# Sagittal Balance of the Spine

## From Normal to Pathology: A Key for Treatment Strategy

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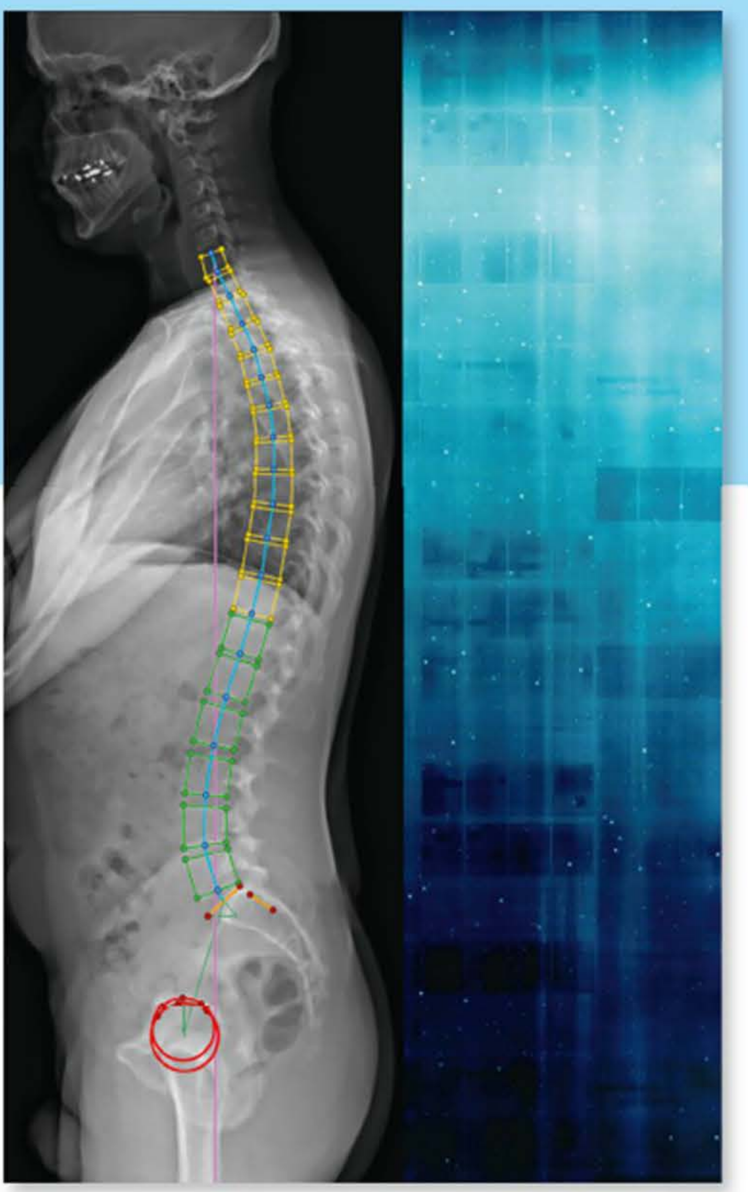

Thieme

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**Pierre Roussouly, MD**
Senior Surgeon
Spinal Surgery Unit
Croix Rouge Française-CMCR des Massues
Lyon, France

**João Luiz Pinheiro-Franco, MD, AFS**
Neurosurgeon and Spine Surgeon
Samaritano Hospital of São Paulo
São Paulo, Brazil

**Hubert Labelle, MD**
Professor of Surgery
Division of Orthopedic Surgery
University of Montreal
Montréal, Québec, Canada

**Martin Gehrchen, MD, PhD**
Associate Professor and Head of Spine Surgery
Spine Unit
Department of Orthopaedic Surgery
Rigshospitalet and University of Copenhagen
Copenhagen, Denmark

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# 2 The Acquisition of Human Verticality

*Christine Tardieu and Martin Haeusler*

**Abstract**
The shift from facultative to permanent bipedalism was a pivotal step in human evolution. Skeletal adaptations to efficient sagittal balance of the trunk are therefore key to identify fossils as our ancestors, the hominids. Morphological modifications of the pelvis and spine had a major role in this process. Here, we review these evolutionary adaptations that resulted in the formation of the spinopelvic functional unit. We suggest that the double S-shape of the vertebral column evolved secondary to the functionally linked pelvic modifications. Together with the lumbar lordosis, the approximation of the sacroiliac and hip joints brought the center of body mass closer to the hip joints, thus minimizing muscular work to maintain equilibrium. A prerequisite for the adoption of lumbar lordosis in early hominids was a long and mobile lumbar spine. As great apes have a rigid spine with three to four lumbar vertebrae, different scenarios have been proposed for the evolution of the human spinal segmentation. We argue that the common ancestor of chimpanzees and humans already possessed five lumbar vertebrae, and a pelvic incidence of ~ 30° that increased during evolution as the sacro-acetabular distance decreased. The strong correlation in humans between pelvic incidence and lumbar lordosis points toward an elaborated functional link that was shaped by natural selection. A review of the hominid fossil record, including *Sahelanthropus*, *Orrorin*, *Ardipithecus ramidus*, *Australopithecus afarensis*, *Australopithecus africanus*, *Australopithecus sediba*, *Homo erectus*, and Neanderthals, suggests that this link between pelvis and spine was probably only established with *H. erectus* 1.5 million years ago.

*Keywords:* bipedalism, hominid evolution, lumbar lordosis, pelvis, sagittal balance, spine

## 2.1 Introduction

The adaptation to bipedalism represents the primary change during human evolution that permits to diagnose fossils as our ancestors, the hominids. This group includes all forms in the lineage leading to modern humans after the split from the chimpanzee lineage some 5 to 8 million years ago. Adaptation to bipedalism therefore occurred long before the production of stone tools, the loss of dense body hair, and the increase in brain size.

Nonhuman primates live mostly in trees and show a diverse locomotor repertoire. This polyvalence with versatile locomotor abilities is therefore also expected in our earliest hominid ancestors. Their varied arboreal locomotor repertoire included quadrupedalism, vertical climbing, suspension, and occasional bipedalism. It was the percentage of terrestrial bipedalism that increased in our first ancestors in relation to the environment, together with its advantages and its constraints. Only later during human evolution, our ancestors became permanent bipeds, which represents a strong specialization.

Sagittal balance of the trunk over the hip joints is essential for efficient bipedal locomotion. Consequently, its acquisition during the evolution of hominids was crucial in the shift from a facultative to a permanent form of bipedalism. The modification of the sagittal morphology of the pelvis and spine played a major role in the process of this evolutionary adaptation, which resulted in the formation of a spinopelvic functional unit.[1] We suggest that the double S-shape of the vertebral column, often considered as one of the most important evolutionary adaptations to bipedal locomotion, evolved secondary to the functionally linked modifications of the pelvis.

## 2.2 Compared Anatomy: The Axial Skeleton in Quadrupeds, Apes, and Hominids

To understand and interpret the evolution of the human morphology, we must use the tool of comparative anatomy. Here, we focus on a comparison of quadrupeds, great apes, and humans with australopithecines. This group of fossil hominids lived in South and East Africa 2 to 4 million years ago and is considered to represent the first true bipeds. Their growth period was short and they became mature at an age of around 12 years, similar to chimpanzees.

In the sagittal view, the skeletons of a quadrupedal monkey, a great ape, and a human reveal very different body proportions (► Fig. 2.1a). The prehensile foot of macaques and gorillas contrasts with the human foot that is strongly adapted to provide support and propulsion during bipedal locomotion. The cranial capacity is around 400 to 600 cm³ in great apes, while the mean is 1400 cm³ in modern humans (► Fig. 2.1b). Facial prognathism is strong in great apes and the canines are very salient. The occipital foramen is positioned posteriorly in the cranial base, and the nuchal musculature is powerful. This cranial morphology results in a distinctive balance of the head on the cervical spine. Australopithecines have a cranial capacity of around 400 cm³, which implies an increased brain size relative to their small body size compared to great apes. The prognathism is reduced, the position of the occipital foramen is more anterior and the nuchal musculature is modified. The small canines are aligned with the other teeth.

### 2.2.1 Pelvis and Rib Cage in Frontal View

### Pelvis

In frontal view, the marked reduction of the distance between the hip joint and the sacroiliac joint is clearly visible in humans. This played a key role in the evolution of bipedalism and was present in australopithecine pelves (► Fig. 2.1c). The approximation between the sacroiliac and hip joints reduces the rotational moments of the iliac segment transmitting trunk weight to the lower limbs, thus reducing muscular work to maintain the equilibrium.[2]

Another important difference is the loss of the tail in hominoids (i.e., great apes and humans). Monkeys such as macaques

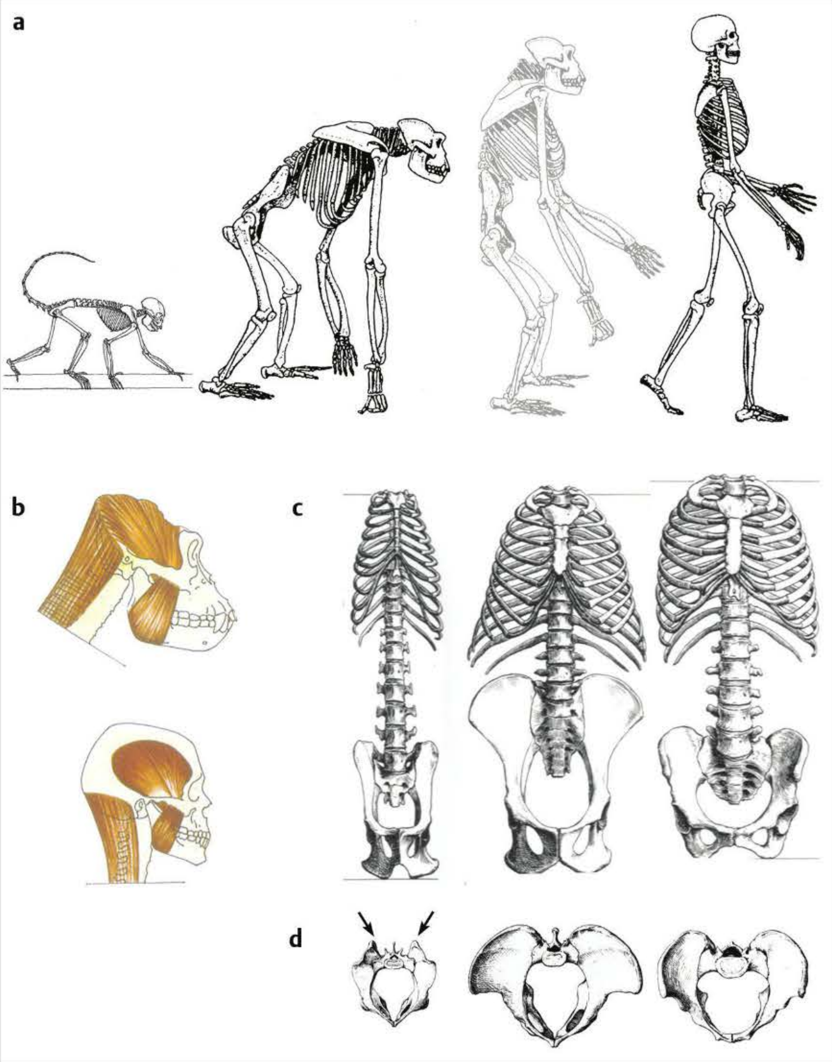

**Fig. 2.1** Skeletal differences among quadrupedal monkeys, great apes, and humans. **(a)** macaque, knuckle-walking gorilla, fictive gorilla in bipedal posture with bent hips and bent knees, and modern human (adapted from Ref. 52). **(b)** Differences in head posture: head of a gorilla with projecting face, powerful jaws, strong chewing muscles, and strong neck muscles, whereas modern humans show a reduced facial skeleton with relatively weak chewing and neck muscles. **(c)** Trunk skeleton: narrow thorax and elongated lumbar spine in a macaque; broad, funnel-shaped thorax, short lumbar spine and elongated ilium in a chimpanzee, and barrel-shaped thorax with long lumbar spine and short ilium in modern humans (adapted from Ref. 5). **(d)** Cranial view of the pelvis of a macaque, chimpanzee, and modern human; arrows, strong iliac tuberosities in macaque (adapted from Ref. 5).

possess a long tail with strong caudal muscles that originate on the sacrum. Their erector spinae muscles are inserted on the very developed iliac tuberosities (▶ Fig. 2.1d). In hominoids that have lost their tail, the erector spinae is inserted on the iliac crest and the sacrum. Humans differ from great apes by a broad sacrum with an extended insertion area of the erector spinae. The entire iliac blade of great apes and humans is considerably broader than that of monkeys. In the brachiating great apes, this provides an extensive area of origin for the latissimus dorsi and the quadratus lumborum, important muscles that support the trunk and pelvis during arm suspension (▶ Fig. 2.1d). In humans, the latissimus dorsi has a smaller area of origin, and the iliac crest can be divided in three sections that provide origin for the muscles balancing the trunk. From the lateral section of the iliac blade originate the oblique and transverse abdominal muscles, in the intermediate section latissimus dorsi and quadratus lumborum, and in the medial section the trunk erectors and gluteus maximus (▶ Fig. 2.2). While in great apes the origin of the gluteus maximus does not reach higher than the base of the sacrum, it has in humans a very high origin on the pelvis at the level of the iliac crest. The capacity of this muscle for trunk erection is thus far greater in humans than in great apes (▶ Fig. 2.2).

Humans also have an anteriorly curved lateral section of the iliac blades that modified the position of the lesser gluteal muscles. They thus became abductors on an extended hip while they were medial rotators on a flexed hip in great apes. This implies a different mechanism of lateral pelvic balance during bipedalism[3] (▶ Fig. 2.1).

The pelvis of australopithecines has laterally flaring and frontally oriented iliac blades similar to great apes with an extensive area of origin of the latissimus dorsi.[4] This implies a different hip abductor mechanism and thus a different mode of bipedalism than in modern humans.[3] On the other hand, they resemble the human condition in having a broad sacrum, and the gluteus maximus muscle originated from the posterior ilium.[4]

## Rib Cage

The rib cage is funnel-shaped in great apes and barrel-shaped in modern humans[5] (▶ Fig. 2.1c). This conforms to the wide and frontally oriented iliac blades in great apes and an anteriorly curved iliac crest in modern humans. The long and robust last rib of great apes provides an ideal attachment for the quadratus lumborum. Together with the reduced gap between the thorax and the iliac crest, this provides the necessary rigidity for the

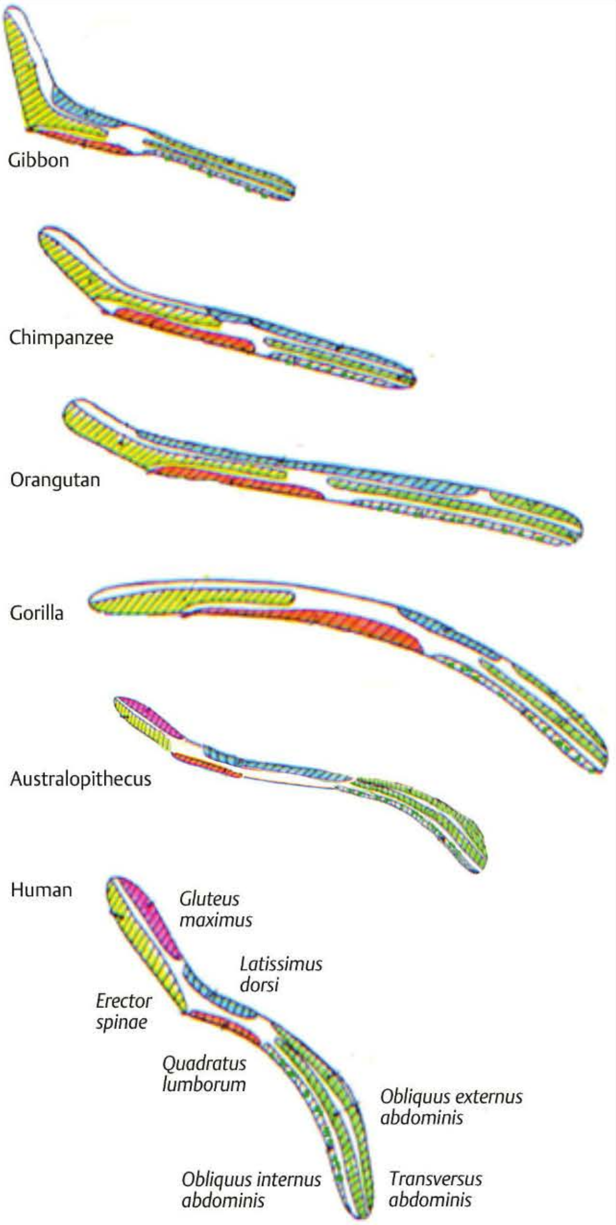

**Fig. 2.2** Iliac crest with muscle origins. Great apes show an extensive area of origin of latissimus dorsi and quadratus lumborum that are important during forelimb dominated locomotion, while in hominids gluteus maximus also originates on the ilium (adapted from Ref. 53).

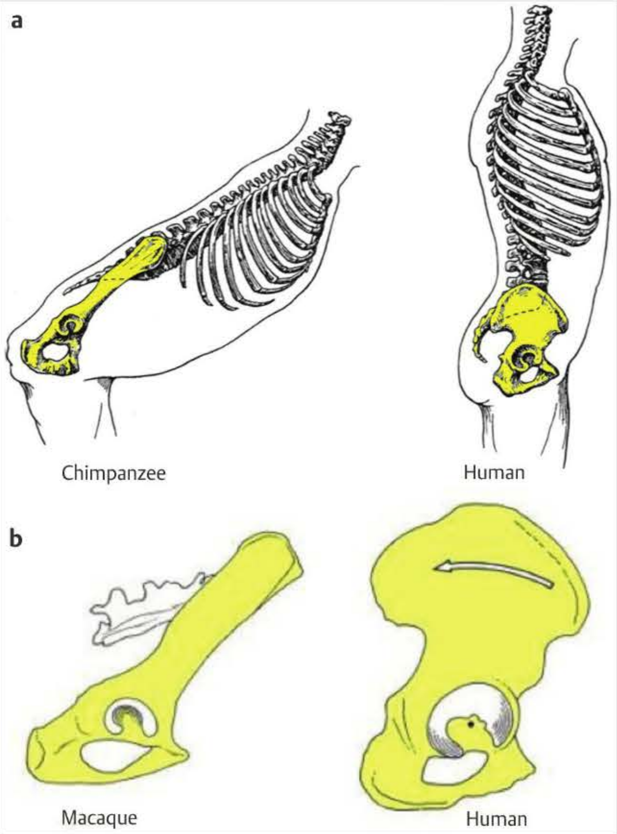

**Fig. 2.3** Spinal curvature and pelvis. **(a)** Nonhuman primates possess a single thoracolumbar curve, while humans additionally have a marked lumbar lordosis that contributes to bring the center of body weight close to the hip joint (adapted from Ref. 55). **(b)** In humans, the sacrum, ischium, and pubis are oriented similar to quadrupeds, whereas the ilium is curved lordotically, leading to the development of the greater sciatic notch (adapted from Ref. 2).

trunk in the forelimb-dominated locomotion of great apes.[6] Humans have a relatively wide upper thoracic aperture. This allows a greater respiratory efficiency and heavy breathing used for running while it reduces shoulder mobility. On the other hand, the lower thorax is narrower compared to great apes, and together with the longer lumbar spine this leads to a slim waistline. This plays an important role for our ability to run as it allows to exploit the greater flexibility of the lumbar spine.[6]

Australopithecines such as the 3.2 million years old Lucy (*Australopithecus afarensis*, Ethiopia), also show a funnel-shaped thorax. Together with their cranially oriented shoulder girdle, this reflects their adaptation for climbing that they retained from the common ancestor with chimpanzees.[6,7] However, these characters make them unable to run long distances.[6,7]

## 2.2.2 Sagittal View of Spine and Pelvis

### Spine

#### Spinal Curvature

Modern humans have a double S-shaped vertebral column with four curvatures (i.e., a cervical lordosis, a thoracic kyphosis, a lumbar lordosis, and a sacral kyphosis). Great apes, in contrast, possess a weak kyphotic thoracolumbar curvature and a relatively short and stiff neck, which mainly results from a highly positioned shoulder girdle and massive pectoral muscles[6] (► Fig. 2.1, ► Fig. 2.3). In association with a narrow sacrum and a short lumbar column there is an “entrapment” of the lumbar vertebrae between the iliac blades in great apes and thus a reduced lumbar mobility.

#### Number of Vertebrae

The length of the spinal regions and particularly of the lumbar region plays an important role for its mobility and capacity for lordosis. A long lumbar region is thought to be fundamental for having facilitated the adoption of bipedal locomotion in early hominids. The evolution of a human-like segmentation of the vertebral column is therefore of particular interest. In primates, the total number of precaudal vertebrae is surprisingly stable at 29. Quadrupedal monkeys have 12 to 13 thoracic vertebrae coupled with a long and flexible lumbar spine of six to seven elements and a short sacrum of three segments (▶ Fig. 2.1).[5] This allows them extensive flexion–extension movements needed for quadrupedal climbing, running, and springing. In contrast, apes show a stiffer and more rigid trunk adapted to forelimb-dominated locomotion. By integrating the last one or two lumbar vertebrae into the sacrum, their lumbar spine is accordingly reduced to five segments in gibbons and to four in orangutans, chimpanzees, and gorillas, while the sacrum became compensatorily elongated to four in gibbons and five elements in great apes on average.[5] A large percentage of chimpanzees and gorillas even possesses only three lumbar vertebrae and a correspondingly elongated sacrum. Such vertebral border shifts are associated with alterations in the expression of Hox genes that control the regional identity of vertebrae.

Another border shift occurred at the thoracolumbar junction in the ancestors of modern humans, leading to 12 thoracic and 5 lumbar segments on average, which makes the lumbar spine longer and more flexible than in great apes. This flexibility is a prerequisite for our lumbar lordosis, which cannot be achieved with the short and stiff lumbar spine of chimpanzees and gorillas. Different scenarios have been proposed for the evolution of this characteristic of modern humans: the short-backed scenario[8] suggests that the short lumbar column of chimpanzees and gorillas is primitive. The long-backed scenario proposes that a six-segment-long lumbar spine was retained in the ancestors of apes and humans.[9] This hypothesis was rejected by the discovery of new vertebral fossils that demonstrate the presence of five lumbar vertebrae in early hominids and not six as claimed before.[10,11,12] We therefore argue for an intermediate scenario with five lumbar vertebrae as the primitive condition in great apes and humans. Such a scenario is further supported by *Oreopithecus*, a great ape that lived 8 million years ago in Italy and also had five lumbar vertebrae.[13] The scenario has the advantage that the last common ancestor of chimpanzees and humans already had five lumbar vertebrae, which facilitated the adoption of lumbar lordosis and thus of bipedal locomotion.

## Orientation of Facet Joints at the Thoracolumbar Junction

Early hominids seem to have differed from humans in the orientation of the facet joints at the thoracolumbar junction. In modern humans, the transition from thoracic to lumbar-like orientation is usually at T12, but in up to 40% of the population at T11. In contrast, all early hominid fossils show the transition at T11,[11,12,14,15] and it is likely that in the future hominid fossils will be discovered with the transitional vertebra at T10. Lumbar-like facet joints allow flexion–extension but restrict spinal rotation, while thoracic-like facet joints do not restrict mobility. The functional implication of a more cranially located transitional vertebra in early hominids might be related to a greater rotational stability of the trunk.[16] This might represent a climbing adaptation in early hominids, while a greater rotational capacity was needed in later *Homo* for running.

# Pelvis

## Quadrupedal-Like Orientation of the Human Sacrum, Ischium, and Pubis (▶ Fig. 2.3)

Very early it was noticed that the longitudinal axis of the sacrum is only slightly inclined with respect to the horizontal plane in upright standing humans, thus closely corresponding to the spatial orientation in quadrupeds (▶ Fig. 2.3a).[17] Also, the longitudinal axis of the pubis and ischium has retained the same angulation with the femur as in quadrupeds; only the ilium axis is bent backward (▶ Fig. 2.3b). It has, therefore, been asserted that the acquisition of upright posture in hominids occurred only above the pelvis with the lumbar lordosis, and that the hominid lower pelvis is essentially that of quadrupeds. Because of the relatively stiff lumbar spine of great apes, they have to rotate their trunk in the hip joints when they want to stand up on their hind legs (▶ Fig. 2.1a). This brings the ischium into a vertical orientation, which would offset the lever arm of the hamstrings if the femur is fully extended, and forces great apes to stand upright with bent hips and bent knees.[2] The quadrupedal-like posteroinferior angulation of the ischium in modern humans is therefore important for preserving an optimal lever arm for the hamstrings as extensors of the hip joint, and the backward rotated ilium together with the S-shaped curvature of the spine is crucial to shift the whole trunk backward, thus bringing the body's center of gravity close to the hip joints.[2]

## The Angle of Pelvic Incidence in Human and Nonhuman Primates

The interpretation of the sagittal aspect of the pelvis was greatly aided by the description of the angle of pelvic incidence by the research team of G. Duval-Beaupère in Paris. This new pelvic parameter was initially called "angle of sacral incidence."[18,19,20] It is defined by the line from the midpoint between the two femoral heads to the center of the upper surface of the sacrum and perpendicular to the upper surface of the sacrum (▶ Fig. 2.4a). The incidence angle is an anatomical variable that is specific to each individual. It represents the sum of the two positional parameters, sacral slope ($\alpha$) and pelvic tilt ($\beta$), and determines the amount of lordosis that provides the most economical upright posture for each individual at a given pelvic tilt in terms of muscle fatigue and vertebral strain.

The first paper that introduced the pelvic incidence in (palaeo) anthropology was published in 2006 by Tardieu et al.[21] It described the variability of the angle of incidence and its correlation with other pelvic parameters in an osteological sample of 51 macerated adult modern human pelves (of 26 men and 25 women) (▶ Fig. 2.4b). This study showed that a low angle of incidence is correlated with a weak sacral slope, a less curved sacrum, and a higher sacral position in relation to the iliac crests. A high angle of incidence is correlated with a strong sacral slope, a curved sacrum, and a low position of the sacrum in relation to the iliac crests. These observations were confirmed by the negative correlation obtained between incidence and sacro-acetabular distance (pelvic thickness) (-0.52, $p < 0.0001$). A tendency to a backward displacement of the sacrum in relation to the acetabulum is observed with a high pelvic incidence.

Tardieu et al.[22] compared intact pelves of newborns and adults. The mean angle of incidence was 27° in the newborns

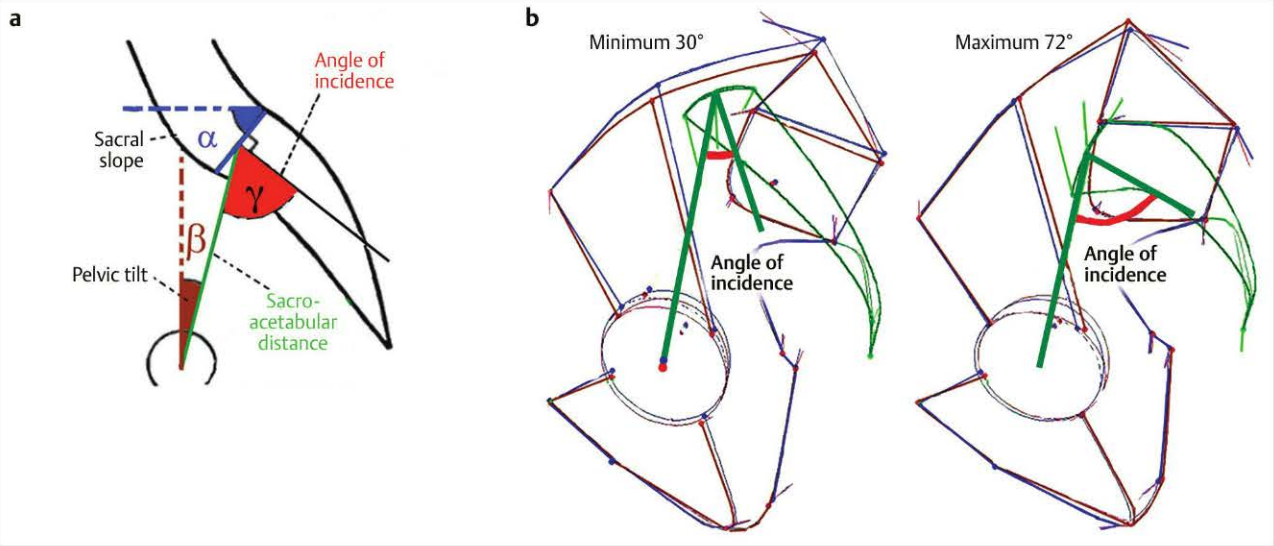

**Fig. 2.4** Angle of pelvic incidence. **(a)** Description of the pelvic incidence. **(b)** Relationship of the angle of incidence, sacral slope, and sacro-acetabular distance (see text for details; for methods, see Refs. 21 and 22; figures adapted from Ref. 1).

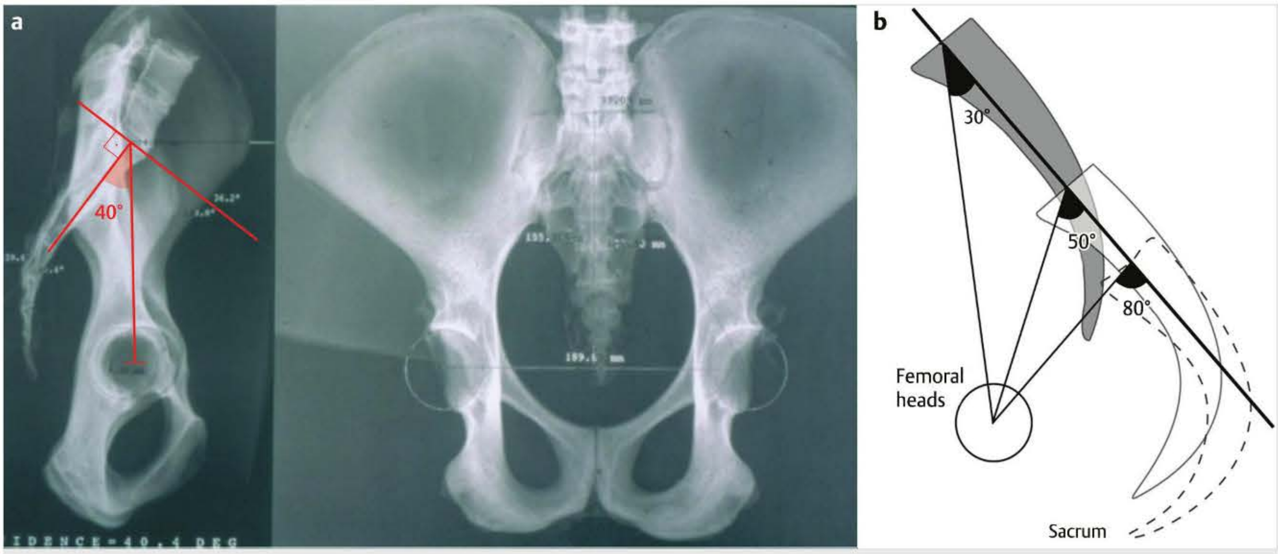

**Fig. 2.5** Evolution of the pelvic incidence. **(a)** lateral and anteroposterior radiograph of a gorilla pelvis, showing a pelvic incidence of 40°. **(b)** Simplified model of pelvic evolution. The sacral slope is kept constant to emphasize the inverse relationship of the sacro-acetabular distance with increasing incidence (adapted from Ref. 1).

compared to 54° in the adults. The newborn pelves showed a correspondingly low sacral slope and the sacrum was straight and anchored high upon the ilia. In lateral view, the plane through the centers of the superior sacral surface and the hip joints was almost parallel to the plane of Lewinnek and thus aligned vertically. As this configuration does not favor the balance of the trunk, the sacrum moves backward from gait acquisition until the end of the growth period. At the same time, the sacrum rotates anteriorly, so that it becomes more horizontally in its cranial part and more curved caudally.

Radiographic measurements of the angle of incidence of nonhuman primates were presented by Tardieu et al.[21,22] In nonhuman primates, the pelvic incidence is small and always inferior to 40° as expected from the long distance between the sacroiliac and hip joints (▶ Fig. 2.5a; see also Table 4 in Ref. [1]). It is important to specify that this angle does not offer any correlation with the spinal curvature in nonhuman primates.

## Sagittal Model of the Evolution of the Pelvis

We proposed a simplified model of the evolution of the pelvis in lateral view (▶ Fig. 2.5b).[1] Because the mean angle of incidence of great apes seems to be identical to that of quadrupedal monkeys such as baboons, it can be hypothesized that the last common ancestor of chimpanzees and hominids also possessed a pelvic incidence between 30° and 40°. Corresponding to the inverse relationship between the angle of incidence and the sacro-acetabular distance observed both during the growth of the human pelvis and within adults, we proposed a similar inverse relationship in hominid evolution. While the angle of incidence progressively increased, the sacro-acetabular distance decreased at the same time by a more and more backward positioned superior sacral surface in relation to the hip joints. We also suggested that the increase in incidence would have been under positive selection at the same time as the distance between the sacroiliac and hip joints was reduced, as it provided a clear advantage to improve sagittal balance of the trunk during bipedal walking in early hominids. For the interpretation of hominid fossils, it is very important to recall the fundamental positive correlation that links the angles of incidence and lumbar lordosis in extant humans[1] ($R = 0.55$, $p < 0.0001$). This correlation establishes a functional link between the spine and the pelvis, which distinguishes the spinal balance of humans from extant nonhuman primates during occasional bipedalism. The association between two very different elements, the mobile vertebral column and the rigid pelvis, is a critical process of functional integration. Moreover, it is very delicate to decipher this process as it becomes only manifest during postnatal growth in tight association with gait acquisition and takes place very progressively. Are we able to recognize some traces of the establishment of this crucial link in the history of fossil hominids?

## 2.3 Interpretation of Hominid Fossils

In this chapter, we present hominid fossils that preserve an associated pelvis and spine or give other indications for sagittal balance. The earliest claimed hominid fossils still had a very polyvalent locomotor repertoire and their taxinomic interpretation is controversial. This includes *Sahelanthropus*, which is known from a 7-million-year-old crushed skull from Chad. Based on an anteriorly placed foramen magnum, it was inferred that *Sahelanthropus* walked bipedally upright.[23] However, the skull needed extensive reconstruction and the neck musculature seems to have been unusually powerful for a biped, which raised doubts regarding its hominid status.[24]

The second oldest early hominid fossil is *Orrorin tugenensis*, which was found in 6-million-year-old sediments in Kenya. *Orrorin* is mainly known from skull and teeth fragments as well as isolated femora. They have been described to show evidence for upright bipedalism, including an elongated femoral neck and an asymmetric distribution of cortex in the femoral neck.[25]

A more complete, though severely crushed skeleton is known for the 4.4-million-year-old *Ardipithecus ramidus* from Ethiopia. With limb proportions similar to monkeys, it was a palmigrade tree climber, and showed no adaptations for suspensory or knuckle-walking behavior characteristic of living great apes. Although lumbar vertebrae are not preserved, the relatively short ilium associated with a wide sacrum does suggest that *Ardipithecus* did not have a rigid lumbar spine. The morphology of this hominid would thus imply that a long ilium that entraps the last lumbar vertebrae, a narrow sacrum, and a reduced number of lumbar vertebrae are derived rather than primitive characteristics in great apes (i.e., they were acquired during the course of evolution of gorillas and chimpanzees rather than present in the last common ancestor of chimpanzees and hominids).[26] It is, however, also conceivable that *Ardipithecus ramidus* belonged to an extinct ape genus not closely related to the human lineage.[27]

The earliest fossils that are undisputedly hominids belong to australopithecines. Their pelvis demonstrates a human-like reduction of the sacro-acetabular distance and a pelvic incidence close to the mean of modern humans. The reconstructions of Häusler and Schmid[28] indicates an incidence of approximately 52° in the 3.2-million-year-old Lucy skeleton AL 288–1 (*A. afarensis*), 45°–54° in the 2.4 million-year-old Sts 14 (*Australopithecus africanus*), and 50° in the 2.0-million-year-old MH2 *Australopithecus sediba*[29] (▶ Fig. 2.6).

The Lucy skeleton preserves six thoracic and a midlumbar vertebra. Other partial skeletons with vertebral columns are Sts 14 and Stw 431 (*A. africanus*)[10] as well as the *A. sediba* skeletons

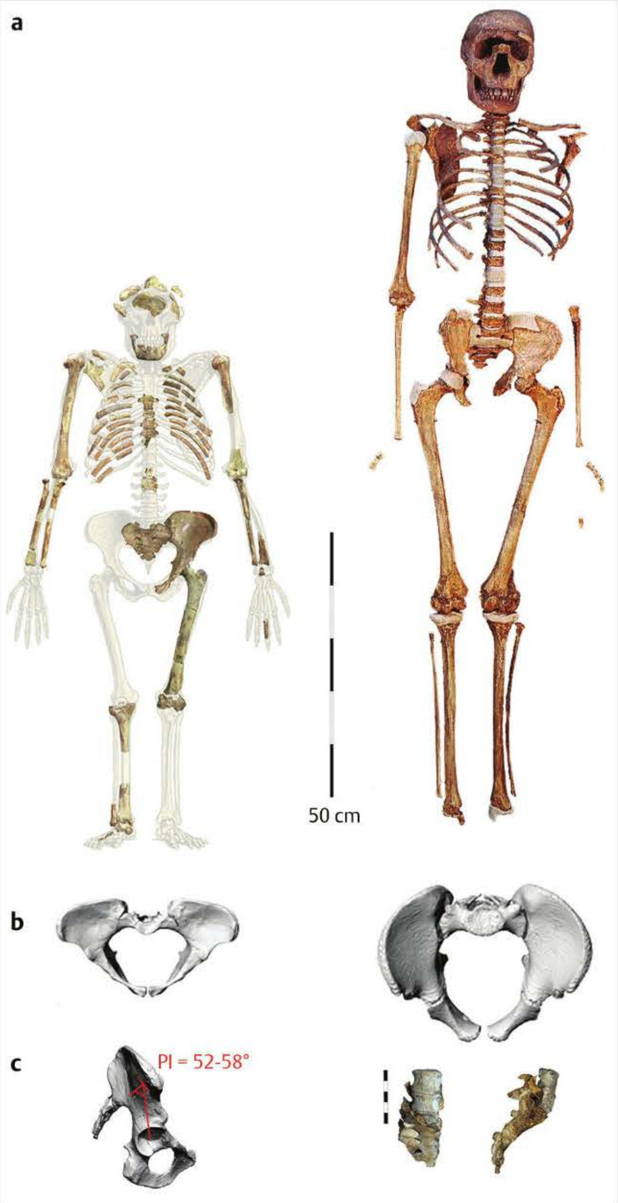

**Fig. 2.6** Fossil hominid skeletons. **(a)** Lucy skeleton (AL 288–1, *Australopithecus afarensis*) and KNM-WT 15000 (*Homo erectus*). **(b)** Superior view of the pelvis of Lucy and a modern human. **(c)** Lateral view of Lucy and frontal and sagittal view of the sacrum and lower lumbar vertebrae of MH2 (*Australopithecus sediba*) (adapted from Ref. 14).

MH1 and MH2.[14] Their vertebral wedging suggests a well-developed lumbar lordosis that was made up of five lumbar vertebrae as in modern humans[11,12] (▶ Fig. 2.7). Both Lucy and Sts 14 show changes suggestive of Scheuermann's disease[30] and several isolated australopithecine vertebrae show similar alterations.[31] This high prevalence of Scheuermann's disease might indicate a greater loading of the vertebral column during juvenile growth period than in modern humans, which is perhaps related to the relatively small cross-sectional area of the early hominid vertebrae[31] (▶ Fig. 2.8).

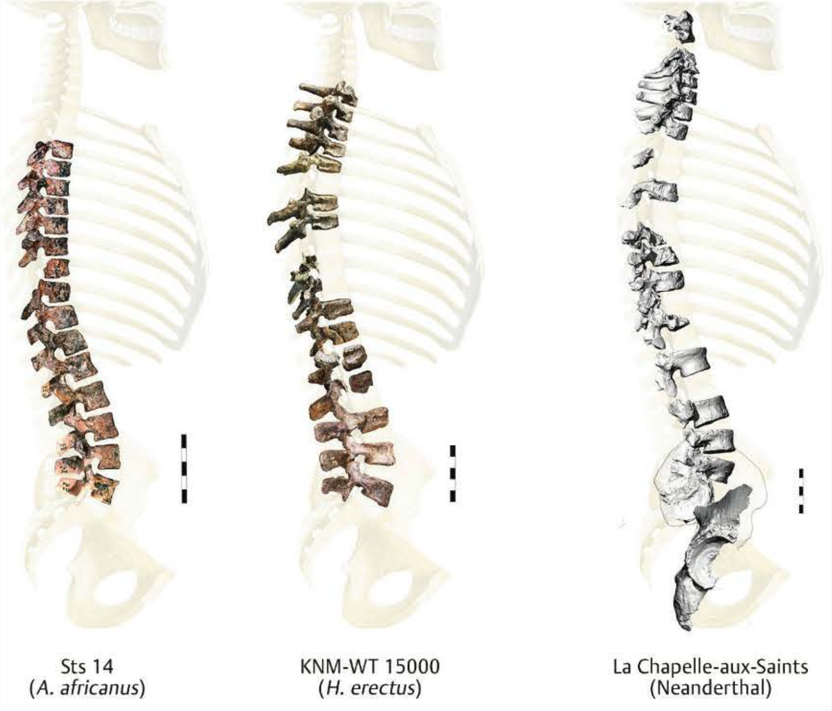

**Fig. 2.7** Fossil hominid vertebral columns: Sts 14 (*Australopithecus africanus*), KNM-WT 15000 (*Homo erectus*), and the Neanderthal from La Chapelle-aux-Saints showing well-developed spinal curvatures (adapted from Ref. 54).

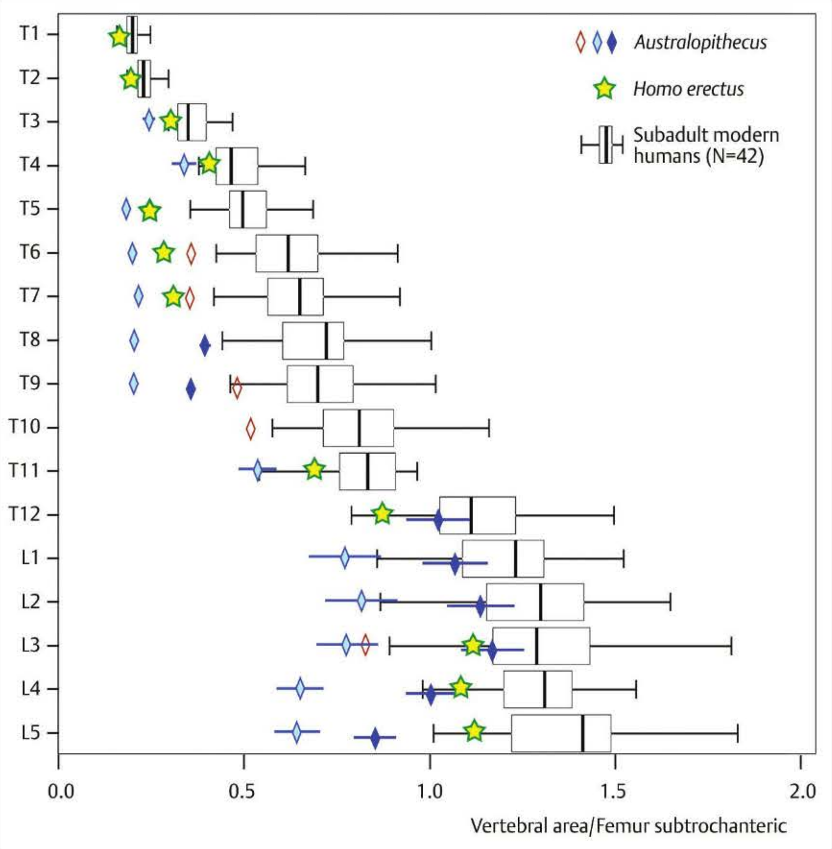

**Fig. 2.8** Superior endplate area of the vertebrae relative to proximal femur size as a measure for body size for *Australopithecus* (open diamonds, AL 288–1; light blue diamonds, Sts 14; dark blue diamonds, Stw 431), *Homo erectus* (stars, KNM-WT 15000), and subadult modern humans (box plots).

The human-like pelvic incidence in australopithecines, on the other hand, does not necessarily imply that they possessed an identical spinopelvic balance as modern humans. Thus, the large, funnel-shaped thorax and the prominent face suggest a more ventrally located center of body weight, and their frontally oriented ilium implies a different mechanism of lateral pelvic stabilization. With its short lower limbs, *Australopithecus* was not as adapted to long distance walking and running (e.g., *Homo erectus*). *Australopithecus* was therefore called a "compromise biped" who still possessed a surprisingly versatile locomotor repertoir.[32] The modern human-like functional link between the pelvis and the vertebral curvatures therefore seems to have been a long process of trial and error. The strong correlation between lordosis and incidence in extant humans is tightly linked with our exclusive bipedalism and stereotypical gait pattern, expressed by periodicity of the movement.[33,34] Before the acquisition of a regular and stereotypical gait, the correlation was likely absent or only weak. A progressively stronger correlation was only established when bipedalism became a major element within the locomotor repertoire so that early hominids became "committed" bipeds and developed a similarly specialized postcranial morphology.[32]

*H. erectus* is known by the almost complete skeleton KNM-WT 15000, which is dated to 1.5 million years ago. Its skeletal age is roughly similar to a 15-year-old modern human boy, and it demonstrates that the growth period in *H. erectus* was longer than in *Australopithecus*.[35] It only misses the first six cervical and two midthoracic vertebrae and displays fully human-like body proportions and thoracic shape.[36] This is confirmed by a reanalysis of KNM-WT 15000 that refutes earlier claims for disproportions because of congenital skeletal dysplasia but indicates that this individual suffered from juvenile disk herniation.[11,12,37,38,39,40] *H. erectus* demonstrates an almost modern bauplan of the axial skeleton. Its long lower limbs emphasize its capacity for running. *H. erectus*, therefore, can be considered an obligate biped with a posture and mode of locomotion close to modern humans. Although there are some uncertainties in Walker and Ruff's[41] reconstruction of the KNM-WT 15000 sacroiliac joint, its pelvic incidence of about 49°–52° is close to the mean of the modern human range of variation.[22] A recent new reconstruction of its pelvis will provide more precise insight into the mode of walking and running of this individual.[42] A second *H. erectus* pelvis, an adult female from Gona, Ethiopia, has a very similar incidence angle of 48°–50°.[22] Interestingly, however, the wedging angles of lumbar vertebrae L3-L5 of KNM-WT 15000 are in the upper range of modern humans, while the degree of anterior wedging at L1 also clearly exceeds the mean of modern humans.[39] This might imply a more marked lumbar lordosis in this specimen than on average today, and thus a stronger curve than expected from the pelvic incidence.

Neanderthals are the successors of *H. erectus* and lived in Europe and large parts of Asia between about 400,000 and 40,000 years ago. Several different skeletons have been discovered. One of the earliest fossils of the Neanderthal lineage from Spain shows an isthmic spondylolisthesis at L5,[43] a typical pathology that is exclusively associated with bipedalism.[44] Moreover, the lumbar vertebrae of this individual are anteriorly wedged and elongated, which is suggestive of the lumbar form of Scheuermann's disease.

All Neanderthals have been described to possess a much weaker cervical lordosis, thoracic kyphosis, and lumbar lordosis than modern humans and their pelvic incidence is said to be in the range of great apes.[45,46] However, the small sample size, pathological changes, and deformations by earth pressure call for further study of incidence and spinal curvature in Neanderthals. Thus, a new reconstruction of the La Chapelle-aux-Saints Neanderthal demonstrates that this individual possessed a pelvic incidence of 56° and a human-like degree of lumbar lordosis.[1,47,48]

From this review of the fossils, it appears that the pelvis and the vertebral column might have become a functional unit in human evolution during the transition from occasional to permanent bipedalism. This functional link was probably established at the stage of *H. erectus*. Developmental data suggest that this process of integration possesses a solid genetic basis, for which selection acted both on the pelvis and the vertebral column.[1] The genetic modifications of the pelvis included the reduction of the distance between sacroiliac and hip joints, which entailed an increase in the angle of incidence and the widening of the sacrum with respect to the last common ancestor with African great apes. Concomitantly, the preservation of a five-segment-long lumbar spine permitted the development of the vertebral curvatures. The superior part of the vertebral column was of course also involved in this process of integration as the target of selection was the efficiency of the bipedal balance of the whole body. The correlation between the thoracic kyphosis and the lumbar lordosis ($R = 0.50$)[1] illustrates this association as the geometries of the lumbar and thoracic curvatures are tightly interrelated.[49] The balance of the head on the cervical spine, which was very important in this context, also involved an adaptation of the morphology of the head.[50] We therefore can speak of a complex process of integration, which we are only beginning to understand.

## 2.4 Conclusion

In an evolutionary point of view, the establishment of the relationship between the angle of incidence, a fixed anatomical pelvic parameter specific to each individual, and variable positional parameters pertaining to the pelvis and vertebral curvatures were crucial steps in the acquisition of hominid sagittal balance. We interpret this relationship as the foundation of an optimal compromise between stability and mobility that is necessary for balancing the trunk above the lower extremity.[51] Mobility is necessary for the vertebrae to modulate the degree of spinal curvature, while stability in the pelvis is necessary to allow the exploitation of these curvatures, and it guarantees the dampening effect of the four compensatory spinal curvatures.

The strong correlation between the angle of incidence and the degree of lumbar curvature in extant humans points toward an elaborated functional response of the postcranial skeleton that was shaped by natural selection. It corresponds to a very derived process of integration between sagittal pelvic morphology and the lumbar spine, which was probably progressive and of long duration. It reveals an advanced stage of specialization to permanent bipedalism and to an economical sagittal balance in extant humans. This specialization was not present among australopithecines. It might only have been reached among *H. erectus* populations, and thus we may expect that an effective step of integration had begun at this stage of evolution.

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