

Chapter 7

The Spine of *Australopithecus*



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7.1 Introduction

Early hominins evolved in the late Miocene (roughly 5–7 million years ago) and proliferated into many varieties, one lineage of which gave rise to the australopiths. This ancestor was ape-like in many ways yet was probably a facultative biped that spent its time both on the ground and in the trees, as demonstrated by analyses of *Ardipithecus ramidus* (Lovejoy et al. 2009a, b; White et al. 2009, 2015; Prang 2019). A subsequent group of species colloquially referred to as australopiths (after the genus *Australopithecus*) initially evolved in the early Pliocene and demonstrate unequivocal evidence for bipedal locomotion on the ground (Lovejoy 2005a, b, 2007; Prang 2015). Restricted to parts of East, Central, and Southern Africa, the ten or so species of australopiths differed in size, diet, and behavior, in addition to the environments in which they lived (see Reed et al. 2013).

Bipedal locomotion is one of the defining characteristics of hominins and is thought to be one of the earliest autapomorphies that appeared in the hominin lineage. Fossils of the ca. 4.4 Ma *Ardipithecus ramidus* demonstrate that a non-grasping, adducted hallux, long considered a primary adaptation to bipedalism, did not accompany the initial evolution of bipedalism (Lovejoy et al. 2009a). Therefore, a grasping, abducted hallux persisted for the first few million years of hominin evolution and eventually evolved into a foot with distinct weight transfer and propulsion mechanisms known in later fossil hominins and modern humans

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(Haile-Selassie et al. 2012; Prang 2015, 2019). Morphologies related to hip (Lovejoy et al. 1973; Lovejoy 1988, 2007), knee (Johanson and Taieb 1976; Leakey et al. 1995; Lovejoy 2005b), and spine posture (Lovejoy 2005a; Whitcome et al. 2007), then, may have been some of the first skeletal structures modified for bipedal locomotion. Indeed, *Ar. ramidus* demonstrates a mosaic pelvic morphology, with a derived, *Australopithecus*-like upper pelvis and a more primitive, ape-like ischium (Lovejoy et al. 2009c); nevertheless, Kozma et al. (2018) showed that *Ar. ramidus* would have been capable of human-like hip extension.

Spinal posture is contributed to by both soft and hard tissues (Shapiro and Frankel 1989; Been et al. 2010a, 2014; Been and Kalichman 2014; Nalley and Grider-Potter 2015, 2017), including the vertebral bodies, intervertebral discs, zygapophyseal morphology, and epaxial and hypaxial musculature. The vertical orientation and sigmoid curvature of the vertebral column balance the upper body over the pelvis, and the strap-like erector spinae muscles provide support and allow extension of the spine. Morphologies related to spinal orientation and curvature on the cranial base and vertebral column may have been some of the earliest adaptations to bipedalism, along with changes in *Hox* gene expression patterns to generate a homeotic shift at the thoracolumbar border and a longer lumbar column (Pilbeam 2004; Williams et al. 2016).

7.2 Numbers of Vertebrae

The last common ancestor (LCA) of hominins and panins (chimpanzees and bonobos) most likely possessed 17 thoracolumbar vertebrae with a panin-like vertebral formula consisting of 13 thoracic vertebrae and 4 lumbar vertebrae (Pilbeam 2004; Williams 2011; Williams and Russo 2015; Williams et al. 2016, 2019a, b; Thompson and Almécija 2017; but see Haeusler et al. 2002; McCollum et al. 2010). At some point in early hominin evolution, a rostral shift in *Hox* gene expression at the thoracolumbar border was selected for, resulting in the regionalization of 12 thoracic and 5 lumbar vertebrae, with no meristic change in total thoracolumbar number (Pilbeam 2004; Williams 2012a; Williams et al. 2016). Such homeotic shifts involve not only costal components (i.e., rib presence or absence, and hence what determines thoracic and lumbar identification traditionally) (Wellik and Capecchi 2003; Mallo et al. 2010) but also the shape and orientation of the articular facets (and thus the location of the transitional or diaphragmatic vertebra, that vertebra with flat, coronally oriented “thoracic-like” superior articular facets and curved, sagittally oriented “lumbar-like” inferior articular facets, which serve as an alternate demarcation of thoracic and lumbar regions; see Washburn 1963; Shapiro 1993; Whitcome 2012) (Pollock et al. 1995; Carapuço et al. 2005). All known early fossil hominins with adequate preservation of the vertebral column possess five lumbar vertebrae (Haeusler et al. 2002, 2011; Williams et al. 2013); however, the transitional vertebra is not the last thoracic vertebra as is the case with modern humans and other extant

hominoids (Williams 2012a, b), but rather the penultimate thoracic vertebra (Haeusler et al. 2002, 2011; Williams et al. 2013; Meyer et al. 2015). Ward et al.'s (2017) analysis of the “Dikika child” (DIK-1-1) confirmed this configuration, and although lacking a lumbar column, this infant *Au. afarensis* preserves 12 thoracic vertebrae, with the 11th thoracic (T11) the transitional vertebra. Together, the fossil evidence suggests that, by the Pliocene, early hominins evolved an elongated lumbar column and an even longer post-transitional vertebral column (5 and 6 elements, respectively), in both cases at the expense of the numerical composition of the thoracic and pre-transitional columns (12 and 11 elements, respectively). This configuration probably facilitated the evolution of bipedalism by allowing for sufficient lordosis and thus overall spinal posture (Lovejoy 2005a; Williams et al. 2013).

7.3 Fossil Record

The oldest known vertebral material in the hominin fossil record belongs to 4.4 Ma *Ardipithecus ramidus* from the Middle Awash site of Aramis (White et al. 2009). The best preserved element is a somewhat crushed subaxial cervical vertebra (ARA-VP-6/500-057); a crushed partial thoracic vertebra (ARA-VP-6/500-084) and an inferior segment of the sacrum (ARA-VP-6/500-038) are both associated with the inferred female partial skeleton known as “Ardi” (ARA-VP-6/500). Several other partial vertebrae from the site are associated with *Ar. ramidus*, but do not belong to the partial skeleton (White et al. 2009). Detailed studies of these vertebrae have not been published but when carried out will provide glimpses into the posture and locomotor repertoire of one of the earliest putative bipeds.

The oldest vertebral material belonging to a member of the genus *Australopithecus* hails from the site of Asa Issie in the Middle Awash of Ethiopia attributed to *Australopithecus anamensis* (White et al. 2006; Meyer and Williams 2019). Several partial vertebrae, including an atlas (ASI-VP-2-220), an axis (ASI-VP-2-214), and lower cervical and thoracic vertebrae, are known but not associated with a single individual. White et al. (2006) point out that the axis and thoracic neural arch are larger than those from A.L. 333 and A.L. 288 (belonging to *Au. afarensis*). The vertebral fragments are described in Meyer and Williams (2019).

Australopithecus afarensis is the earliest hominin with fully described, reasonably complete vertebrae, and all of the vertebrae known for this species derive from the Afar region of Ethiopia. The earliest *Au. afarensis* vertebrae yet discovered belong to KSD-VP-1/1 dated to ~3.6 Ma from Woranso-Mille in Ethiopia (Haile-Selassie et al. 2010). The vertebrae of Kadanuumuu, the “Big Man,” include parts of six cervical vertebrae (C2–C6), none of which are well-preserved, although several of the vertebral bodies are nearly complete (Meyer 2016). The Dikika child is the partial skeleton of a young juvenile *Au. afarensis* dated to ~3.3 Ma (Alemseged et al. 2006). It includes the most complete cervical and thoracic vertebral columns in the early hominin fossil record (Ward et al. 2017). These vertebrae are essentially

complete, but the centra are not yet fused to the neural arches due to the young age of this individual (Ward et al. 2017).

The partial skeleton of an adult female from ~3.2 Ma Hadar, A.L. 288-1 (“Lucy”), preserves eight vertebral elements (one of the original nine, a neural arch fragment, was shown not to belong to Lucy; Meyer et al. 2015). Fossil hominin vertebrae are shown in a comparative context in Figs. 7.1, 7.2, 7.3, 7.4, 7.5, 7.6, 7.7, 7.8, 7.9, 7.10, 7.11, 7.12, 7.13, 7.14, 7.15, 7.16, and 7.17. Johanson et al. (1982) and Cook et al. (1983) describe nonconsecutive thoracic vertebrae, but Meyer et al. (2015) make a case that the thoracic elements are consecutive (T6–T11) (see Fig. 7.10). In addition, there is a nearly complete lumbar vertebra (sans lumbar transverse processes) (Fig. 7.13) and an isolated lumbar spinous process. Vertebrae from other sites at Hadar (A.L. 333 and A.L. 444) represent all three presacral regions, some of which are nearly complete (Lovejoy et al. 1982; Ward et al. 2012). These vertebrae are isolated and have not been associated with one another, although A.L. 444-7, a large lumbar vertebral body (Fig. 7.14), has been suggested to belong to the same individual as the A.L. 444-2 male skull (Kimbel et al. 2004; Ward et al. 2012).

Potentially the oldest hominin material from South Africa comes from the lower members of Sterkfontein Caves (Granger et al. 2015; but see Pickering et al. 2019a). StW 573 is a yet fully described partial skeleton from Member 2 in Silberberg Grotto (Clarke 2019). Clarke (2019) reports 16 preserved vertebrae in this individual: an atlas, 4 other cervical vertebrae, 6 thoracic vertebrae, and 5 lumbar vertebrae

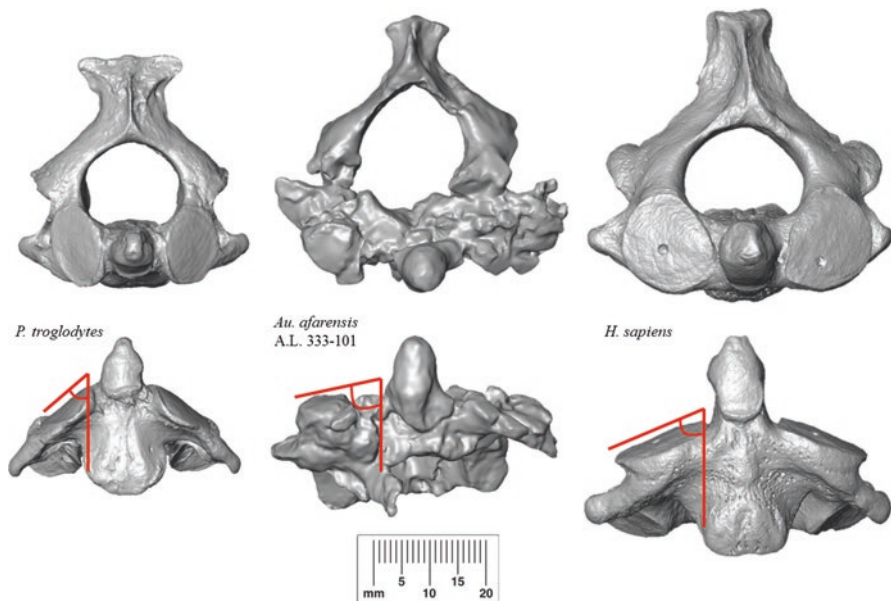


Fig. 7.1 Axis vertebrae in superior and anterior views. Angles indicate the angle of the superior articular facets, which are more steeply sloped in *Au. afarensis* and modern humans than in chimpanzees

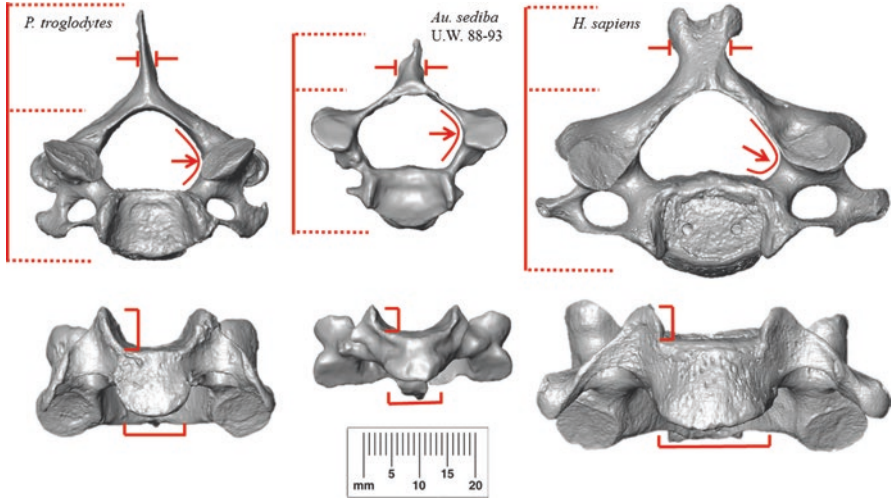


Fig. 7.2 Third cervical vertebrae in superior and anterior views. Spinous processes are shorter and wider in *Au. sediba* and modern humans than in chimpanzees. Arrows indicate the widest part of the spinal canal, which is more posteriorly located in *Au. sediba* and chimpanzees than in modern humans. Brackets show the height of the uncinated processes, which are shorter in *Au. sediba* and modern humans than in chimpanzees, and the width of the vertebral body, which is narrower in *Au. sediba* and chimpanzees than in modern humans

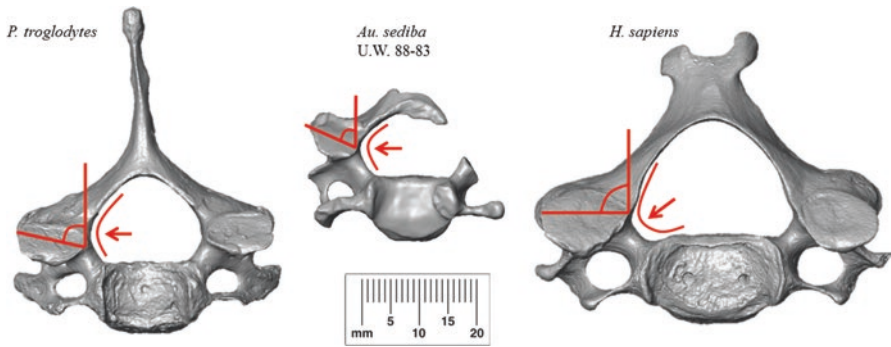


Fig. 7.3 Fourth cervical vertebrae in superior view. Orientations of the superior articular facets are more acute in *Au. sediba* and chimpanzees than in modern humans, which are obtuse. As with the third cervical vertebra, the widest portion of the spinal canal is more posterior in *Au. sediba* and chimpanzees than in modern humans

(in addition to a badly crushed sacrum). It is currently unknown whether StW 573 belongs to *A. africanus* or a second species in the lower members at Sterkfontein, the latter of which has been suggested by Clarke (2008). Two additional, mostly complete lumbar vertebrae are known from Member 2 of Jacovec Cavern in Sterkfontein: middle lumbar vertebrae (StW 656) and last lumbar vertebrae

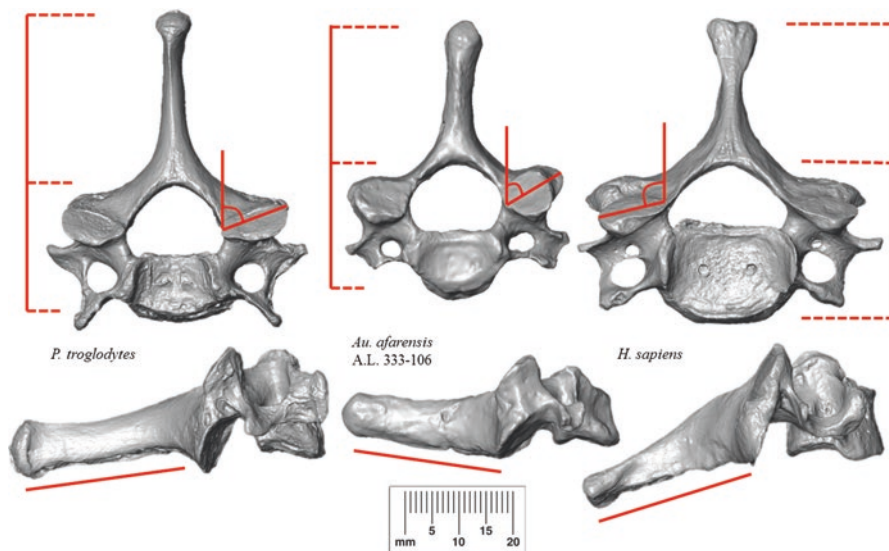


Fig. 7.4 Sixth cervical vertebrae in superior and lateral view. The relative length of the spinous process is shorter in *Au. afarensis* and humans than in chimpanzees. The superior articular facets are acutely angled in *Au. afarensis* and chimpanzees and obtusely angled in modern humans. The spinous process is cranially oriented in *Au. afarensis*, slightly caudally oriented in chimpanzees, and more strongly caudally oriented in modern humans

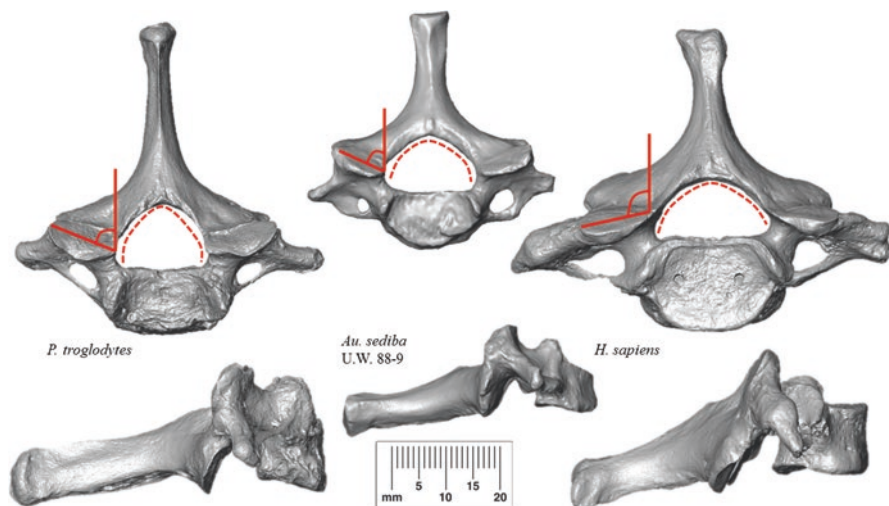


Fig. 7.5 Last cervical vertebrae in superior and lateral view. Superior articular facets are acutely angled in *Au. sediba* and chimpanzees and obtusely angled in modern humans. Spinal canal shape is wider in *Au. sediba* and modern humans than in chimpanzees

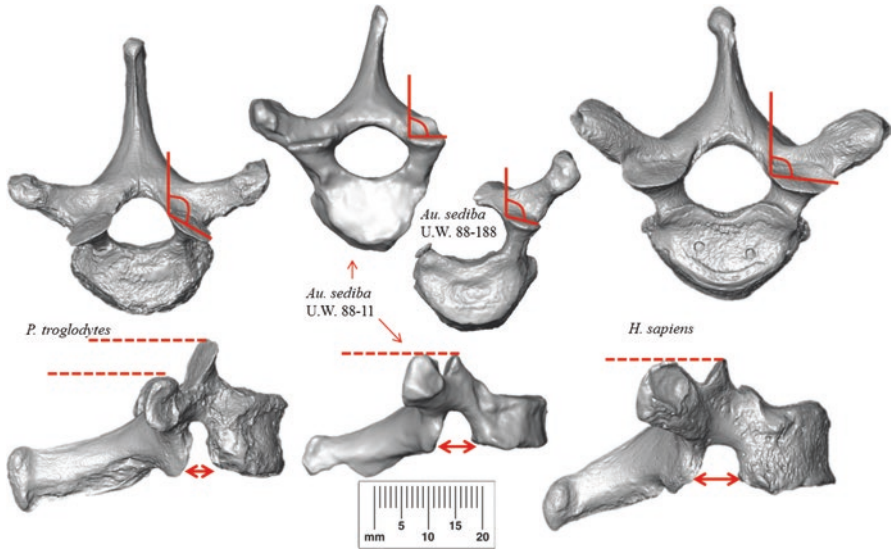


Fig. 7.6 Second thoracic vertebrae in superior and lateral view. Superior articular facets are less obtusely angled in *Au. sediba* and modern humans than in chimpanzees. The transverse processes are more superiorly positioned relative to the superior articular facets in *Au. sediba* and modern humans than in chimpanzees. The vertebral notch is wider in *Au. sediba* and modern humans than in chimpanzees

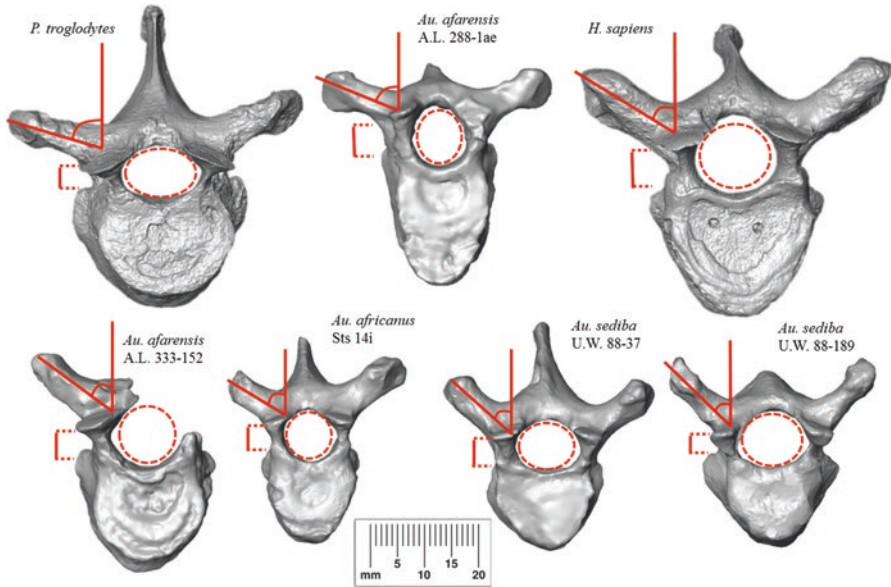


Fig. 7.7 Middle thoracic vertebrae in superior view. Transverse processes are generally more dorsally oriented in hominins than in chimpanzees (A.L. 288-1ae, but not A.L. 333-152, is an exception). Pedicles are anteroposteriorly longer in hominins than in chimpanzees (U.W. 88-189, but not U.W. 88-37, is an exception). Spinal canal shape is more round in hominins than in chimpanzees

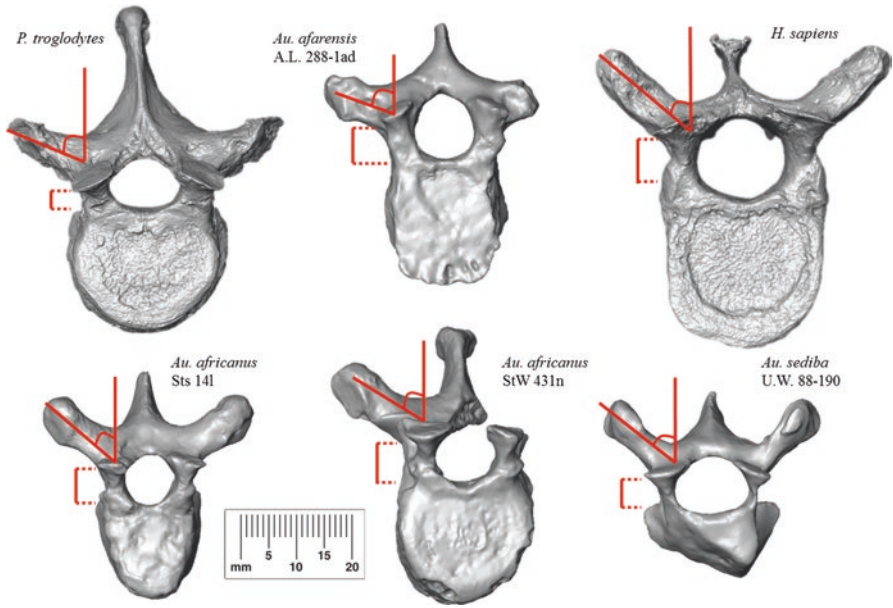


Fig. 7.8 Ninth thoracic vertebrae (tenth thoracic in a chimpanzee) in superior view. Transverse process orientation is more acute in *Au. africanus*, *Au. sediba*, and modern humans than in *Au. afarensis* and chimpanzees. Pedicles are anteroposteriorly longer in hominins than in chimpanzees

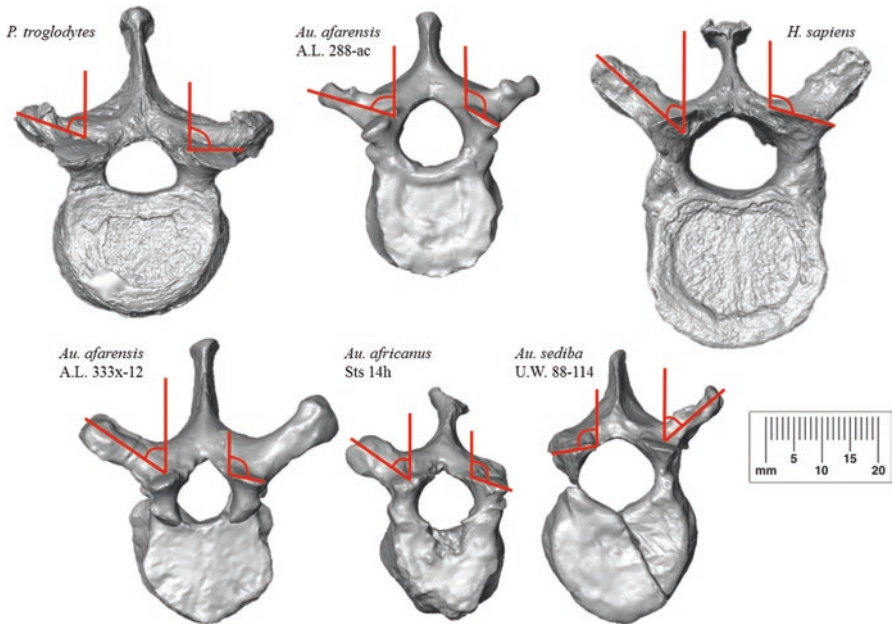


Fig. 7.9 Antepenultimate thoracic vertebrae in superior view. Transverse processes are generally more dorsally oriented in hominins than in chimpanzees (A.L. 288-1 ac, but not A.L. 333x-12, is an exception). Superior articular facets are more obtusely oriented in hominins than in chimpanzees

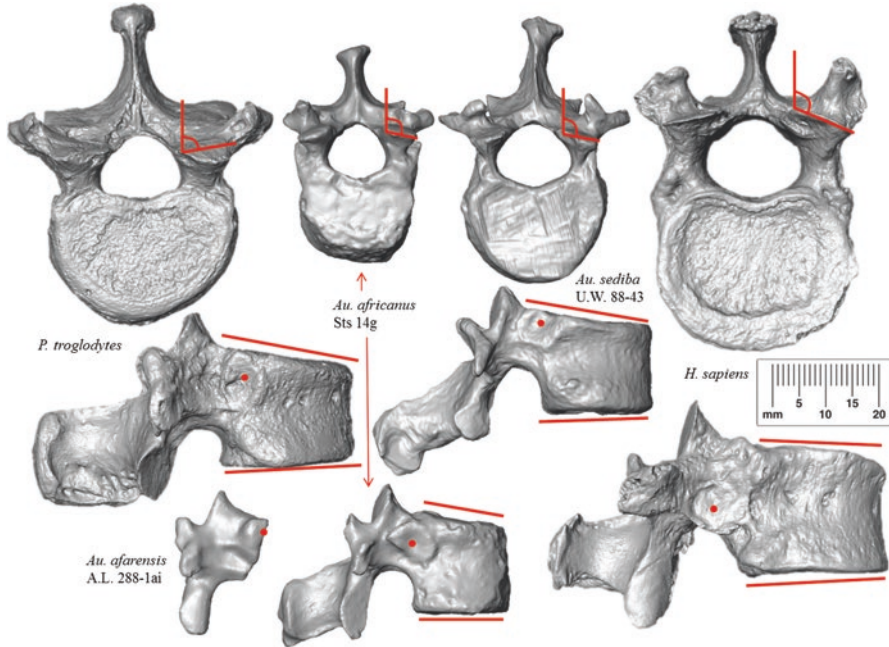


Fig. 7.10 Penultimate thoracic vertebrae in superior and lateral view. Superior articular facets are obtusely oriented in hominins and acutely oriented in chimpanzees. Vertebral bodies are more strongly ventrally wedged in *Australopithecus* and chimpanzees than in modern humans. Red dots indicate the center of the costal facets, which are located more cranially and anteriorly in fossil hominins and chimpanzees than in modern humans. Notice that extant taxa with the transitional vertebra located at the penultimate thoracic level were chosen, whereas the transitional vertebra occurs modally at the last thoracic vertebra in modern humans and chimpanzees

(StW 600) (Partridge et al. 2003; Pickering et al. 2019b). Both vertebrae are similar to those of *Au. africanus* discussed below (Pickering et al. 2019b).

Arguably, *Au. africanus* vertebrae are the best known in the early hominin fossil record, although, as we previously mentioned, no cervical vertebrae are known for this species. All specimens discussed here derive from Member 4 of Sterkfontein. The first early hominin partial skeleton recovered (d. 1947), Sts 14, was announced in Broom et al. (1950) and fully described in Robinson (1972). This individual's vertebral and sacral annular epiphyses are in various stages of fusion, and the iliac crest is not fully fused, suggesting that Sts 14 is a subadult (Bonmatí et al. 2008). The original identification and seriation of the vertebrae was challenged by Haeusler et al. (2002), who argued for a consecutive series of 15 thoracolumbar vertebrae (T3–L5). The fossils were found in cement-like breccia alongside a partial pelvis and were treated with acid for removal, which unfortunately dissolved some morphological aspects of the vertebrae. Additionally, a number of the vertebrae were “reconstructed” with plaster permanently applied directly to the fossils, in some cases fairly extensively (e.g., Sts 14a, the last lumbar vertebra; see Fig. 7.15).

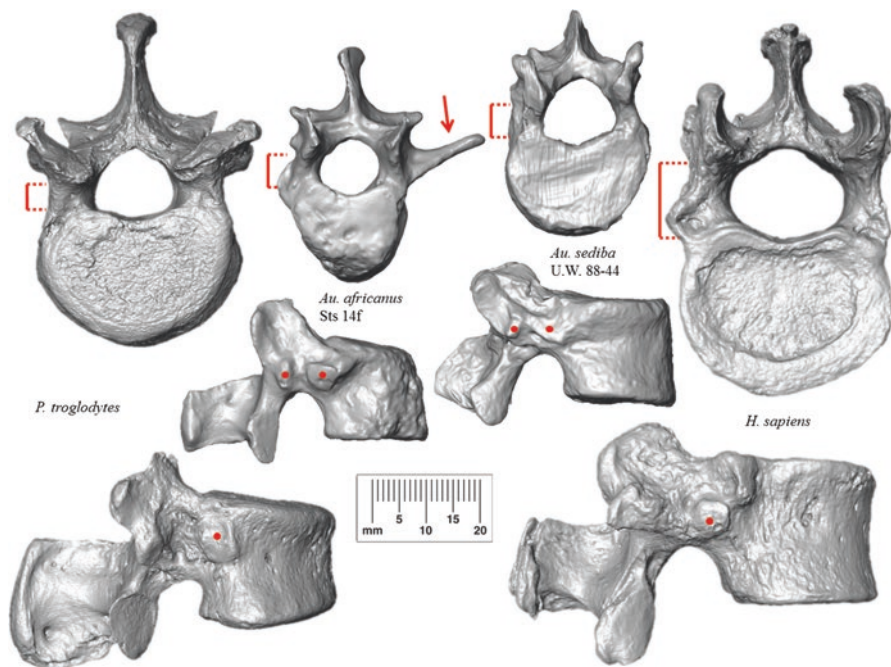


Fig. 7.11 Ultimate thoracic vertebrae in superior and lateral views. Anteroposterior pedicle length is short in chimpanzees, long in modern humans, and somewhat intermediate in fossil hominins. Costal facets are indicated with red dots: notice that those of *Au. africanus* and *Au. sediba* are bifurcate. The red arrow indicates a lumbar transverse process or ankylosed last rib of Sts 14f. Both Sts 14f and U.W. 88-44 are fairly lumbar-like in their overall morphology. Extant taxa with post-transitional thoracic vertebrae are shown for comparison with the fossil hominins

Another *Au. africanus* partial skeleton, StW 431, was discovered in 1987 and published by Toussaint et al. (2003), although the vertebrae were fully described previously by Benade (1990). Haeusler et al. (2002) reassessed the vertebrae and seriated them as ten consecutive elements (T8–L5). StW 431 is an adult and, given its large size compared to Sts 14, is probably a male. Similar-sized adult vertebrae recovered in 1969 and 1975, StW 8, a series of four articulated lumbar vertebrae, and StW 41, two articulated lower thoracic vertebrae, were proposed to be from the same individual by Tobias (1978). Seriation attempts were made by Benade (1990) and Sanders (1998), with the consensus that a continuous series of lower thoracic and lumbar vertebrae (T11–L4) are represented. Two other vertebrae from Member 4 at Sterkfontein, attributed by Robinson (1972) to *Au. africanus*, are the large lower thoracic vertebral body Sts 73 (Robinson 1972) and the partial lumbar vertebra Sts 65 associated with the homonymous female ilium and pubis (Claxton et al. 2016).

The site of Malapa bears *Au. sediba* fossils dated to just under 2 Ma and yields vertebrae from two individuals: an adult female (MH2) and a juvenile male (MH1) (Berger et al. 2010). Additional vertebrae are described in Williams et al. (2013, 2018), with analyses of cervical vertebrae published in Meyer et al. (2017). Eight

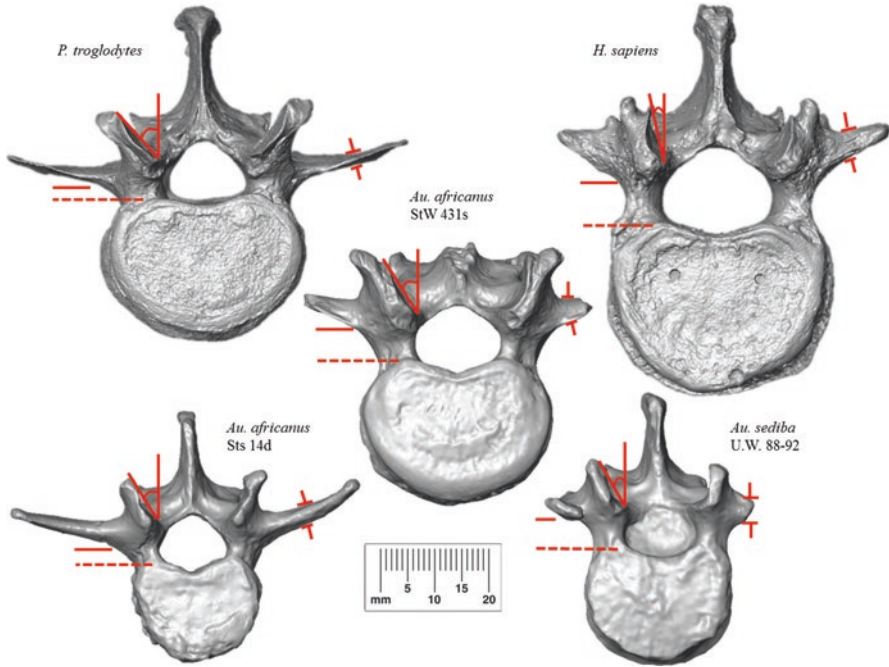


Fig. 7.12 First lumbar vertebrae in superior view. Superior articular facets are more acutely oriented in hominins than in chimpanzees. This is the opposite pattern than what is found at the last lumbar level. Pedicles are longer and lumbar transverse processes are anteroposteriorly more robust in hominins than in chimpanzees

nonconsecutive cervical, thoracic, and lumbar vertebrae are associated with MH1, while 14 vertebrae of MH2 have been recovered, with at least 3 consecutive thoracic vertebrae and 2 lower lumbar vertebrae preserved in articulation with a sacrum (Kibii et al. 2011; Williams et al. 2013, 2018). Overlapping elements belonging to MH1 and MH2 allow for unprecedented comparisons of contemporaneous adult and juvenile, female and male australopiths, which will provide insights into ontogeny and sexual dimorphism of this species.

7.4 Head Carriage and Neck Mobility

Basicranial morphology and cervical vertebral morphology correlate with positional behavior and head and neck posture in primates (Strait and Ross 1999; Manfreda et al. 2006; Russo and Kirk 2013, 2017; Nalley and Grider-Potter 2015; but see caveats in Ruth et al. 2016; Nalley and Grider-Potter 2017; Villamil 2017). Upright posture and bipedal locomotion in early hominins were first inferred from the cranial base in the Taung child, a juvenile member of *Australopithecus africanus*

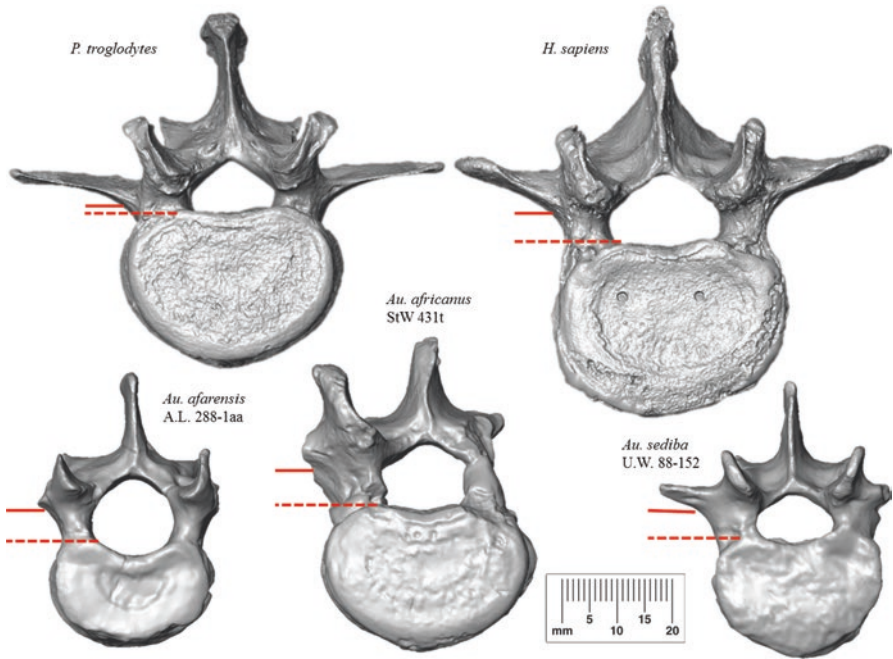


Fig. 7.13 Middle lumbar vertebrae in superior view. Pedicles are anteroposteriorly longer in hominins than in chimpanzees. Notice that superior articular facet orientation is similar across taxa at this level

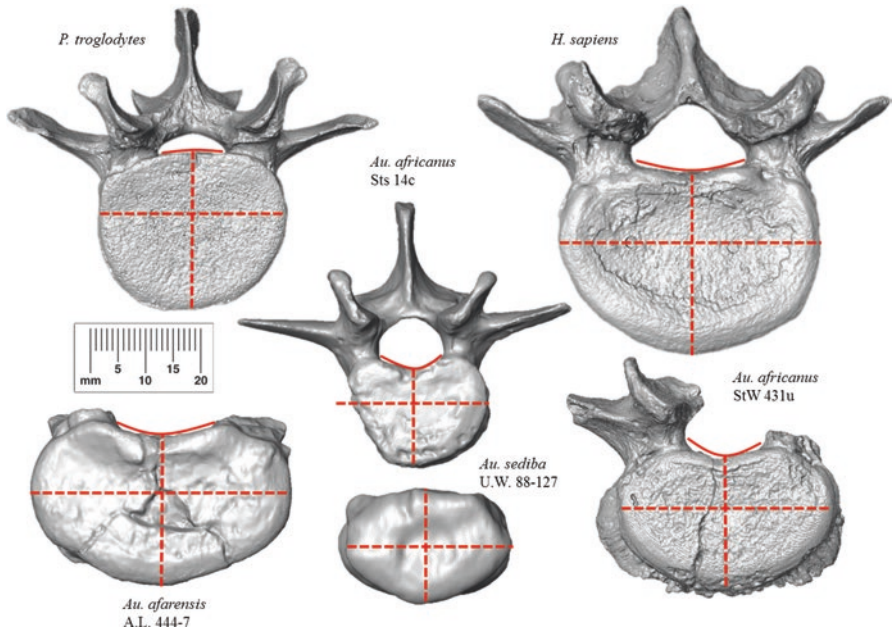


Fig. 7.14 Penultimate lumbar vertebrae (middle lumbar vertebra of *Au. africanus*) in superior view. The hominin vertebral body is kidney-shaped (reniform), with a dorsal concavity that the chimpanzee lacks. Notice that the mediolateral width of the hominin vertebral body is greater than its dorsoventral dimension

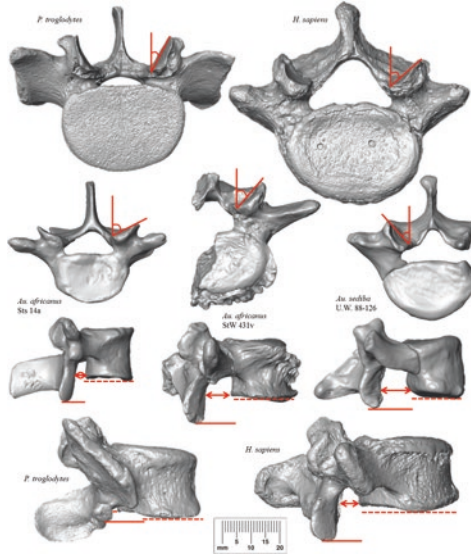


Fig. 7.15 Ultimate lumbar vertebrae in superior and lateral views. Hominin superior articular facets are less acutely angled than chimpanzees. This reflects the oblique (more coronal) orientation of hominin inferior articular facets, which meet the articular facets of the sacrum. The inferior articular facets project more caudally in hominins than in chimpanzees. Hominins also have wider vertebral notches than chimpanzees, although Sts 14a demonstrates a fairly narrow notch compared to other hominins

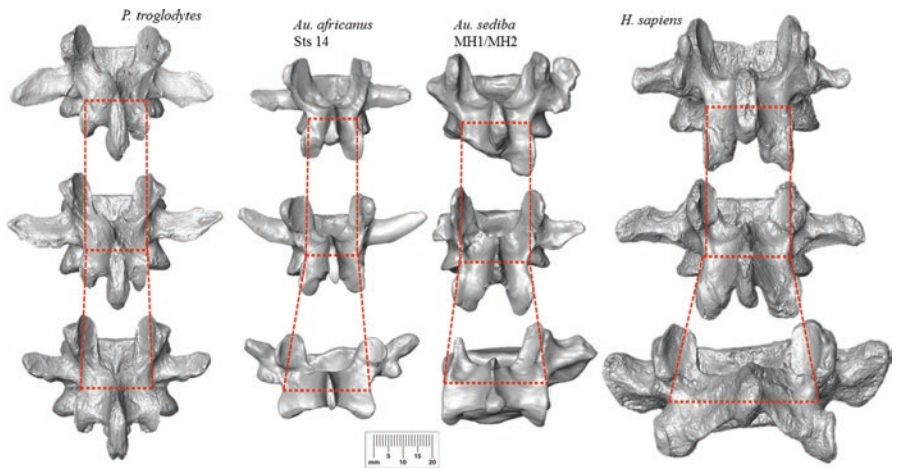


Fig. 7.16 Upper, middle, and lower lumbar vertebrae in posterior view in fossil hominins and extant taxa. Notice that lamina breadth increases caudally in hominins and remains consistently narrow in chimpanzees

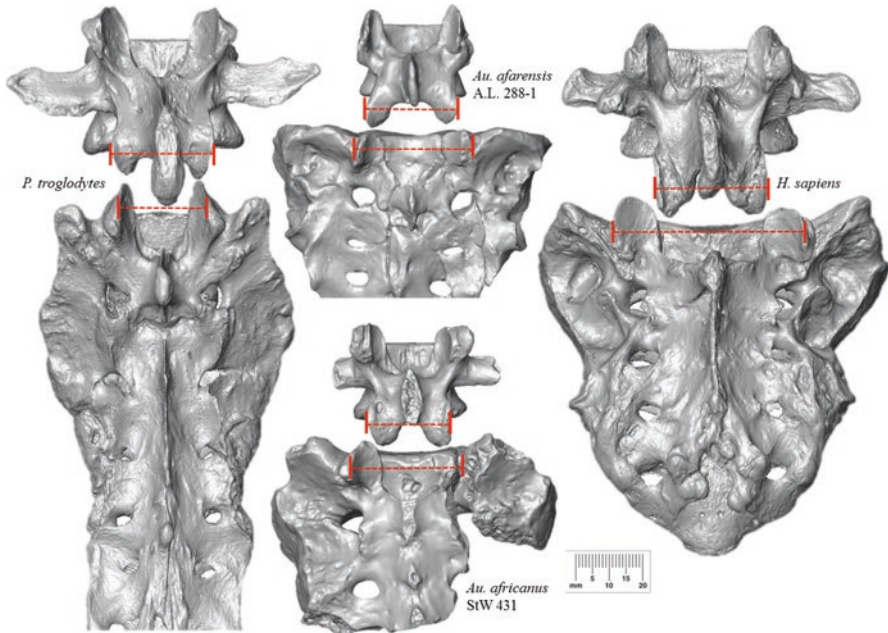


Fig. 7.17 Second lumbar vertebrae and sacra in posterior view in fossil hominins and extant taxa. Comparing the lower articular facet breadth of L2 to superior articular facet breadth of the sacrum reveals an increase in hominins (more drastic in modern humans than in *Australopithecus*) and a decrease or consistency in breadth in chimpanzees. Notice that the sacral alae are much broader in hominins than in chimpanzees

(Dart 1925). The cranial base has also been used to infer bipedalism, and, by implication, hominin status, of the late Miocene *Sahelanthropus tchadensis* cranium, a candidate for the earliest known member of the human lineage (Brunet et al. 2002; Zollikofer et al. 2005; but see Wolpoff et al. 2002). An anteriorly positioned and anteriorly oriented foramen magnum characterizes modern humans to the exclusion of chimpanzees and other apes (Strait and Ross 1999; Russo and Kirk 2013; Been et al. 2014). This places the human skull atop a vertical vertebral column, with minimal neck musculature needed to support the head compared to great apes (Le Gros Clark 1947; Adams and Moore 1975; Aiello and Dean 1990; Lieberman 2011). Neck posture, quantified as cervical lordosis, is correlated with foramen magnum orientation in modern humans, suggesting that cranial base morphology can be informative for reconstructing neck posture in extinct hominins (Been et al. 2014, 2017; see reference to Zollikofer et al. 2005 and Kimbel and Rak 2010 below).

Cervical vertebrae are rare in early hominins. Associated cervical vertebrae are even rarer and are currently known only for *Au. afarensis* (KSD-VP-1/1) and *Au. sediba* (MH1 and MH2). Recent work has shown that australopith cervical vertebrae are intermediate in morphology (and potentially in terms of function) between chimpanzees and modern humans (Gommery 2006; Kimbel and Rak 2010; Nalley 2013; Meyer 2016; Arlegi et al. 2017; Meyer et al. 2017; see also Lovejoy et al.

Table 7.1 List of specimens and species to which they belong

Level	Specimen	Comments	References
<i>Ardipithecus ramidus</i> , Aramis			
?	ARA-VP-6/500-070	Possible vertebra	White et al. (2009)
?	ARA-VP-6/500-086	Possible vertebra	White et al. (2009)
C	ARA-VP-6/500-057	Mostly complete	White et al. (2009)
T	ARA-VP-6/500-084	Thoracic arch	White et al. (2009)
T	ARA-VP-6/1001	Thoracic arch	White et al. (2009)
T	ARA-VP-6/1012	Thoracic spine	White et al. (2009)
<i>Australopithecus anamensis</i> , Asa Issie			
C1	ASI-VP-2/219	Neural arch fragment	Meyer and Williams (2019)
C1	ASI-VP-2/220	Neural arch fragment	White et al. (2006), Meyer and Williams (2019)
C2	ASI-VP-2/214	Body/partial arch	Meyer and Williams (2019)
C6	ASI-VP-2/218	Partial neural arch	Meyer and Williams (2019)
T1	ASI-VP-2/224	Neural arch fragment	White et al. (2006), Meyer and Williams (2019)
T1	ASI-VP-2/470	Body	Meyer and Williams (2019)
T9	ASI-VP-2/223	Partial neural arch	White et al. (2006), Meyer and Williams (2019)
<i>Australopithecus afarensis</i> , Woranso Mille			
C2	KSD-VP-1/1h	Body/partial arch	Haile-Selassie et al. (2010), Meyer (2016)
C3	KSD-VP-1/1i,x	Body/partial arch	Haile-Selassie et al. (2010), Meyer (2016)
C4	KSD-VP-1/1j,ac,z	Body/partial arch	Haile-Selassie et al. (2010), Meyer (2016)
C5	KSD-VP-1/1k,aa,y	Body/partial arch	Haile-Selassie et al. (2010), Meyer (2016)
C6	KSD-VP-1/1l	Body	Haile-Selassie et al. (2010), Meyer (2016)
C7	KSD-VP-1/1ad,ae,af,ag,ab	Partial neural arch	Haile-Selassie et al. (2010), Meyer (2016)
?	KSD-VP-1/1m	Body	Haile-Selassie et al. (2010)
<i>Australopithecus afarensis</i> , Dikika			
C1	DIK-1-1 C1	Mostly complete	Alemseged et al. (2006)
C2	DIK-1-1 C2	Mostly complete	Alemseged et al. (2006)
C3	DIK-1-1 C3	Mostly complete	Alemseged et al. (2006)
C4	DIK-1-1 C4	Mostly complete	Alemseged et al. (2006)
C5	DIK-1-1 C5	Mostly complete	Alemseged et al. (2006)
C6	DIK-1-1 C6	Mostly complete	Alemseged et al. (2006)
C7	DIK-1-1 C7	Mostly complete	Alemseged et al. (2006)
T1	DIK-1-1 T1	Mostly complete	Alemseged et al. (2006), Ward et al. (2017)
T2	DIK-1-1 T2	Mostly complete	Alemseged et al. (2006), Ward et al. (2017)
T3	DIK-1-1 T3	Mostly complete	Alemseged et al. (2006), Ward et al. (2017)
T4	DIK-1-1 T4	Mostly complete	Alemseged et al. (2006), Ward et al. (2017)
T5	DIK-1-1 T5	Mostly complete	Alemseged et al. (2006), Ward et al. (2017)
T6	DIK-1-1 T6	Mostly complete	Alemseged et al. (2006), Ward et al. (2017)
T7	DIK-1-1 T7	Mostly complete	Alemseged et al. (2006), Ward et al. (2017)

(continued)

Table 7.1 (continued)

Level	Specimen	Comments	References
T8	DIK-1-1 T8	Mostly complete	Alemseged et al. (2006), Ward et al. (2017)
T9	DIK-1-1 T9	Mostly complete	Alemseged et al. (2006), Ward et al. (2017)
T10	DIK-1-1 T10	Mostly complete	Alemseged et al. (2006), Ward et al. (2017)
T11	DIK-1-1 T11	Mostly complete	Alemseged et al. (2006), Ward et al. (2017)
T12	DIK-1-1 T12	Mostly complete	Alemseged et al. (2006), Ward et al. (2017)
<i>Australopithecus afarensis</i> , Hadar			
T6	A.L. 288-1ae/ah	Mostly complete	Johanson et al. (1982), Cook et al. (1983)
T7	A.L. 288-1af	Body	Johanson et al. (1982), Cook et al. (1983)
T8	A.L. 288-1ag/aj	Mostly complete	Johanson et al. (1982), Cook et al. (1983)
T9	A.L. 288-1ad	Mostly complete	Johanson et al. (1982), Meyer et al. (2015)
T10	A.L. 288-1ac	Mostly complete	Johanson et al. (1982), Meyer et al. (2015)
T11	A.L. 288-1ai	Partial dorsal pillar	Johanson et al. (1982), Meyer et al. (2015)
L2	A.L. 288-1ab	Spinous process	Johanson et al. (1982), Meyer et al. (2015)
L3	A.L. 288-1aa/ak/al	Mostly complete	Johanson et al. (1982), Meyer et al. (2015)
C1	A.L. 333-83	Partial neural arch	Lovejoy et al. (1982)
C2	A.L. 333-101	Mostly complete	Lovejoy et al. (1982)
C5/6	A.L. 333-106	Mostly complete	Lovejoy et al. (1982), Cook et al. (1983)
T2	A.L. 333-81	Mostly complete	Lovejoy et al. (1982), Cook et al. (1983)
T6	A.L. 333-152	Body/partial arch	Ward et al. (2012)
T7/8/9	A.L. 333-51	Body	Lovejoy et al. (1982), Cook et al. (1983)
L3	A.L. 333-73	Body	Lovejoy et al. (1982), Cook et al. (1983)
C/T	A.L. 333w-14	Lower C/Upper T spinous process	Lovejoy et al. (1982), Cook et al. (1983)
T10	A.L. 333x-12	Mostly complete	Lovejoy et al. (1982), Cook et al. (1983)
C	A.L. 444-9	Partial neural arch	Ward et al. (2012)
T	A.L. 444-8	Spinous process	Ward et al. (2012)
T	A.L. 444-10	Partial neural arch	Ward et al. (2012)
T	A.L. 444-11	Partial neural arch	Ward et al. (2012)
L	A.L. 444-7	Body	Ward et al. (2012)
?	A.L. 444-12	Partial neural arch	Ward et al. (2012)
<i>Australopithecus</i> sp., Sterkfontein			
L3	StW 656	Mostly complete	Pickering et al. (2019a)
L5	StW 600	Mostly complete	Partridge et al. (2003), Pickering et al. (2019a)
L	StW 573	Partial column	Clarke (2002, 2019)
<i>Australopithecus africanus</i> , Sterkfontein			
T3	Sts 14p	Partial arch, body	Robinson (1972), Haeusler et al. (2002)
T4	Sts 14n	Mostly complete	Robinson (1972), Haeusler et al. (2002)
T5	Sts 14m	Mostly complete	Robinson (1972), Haeusler et al. (2002)
T6	Sts 14i	Mostly complete	Robinson (1972), Haeusler et al. (2002)
T7	Sts 14k	Mostly complete	Robinson (1972), Haeusler et al. (2002)
T8	Sts 14l	Mostly complete	Robinson (1972), Haeusler et al. (2002)
T9	Sts 14o	Body	Robinson (1972), Haeusler et al. (2002)

(continued)

Table 7.1 (continued)

Level	Specimen	Comments	References
T10	Sts 14h	Mostly complete	Robinson (1972), Haeusler et al. (2002)
T11	Sts 14g	Mostly complete	Zihlmann (1971), Robinson (1972), Haeusler et al. (2002)
T12	Sts 14f	Mostly complete	Robinson (1972), Haeusler et al. (2002)
L1	Sts 14e	Mostly complete	Robinson (1972), Haeusler et al. (2002)
L2	Sts 14d	Mostly complete	Robinson (1972), Haeusler et al. (2002)
L3	Sts 14c	Mostly complete	Robinson (1972), Haeusler et al. (2002)
L4	Sts 14b	Partial arch, body	Robinson (1972), Haeusler et al. (2002)
L5	Sts 14a	Partial arch, body	Zihlmann (1971), Robinson (1972), Haeusler et al. (2002)
T8	StW 431o	Body	Toussaint et al. (2003), Haeusler et al. (2002)
T9	StW 431n	Mostly complete	Toussaint et al. (2003), Haeusler et al. (2002)
T10	StW 431ma/mb	Partial arch, body	Toussaint et al. (2003), Haeusler et al. (2002)
T11	StW 431l	Partial arch	Toussaint et al. (2003), Haeusler et al. (2002)
T12	StW 431qa/qb	Partial arch, body	Toussaint et al. (2003), Haeusler et al. (2002)
L1	StW 431r	Body	Toussaint et al. (2003), Haeusler et al. (2002)
L2	StW 431s	Mostly complete	Toussaint et al. (2003), Haeusler et al. (2002)
L3	StW 431t	Body, partial arch	Toussaint et al. (2003), Haeusler et al. (2002)
L4	StW 431u	Body, partial arch	Toussaint et al. (2003), Haeusler et al. (2002)
L5	StW 431v	Partial arch, body	Toussaint et al. (2003), Haeusler et al. (2002)
T11	StW H41a	Body	Tobias (1992), Sanders (1998)
T12	StW H41b	Body	Tobias (1992), Sanders (1998)
L1	StW H8a	Partial arch, body	Tobias (1992), Sanders (1998)
L2	StW H8b	Body, partial arch	Tobias (1992), Sanders (1998)
L3	StW H8c	Body, arch fragment	Tobias (1992), Sanders (1998)
L4	StW H8d	Partial body	Tobias (1992), Sanders (1998)
T12	Sts 73	Body	Zihlmann (1971), Robinson (1972), Sanders (1998)
<i>Australopithecus sediba</i> , Malapa			
C3	U.W. 88-72 (MH1)	Partial arch, body	Berger et al. (2010), Williams et al. (2013, 2018), Meyer et al. (2017)
C7	U.W. 88-09 (MH1)	Mostly complete	Berger et al. (2010), Williams et al. (2013, 2018), Meyer et al. (2017)

(continued)

Table 7.1 (continued)

Level	Specimen	Comments	References
Upr T	U.W. 88-11 (MH1)	Mostly complete	Berger et al. (2010), Williams et al. (2013, 2018), Meyer et al. (2017)
Mid T	U.W. 88-37 (MH1)	Mostly complete	Berger et al. (2010), Williams et al. (2013, 2018)
Lwr T	U.W. 88-70 (MH1)	Partial arch, body	Berger et al. (2010), Williams et al. (2013, 2018)
Lwr T	U.W. 88-90 (MH1)	Partial arch, body	Berger et al. (2010), Williams et al. (2013, 2018)
Mid L	U.W. 88-92 (MH1)	Mostly complete	Berger et al. (2010), Williams et al. (2013, 2018)
Mid L	U.W. 88-152 (MH1)	Mostly complete	Williams et al. (2013, 2018)
C3	U.W. 88-93 (MH2)	Mostly complete	Berger et al. (2010), Williams et al. (2013, 2018), Meyer et al. (2017)
C6	U.W. 88-83 (MH2)	Body, partial arch	Berger et al. (2010), Williams et al. (2013, 2018), Meyer et al. (2017)
Upr T	U.W. 88-188 (MH2)	Body, partial arch	Williams et al. (2013, 2018)
Mid T	U.W. 88-189 (MH2)	Mostly complete	Williams et al. (2013, 2018)
T	U.W. 88-190 (MH2)	Partial arch, body	Williams et al. (2013, 2018)
T	U.W. 88-191 (MH2)	Partial arch, body	Williams et al. (2013, 2018)
T	U.W. 88-96 (MH2)	Mid-Lower T neural arch fragment	Berger et al. (2010), Williams et al. (2013, 2018)
Lwr T	U.W. 88-114 (MH2)	Mostly complete	Williams et al. (2013, 2018)
Lwr L	U.W.88-43 (MH2)	Mostly complete	Berger et al. (2010), Williams et al. (2013, 2018)
Ult T	U.W. 88-44 (MH2)	Mostly complete	Berger et al. (2010), Williams et al. Williams (2012a, b), (2018)
Lwr L	U.W. 88-127/153/234	Body, partial arch	Williams et al. (2013, 2018)
Ult L	U.W. 88-126/138	Body, partial arch	Williams et al. (2013, 2018)

1982) (Figs. 7.1, 7.2, 7.3, 7.4, and 7.5). However, the presumed retention of primitive features (present in extant great apes) in *Au. sediba* cervical vertebrae such as relatively gracile vertebral bodies and robust dorsal pillar morphologies; acute (versus obtuse) superior articular facet angles; long, dorsally oriented lower cervical spinous processes; and inferred lack of the nuchal ligament (Meyer et al. 2017; see Figs. 7.2, 7.3, 7.5) suggests limited neck mobility in australopiths relative to modern humans (Nalley 2013; Meyer 2016; Arlegi et al. 2017). While only the latter two features are shared by the KSD-VP-1/1 *Au. afarensis* (Meyer 2016), this morpho-functional condition appears corroborated by evidence for posteriorly oriented foramina magna on australopith basicrania (Zollikofer et al. 2005; Kimbel and Rak 2010). However, relatively short spinous processes on upper subaxial cervical vertebrae and vertebral body wedging angles similar to modern humans suggest cervical lordosis and a human-like neck posture (Meyer 2016; Meyer et al. 2017; Arlegi et al. 2017) (Figs. 7.2, 7.4).

7.5 Number and Configuration of Thoracic and Lumbar Vertebrae

Regional vertebral numbers are relatively stable in mammals, with nearly all possessing seven cervical vertebrae, and many clades fixed at either 19 or 20 thoracolumbar vertebrae, with little variation (Galis 1999; Narita and Kuratani 2005; Asher et al. 2011; Williams et al. 2019). The same is true for the majority of primate clades (Schultz and Straus 1945; Pilbeam 2004). In particular, reduction in the number of thoracolumbar vertebrae in primates and other mammals is rare, with bats, giant pandas, and hominoids as notable exceptions (Schultz and Straus 1945; Pilbeam 2004; Williams 2011; Russo and Williams 2015; Williams and Russo 2015; Williams et al. 2017, 2019). No single fossil hominin skeleton preserves a complete thoracolumbar column. As Table 7.1 indicates, Sts 14 and StW 431 (*Au. africanus*) preserve five lumbar vertebrae each, but neither preserves a complete thoracic column. DIK-1-1 (*Au. afarensis*), on the other hand, does preserve a putatively complete thoracic (and cervical) column but lacks any lumbar vertebrae (Ward et al. 2017). A.L. 288-1 (*Au. afarensis*) preserves a series of thoracic vertebrae and parts of two lumbar vertebrae, StW 8/41 (*Au. africanus*) probably represents the last two thoracic vertebrae and the first four lumbar vertebrae, and MH1 and MH2 (*A. sediba*) preserve a number of thoracic vertebrae and two lumbar vertebrae each (Table 7.1).

Thoracolumbar vertebrae have also been identified functionally (as opposed to developmentally, based on the presence or absence of ribs) on the basis of articular facet (zygapophysis) orientation and location of the transitional vertebra (e.g., Shapiro 1993; Whitcome 2012). This so-called zygapophyseal definition of thoracic versus lumbar vertebrae identifies the transitional vertebra as the last thoracic vertebra (but see Haeusler et al. 2002; Williams 2012a; Williams et al. 2013). Whereas the distinction does not affect regional counts in most hominoids because the transitional vertebra is modally the last rib-bearing vertebra, it is located one to several elements cranial to the last thoracic vertebra in non-hominoid primates (e.g., at the T10 level in a primate with 12 or 13 thoracic vertebrae), which retain the primitive mammalian configuration (Shapiro 1993; Williams 2012a). Importantly, fossil hominins seem to be distinct from modern humans and other hominoids in this regard (Williams 2012b; Williams et al. 2016). The transitional vertebra is located at the penultimate thoracic level in all early hominins preserving this region (Haeusler et al. 2002; Williams 2012a; Williams et al. 2013, 2016; Meyer et al. 2015; Ward et al. 2017). This displacement of transitional and last thoracic vertebra morphologies has led to confusion and debate over the total number of thoracolumbar vertebrae in hominin evolution (Robinson 1972; Sanders 1995; Pilbeam 2004; Lovejoy et al. 2009d; McCollum et al. 2010; Williams and Russo 2015; Williams et al. 2013, 2017; Thompson and Almécija 2017).

7.6 Lumbar Morphology

Due to both lack of ribs and sagittal mobility allowed by post-transitional vertebrae, the lumbar column is thought to be particularly relevant to function and locomotion. Compared to the short, stable lower backs of great apes, hominins have longer, more mobile lower backs. In addition to a numerically longer lumbar column than great apes (five lumbar vertebrae as opposed to four or even just three), hominins have fewer rib pairs (and fewer thoracic vertebrae resulting from a cranially directed homeotic shift at the thoracolumbar border; see Pilbeam 2004; Williams et al. 2017) and fewer lower lumbar vertebrae “entrapped” between the iliac blades (Lovejoy 2005b; Lovejoy and McCollum 2010; McCollum et al. 2010; Machnicki et al. 2016). The presence of an additional post-transitional vertebra in early hominins would conceivably allow more sagittal mobility, which may be related to the achievement of adequate lumbar lordosis for bipedal posture and locomotion (Lovejoy 2005a; Williams et al. 2013).

Hominins are characterized by lumbar lordosis (ventral convexity of the lower back), a combination of bony and soft tissue wedging of lumbar vertebrae, and angulation of the sacrum that counters the primary kyphotic curve (ventrally concavity of the upper back) of the vertebral column, which is found in nonhuman primates and many other mammals. In addition to wedging of the vertebral body and intervertebral discs, the lamina and articular facets increase in width starting in the middle of the lumbar column (Lovejoy 2005a; Ward and Latimer 2005), the postzygapophyses (inferior articular processes) are more dorsally angled (Been et al. 2010b, 2012), and laminar fossae (also known as “imbrication pockets”) form via bone remodeling on nonarticular areas of the pars interarticularis from hyperextension of the articular facet joints (Latimer and Ward 1993; Ward and Latimer 2005; Williams et al. 2013; see Fig. 7.16). In combination with thoracic kyphosis, lumbar lordosis contributes to the sinusoidal curvature of the human spine and is considered a primary adaptation to bipedalism and of our lineage. This configuration evolved to balance and stabilize the upright trunk over two legs and dissipate loads through the vertebral column, pelvis, and lower limbs during bipedal posture and locomotion (Sanders 1995; Lovejoy 2005b). Australopiths are widely considered to have possessed modern human-like lordosis, evidenced by dorsal wedging of lower lumbar vertebrae and a pattern of caudad widening of the lamina and articular facets in *Au. africanus* (Sts 14, StW 431) and *Au. sediba* (MH2) (Robinson 1972; Sanders 1995; Whitcome et al. 2007; Been et al. 2012; Williams et al. 2013) and caudally progressive widening of the articular facets in *Au. afarensis* (A.L. 288-1) (Lovejoy 2005a) (Figs. 7.16 and 7.17). Additionally, sexual dimorphism in lumbar lordosis is present in both modern humans (Masharawi et al. 2010; Ostrofsky and Churchill 2015) and *Au. africanus* (Whitcome et al. 2007) and presumably in other australopiths.

7.7 Paleopathology

The evolution of bipedalism seems to have taken a toll on the lower back, a region prone to injury and chronic pain in modern human populations (Balagué et al. 2012; Castillo and Lieberman 2015). Although prolonged use of furniture and the poor postures promoted by its use are a probable culprit for many of these maladies (Black et al. 1996; Castillo and Lieberman 2015), vertebral pathologies are prevalent in the hominin fossil record (see Haeusler 2019). The A.L. 288-1 vertebral column shows evidence of the modern human disease known as Scheuermann's kyphosis, where the thoracic vertebral bodies are characterized by "hyperostotic" anterior bone growth that affects the wedging of vertebrae and increases thoracic kyphosis (Johanson et al. 1982; Cook et al. 1983) (Figs. 7.7 and 7.8). Cook et al. (1983) proposed that habitual ventral flexion of the trunk during flexed trunk climbing or object carrying might be responsible for Lucy's vertebral pathologies. The degree of anterior bone growth in her spine appears to be greater than that normally seen in modern humans with Scheuermann's disease (DiGiovanni et al. 1989). The isolated thoracic vertebra A.L. 333-51 and middle thoracic vertebrae of Sts 14 (Fig. 7.8) show evidence of slight to moderate anterior bone growth, suggesting Scheuermann's kyphosis or something like it occurred frequently in the australopiths.

Juvenile male *Au. sediba* MH1 bears the earliest evidence in the hominin fossil record for a neoplasm. A middle thoracic vertebra (U.W. 88-37) from this individual (Fig. 7.7) carries a lytic lesion on its right lamina and base of the spinous process that was diagnosed as an osteoid osteoma, a benign tumor that probably resulted in chronic pain and affected the individual's use of his right arm (Randolph-Quinney et al. 2016). Finally, the male *Au. africanus* partial skeleton StW 431 includes lower lumbar vertebrae with lesions and lipping (Figs. 7.14 and 7.15) that were originally interpreted as pathological (osteophytic lipping; Toussaint et al. 2003). D'Anastasio et al. (2009) later interpreted the lesions as a possible case of early brucellosis, an infectious disease often caused by ingestion of *Brucella*-infected animal proteins such as milk and meat. Recently, however, Odes et al. (2017) proposed taphonomic and pathological origins of the lesions, a combination of degenerative joint disease and insect burrowing in the bone prior to fossilization.

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