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2.1 Introduction

The human vertebral column (or the spine) serves two main functions: a biomechanical one and a protective one. The spine gives the body longitudinal support (while retaining a degree of mobility), connects the head and limbs, offers muscle attachment sites and protects the spinal cord. In this chapter, we will explore how these functions have developed during evolution and have led to the very specific structure that is unique to the only habitual striding biped among mammals: man.

2.2 The Origin of the Basic Mammalian Vertebral Structure

Many aquatic animals do not need a structural support of the body, e.g. jellyfish, which are neutrally buoyant and move by jet propulsion. Other animals, e.g. many molluscs and insects, use some type of exoskeleton. Vertebrates, however, are named after their endoskeleton with a segmented vertebral column. If we want to understand its origins, we have to go back to the parental group of the vertebrates: the chordates. In the most primitive members of this group, longitudinal body support is provided by the notochord, an unsegmented structure consisting of fibrous connective tissue around a core of fluid.

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This 'hydrostatic skeleton', which can be seen in extant hagfishes and lancelets, allows for longitudinal stiffness but provides no muscular attachment sites. The notochord can still be seen during embryonic development in all vertebrates and defines the axis of the body, around which the axial skeleton forms. It is also seen in the adult stages of some vertebrates (e.g. lungfish), and it persists as the nucleus pulposus in mammals, including humans.

Segmented vertebrae first showed as ventral (haemal) and dorsal (neural) arches. They served to protect, respectively, blood vessels and the neural tube. The supportive function of the spine only came later.

The next evolutionary stage was the development of two centra (the pleurocentrum and the intercentrum), which supported the ventral arches but did not surround the notochord completely. Such arrangement can be seen in primitive gnathostomes [1], and it fundamentally persists in all of the vertebrae we can see to date – all consisting of arches and centra (Fig. 2.1). Evolution has acted upon these structures; some have enlarged, while others have reduced, explaining for a large part the vertebral diversity we can observe today.

During the course of evolution, the vertebrae became strong units (particularly because of the enlarged centra) replacing the notochord as the fundamental support structure. They also became regionally differentiated. Fish have two regions (trunk and caudal), while amniotes (amphibians, reptiles, birds and mammals) have up to five regions: cervical, thoracic, lumbar, sacral and caudal, with varying vertebral numbers in these regions.

In amniotes, the pleurocentrum dominates and forms the body of each vertebra. The intercentra initially form the cartilaginous intervertebral disks but in mammals, they only remain present as the rib's capitulum. The centra link up into an axial vertebral column assisted by interspinal ligaments. The articular shape defines the intervertebral articular surfaces and thus largely determines in which plane movement is allowed. Articular shapes strongly differ between animal groups and even within a single body, while many show high intervertebral mobility due to their biconcave or concave/convex joint shapes; in mammals, the centra have flat articulations, which have reduced mobility but can withstand high compressive forces.

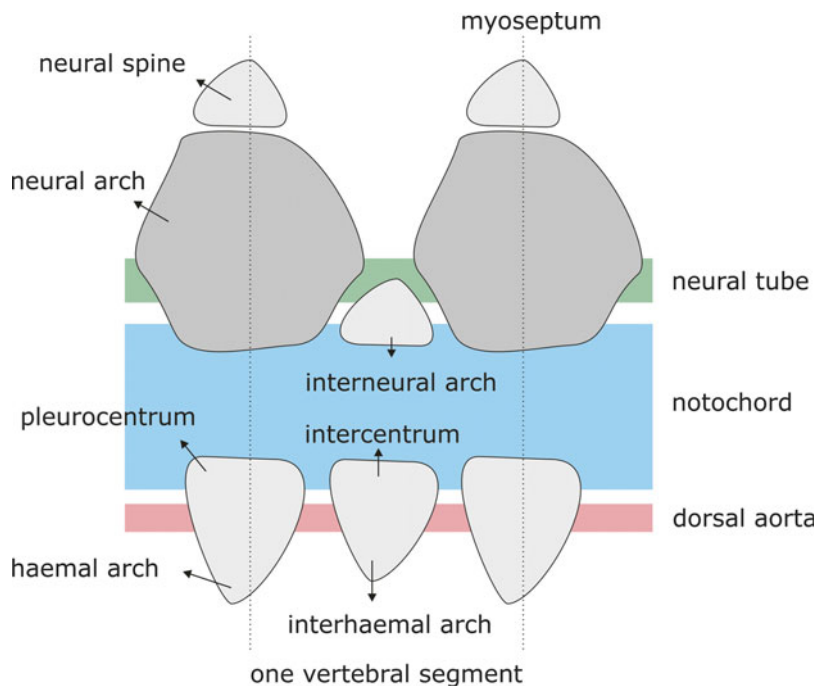


Fig. 2.1 Schematic representation of the primitive vertebral structure, here in a gnathostome [1]

In fish, lizards and snakes, the movement of the spine is characterised by a lateral undulation. In crocodiles, the spine can, in addition, move dorsoventrally as can be seen in mammals. Dolphins, reflecting their mammalian heritage, move in the water with a dorsoventral movement of their spine in contrast to fish.

During evolution, the ventral arch decreases in importance or disappears (e.g. in mammals, it is only occasionally found in the tail), while the dorsal arch dominates. The dorsal arch persists in mammals, including humans, as the vertebral arch. It serves to protect the spinal cord, it provides attachment sites for both hypaxial and epaxial musculature and it provides attachment for numerous processes.

In addition to the centrum and arches, vertebrae can develop a number of processes – apophyses. Some of these (the pre- and postzygapophyses) provide resistance to twisting.

Other apophyses carry ribs, which serve locomotor, respiratory and protective functions. Basapophyses are paired remnants of the haemal arch bases, which may articulate with the ventral ribs of fish (which are probably homologous to the haemal arches). Tetrapods only retain dorsal ribs (termed the trunk ribs), which have a bicapital articulation. The ventral head (capitulum) articulates with the pleurocentrum (in most reptiles and birds) or, in mammals, between the centra. The dorsal head (tuberculum) articulates with the diapophysis, a process on the neural arch.

Processes also change between species and between regions, e.g. in mammals, where processes disappear towards the end of the tail and only centra remain.

In mammals, the vertebral column is highly regionalised, and vertebral numbers are much more conservative than in other groups.

Typically (with very few exceptions), there are seven cervical vertebrae, of which the first two (as in other amniotes), the atlas and the axis, are highly specialised in order to support the head while allowing for great range of motion. There are typically 15–20 thoracic and lumbar vertebrae (combined) and 2–3 sacral vertebrae (5 in humans). The number of caudal vertebrae is highly variable [2]. The basic structure of the

human vertebrae is similar to that of other mammals.

At this point, it should be clear that the evolution of the vertebrae is complex, with specific components gaining importance while others are reduced, depending on the phylogenetic history and locomotor demands of the animal. We will therefore outline first some of the most important differences between the human spine and the non-human primate spine and subsequently focus on the evolution of the spine in hominins.

2.3 The Primate Spine

Humans are hominoid primates (apes), and it is instructive to consider the extant primate spine as a model or analogue to understand our ancestral spine structure, which later became adapted to our specific life style and, most importantly, our unique form of locomotion – habitual striding bipedalism (for details on the evolution of primate morphology, we refer to the literature [3]).

The generalised primate vertebra consists of a well-developed body with a neural (also named dorsal or vertebral) arch. The base of this arch is formed by the paired pedicles, joining into the paired laminae onto which the spinal process sits (which is unpaired but might end in double tubercles; [4]). The spinous process can vary in its length, strength and direction.

Laterally, the neural arch possesses transverse processes and articular processes (zygapophyses).

The intervertebral disks are important, and the makeup is approximately one fourth of the presacral spine length in humans, but they vary in thickness and shape.

2.3.1 Vertebral Structure Varies Across the Regions in All Primates

In the cervical (C) region, the vertebral foramen is at its largest, and there is a transverse foramen through the transverse processes. The two first vertebrae, the atlas (C1) and the axis (C2), are atypical: they are much derived, and there is no

intervertebral disk between them. The atlas has no body or spinous process and transmits the weight of the head from the two occipital condyles (allowing movement in the sagittal plane, as in nodding 'yes') onto the axis. The axis has cranially oriented dens, which articulate firmly with what is left of the ventral arch of the atlas. Movement between the atlas and the axis is rotation along the longitudinal axis (as in 'no'). The orientation of the dens differs among primates. It is retroflexed in typical pronograde quadrupeds, which (together with the position of the foramen magnum) positions the head rather in line with the vertebral column. The dens is slightly bent in knuckle walkers (African great apes who have much longer forelimbs than hind limbs) and completely along the longitudinal axis in the orthograde habitual bipeds (humans), helping to balance the head vertically into the vertebral column.

The typical cervical vertebrae (C3–C6) have kidney-shaped bodies in a cross-sectional view and possess uncinat processes, which are facing cranially and articulate with the previous vertebra's body.

C7 is atypical and has a very long spinous process (which is not bifid, unlike in the typical cervical vertebrae). All primates, like all mammals, possess seven cervical vertebrae.

The thoracic (T) vertebrae are typically heart shaped in cross section and bear ribs. In order to do so, they have facets on the body (two demifacets per side, one cranially and one caudally) and on the transverse processes. A rib typically articulates with a demifacet of its vertebra a demifacet of the vertebra above, and its tubercle articulates with the transverse process. However, the ribs of the first thoracic vertebra, in humans, and the last two thoracic vertebrae, in humans as well as apes, articulate only via a single facet, not two demifacets (Fig. 2.2).

Caudally, the thoracic vertebral bodies become bigger (longer and wider), the rate at which varies between species. Neural arch size often (but not always) decreases.

The shape of the superior and inferior articular process is of great interest because of its functional meaning. While oriented almost in the frontal plane cranially, then there is a sudden change

to the lumbar arrangement (i.e. angled steeply) at the transitional (or diaphragmatic) vertebra [5, 6], making the subregions very stable. The pre-diaphragmatic region allows for rotational movements, whereas the post-diaphragmatic region does not.

Usually, the functional region of the thoracic region is shorter than the rib-bearing region. The ribs are very interesting from a comparative point of view but fall outside the scope of this chapter. The spinous processes are usually oriented caudally, to varying degrees (e.g. in humans more steeply than in non-human primates).

The lumbar (L) region possesses vertebrae with laterally projecting transverse processes and facet joints which interlock tightly between two vertebrae. This arrangement increases stability and limits rotational motion (but allowing flexion and extension). Some primates have accessory processes on the posterior articular processes, locking with the anterior articular process of the next (more caudal) vertebra. Spinous processes in the lumbar region are usually well developed and oriented cranially (not caudally, as in the thoracic region).

It should be noted that the lumbar vertebral bodies are more robust in primates than in other mammals, which has been related to their more upright postures (if not habitual) [7].

In the sacral (S) region, the vertebral bodies, the articulations between the neural arches and the neural spines (partly or completely) are fused, and there are no intervertebral disks. Therefore, the sacrum is a rigid region.

The caudal region is highly variable in primates. Only the first few caudal vertebrae have a fully developed neural arch, but most also have ventral arches (connected to the body by ligaments) that protect the caudal artery.

While the basic anatomy and function of the regions, outlined here, holds for all primates, substantial variation exists within primate taxa, and we will here outline some of this variation in hominoids (apes, including humans), stating how they differ from other primates.

One main point of variation is in the number of vertebrae per region, which differs inter- (and sometimes intra-) specifically. We will focus on

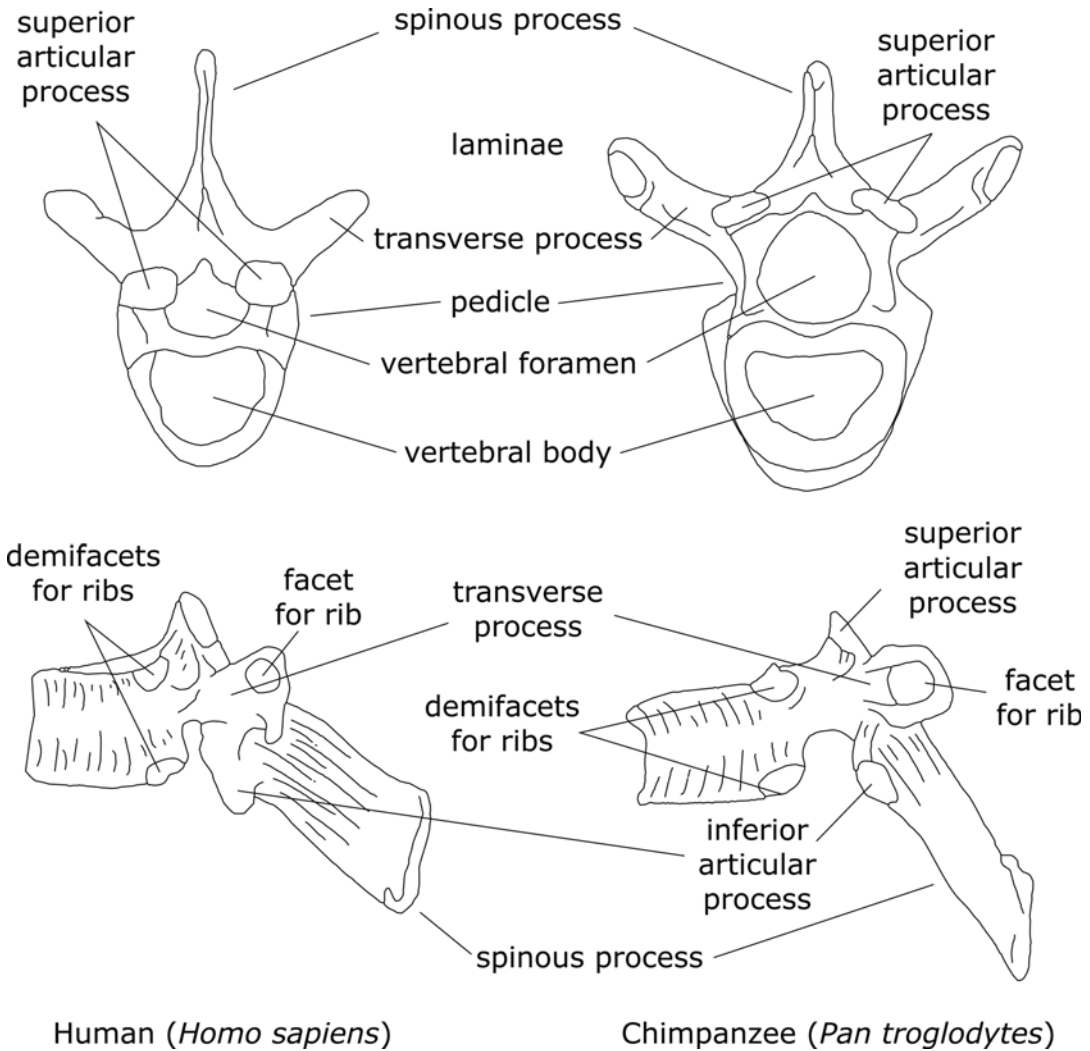


Fig. 2.2 Schematic drawing of the sixth thoracic vertebra (T6) of a chimpanzee and a human. *Top*, axial view; *bottom*, lateral view (After Aiello and Dean [8])

the thoracic, lumbar and sacral regions, since the cervical region is highly conservative, even across mammals, with seven vertebrae, and the caudal region is very variable (e.g. ranging from no caudal vertebrae in some gibbons to more than 30 in the robust prehensile tail of spider monkeys) but less relevant for humans. Interestingly, the total number of thoracic, lumbar and sacral vertebrae is usually 22 across apes and even monkeys [9], and it is the distribution between regions that differs (Table 2.1, adapted from after Schultz [10]).

Apes, as well as other non-human primates, usually have more than 12 thoracic vertebrae

(e.g. up to 14 in chimpanzees, *Pan*, and up to 16 in the New World monkeys *Alouatta*). For the lumbar region, it is interesting that the apes, our closest relatives, have less vertebrae than humans (typically three or four), which increased stiffness is associated with the demands of climbing, but primates in general often have more than five lumbar vertebrae (e.g. up to nine in the Old World monkeys *Presbytis*). A long lumbar region may thus be the primitive primate condition, with an independent reduction in vertebral numbers in apes (see [10–12]). It has been stated in the past that early hominins had six lumbar vertebrae but

Table 2.1 Vertebral numbers per region in some primates

	Thoracic	Lumbar	Sacral	Caudal	TL total	TLS total
Human (<i>Homo</i>)	12.0 (11–13)	5.0 (4–6)	5.2 (4–7)	4.0 (2–5)	17	22.2
Chimpanzee (<i>Pan</i>)	13.2 (12–14)	3.6 (3–4)	5.7 (4–8)	3.3 (2–5)	16.8	22.5
Gorilla (<i>Gorilla</i>)	13.0 (12–14)	3.6 (3–5)	5.7 (4–8)	3 (1–5)	16.6	22.3
Orang-utan (<i>Pongo</i>)	11.9 (11–13)	4.0 (3–5)	5.4 (4–7)	2.6 (1–5)	15.9	21.3
Gibbon (<i>Hylobates</i>)	13.1 (12–14)	5.1 (4–6)	4.6 (3–6)	2.7 (0–6)	18.2	22.8
Macaque (<i>Macaca</i>)	12.1 (12–13)	6.9 (6–8)	3.0 (2–4)	17.0 (5–28)	19	22.0
Spider monkey (<i>Ateles</i>)	13.8 (13–15)	4.2 (4–5)	3.0 (2–4)	31.1 (28–35)	18	21.0

After Schultz [10]

[6] have shown that they had five, still one more than typical for great apes.

The number of sacral vertebrae within apes is somewhat variable but usually 5–6. Thus, compared to the other apes, humans typically have an extended lumbar region (+1 or 2 vertebrae) but a shorter thoracic (–1 vertebra) and sometimes sacral (–1 vertebra) region.

The hominoids deviate from the generalised primate pattern in some other ways.

In the cervical region, the dorsal processes are very large, especially in the largest individuals (male gorillas and orang-utans), with the seventh being the longest, as in humans.

In contrast to non-hominoid primates, the volume increase from cranial to caudal in the thoracic and (especially) lumbar region is mostly due to widening but not lengthening of the vertebrae. This is often regarded as an adaptation to the more frequent use of upright (orthograde) postures and is associated also with a broad thorax.

The lumbar articulation with the sacrum is strongly enlarged, especially in humans (Fig. 2.3).

Non-human primates, including apes, have relatively straight vertebral columns, with typically very moderate lumbar lordosis and thoracic kyphosis compared to the situation in adult humans, as seen in our closest relatives, chimpanzees (*Pan*). However, it should be noted that the spine can show some lordosis and

a long lumbar region, as seen in, for example, macaques [13].

2.4 The Hominin Spine

The previous section dealt with extant species; now we will focus on extinct hominins (humans and their direct ancestors) in an attempt to illustrate how the typically human spine anatomy evolved within our lineage. The fossil record of the human spine is, however, very scarce and fragmentary. We have vertebral fossils for five Plio-Pleistocene hominins, excluding the relatively recent and in the framework of spine evolution, less interesting species such as *H. neanderthalensis* and *H. sapiens*. Out of the five species, *Australopithecus africanus* and *Homo erectus*, and recently *Australopithecus sediba*, are best documented and have adequately preserved detail [5], although for all of these species, we lack a complete vertebral column.

All fossil vertebrae for Plio-Pleistocene hominins we know have relatively long (compared to modern humans) spinal and transverse processes.

Australopithecus afarensis (approx. 4–3 million years ago, mya) is a key species for our understanding of hominin evolution in general. Fifteen vertebral elements are known for the AL 288-1 subject ‘Lucy’ and nine for the AL 333 sample ‘the first family’. They show long cervical

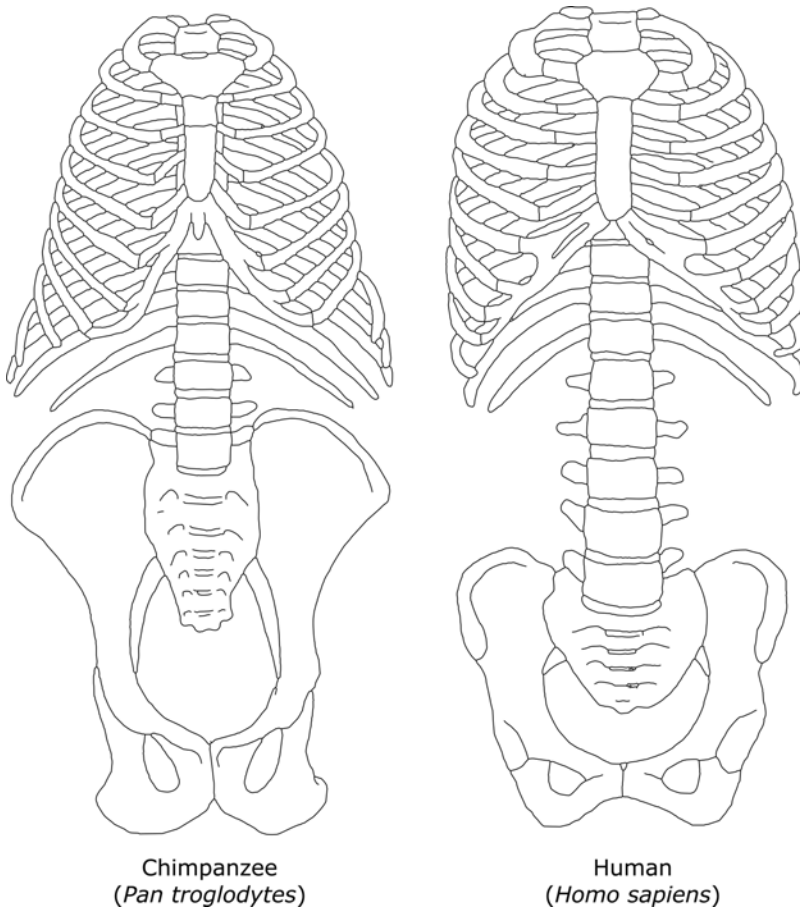


Fig. 2.3 Schematic drawing of the vertebral column, rib cage and pelvis in a chimpanzee and a human (frontal view). Note the higher pelvis, shorter lumbar region and

narrow gap between the rib cage and the iliac crests in the chimpanzee as compared to the human (After Schultz [10])

and probably also upper thoracic spinous processes, which have been suggested that the erector spinae, rhomboids and trapezius muscles were particularly well developed [14].

Australopithecus africanus (approx. 3–2 mya) vertebral fossils are from Sts 14 (15 elements) and Stw 431 (12 elements) [15] subjects, plus one each for Sts 65 and Sts 73. The species possessed very long transverse processes (Fig. 2.4) in the lumbar region (esp. L3) and L3 and L4 very upwardly curved [16]. Sts 14 had five lumbar vertebrae [15].

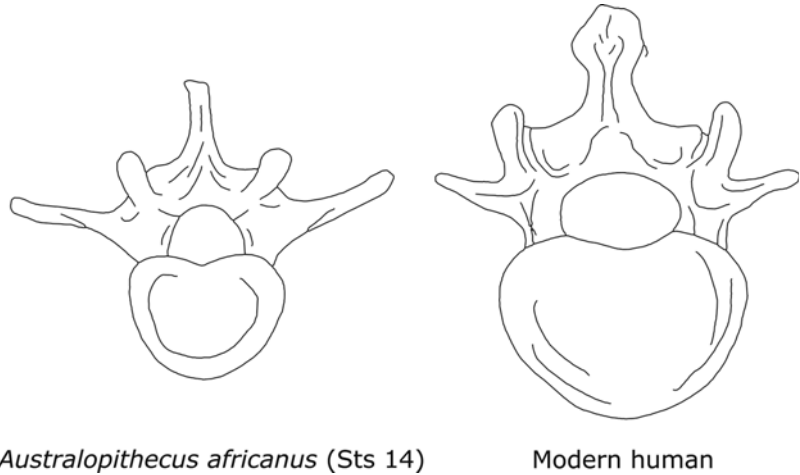
Paranthropus fossil vertebrae number only three, from Swartkrans in South Africa (SK 3981b; [17], approx. 1.9 mya), and they are in poor state. As in *Australopithecus*, they also possess long processes. The last lumbar vertebra has

transverse processes, which are up curved (as in *Australopithecus africanus*) but very long compared to both *Australopithecus africanus* and modern humans; however, *Paranthropus* is considered not to be a direct ancestor to the latter.

Homo erectus vertebrae are best known from KNM-WT 15000 ‘Turkana boy’ (approx. 1.5 mya), and the sample consists of 14 presacral vertebrae. Haeusler et al. [18] describe the spine as an overall rather modern human-like structure, with five lumbar vertebrae and a human-like mobility and capacity for lordosis (notably, with even stronger lumbar wedging than in modern humans and in australopithecines).

Australopithecus sediba (approx. 2.0 mya) vertebral fossils have been recently described for

Fig. 2.4 Schematic drawing of the second lumbar vertebra (L2) in an axial view for an australopithecine and a modern human (After Robinson [16])



two individuals: MH1 (a juvenile male) and MH 2 (an adult female) [19]. They show very strong lumbar wedging (and thus lordosis), comparable to *Homo erectus*.

The picture of hominin vertebral evolution is still quite fragmentary, but some features are seen in all hominins for which sufficient fossils are available: lordosis [20–22], a pyramidal configuration of articular facets with descent through the lower lumbar column, and a wide curved sacrum. In some species (but not in *Australopithecus afarensis* and *Australopithecus africanus*), a large relative lumbosacral body size is observed [19]. Overall, key features linked to habitual bipedalism, detailed below, can be seen in all fossil hominins.

2.5 The Human Spine: Characteristics and Function

We have described the basic anatomy of the human spine, how it has evolved, and outlined some unique features in humans. In this final section, we will try to relate some of the most striking features to function. This is not always straightforward, since anatomy is not exclusively determined by function but also by evolutionary constraints. Even the functional requirements are multiple, and especially the requirement for a large birth canal in humans strongly dictates pelvic shape and, secondarily, spinal architecture (see ‘spinal curvature’). However, in the case of the human spine, there is a very large consensus that habitual upright

locomotion is the major driver (in evolutionary and developmental terms) and that the requirements of stability and mobility are both important (and potentially conflicting).

2.5.1 Spinal Curvature

For efficient, straight-legged, upright locomotion as seen in humans, the trunk needs to be fully erect with its centre of mass directly above the base of support. This is achieved in two ways. Firstly, by having ischio-iliac lordosis (which is outside the scope of this chapter, but see [23]) and, secondly, by having lumbar lordosis (Fig. 2.5).

Lumbar lordosis (a forward-facing convexity) in humans is, for a great part, a phenotypically plastic feature that develops as a result of upright walking. This is shown, firstly, because it is not seen in babies. Prior to the ability to walk, all sections of the vertebral column show a dorsal convex curvature [24], and it is also not seen in permanent bed-bound adults. Secondly, non-human primates can develop human-like spinal curvature during development, as seen, for example, in Japanese monkeys trained for bipedal walking (although the lordosis is largely the result of the intervertebral disk rather than the result of vertebral wedging; e.g. see [25]).

Apart from pronounced lumbar lordosis, the human spine displays thoracic kyphosis (backward-facing convexity), as well as cervical lordosis and sacral kyphosis. The combined

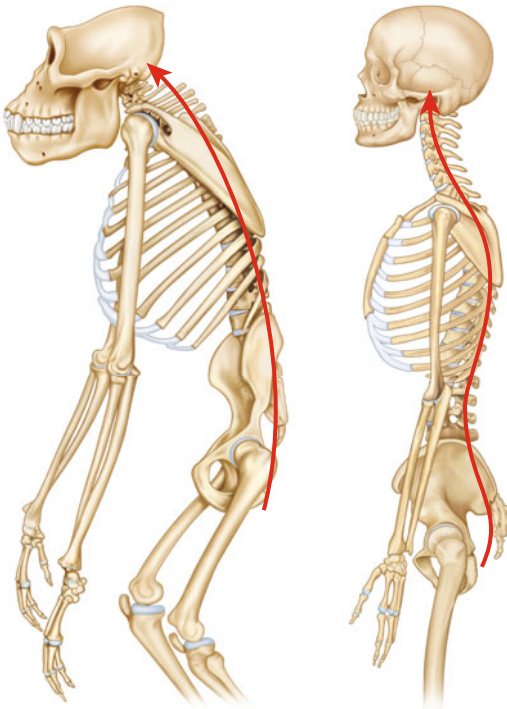


Fig. 2.5 Note the lumbar lordosis in humans (*right figure*), necessary to keep upright position of the spine, as compared to the general kyphosis of the spine in hominoids (*left figure*)

curvature of the spine also helps (with the intervertebral disks) to absorb shocks. Interestingly, an average lumbar lordosis in women seems to be most attractive in men (see Chap. 39).

Anatomically, lumbar lordosis is a result of dorsal wedging in L4 and L5 (in males) and L3–L5 (in females, [26]) and of the deformable, intervertebral disks. Furthermore, these disks are higher ventrally than dorsally. This is an important finding when considering lumbar spine reconstruction.

2.5.2 Spinal Mobility

The second fundamental difference between the ape and the human spine lies in its overall increased mobility. This is a result of mobility of the spine itself, combined with the shape of the rib cage and the pelvis, which are also very different in humans and apes.

The increased mobility in humans is caused by the increased number of lumbar vertebra, outlined higher, but further enhanced by a number of other features. The pelvis of great apes is much higher than that of humans, and the iliac blades virtually enclose the lowest lumbar vertebrae. This iliac structure combined with the extended rib cage (which further reduces flexion and extension movements in the thorax) also means that the gap between these is very small, sometimes only a few centimetres (Fig. 2.3). This further limits overall trunk mobility in apes but not in humans, where the lumbar region is the most mobile one, after the cervical region. Since all the great apes, with which we share a common ancestor, had such a stiff trunk (suited for arboreal locomotion), it has been argued that hominins started with a similarly short trunk; however, it has also been proposed that they did not and that the short lumbar regions of apes have evolved independently from a longer primitive primate lumbar region [11].

Motion is also to a great extent explained by articular processes. Humans have relatively short transverse and spinous processes (the latter angles downwards more steeply than in apes), which provides shorter leverage for the muscles but enhances mobility. Moreover, the surfaces of the articular processes are oriented in order to allow movement, being curved and sagittally oriented in the lumbar region, allowing for flexion and extension, but flat and coronally oriented in the thoracic region, allowing primarily lateral bending and rotation, but much less flexion and extension.

2.5.3 A Strong Lumbosacral Region

Lumbar vertebrae increase in size caudally; in humans (but not in apes) the left-to-right distance between the facets of the paired articular processes (which are, moreover, very well developed) also increases [8]. This is necessary for the articulation with the wide sacrum (see below). At lumbosacral joint, the inferior facet joints are reoriented to prevent the entire spine sliding off the highly angled sacrum (further helped by the enlarged sacrospinous ligament).

The human sacrum is absolutely and relatively enlarged (notably in width) compared to the ape sacrum; it is more curved and has a larger articulation (the auricular surface) with the pelvis. Compared to apes, humans display less partial sacralisation of lumbar vertebrae [9].

Human bipedal walking requires both an increased stability (due to the important loads involved) and an increased mobility. These are conflicting demands, which (with some other, notably obstetric factors) have shaped the human spine throughout the course of hominin evolution. This has led to a compromise anatomy (see Putz et al. [27]), which together with the relatively poorly developed erector spinae might help explain the predisposition for lower back injuries in humans [28].

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