



# Thoracic vertebral count and thoracolumbar transition in *Australopithecus afarensis*

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The evolution of the human pattern of axial segmentation has been the focus of considerable discussion in paleoanthropology. Although several complete lumbar vertebral columns are known for early hominins, to date, no complete cervical or thoracic series has been recovered. Several partial skeletons have revealed that the thoracolumbar transition in early hominins differed from that of most extant apes and humans. *Australopithecus africanus*, *Australopithecus sediba*, and *Homo erectus* all had zygapophyseal facets that shift from thoracic-like to lumbar-like at the penultimate rib-bearing level, rather than the ultimate rib-bearing level, as in most humans and extant African apes. What has not been clear is whether *Australopithecus* had 12 thoracic vertebrae as in most humans, or 13 as in most African apes, and where the position of the thoracolumbar transitional element was. The discovery, preparation, and synchrotron scanning of the *Australopithecus afarensis* partial skeleton DIK-1-1, from Dikika, Ethiopia, provides the only known complete hominin cervical and thoracic vertebral column before 60,000 years ago. DIK-1-1 is the only known *Australopithecus* skeleton to preserve all seven cervical vertebrae and provides evidence for 12 thoracic vertebrae with a transition in facet morphology at the 11th thoracic level. The location of this transition, one segment cranial to the ultimate rib-bearing vertebra, also occurs in all other early hominins and is higher than in most humans or extant apes. At 3.3 million years ago, the DIK-1-1 skeleton is the earliest example of this distinctive and unusual pattern of axial segmentation.

*Australopithecus afarensis* | vertebrae | Dikika | segmentation | thoracic

A partial skeleton attributed to *Australopithecus afarensis* from Dikika, Ethiopia, dated to 3.3 Ma (1), provides the only known complete cervical and thoracic vertebral column of any early hominin prior to 60,000 years ago (2).

The modal number of thoracic and lumbar vertebrae has been a key factor in interpretations of the evolution of locomotor adaptations in hominoids (3–15). A larger number of thoracic and smaller number of lumbar vertebrae increase dorsostability of the trunk (8, 16–19) and are found in various combinations in extant apes (10, 11, 13, 15, 17, 19). Like humans, early hominins had five non-rib-bearing lumbar vertebrae, as demonstrated in three species: *Australopithecus africanus*, *Australopithecus sediba*, and *Homo erectus* (3, 4, 6, 7, 10, 14, 20). However, a lack of a complete thoracic column for any early hominin has made it difficult to determine whether early hominins had only 12 thoracic vertebrae like humans, or 13, as in extant African apes, or whether variation in segmentation patterns involved addition or deletion of segments or a shift in identity among segments (10, 11, 13, 15).

In addition to uncertainty in thoracic count, there is also variation in the configuration of the thoracolumbar transition, in which early hominins differ from most extant hominids (4, 7, 10, 20). In most extant hominids, the caudal-most rib-bearing vertebra usually has flat cranial zygapophyseal facets facing dorsally or very slightly dorsolaterally, as is typical of thoracic vertebrae. In contrast, the caudal zygapophyseal facets of this vertebra are transversely convex

and are generally oriented posteromedially, averaging about 30° to 45° to a sagittal plane, like those of upper lumbar vertebrae (21–23). This vertebra, which exhibits the transition from thoracic-like to lumbar-like zygapophyses, is referred to as the transitional or diaphragmatic vertebra. The transition in facet orientation from thoracic to lumbar patterns occurs gradually over two to three segments in 43 to 93% of human individuals (depending on how facet morphology is quantified), but the transition is usually complete no higher than the last rib-bearing thoracic vertebra (21–30). When an abrupt transition occurs within only a single vertebra, it typically occurs at the last rib-bearing element but can be found one segment higher (11th thoracic, or T11) in up to ~10 to 23% of individuals (10, 23, 28, 29). Thus, when a transition is abrupt, most modern humans and extant great apes have a transitional vertebra at the last rib-bearing vertebra. Due to differences in the numbers of non-rib-bearing lumbar vertebrae among apes and humans, this transition usually occurs at the sixth presacral level (T12) in modern humans versus the fourth or fifth presacral levels (T13) in extant great apes (8–10).

All four early hominin fossils that preserve the transitional region exhibit a different pattern, compared with the most frequent pattern seen in extant hominoids (4, 7, 10). The *A. africanus* skeleton Sts 14 has an abrupt transitional element situated at the seventh—not sixth—presacral level (Sts 14g), even though the sixth presacral element has a distinct rib on the right side (4, 6). The *A. africanus* skeleton StW 431 also has an abrupt transitional element at the seventh presacral level and probably had only five

## Significance

The discovery of a 3.3 million-year-old partial skeleton of *Australopithecus afarensis*, from Dikika, Ethiopia, preserved all seven cervical (neck) vertebrae and provided the only known evidence for the presence of 12 thoracic (rib-bearing) vertebrae in hominins prior to 60,000 years ago. This skeleton has seven cervical and only 12 thoracic vertebrae like humans, rather than 13 like African apes. However, the anatomical transition from thoracic to lumbar (lower back) vertebral form occurs at the 11th thoracic segment. This distinctive pattern of vertebral segmentation, rare in modern apes and humans, is also seen in the three other early hominins for which this area is known, with the Dikika skeleton providing the earliest and most complete example.

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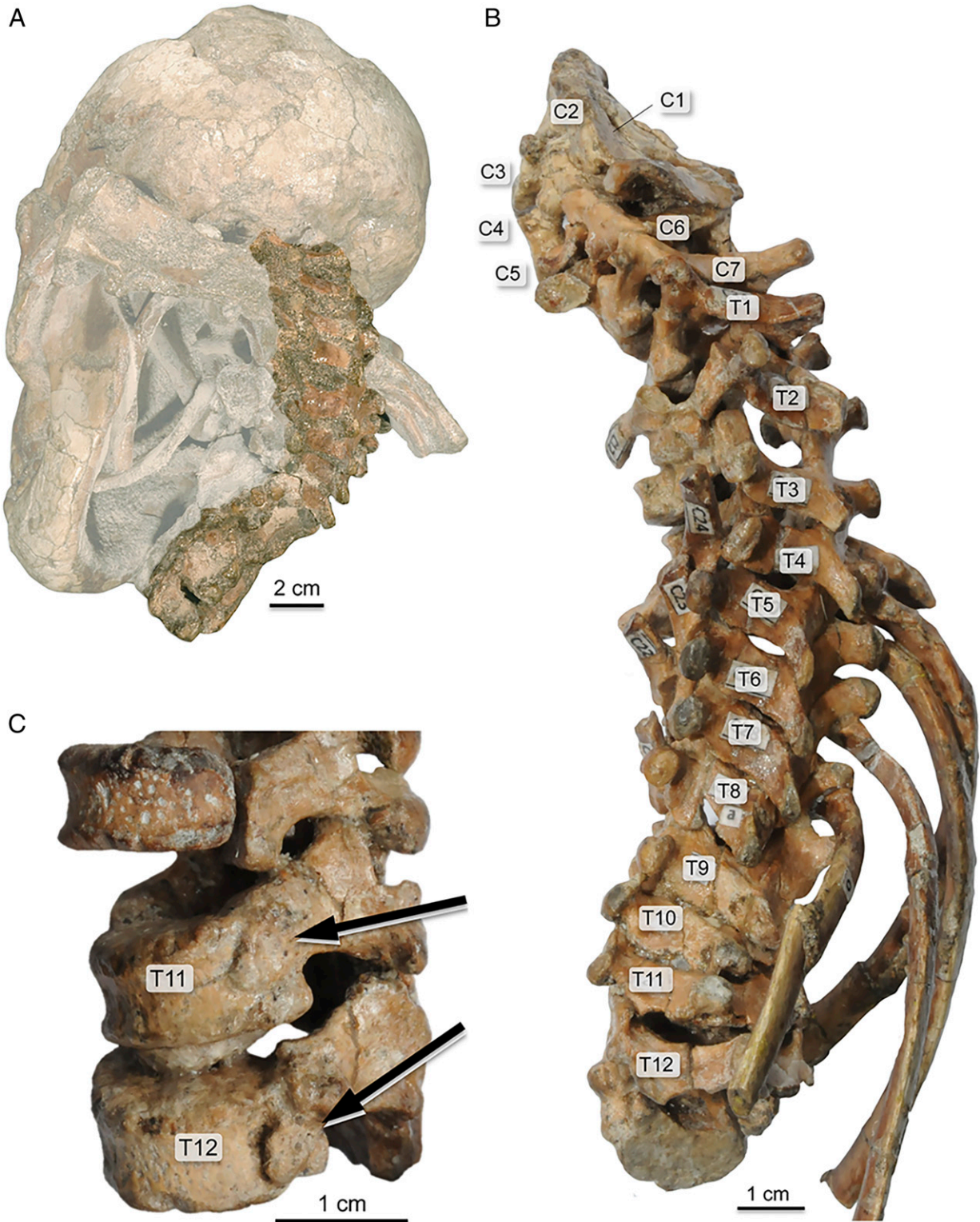
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non-rib-bearing lumbar vertebrae, based on a tiny raised area adjacent to where a costal facet would be on the sixth presacral vertebra (4, 5). The *A. sediba* specimen MH2 preserves the

penultimate and ultimate rib-bearing vertebrae, with the penultimate vertebra being an abrupt transitional element, as in the *A. africanus* skeletons (7). Similar to what is seen in these



**Fig. 1.** (A) Photograph of the DIK-1-1 vertebrae in block with skull, pectoral girdle, and rib fragments before complete preparation. The vertebral column is highlighted. (B) Entire articulated cervical and thoracic column of DIK-1-1, with vertebral levels indicated on each bone, demonstrating the presence of seven cervical and 12 thoracic (rib-bearing) vertebrae. Most of these vertebrae cannot be disarticulated mechanically. (C) The three caudal-most preserved vertebrae—T10, T11, and T12—with rib facets indicated (arrows) on T11 and T12.



## Discussion

The DIK-1-1 skeleton demonstrates that the distinctive vertebral segmentation pattern seen in four other early hominins, with an abrupt facet transition at the penultimate rib-bearing vertebra, was present at least by 3.3 million years ago in *A. afarensis*. This specimen also preserves 12 thoracic vertebrae. Because the presence of a transitional vertebra cranial to the penultimate or second-to-last rib-bearing element is very rare among extant hominoids (*H. sapiens* <0.1%; *Pan troglodytes* 0.4%; *Gorilla gorilla* 1.5%; *Gorilla beringei* 1.5%; *Symphalagus syndactylus* 2.8%; unobserved in *Pan paniscus*, *Pongo pygmaeus* and *Hylobates lar*) (8–10), it is highly improbable that other *A. afarensis* would have had 13 thoracic vertebrae. We therefore can conclude confidently that *A. afarensis* had 12 thoracic vertebrae, as is modal for humans and unlike the pattern in all but a few African apes (10, 11, 13, 15, 16, 18).

The A.L. 288-1 partial skeleton (*A. afarensis* from Ethiopia) (31) preserves some lumbar and thoracic vertebrae. Specimen A.L. 288-1ai has been referred to as a last thoracic vertebra, based on the transitional morphology of its cranial and caudal facets, with the latter being elongated, convex, and facing anterolaterally, and called T12 under the assumption that *A. afarensis* had 12 thoracic elements and that the transition was at T12 (20). However, based on the transition pattern typical for all other early hominins, including DIK-1-1, A.L. 288-1ai is likely a penultimate thoracic (see also ref. 31). If so, the more cranially positioned thoracic vertebrae may also represent higher levels than originally reported.

Comparison between the DIK-1-1 T11 and A.L. 288-1ai shows that the curvature and oblique orientation of the caudal zygapophyseal facets are even more prominent in A.L. 288-1, probably reflecting ontogenetic differences in morphology. Developmental changes in lumbar zygapophyseal facet orientation and curvature have been reported for humans (32, 33). Lumbar zygapophyseal joints lie in the coronal plane at birth, similar to those of thoracic vertebrae, and subsequently rotate inward a sagittal plane and become more curved during growth, reaching adult morphology by late adolescence or early adulthood (34), which suggests that the rotation into the sagittal plane and curvature of the T11 caudal facets of DIK-1-1 and both sets of T12 facets would likely have increased during development.

Because DIK-1-1 has no preserved lumbar vertebrae, its lumbar count cannot be assessed. However, it is reasonable to hypothesize that DIK-1-1 would have had five lumbar segments, as do all sufficiently preserved ( $n = 3$ ) early hominins. DIK-1-1 is unlikely to have had more than five non-rib-bearing lumbar vertebrae because it has the transitional element at the second-to-last rib-bearing segment. No extant African ape has a transitional element cranial to the seventh presacral vertebra, and this morphology is extremely rare in humans (<0.1%,  $n = 1,159$ ) (10). It is unlikely, though less certain, that DIK-1-1 had fewer than five non-rib-bearing lumbar segments. Given that a count of only 16 thoracolumbar vertebrae is rare in modern humans (4.9%,  $n = 1,159$ ) (10) and unknown in other early fossil hominins, this scenario is much less likely. Seventeen thoracolumbar vertebrae also is the most common pattern in most African apes although a count of 16 or fewer is slightly more common in apes than in humans [*P. paniscus* 6.3% ( $n = 48$ ), *P. troglodytes* 24.3% ( $n = 239$ ), *Gorilla gorilla gorilla* 29.6% ( $n = 86$ ), although *Gorilla beringei beringei* is 95.5% ( $n = 66$ )] (10). It is therefore possible to infer that early hominins modally had 12 thoracic and five non-rib-bearing lumbar vertebrae as their modal vertebral counts, with a transitional element at T11. This evidence supports the early hominin modal vertebral formula proposed by Pilbeam (11) and Williams et al. (10). The shifting morphology and identity of the thoracolumbar transitional vertebrae seems to have been a change involving a shift in segment identity, or identity of parts of the segment (i.e., costal articulations versus zygapophyseal morphology), rather than a meristic shift involving addition or deletion of elements (11, 13).

The location of the thoracolumbar transitional element may affect function of the vertebral column. Medially oriented lumbar-like zygapophyseal facets restrict rotation of the vertebral motion segments because the center of rotation is located within the intervertebral disk (29, 34). Having a more cranial transition to this type of facet would in principle result in more limited rotation of the lumbar spine in early hominins, perhaps by 2° to 3°. In DIK-1-1, the mammillary processes of T12 extend dorsally to flank the T11–T12 zygapophyseal joint, forming a “mortice”-style joint like that found in up to 47% of modern humans (25). Such a configuration would have further limited rotational capacity (35–38), at least in this individual (28). However, the range for spinal flexion and extension may have been equivalent to that of modern humans (34, 39), even given the deep lumbar capture between the iliac blades found in *Australopithecus* (40). A higher thoracolumbar transition may have permitted the ability to achieve a lumbar lordosis in *A. afarensis*—a key component of habitual upright bipedal locomotion in hominins (40, 41). Shifting the transition back to the ultimate rib-bearing element in later *Homo*, perhaps also indicating a freed lower lumbar region with reduced lumbar capture within the pelvis, may have increased the capacity for lumbar spinal rotation between the torso and pelvis (8, 13, 40–44) during modern human walking and running. This movement, in conjunction with other joint rotations (e.g., shoulders and knees), acts to balance and cancel angular moments around the spinal column during bipedal locomotion (45–48). The caudal shift in the thoracolumbar transition may be a component of a suite of derived features that have been argued to represent an adaptation for more efficient long-distance walking and endurance running in later *Homo*, and, if so, this particular component would have occurred only after 1.6 Ma with KNM-WT 15000 (48, 49).

Regardless of the functional significance of the modern human pattern, the DIK-1-1 skeleton provides evidence that *A. afarensis* had 12 thoracic vertebrae, with a thoracolumbar transitional element at T11, and that the thoracolumbar transitional morphology, present in four other known early hominins, evolved by at least 3.3 million years ago. This distinctive early hominin vertebral configuration may be a key to building and testing scenarios for the evolution of bipedality and body form in early hominins.

## Materials and Methods

The upper part of the DIK-1-1 skeleton, which includes the skull and most of the torso, was found largely articulated and encased in a highly compact sandstone block, making preparation difficult and time-consuming. Significant mechanical preparation has been done at the National Museum of Ethiopia by Z.A. and Christopher Kiarie for over 13 years since its discovery and continues. Many of the elements, particularly the vertebrae, are now exposed (Fig. 1). In addition, the fossil was scanned using propagation phase contrast synchrotron microtomography on beamline ID17 at the European Synchrotron Radiation Facility (ESRF) in Grenoble, France, using a 100-keV monochromatic beam, with a voxel size of 45  $\mu\text{m}$  and 5 m of propagation, providing us with the opportunity to virtually examine the vertebrae. These tomographic images were segmented by T.K.N. to isolate individual vertebral elements and their morphology. The DIK-1-1 fossil is housed at the National Museum of Ethiopia. Requests to study it should be made to the museum and to Z.A. (alemseged@uchicago.edu). Scan data are archived at the University of Chicago and the European Synchrotron Radiation Facility (requests for these data should also be made to Z.A.).

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