The Vertebral Column of Australopithecus sediba

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Two partial vertebral columns of Australopithecus sediba grant insight into aspects of early hominin spinal mobility, lumbar curvature, vertebral formula, and transitional vertebra position. Au. sediba likely possessed five non–rib-bearing lumbar vertebrae and five sacral elements, the same configuration that occurs modally in modern humans. This finding contrasts with other interpretations of early hominin regional vertebral numbers. Importantly, the transitional vertebra is distinct from and above the last rib-bearing vertebra in Au. sediba, resulting in a functionally longer lower back. This configuration, along with a strongly wedged last lumbar vertebra and other indicators of lordotic posture, would have contributed to a highly flexible spine that is derived compared with earlier members of the genus Australopithecus and similar to that of the Nariokotome Homo erectus skeleton.

The vertebral column plays a central role in posture, locomotion, and overall trunk stability and mobility in vertebrate animals. The hominin vertebral column is distinct in its role in force transmission and weight-bearing in an upright torso balanced over two legs. Owing to these biomechanical demands, the hominin spine has several specialized traits not seen in other mammals, including sigmoid curvature; a pyramidal configuration of articular facets with descent through the lower lumbar column; and a wide, curved sacrum (1–6). Whereas these adaptations are present in modern humans and currently known extinct hominins, other aspects of the modern human vertebral column—for instance, large relative lumbosacral body size—are not present in early hominins such as Australopithecus afarensis and Au. africanaus (2, 3, 7), suggesting that the vertebral column evolved in a mosaic fashion. Therefore, an understanding of which adaptations characterized various fossil species and when the full complement of modern humanlike features evolved is integral to reconstructing postural and locomotor evolution in the hominin lineage.

Recently, two key components of the hominin vertebral column—its numerical composition and degree of lumbar lordosis—have been at the forefront of discussion (4, 6, 8–17). However, adequately preserved vertebral columns that lend themselves to reconstructions of regional vertebral numbers are rare in the hominin fossil record, particularly before 50 thousand years ago, and are best represented by partial skeletons assigned to Au. africanaus (Sts 14 and Stw 431) and Homo erectus (KNM-WT 15000). Thoracic and lumbar vertebrae have been defined in two ways in the recent literature: (i) based on the presence and absence of ribs (i.e., the last thoracic vertebra is identified as the last rib-bearing vertebra) (8, 15, 16), and (ii) based on the orientation of the articular facets (i.e., the last thoracic vertebra is identified as the transitional vertebra, one that bears thoracic-like, coronally oriented superior articular facets and lumbar-like, curved and laterally directed inferior articular facets) (6, 17, 18). In modern humans and other extant hominoids, the last rib-bearing vertebra and the transitional vertebra generally occur at the same vertebral level (i.e., are the same vertebral element) and, therefore, yield identical numbers of thoracic and lumbar vertebrae under either definition [15, 18, 19], but see (20).

In contrast, recent evidence indicates that early fossil hominins may not follow this pattern (9, 15). Newly identified vertebral column and fragment associations with KNM-WT 15000 show that the transitional vertebra is cranially adjacent to the last rib-bearing vertebra in this specimen (9). This configuration yields contrasting numbers of lumbar vertebrae when different operational definitions are employed: five nonribbed lumbar vertebrae and six vertebrae with sagittally oriented upper articular facets (posttransitional vertebral). Sts 14 also seems to demonstrate this pattern (8, 15), although the last rib-bearing vertebra in this specimen is somewhat anomalous in that it bears a lumbar-like structure on one side, giving it an intermediate (half-thoracic, half-lumbar) appearance (8, 10, 15, 21, 22). Dissociated vertebral bodies and neural arches at the thoraco-lumbar border in Stw 431 have led to contrasting reconstructions of this specimen (8, 23), precluding a definitive assessment of the relationship between last rib-bearing and transitional vertebrae. Clearly, additional specimens that preserve this region of the vertebral column are needed. The 1.977 Ma partial skeletons of Au. sediba from Malapa, Gauteng, South Africa (24, 25) preserve 23 presacral vertebrae and a partial, five-element sacrum (Fig. 1). Here, we describe vertebrae assigned to the juvenile male holotype [Malapa Hominin 1 (MH1)] and the adult female paratype (MH2), in addition to the previously published sacrum of MH2 (26).

The MH1 partial vertebral column consists of four cervical, six thoracic, and two lumbar vertebrae; that of MH2 is composed of two cervical, seven thoracic, and two lumbar vertebrae, as well as a sacrum. Specimen numbers and identifications are provided in table S1. Vertebrae belonging to MH1 are readily distinguished from those of MH2 by their lack of apophyseal rings. As with modern human juveniles and the Nariokotome juvenile skeleton (KNM-WT 15000) (1), MH1 possesses short vertebral centra relative to superior-inferior interfacet distance, consistent with its juvenile status (27). In contrast, MH2’s centra demonstrate ratios similar to those of adult modern humans.

Cervical Vertebrae

A small cervical body fragment of unknown serial position, two fragmentary mid-cervical vertebrae, and a nearly intact last cervical (C7) vertebra (Fig. S1) are associated with MH1. Two mid-level cervical vertebrae are attributed to MH2: a nearly complete C3 or C4 (fig. S2) and a partially complete C5 or C6. These vertebrae do not articulate and, thus, likely represent either C3 and C5 or C4 and C6.

Rib-Bearing Vertebrae

Six rib-bearing vertebrae are attributed to MH1: two upper thoracic, one mid-thoracic, and three lower thoracic vertebrae. An upper thoracic vertebra (fig. S3) demonstrates superior articular facet shape and orientation and relationships among the body, transverse process, and superior articular facets diagnostic of a second thoracic vertebra (T2). The middle thoracic vertebra, which likely represents T7, is complete but pathological: The dorsal surface of the right lamina exhibits a rounded triangular lytic lesion extending ventrally into the lamina (fig. S4). Poor preservation precludes certainty of articulation between the three lower thoracic vertebrae, although spinous and transverse process morphologies and orientations and costal facet configurations suggest the association and possible affiliation of two of these vertebrae as T9 and T10.

There are seven rib-bearing vertebrae associated with MH2 (table S1), including a block of four consecutive upper–to-mid-thoracic vertebrae and a block of three articulating lower rib-bearing vertebrae. The upper block contains variably complete fragments of what likely represent either a T3-T6 or T4-T7 series. The lower block is of particular interest because it preserves in articulation the penultimate and ultimate rib-bearing vertebrae (Fig. 2). The antepenultimate rib-bearing vertebra is also preserved but is displaced slightly
from articulation with the penultimate vertebra. The penultimate vertebra bears a full costal facet at the body-pedicle border and lacks an inferior facet or demi-facet. The zygapophyses bear flat, dorsally (and slightly laterally) directed superior articular facets and curved, laterally directed inferior articular facets; that is, the penultimate rib-bearing vertebra is the transitional vertebra. The ultimate thoracic vertebra bears a full costal facet on the superior aspect of the posterior vertebral body that extends onto the pedicle. Its superior and inferior articular facets are curved and dorso-medially directed; therefore, it is both rib-bearing and posttransitional.

Lumbar Vertebrae

There are two non-rib-bearing lumbar vertebrae associated with MH1, both lacking apophyseal rings. One is a nearly complete first lumbar (L1) vertebra that bears asymmetrical lumbar transverse processes (fig. S5). Another lumbar vertebra is also nearly complete, with a broken left transverse process (fig. S6). Body-proportion differences that can be observed between the two vertebrae suggest that they were separated by an additional element, rendering this likely the third lumbar vertebra (L3). In both vertebrae, but particularly marked on L3, “imbrication pockets” (4) are present on the dorsal neural arch inferior to the superior articular facets in a region known as the pars interarticularis (1, 5). These laminar fossae are nonarticular and thought to be mechanically induced (5). They allow room for the inferior zygapophyses of the cranially adjacent vertebra during extension of the articular facet joints and are indicative of a lordotic spine (1, 4, 5). Body dimensions and vertebral wedging are reported in table S2. These measurements and wedging estimates should be treated with caution due to both the lack of apophyses and the associated juvenile developmental status of MH1. The first lumbar vertebra is ventrally wedged (4.1°), whereas L3 is wedged dorsally (−1.6°).

The penultimate and ultimate lumbar vertebrae belonging to MH2 directly articulate with each other and, in turn, with the sacrum (Fig. 3). The lumbar bodies and neural arches are separated, broken at the pedicle bases. The neural arches were discovered in articulation with each other and with the articular facets of the sacrum; the vertebral bodies were found in articulation with each other (with a fragment of the sacral S1 body) and refit cleanly with their respective neural arches. The MH2 lumbar vertebrae were reconstructed digitally (fig. S7), combining the broken neural arches with the vertebral bodies. The cranial portion of the neural arch of the penultimate lumbar vertebra is missing and preserves only a partial spinous process and inferior zygapophyses; that of the ultimate lumbar is intact, except for the left transverse process and pedicle, the latter of which is broken along with part of the superior zygapophysis. The ultimate lumbar vertebra bears strong imbrication pockets on the pars, again consistent with extension of the articular facet joints onto the laminae and habitual lordotic posture (fig. S7). Both the penultimate and ultimate lumbar vertebrae are wedged dorsally (−1.5° and −10.9°, respectively) (fig. 4, fig. S8, and table S2).

Sacrum

The MH2 sacrum is cranio-caudally complete along the anterior midline (except for the detached portion of the S1 body) from the cranial body of S1 through the caudal body of S5; five distinct sacral bodies are recognizable. The sacrum is incomplete medio-laterally, with the alae broken at its lateral aspects on both sides. The left ala and sacral foramina are missing entirely, whereas the right side retains four large and complete sacral foramina and part of the auricular surface. The preserved right zygapophysis is curved and postero-medially oriented at an angle of ~45°. The posterior surface of the sacrum

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**Fig. 1.** Vertebral specimens for MH1 (left) and MH2 (right). See corresponding specimen identifications in table S1. MH1 cervical vertebrae UW88-71 and UW88-73 are encased in matrix and, thus, not shown here.
is mostly complete on the right side and along the midline, with the maintenance of largely separate S1, S2, S3, and S4 spinous processes. Overall sacral curvature is greater and more humanlike in MH2 than in A.L. 288-1 (fig. S9).

**Thoraco-Lumbar Transition and Inferred Numerical Composition**

Ever since the description and interpretation of a partial *Au. africanus* skeleton (Sts 14) from Sterkfontein, Gauteng, South Africa more than 40 years ago (21), researchers have grappled with the number of lumbar vertebrae in early hominins (1–3, 8–13, 16, 17, 21–23, 28–32). Although a full complement of lumbar vertebrae is not associated with either MH1 or MH2, both the thoraco-lumbar transition and the sacrum of MH2 provide indirect evidence that *Au. sediba* possessed five non–rib-bearing lumbar vertebrae. Hypotheses for six lumbar vertebrae in early hominins due to an interspecific homeotic shift at the lumbo-sacral border have been proposed on the basis of recent interpretations of four-element sacra in A.L. 288-1 and KNM-WT 15000 (10, 13, 33). However, both fossil specimens are damaged and preclude certainty in this assessment (22). The presence of five sacral elements in MH2 challenges the hypothesis of a six-four configuration (6L:4S) due to homeotic change and, rather, suggests a five-five configuration (5L:5S), which is consistent with the majority of modern humans. Although this does not entirely rule out the possibility of six lumbar vertebrae in combination with a five-element sacrum (6L:5S), this configuration occurs at a very low frequency in modern humans (10, 34).

Additionally, the dissociation between the transitional and last rib-bearing vertebrae in MH2 provides further support for the presence of five non–rib-bearing lumbar vertebrae in this specimen. In other early hominins, the thoraco-lumbar transition is either anomalous in appearance (Sts 14, which includes what superficially resembles a half-thoracic, half-lumbar vertebra) (8, 15, 21, 22) or damaged (Stw 431 and KNM-WT 15000); reconstructions of the latter differ and result in divergent numbers of lumbar vertebrae (1, 3, 8, 9, 23, 28, 29). In MH2, if six instead of five non–rib-bearing lumbar vertebrae were present, seven vertebrae with curved, sagittally oriented articular facets would follow the transitional vertebra, a configuration that is not observed in other fossil hominins or modern humans ([9, 15, 19], but see (20)). Rather, cranial placement of the transitional vertebra relative to the last rib-bearing vertebra suggests that the MH2 vertebral column consisted of five non–rib-bearing lumbar vertebrae and six posttransitional vertebrae. In fact, recent evidence and interpretations suggest that other early hominins demonstrate this configuration as well, including KNM-WT 15000 (9), Sts 14 (8, 15), and possibly Stw 431, depending on the association between its broken neural arches and vertebral bodies (8, 23, 29). Unlike the case with other partial hominin vertebral columns, the penultimate and ultimate thoracic vertebrae of MH2 are articulated and were found as such in situ, rendering discrepancies
in reconstructions that plague other specimens a nonissue.

**Function, Posture, and Locomotion**

The presence of lumbar dorsal wedging and other morphological features (for instance, imbrication pockets on lumbar laminae) in the MH1 and MH2 partial vertebral columns demonstrates an intrinsic lumbar lordosis and adaptation to upright posture and bipedal locomotion in *Au. sediba*. MH2 also shows a cranial position of the transitional vertebra relative to the last rib-bearing vertebra, resulting in six vertebrae with curved, sagittally oriented articular facets on the zygaphyses that allow flexion and extension of the torso and constrain its rotation (35, 36). A numerically longer posttransitional regional trend would, therefore, facilitate postural lordosis over a longer range of the lower back than the modal condition in modern humans ([1, 2, 4, 15, 17], but see (9)). In addition, the L5 vertebra of MH2 is extremely dorsally wedged (−10.9°), greatly surpassing l令dotic wedging observed at the last lumbar vertebrae in other *Australopithecus* specimens and, although within the range of modern human variation, outside the lower limit of their 95% prediction intervals. In this regard, the MH2 L5 vertebra is very similar to that of KNM-WT 15000 (Fig. 4). When lordotic wedging is estimated from both L4 and L5, KNM-WT 15000 possesses a greater degree of summed dorsal wedging (−16.0°) than MH2 (−12.4°), both surpassing values calculated for *Au. africanaus* specimens (Stw 431 at −5.7°, Sts 14 at −8.9°) (fig. S8 and table S2). Although a complete lumbar column is required to measure the overall lumbar angle (1/4), this trend toward strong lordotic wedging of the lower lumbar bodies may represent an evolutionary trend in *Au. sediba* and *H. erectus* relative to earlier species; together with a more anterior position of the shoulder joint (37), this high degree of lordosis helps to position the center of gravity of the trunk more posteriorly. However, as other partial skeletal elements belonging to early members of the genus *Homo* do not preserve lower lumbar vertebrae (38–41), this hypothesis awaits future discoveries.

The likely presence of six posttransitional vertebrae (probably shared with other early hominins), in combination with dorsal wedging of the lower lumbar vertebrae (MH1 L3, as well as MH2 L4 and L5), including extreme dorsal wedging at L5, reveals a highly mobile lower back in *Au. sediba* (Fig. 4 and fig. S8). Functional analyses of lower lumbar vertebrae in other hominins have been proposed and tested in modern humans, with mixed results (44–47). Previous studies have assessed these relationships only during quiet stance on two feet, and data on the kinematics of bipedal locomotion are needed; nevertheless, the relatively strong lordotic morphology observed in the lower back of MH2 is consistent with such a kinematic hypothesis (43). Additionally, this finding suggests that MH2 may have been characterized by a pelvis tilted more anteriorly than that of modern humans (fig. S10), which has also been proposed for other members of the genus *Australopithecus* (48, 49). Whether or not these morphologies characterized *Au. sediba* as a species is unknown and will require the recovery and biomechanical analysis of additional skeletal materials. The relationship between the orientation of the pelvis and vertebral column (48–50) and integration within (51, 52) and between morphologies in these complex anatomical systems is understood areas (49, 50) that will undoubtedly contribute to our understanding of posture and gait in *Au. sediba* and other early hominins.

**References and Notes**

20. M. Haeusler, S. Regula, B. Thomas, Modern or distinct axial bauplan in early hominins? A reply

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**Fig. 4. Wedging angle of the last lumbar vertebra in MH2 compared with other fossil hominins and modern humans.** Modern human (n = 88 specimens) sex differences are not significant [female (n = 45); μ = −6.4°, male (n = 43); μ = −6.6°, PS = 0.576]. Notice that MH2 is at the extreme end of modern human variation and lies outside the range of 95% prediction intervals (μ ± 1.96σ) (−2.2°, −10.8°) for *H. sapiens*. Whiskers represent the minimum and maximum values of the modern human data set. See table S1 for raw data used to calculate wedging angles.
Early Hominid Posture and Locomotion from Dmanisi, Georgia.

We thank the South African Heritage Resources Agency for the permits to work at the Malapa site; the Nash family for granting access to the Malapa site and continued support of research on their reserve; the South African Department of Science and Technology, the Gauteng Provincial Government, the South African National Research Foundation and the African Origins Platform, the Institute for Human Origins, University of the Witwatersrand, the University of the Witwatersrand’s Vice Chancellor’s Discretionary Fund, the National Geographic Society, the Palaeoanthropological Science Trust, The Andrew W. Mellon Foundation, the Ford Foundation, the U.S. Diplomatic Mission to South Africa, the French Embassy of South Africa, the A.H. Schultz Foundation, Duke University, the Ray A. Rothrock ’77 Fellowship and International Research Travel Assistance Grant of Texas A&M University, and the Oppenheimer and Ackerman families. Support was provided by the University of the Witwatersrand’s Schools of Geosciences and Anatomical Sciences and the Bernard Price Institute for Palaeoanthropology for support and facilities; the Gauteng Government, and the Gauteng Department of Agriculture, Conservation and Environment and the Cradle of Humankind Management Authority; and our respective universities for ongoing support. We thank E. Mbuva, P. Kiura, V. Iminjili, the National Museums of Kenya, B. Billings, B. Zipfel, the School of Anatomical Sciences at the University of the Witwatersrand, S. Potze, L. C. Kgasii, and the Ditsong Museum for access to comparative specimens; the Virtual Image Processing lab of the Palaeosciences Centre and the Microfocus X-ray CT facility of the Palaeosciences Centre at Wits for funding these facilities; the University of the Witwatersrand Office of Research and the National Research Fund Strategic Research Infrastructure Grant and African Origins Platform funding programs; and Duke University and the University of Zurich 2009 and 2010 Field Schools for technical and material support. Numerous individuals have been involved in the ongoing preparation and excavation of these fossils, including C. Dube, C. Kemp, M. Kgasi, M. Languza, J. Malaza, G. Mokoma, P. Mukanla, T. Nembhuri, M. Ngamphalala, S. Jirah, S. Tbhabala, and C. Yates. Other individuals who have given substantial support to this project include B. de Klerk, W. Lawrence, C. Steininger, B. Kuhn, L. Pollaro, B. Zipfel, J. Kretzen, D. Conforti, J. McCaffrey, C. Diamini, H. Visser, R. McClure-Samuel, B. Nikosi, B. Louw, L. Backwell, F. Thackeray, and M. Peltier. S. Smilg facilitated computed tomography scanning of the specimens, A. Val provided information of CT slices, W. Sanders and K. Whitcome made data on fossil specimens and casts available, M. Grabowski provided helpful comments on the manuscript, and M. Shattuck provided valuable comments and assisted substantially with the revision of this manuscript. The Au. sediba specimens are archived at the Evolutionary Studies Institute at the University of the Witwatersrand. All data used in this study are available upon request, including access to the original specimens. Data reported in this study are available in the supplementary materials.

Acknowledgments: We thank the South African Heritage Resource agency for the permits to work at the Malapa site; the Nash family for granting access to the Malapa site and continued support of research on their reserve; the South African Department of Science and Technology, the Gauteng Provincial Government, the South African National Research Foundation and the African Origins Platform, the Institute for Human Origins, University of the Witwatersrand, the University of the Witwatersrand’s Vice Chancellor’s Discretionary Fund, the National Geographic Society, the Palaeoanthropological Science Trust, The Andrew W. Mellon Foundation, the Ford Foundation, the U.S. Diplomatic Mission to South Africa, the French Embassy of South Africa, the A.H. Schultz Foundation, Duke University, the Ray A. Rothrock ’77 Fellowship and International Research Travel Assistance Grant of Texas A&M University, and the Oppenheimer and Ackerman families. Support was provided by the University of the Witwatersrand’s Schools of Geosciences and Anatomical Sciences and the Bernard Price Institute for Palaeoanthropology for support and facilities; the Gauteng Government, and the Gauteng Department of Agriculture, Conservation and Environment and the Cradle of Humankind Management Authority; and our respective universities for ongoing support. We thank E. Mbuva, P. Kiura, V. Iminjili, the National Museums of Kenya, B. Billings, B. Zipfel, the School of Anatomical Sciences at the University of the Witwatersrand, S. Potze, L. C. Kgasii, and the Ditsong Museum for access to comparative specimens; the Virtual Image Processing lab of the Palaeosciences Centre and the Microfocus X-ray CT facility of the Palaeosciences Centre at Wits for funding these facilities; the University of the Witwatersrand Office of Research and the National Research Fund Strategic Research Infrastructure Grant and African Origins Platform funding programs; and Duke University and the University of Zurich 2009 and 2010 Field Schools for technical and material support. Numerous individuals have been involved in the ongoing preparation and excavation of these fossils, including C. Dube, C. Kemp, M. Kgasi, M. Languza, J. Malaza, G. Mokoma, P. Mukanla, T. Nembhuri, M. Ngamphalala, S. Jirah, S. Tbhabala, and C. Yates. Other individuals who have given substantial support to this project include B. de Klerk, W. Lawrence, C. Steininger, B. Kuhn, L. Pollaro, B. Zipfel, J. Kretzen, D. Conforti, J. McCaffrey, C. Diamini, H. Visser, R. McClure-Samuel, B. Nikosi, B. Louw, L. Backwell, F. Thackeray, and M. Peltier. S. Smilg facilitated computed tomography scanning of the specimens, A. Val provided information of CT slices, W. Sanders and K. Whitcome made data on fossil specimens and casts available, M. Grabowski provided helpful comments on the manuscript, and M. Shattuck provided valuable comments and assisted substantially with the revision of this manuscript. The Au. sediba specimens are archived at the Evolutionary Studies Institute at the University of the Witwatersrand. All data used in this study are available upon request, including access to the original specimens. Data reported in this study are available in the supplementary materials.

Supplementary Materials
www.sciencemag.org/cgi/content/340/6129/1232996/suppl/DC1

Supplementary Text
Figs. S1 to S11
Tables S1 and S2
References (S4–S58)
20 November 2012; accepted 12 March 2013
10.1126/science.1232996