

Ella Been · Asier Gómez-Olivencia
Patricia Ann Kramer *Editors*

Spinal Evolution

Morphology, Function, and Pathology of
the Spine in Hominoid Evolution

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Editors

Ella Been

Department of Sports Therapy
Faculty of Health Professions
Ono Academic College
Kiryat Ono, Israel

Department of Anatomy and Anthropology
Sackler Faculty of Medicine
Tel Aviv University
Tel Aviv, Israel

Patricia Ann Kramer
Departments of Anthropology and
Orthopaedics and Sports Medicine
University of Washington
Seattle, WA, USA

Asier Gómez-Olivencia

Departamento de Estratigrafía y
Paleontología
Facultad de Ciencia y Tecnología
Universidad del País Vasco/Euskal Herriko
Unibertsitatea (UPV/EHU)
Leioa, Spain

IKERBASQUE

Basque Foundation for Science
Bilbao, Spain

Centro Mixto UCM-ISCIH de Evolución y
Comportamiento Humanos
Avda. Monforte de Lemos
Madrid, Spain

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Foreword

Since the publication of J. T. Robinson's *Early Hominid Posture and Locomotion* in 1972, there hasn't been such a comprehensive, detailed analysis of the hominid vertebral column as in this splendid volume. True, this topic has attracted much attention in highly regarded publications (see, e.g., Aiello and Dean's *An Introduction to Human Evolutionary Anatomy* [1990] and Cartmill and Smith's *The Human Lineage* [2009]), but in most cases, the discussion either constitutes part of a broad treatment of human anatomy and its evolution, is focused on a specific structure, or simply reports on the inventory of recently discovered fossil vertebrae, giving a basic list of their metric characteristics. Here comes Been, Gómez-Olivencia, and Kramer's *Spinal Evolution: Morphology, Function, and Pathology of the Spine in Hominoid Evolution*, whose 17 chapters are dedicated to elucidating diverse biological and evolutionary aspects of the vertebral column.

During the decades that have elapsed since Robinson published his book, we have witnessed an unprecedented expansion of our inventory of fossil remains relevant to locomotion and posture. This rich assemblage affords us a view of anatomical elements that for many years were terra incognita in the human fossil record, such as the pelvis of *Australopithecus afarensis* and that of the more primitive *Ardipithecus*; vertebrae of various hominid species, including a complete Neandertal vertebral column accompanied by an entire pelvis; structures that indicate body proportions; hand and foot bones, including two medial navicular bones, one resembling a modern human big toe and the other indicating a medially divergent big toe; and even a rare tiny pisiform bone that appears to represent an intermediate stage between the morphology of modern humans and that of chimpanzees. All of these elements have no doubt influenced the vertebral column, both as a single anatomical unit and a collection of individual components.

The increase in the number of available fossils has not only added new links in our own evolutionary chain, making the fossil record denser, but also provided evidence of numerous species that we have reassigned to side branches of the hominin clade. These species have been placed in different clades because their skulls, mandibles, and teeth are incompatible with the morphocline leading to modern humans, even though these cranial elements represent bipedal species. Nevertheless, it is

both interesting and surprising that most researchers continue to arrange the postcranial remains of the side branches in a single morphocline, as if the only possible mode of bipedality is that of humans.

On the contrary, I see bipedality as manifested in many forms, just as animal flight takes many forms. Consider, for example, the hummingbird, which flaps its wings hundreds of times a minute, can hover in midair and can even fly backwards, as opposed to the albatross, which glides for days without flapping its wings even once. Sure, the substantially longer evolutionary history of birds is expressed in much richer and more dramatic anatomical differentiation than what we would expect of the hominin clade. Nevertheless, the principle is what counts: we cannot assume a priori that the locomotion system in the hominin clade falls into a single morphocline and that each specimen (or even each postcranial fragment) represents a character state in that morphocline. In other words, we should not be content with the hypothesis that all hominids walked “upright” and that there is no difference between the mode of locomotion found in various hominids and that of modern humans. Accepting such a hypothesis would be a blatant repetition of the historical mistake of arranging all fossil hominid skulls into a single lineage that is based on a morphocline of brain capacity, even when specimens clearly did not fit into the evolutionary sequence.

Take, for example, the remains of hominid pelvises and their accompanying vertebral column. One configuration is seen in *Homo sapiens*, a different one in Neandertals, a still different one in Lucy (and maybe also in *Au. africanus*), and a much different one in *Ardipithecus*. Still, we have only a vague idea of the pelvic anatomy of other hominids, such as *Au. robustus*, *Au. boisei*, *H. heidelbergensis*, and even the well-known Peking assemblage. Do all these pelvises and vertebral columns fall into a single morphocline (in which every pelvis represents a different character state), and does that morphocline lead to the anatomy of modern humans? I seriously doubt it. If we happen to find a robust australopith pelvis and vertebral column, would they fit into a morphocline that leads to modern humans, or would their degree of specialization force us to remove them from our lineage, just as the unique robust australopith masticatory system has?

Furthermore, when anagenesis was still the dominant theme, Franz Weidenreich had the insight to declare that “the humanlike features of the Australopithecinae are signs of their past rather than of their ‘future.’ In other words, the features they share with man are those retained from an original stock” (1948, p. 158). What he is actually saying is that not every element that resembles the corresponding element in the modern human skeleton signifies a derived anatomy just because the element is found in modern humans today. The “future,” according to Weidenreich, can certainly include morphologies that do not lead to modern humans, morphologies whose character states do not fit into our morphocline, as indeed we have learned from the robust australopith anatomy.

Let us not forget the frequency of parallelism: the fact that extreme orthognathism characterizes some australopithecine faces does not render them “super humans” (a term often applied to describe such faces), nor does the extremely wide birth canal of Lucy render her “wonder woman.” These two traits are manifestations

of unique specializations that bear no relationship to the homologous characters in modern humans.

No doubt that the hominin clade is rich in branches, some of which have brought us to *H. sapiens* and others that are completely unrelated to that journey. The contributions in the present volume clearly observe the cautious, meticulous approach and tight adherence to the common rules of the game (parsimony and the proper identification of outgroups) that are required for recruiting postcranial elements, including the vertebral column and its many components, to arrive at a deeper understanding thereof and an accurate phylogenetic reconstruction. Indeed, *Spinal Evolution* offers a welcome deliverance from the many preconceptions about the vertebral column that have held us captive in recent years.

Tel Aviv, Israel

Yoel Rak

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Chapter 1

The Study of the Human Spine and Its Evolution: State of the Art and Future Perspectives



Ella Been, Asier Gómez-Olivencia, and Patricia Ann Kramer

1.1 Introduction

The vertebral spine is a key element of the vertebrate anatomy. Its two main roles are related to protection of the spinal cord and the main blood vessels and to provision of a structural foundation that is of paramount importance for posture and locomotion. The vertebral column is the axis of the body where the limbs attach; it enables the mobility required for breathing and for locomotion and, at the same time, it provides stability for the attachment of the sensory organs of the head. Despite its great importance, in evolution the human vertebral spine is often overlooked by researchers because (1) vertebrae are fragile in nature, which makes their fossilization a rare event; (2) they are metameric (seriated and repeated elements) which makes their anatomical determination and, thus, their subsequent study difficult

E. Been (✉)

Department of Sports Therapy, Faculty of Health Professions, Ono Academic College, Kiryat Ono, Israel

Department of Anatomy and Anthropology, Sackler Faculty of Medicine, Tel Aviv University, Tel Aviv, Israel

A. Gómez-Olivencia (✉)

Departamento de Estratigrafía y Paleontología, Facultad de Ciencia y Tecnología, Universidad del País Vasco/Euskal Herriko Unibertsitatea (UPV/EHU), Leioa, Spain

IKERBASQUE, Basque Foundation for Science, Bilbao, Spain

Centro Mixto UCM-ISCI3 de Evolución y Comportamiento Humanos, Avda. Monforte de Lemos, 5, Madrid, Spain

e-mail: asier.gomezo@ehu.eus

P. A. Kramer (✉)

Departments of Anthropology and Orthopaedics and Sports Medicine, University of Washington, Seattle, WA, USA

e-mail: pakramer@uw.edu

(Franciscus and Churchill 2002); and (3) the plethora of bones and joints involved in every movement or function of the axial skeleton makes the reconstruction of posture, breathing mechanics, and locomotion extraordinarily difficult (Been et al. 2017; Gómez-Olivencia et al. 2018). Nonetheless, it is well established that the spine has changed dramatically during human evolution. Spinal curvatures, spinal load transmission, and thoracic shape of modern humans are unique among primates. Yet, there are many debates regarding how and when these changes occurred and about their phylogenetic, functional, and pathological implications.

In recent years, renewed interest in the axial skeleton, and more precisely in the vertebral column, has arisen. New and exciting finds, mostly from Europe and Africa, as well as new methods for reconstructing the spine, have been introduced to the research community (e.g., Carretero et al. 1999; Meyer 2005, 2016; Gómez-Olivencia et al. 2007; Bonmatí et al. 2010; Williams et al. 2013, 2017; Bastir et al. 2017). Additionally, the revisions of previously found specimens has provided new information about important aspects of spine evolution (Haeusler et al. 2002, 2011; Been et al. 2010; Gómez-Olivencia et al. 2013, 2017). Methodologies such as finite element analysis, trabecular bone analysis, geometric morphometrics, the study of patterns of integration, and gait analysis that have been applied to the spines of primates and humans (Bastir et al. 2014; Nalley and Grider-Potter 2015; Arlegi et al. 2018) and have become common in parallel with the study of the numbers of vertebrae in primates, including active debates with regard to the vertebral formula of the last common ancestor between chimpanzees and modern humans (Pilbeam 2004; McCollum et al. 2010; Lovejoy and McCollum 2010; Williams 2012a, b; Williams and Russo 2015; Gómez-Olivencia and Gómez-Robles 2016; Williams et al. 2016; Thompson and Almécija 2017). Additionally, advanced biomechanical research regarding posture, range of motion, stability, and shock attenuation of the human spine has interesting evolutionary implications (Castillo and Lieberman 2018). All these new avenues provide novel perspective on the evolution of the spine.

The objective of this book is to explore both these new methodologies and the new data, including recent fossil, morphological, biomechanical, and theoretical advances regarding vertebral column evolution, and to provide “state-of-the-art” information on the evolution of the human spine. The book was born after a session at the 2017 AAPA meeting entitled “The Axial Skeleton: Morphology, Function, and Pathology of the Spine and Thorax in Hominoid Evolution” that was organized by one of us (EB) and Alon Barash.

The book is divided into four main sections: the hominoid spine; the vertebral spine of extinct hominins; ontogeny, biomechanics, and pathology of the modern human spine; and new methodologies of spinal research. Each of these sections is composed of several chapters that complement each other and together provide a wide-ranging and comprehensive examination of different themes of importance to understanding spinal evolution.

1.2 Part One: The Vertebral Spine of Nonhuman Hominoids

The first part of the book focuses on the vertebral spine of nonhuman hominoids. It describes the morphology and biomechanics of the cranial base and the cervical, thoracic, and lumbar areas of extant nonhuman hominoid species and explores the relationships of morphology and biomechanics with posture and locomotion. The last two chapters of this first section deal with the important question of vertebral formulae in hominoid evolution, the early stages of spinal evolution in Miocene apes and the appearance of recent spinal morphology in extant apes.

In Chap. 2, Russo and Kirk (2019) describe the cranial base in hominoids and its relation to posture and locomotion. They find that at the “cranio-cervical interface,” the morphology of the hominoid cranial base offers a wealth of information regarding posture and locomotion. In particular, compared to the other great apes, modern humans exhibit more anteriorly positioned and anteroinferiorly oriented foramina magna, more anteriorly positioned and flatter occipital condyles, and a reduction and reorganization of the nuchal musculature. Anteriorly positioned foramina magna and occipital condyles confer a mechanical advantage for balancing the head above an upright (orthograde) torso in humans rather than in front of a horizontal torso as in great apes. Differences in the head equilibrium are related to the development of neck musculature. In fact, more balanced heads (such as those present in modern humans) require less neck musculature (Aiello and Dean 1990). Extinct hominin taxa resemble modern humans in some (e.g., forward migration of the foramen magnum) but not all (e.g., nuchal plane architecture) aspects of cranial base morphology. They suggest that research on the “cranio-cervical interface” will continue to inform our understanding of how hominoid cranial anatomy relates to posture and locomotion and, in particular, how the modern human cranium evolved in relation to our unique reliance on bipedalism.

In Chap. 3, Nalley and Grider-Potter (2019) review the current knowledge regarding cervical vertebral morphology in relation to head posture and locomotion in nonhuman hominoids. They provide compelling evidence for function-form relationships between cervical bony morphology and behavior, as well as new data detailing the relationship between head shape and cervical variation. They suggest that future efforts should focus on expanding skeletal samples to include more orthograde and antipronograde taxa (e.g., strepsirrhines), as well as on documenting internal bony architecture to further test these proposed functional explanations.

Shapiro and Russo (2019) explore in Chap. 4 the lumbar spine of nonhuman hominoids. Hominoids show a distinct suite of characteristics in their lumbar region. The authors conclude that the evolution of hominoids was accompanied by a transformation of the primate body plan from a monkey-like ancestral condition to one characterized by a distinct suite of postcranial features functionally associated with orthograde posture and/or forelimb-dominated locomotor behaviors. While diagnostic hominoid features can be found throughout the postcranial skeleton, the trunk, and especially the lumbar region, can be considered one of the most functionally important and immediately noticeable aspects of the hominoid body plan. The

most important features of the hominoid body plan include the vertebral formula, relative lumbar spine length, vertebral body shape, and vertebral arch morphology, including the shape of the transverse and spinal processes.

In Chap. 5, Nakatsukasa (2019) provides a thorough review of the study of orthogrady in Miocene ape spinal morphology. This chapter links with previous chapters of this book presenting the derived features present in the vertebral column of extant hominoids, attributable to the frequent forelimb-dominated orthograde positional behavior such as suspension or vertical climbing. These specializations include a cranial shift in the lumbosacral border (decreased number of lumbar vertebrae and increased number of sacral vertebrae), loss of an external tail, spinal invagination into the thoracic and abdominal cavities, and craniocaudally short and dorsoventrally deep lumbar vertebral centra. Despite the large number of Miocene ape genera, only a few preserve sufficiently complete vertebrae to examine these features. Fossil apes (*Ekembo* and *Nacholapithecus*) from the beginning and mid-part of the Miocene in Africa (~19–15 Mya, Kenya) were essentially deliberate arboreal pronograde quadrupeds and retained primitive catarrhine axial skeletal morphology: long and dorsomobile lumbar spine, short sacrum, absence of spinal invagination (although *Nacholapithecus* shows a hint of an early transition to orthograde positional behavior). The penultimate lumbar vertebra of *Morotopithecus* (20.6 Mya, Uganda) exhibits craniocaudally short and dorsoventrally deep centrum and dorsal position of the transverse process, similar to that of extant apes, which seems to be the result of parallel evolution, based on the dentognathic evidence. European ape fossil record (*Pierolapithecus* and *Hispanopithecus*) illustrates a progressive evolution toward orthogrady. Nakatsukasa (2019) also provides insights regarding the current debates on the evolution of orthogrady: whether it evolved in European and African ape lineages (and Asian as well) independently or not; whether the dorsostable spine in the extant African apes is homologous or homoplastic; and whether the last common ancestor of the extant African apes and humans had an intermediate body plan between pronogrady and orthogrady (“multigrady”).

In Chap. 6, Williams et al. (2019) provide an overview of the numbers of vertebrae in extant hominoids, presenting a summary of the largest database of hominoid vertebral numbers. In fact, this database provides, for the first time, data of previously unstudied species and subspecies. They conclude that vertebral formulae, the combination of regional numbers of vertebrae making up the bony spine, vary across vertebrates and within hominoid primates. They found more variation within and between species than expected, particularly in gibbons and in the gorilla and chimpanzee subspecies. Williams et al. (2019) suggest that combined thoracic and lumbar numbers of vertebrae are somewhat phylogenetically structured: while outgroup taxa (two species of cercopithecoids) retain the primitive number of 19 thoracolumbar vertebrae, hylobatids generally possess 18 thoracolumbar vertebrae, and hominids (great apes and humans) have 17 or 16 thoracolumbar vertebrae. When compared to cercopithecoids, and to putative stem hominoids, extant hominoids show evidence for homeotic change at both the lumbosacral (e.g., decrease in lumbar vertebrae; increase in sacral segments) and in the position of the transitional vertebrae. Homeotic changes are probably also responsible for the differences

between African apes and modern humans, with differences in the number of thoracic and lumbar within a 17-segment thoracolumbar framework.

Interesting and promising areas for future research of the vertebral spine of non-human hominoids include, among others, studying the interaction between spinal posture, motion, and mode of locomotion using new methodologies such as digital motion X-rays (Nalley and Grider-Potter 2019). Additionally, more information on how the spine covaries with other anatomical region is necessary, as well as an expanded fossil record that can answer to the current questions regarding hominoid spine evolution.

1.3 Part Two: The Vertebral Spines of Extinct Hominins

The second part of the book gives the most current description of the spines of extinct hominins, from *Australopithecus* to fossil *H. sapiens*.

In Chap. 7, Williams and Meyer (2019) discuss the spinal remains of *Australopithecus* from five sites in East and South Africa: Aramis, Asa Issie, and Hadar from the Afar Depression of Ethiopia and Sterkfontein and Malapa in the Cradle of Humankind, South Africa (Robinson 1972; Lovejoy et al. 1982; Cook et al. 1983; Sanders 1998; Haeusler et al. 2002; Williams et al. 2013, 2018). They indicate that australopith cervical vertebrae are intermediate in morphology (and potentially in function) between chimpanzees and modern humans; their thoracic vertebrae tend to show Scheuermann's hyperkyphosis deformity; and the lumbar vertebrae show human-like lumbar lordosis.

In Chap. 8, Meyer and Williams (2019) summarize vertebral remains from early *Homo*, including *H. erectus* as well as the Middle Pleistocene *H. naledi*. Two partial immature *H. erectus* skeletons preserve vertebrae: KNM-WT 15000 ("Turkana boy"; Latimer and Ward 1993) and the D2700 individual from Dmanisi (Meyer 2005; Lordkipanidze et al. 2007). Vertebrae from *H. naledi* include those from the Dinaledi Chamber (Williams et al. 2017) as well as those from LES1 partial skeleton ("Neo") found in the Lesedi Chamber (Hawks et al. 2017; Williams et al. 2017). Based on the current evidence, the vertebral column of *H. erectus* possessed a modal number of 12 thoracic and 5 lumbar segments, as is the case in australopiths and modern humans. Nonetheless, the spine of *H. erectus* reveals key changes relative to earlier hominins, with an expanded thoracolumbar spinal canal offering increased neurovascular capacities and a ventral pillar (formed by the vertebral bodies) better equipped to mitigate compressive loads and provide energy return (Meyer and Haeusler 2015). These biological developments are germane to understanding the advent of derived human behaviors, including efficient long-range locomotion and the first hominin expansion out of Africa.

In Chap. 9, Gómez-Olivencia and Been (2019) summarize the vertebral fossil record for "late" *Homo*, including *H. antecessor*, Middle Pleistocene *Homo* (except *H. naledi*), Neandertals, and fossil *H. sapiens*. The fossil record of the *H. antecessor* is currently restricted to the fossil remains from Gran Dolina-TD6 (Sierra de

Atapuerca, Spain), the Middle Pleistocene vertebral fossil record is sparse both geographically and chronologically, and the Late Pleistocene fossil record is more abundant. Based on the current evidence, these authors recognize the presence of at least two distinct morphologies arising from the more primitive *H. erectus* spine morphology: that of the Neandertal lineage and that of *H. sapiens*. Neandertals and their Middle Pleistocene ancestors show differences in all the anatomical regions when compared to modern humans related to a more stable spine with less accentuated curvatures (Gómez-Olivencia et al. 2007, 2013, 2017; Been et al. 2010, 2012, 2014, 2017). The Sima de los Huesos (SH) paleodeme does not, however, display the full suite of derived Neandertal features, a pattern also present in the cranium and the rest of the postcranium (Arsuaga et al. 2014, 2015). This implies that the distinctive Neandertal morphology did not arise all at once, but rather in a mosaic fashion. The Neandertal spinal morphology seems to be more stable in both sagittal and mediolateral directions. According to this review, the evolution of the modern human spine is less well known compared to Neandertals due to the scarce Middle Pleistocene fossil record ancestral to *H. sapiens* and the poor preservation of *H. sapiens* remains during the first half of the Late Pleistocene.

In Chap. 10, Haeusler (2019) provides an overview of the spinal disorders found in the hominin fossil record and alternative etiologies for several of them. The spinal disorders present in the hominin fossil record include one case of a benign primary bone tumor in MH2 (*A. sediba*), one case of developmental aplasia of the lumbar spinous processes in the Kebara 2 Neandertal, and many cases of degenerative osteoarthritis and pathologies related to the biomechanical failure of the growing spine. These include spondylolisthesis in the Middle Pleistocene Pelvis 1 individual from Sima de los Huesos (Sierra de Atapuerca; Bonmatí et al. 2010), traumatic juvenile disc herniation in KNM-WT 15000 (*H. erectus*; Schiess et al. 2014), anterior disc herniation (limbus vertebra) in Stw 431 (*A. africanus*; contra D'Anastasio et al. 2009), and Scheuermann's disease in several *Australopithecus* specimens. Haeusler (2019) argued that juvenile disc herniation, traumatic anterior disc herniation, and Scheuermann's disease all result from displacement of disc material and have a higher incidence following strains and trauma to the spine during the increased vulnerability phase of the pubertal growth spurt. He concluded that the remarkably high prevalence of this kind of disorders in our ancestors might suggest that our spine has become less vulnerable during the course of human evolution.

Summarizing the data and knowledge of the spine of extinct hominins made us realize that there are major lacunae in current research. For example, data regarding the spine of early *H. sapiens* (the hominins from Skhul and Qafzeh for example) is based mostly on the original publications (McCown and Keith 1939; Vandermeersch 1981), and it has not been thoroughly reexamined since their discovery. Reinvestigating these remains with modern technologies and methods is of paramount importance in order to understand spinal evolution in hominins. Additionally, this section emphasizes the presence of a significant fossil record that has not published in detail yet, either from old excavations or from recent discoveries, including the thoracic vertebrae of the hominins from Sima de Los Huesos, the cervical vertebrae of El Sidrón, the recently discovered vertebrae from the Little foot individual

(Stw 573), and the spine of immature individuals (e.g., Amud 7). New publications describing and documenting these remains and comparing them to modern humans and to other hominins will broaden our knowledge and understanding of the evolution of the spinal column in hominins. Another important question emerging from this part of the book is the taxonomic value of vertebrae for species recognition. In other words, can a hominin species be defined or recognized based on vertebral morphology?

Of note, this section is also tightly connected with two chapters from the fourth section that describe the reconstruction of the complete spinal columns of fossil hominins based on their vertebral morphology (Bastir et al. 2019; Been et al. 2019b). These reconstructions enable us to measure and understand the relationship between body parts in a way we could not establish before reconstruction and constitute the basis for future biomechanical analysis of the thorax/spine/pelvis in extinct hominins.

1.4 Part Three: The Vertebral Spine of Modern Humans

The third part of the book explores the spine of modern humans. Spinal ontogeny, biomechanics, posture, and pathology are discussed in relation to human evolution.

Chapter 11, by Martelli (2019), presents an overview of the pre- and postnatal ontogeny of the modern human and modern great and lesser ape vertebral column. In this chapter, Martelli introduces the key events in the prenatal development of the human vertebral column and sums up the postnatal development of the size and shape of the different elements—vertebrae, discs—and of the vertebral spine as a whole. At the end of this chapter, Martelli provides a summary of what is known about the pre- and postnatal ontogeny of the modern ape vertebral column. This is followed by an overview on the postnatal growth of various fossil specimens/species, including *A. afarensis* (Dikika 1-1), *A. sediba* (MH1), *H. erectus* (KNM-WT 15000), and Neandertals, compared to both extant nonhuman ape and modern human patterns. Martelli (2019) concludes that the patterns of postnatal development of the vertebral column are roughly similar for all hominoids, but given the overall variation in life history and growth period duration, variation of these patterns is observed. The shift from a great ape-like pattern of postnatal ontogeny happens late in the hominin evolution, and recent data from Neandertal fossils indicate further diversity in those patterns in late hominin evolution.

In Chap. 12, Been and Bailey (2019) describe the association between spinal posture and spinal biomechanics in modern humans and discuss the implications for extinct hominins. They determine the interactions between spinal posture and biomechanics within modern humans and translate those results to extinct hominins. Their main findings indicate that each group/lineage of hominins had special biomechanical characteristics. Early (Mousterian) *H. sapiens* and *H. erectus*, with moderate to high spinal curvatures, similar to the posture of modern humans,

probably had similar spinal biomechanical characteristics as modern humans do. Neandertal lineage hominins (NLH) with small spinal curvatures, reduced from their *H. erectus* ancestors, might have had somewhat different spinal biomechanics characterized by more stability and with reduced shock attenuation abilities compared to modern humans. NLH probably also preferred to squat rather than stoop and had better overhead throwing kinematics compared to modern humans. *Australopithecus* probably had lumbar biomechanical characteristics within the range of modern humans together with very stable cervical spine and a small cervical range of motion (ROM).

In Chap. 13, Been et al. (2019a) review the interaction between spinal posture and pathology in modern humans. They explore the relationship between sagittal spinal posture and spinal pathologies, back pain, and health-related quality of life. Their major findings indicate that spinal posture closely correlates with spinal pathology. Individuals with a well-aligned spine—within the neutral zone defined as moderate spinal curvatures and the line of gravity close to the acetabulum—have a better quality of life, less back pain, and less spinal pathology. Individuals out of the neutral zone, with accentuated or with decreased pelvic incidence and spinal curvatures, are at a higher risk for developing spinal pathology, back pain, and reduced quality of life. In fact, some of the unique spinal pathological lesions in modern humans are related to our distinct locomotion mode and are not present in other primates. This implicates that the emergence of an erect posture and bipedal locomotion was paralleled with the appearance of new pathological lesions.

In Chap. 14, Ezra et al. (2019) discuss the cervical lordosis of modern humans. They explore the ontogeny of the cervical lordosis, its association with pathology, ergonomics, and the evolution of cervical lordosis in hominins. They conclude that many factors influence the amount of cervical lordosis and its internal architecture, including age, sex, and the morphology of the thorax, head, pelvis, and spine. The leading morphologies that associate with cervical lordosis are those of the cervicothoracic junction (C7 or T1 slope), craniofacial features, mandibular morphology, the orientation of the foramen magnum, and pelvic and lumbar posture. They report that certain working groups suffer from neck pain more than others. Neck pain seems typical for sitting occupations and is researched mostly in office workers. Forward head posture and sustained sitting, which are associated with computer use, are typical risk factors, because they produce a prolonged static trunk and neck postures that create the need for excessive nuchal muscle stabilization which causes neck pain. They report cervical pathologies in the spine of extinct hominins and in the spine of pre- and post-agricultural societies, as well as in modern humans. The authors conclude that the possible contribution of the evolution of cervical lordosis in hominins to neck pain and dysfunction is far from being resolved and that future studies should explore the prevalence and nature of cervical pathology in extinct and extant hominoids and in pre- and post-agricultural societies. This might shed light on the different contributors to cervical pain and pathology—evolutionary components and postural and/or functional mechanisms.

Several questions stem from this part. Although it has been shown that back and neck pain/pathology are associated with spinal posture, not enough research has

been done to conclude that changing one's posture will lead to better outcome. Little research suggests that we can create permanent postural change without using surgical intervention, but is that due to the dearth of appropriate research? What kind of impact on spinal posture does the early stages of ontogeny have? Can we influence the development of spinal posture in children? Can we prevent the development of spinal pathologies by intervening early with postural changes? All of these questions are relevant in order to develop preventive medicine to reduce spinal pain and pathology. Enhancing our understanding of spinal biomechanics will provide us with the knowledge to produce better ergonomics solutions in order to ensure better working environments and reduce spinal pain and pathology.

Another major issue that is not well understood yet is the interaction among the morphology of the different body regions, which also has an evolutionary element. For example, how does pelvic morphology influence spinal and thorax morphology (and vice versa)? How does spinal morphology relate to the body bauplan? Given the ubiquity of spinal pain and the consequences of it to quality of life and economic activity, connecting spinal evolution, morphology, and biomechanics to pathology remains a critical research area.

1.5 Part Four: Current Methodologies for the Study of the Vertebral Spine

While the first three parts of the book summarize current knowledge regarding different aspects of spinal evolution in hominoids, hominins, and modern humans, the last part explores some of the current methodologies for the study of the spine, mainly with an evolutionary objective.

In Chap. 15 Been et al. (2019b) describe the methods to reconstruct spinal posture based solely on osseous material and its application to fossil hominins. Despite its importance, researchers face many difficulties in reconstructing spinal posture based solely on osseous material due to the absence of soft tissues. In this chapter, the authors provide information on how to overcome the absence of the intervertebral discs and to align two consecutive vertebrae, and they summarize the methods for measuring/calculating spinal posture based on osseous material. These methods include (1) pelvic incidence (PI) and sacral anatomical angle (SAA) to describe sacral orientation, when the pelvis is relatively complete; (2) lumbar vertebral body wedging (LVBW), inferior articular process angle (IAPA), and lumbar lordosis based on PI (LLPI) to estimate lumbar lordosis; (3) thoracic vertebral body wedging (TVBW) and thoracic vertebral body height difference (TVBHD) to estimate thoracic kyphosis; and (4) the foramen magnum orientation (FMO) for the reconstruction of cervical lordosis. Using these methods, the authors calculate the curvatures of the spine of Kebara 2, and based on these calculations, they have presented a complete 3D virtual reconstruction of the spine of Kebara 2 from the atlas to the sacrum. This is the first reconstruction of a complete vertebral spine that has been

performed for a fossil hominin specimen. The authors recommend utilizing a combination of methods for reconstructing the posture of extinct hominins in order to provide a more robust estimate of spinal curvature.

Bastir et al. (2019) in Chap. 16 provide a brief introduction to geometric morphometrics (GMM) and detail several examples of its application to the spine. GMM is based on the multivariate statistical analysis of Cartesian 2D or 3D landmark coordinates and has seen an exponential increase in its use since its recent development. Bastir et al. (2019) provide an overview of the recent applications of GMM to the human spine anatomy. This overview includes works of general (e.g., Arlegi et al. 2017) and specific aspects (Meyer et al. 2008) of spine anatomy, of how GMM can aid in the reconstruction of fragmentary specimens (Palancar 2017), and of quantitative analysis of sexual dimorphism (Bastir et al. 2014).

Kramer et al. (2019) in Chap. 17 explain the basics of finite element analysis (FEA) and the important considerations and cautions of modeling the spine using this methodology. They conclude that, as with all analysis techniques, the results will only be as good as the assumptions used to create it, so great care and a strong grounding in the first principles of the theory are required to implement an FEA. Of particular importance with the spine is the question of interest. For example, the approach to understand “how do osteophytes form?” will be substantively different from “how does the lumbar curve change when loaded?” The interface of vertebra and soft tissues (such as the intervertebral discs and ligaments) make modeling the spine challenging. Nonetheless, the spine is a 3D structure whose substantial complexity in its morphology and boundary conditions make it worth the effort required to create an FEM to analyze it.

The methods presented in this section have the potential, when applied to both the individual elements (i.e., the vertebrae) and the complete spines of both extinct and extant species, to open new horizons for our understanding of the vertebral spine and its role as the fundamental part of human motion. Using FEM models will enhance our understanding of spinal motion and the development of spinal pathology. It will also enable researchers to simulate the influence of different spinal surgeries.

1.6 Conclusion

The last 20 years has seen substantial improvement in our understanding of the evolution of the spine in hominoids in general and in hominins in particular. New fossils, new approaches, and new methodological applications have multiplied the number of studies published and have drastically changed our perception of how the spine evolved. Moreover, this new information has provided an expansive framework against which new fossil findings can be compared. This book is born from the necessity to provide an overview of the state of the art in the field in a single volume, in order to detect areas in which additional research should be performed. The reviews of the authors of this book do not only provide evidence for substantial

improvement in the understanding of this anatomical region but also demonstrate that the years ahead of us will be exciting: many fossils already excavated have not been published in detail (e.g., Sima de los Huesos, Dinaledi, Little foot), some “classical fossils” need to be restudied using the current methodological frameworks, and the application of new technologies and statistical approaches to new areas of the study of the spine all promise many changes in our understanding of the spine in coming years.

Additionally, much work remains to be done, not only in the field to recover new fossils but also to develop and implement new conceptual and analytical tools that can be useful in the study of the hominoid fossil record. For instance, tackling the always difficult question of homology vs homoplasy requires new perspectives. In fact, the studies of the patterns of integration in extant hominoids, combined with studies of covariation across vertebrae and analyses of the patterns of allometry, may well shed light on this issue. In another example of the work left to be done, we also need more information regarding extant locomotion and its relationship to the morphology (shape, orientation, trabecular organization) of the vertebral bodies in extant hominoids compared to cercopithecoids, in order to infer locomotion patterns in fossil hominoids. Another promising and important area is the implication of erect posture and bipedalism to paleopathology of the spine and to modern human spinal disease and back pain. Our hope is that this volume will serve as a foundation upon which all of these new studies—and many others—will be designed.

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Chapter 2

The Hominoid Cranial Base in Relation to Posture and Locomotion



Gabrielle A. Russo and E. Christopher Kirk

2.1 Introduction

A quick glance at the cover and title of this book promises the reader that it reviews the anatomy and evolution of the hominoid spine. The reader may therefore ask: why does this chapter focus on the *head*? In our view, there are two main reasons to introduce a book on the evolutionary anatomy of the hominoid spine with a chapter on the head. The most obvious answer is that in all vertebrates the head is directly connected to the rest of the body via the spine. The cranial base articulates with the cervical vertebral column, which initially evolved in early tetrapods to allow the head to move independently of the rest of the body (Romer 1950). In modern humans the cervical vertebral column has been modified to allow movements of the head atop an upright torso, rather than in front of the torso as in quadrupedal chimpanzees and most other primates and mammals (Lieberman 2011). Given this unusual positional relationship between the head and the rest of the body in modern humans, extensive research has been dedicated to documenting and understanding the biomechanical interactions between the cranial base and the rest of the axial skeleton among hominoids. The second answer, which is a primary driver behind biological anthropologists' motivation to conduct the aforementioned research, is that cranial anatomy plays a key role in interpreting the primate and human fossil record. Researchers have long appreciated our ability to make phylogenetically and functionally relevant inferences about aspects of postcranial anatomy using clues

G. A. Russo (✉)

Department of Anthropology, Stony Brook University, Stony Brook, NY, USA

e-mail: gabrielle.russo@stonybrook.edu

E. C. Kirk (✉)

Department of Anthropology, University of Texas at Austin, Austin, TX, USA

Jackson School Museum of Earth History, University of Texas at Austin, Austin, TX, USA

e-mail: eckirk@austin.utexas.edu

gleaned from the cranial base, which is particularly important in the absence of direct fossil evidence of the postcranial skeleton. As we will discuss below, cranial base anatomy has historically played a key role in interpreting the postural and locomotor adaptations of some early hominin taxa (e.g., Dart 1925; White et al. 1994; Brunet et al. 2002). With these two answers in mind, in this chapter we focus on the relationship between cranial base morphology, posture, and locomotion in the Hominoidea.

2.2 What Is the Cranial Base?

The cranial base is the region of the skull that intervenes between the bones of the face (splanchnocranium/viscerocranium) and the cranial vault (calvaria). The cranial base forms the floor of the braincase (neurocranium) and supports the inferior surface of the brain. In hominoids, the cranial base is primarily formed by the ethmoid, orbital plates of the frontal, sphenoid, right and left temporals, and occipital (excluding the planum occipitale). The majority of the cranial base develops from multiple centers of ossification that appear early in fetal development within the chondrocranium. The chondrocranium itself is formed via the fusion of multiple smaller cartilages, which grow to surround many of the neurovascular structures that pass between the neck and the interior of the developing braincase. As a result, the adult bones of the cranial base that are derived at least partly from the chondrocranium (ethmoid, sphenoid, temporal, and occipital) contain numerous foramina that transmit major nerves (e.g., the cranial nerves and spinal cord) and vessels (e.g., the internal carotid artery and internal jugular vein). However, several sections of the cranial base are not derived from the chondrocranium and instead develop via intramembranous ossification. These intramembranous parts of the adult cranial base include the orbital plates of the frontal, the squamous portions of the temporals, and the pterygoid and alisphenoid portions of the sphenoid. Superiorly, the bony elements of the cranial base form fossae that accommodate key intracranial structures, including the frontal lobes and olfactory bulbs within the anterior cranial fossa, the temporal lobes within the middle cranial fossae, the pituitary gland within the hypophyseal fossa, and the cerebellum, pons, and medulla within the posterior cranial fossa (Lieberman et al. 2000; Scheuer and Black 2001).

As the bony interface between anatomical structures of the face, neck, and braincase, the cranial base provides a rich source of information about an organism's adaptations and evolutionary history. Accordingly, the morphology of the cranial base may be influenced by selection acting on many different variables, such as brain size, the anatomy of the masticatory apparatus, trunk and/or neck posture, and locomotion. Because the literature on the hominoid basicranium is quite extensive (e.g., Bolk 1909; Weidenreich 1941; Ashton and Zuckerman 1952, 1956; Biegert 1957, 1963; Demes 1985; Lieberman et al. 2000; Ross and Ravosa 1993; Russo and Kirk 2013, 2017; Neaux et al. 2017, 2018; Villamil 2017), in this chapter we primarily focus on those portions of the posterior cranial base that are most closely associated



Fig. 2.1 Inferior views of the crania of *Pan troglodytes* (left, FMNH 18406), *Homo sapiens* (middle), and *Gorilla gorilla* (right, AMNH 167236). Occipital condyles highlighted in red; FM = foramen magnum; blue asterisk = tip of mastoid process. Specimens oriented in the Frankfort horizontal and scaled to the same approximate anteroposterior length

with the cervical spine and related structures in the neck. In this context, we identify these relevant features of the cranial base as the (1) foramen magnum, which transmits the spinal cord from the braincase to the vertebral canal formed by the subjacent vertebrae; (2) occipital condyles, which form the bony articulation with the first cervical vertebra (i.e., the atlas); and (3) adjacent portions of the occipital and temporal bones that provide attachment sites for major muscles involved in head movements relative to the trunk (Fig. 2.1). For clarity, we henceforth refer to these components of the cranial base as the “cranio-cervical interface.” Although our focus is on the morphology of these specific structures among hominoids, we will necessarily provide some discussion about how the cranio-cervical interface relates to other cephalic structures because the cranium as a whole is integrated (Lieberman et al. 2000; Strait 2001).

From a simplified biomechanical perspective, the cranio-cervical interface lies at the center of the first-class lever system primarily responsible for flexion and extension of the head relative to the cervical spine (Şenyürek 1938; Schultz 1942; Demes 1985). The atlanto-occipital joint is formed by the occipital condyles, located immediately lateral to the foramen magnum, and the superior articular facets (prezygopophyses) of the atlas. A point midway between the centers of the occipital condyles represents the “axis/fulcrum” of this joint, the portion of the cranium anterior to the atlanto-occipital joint represents the “resistance/load,” and the nuchal musculature (and passive nuchal ligaments) positioned posterior to the joint represents the “force/effort” (Şenyürek 1938; Schultz 1942; Demes 1985). The anterior projection (i.e., resistance/load arm or out-lever) and weight (i.e., the actual resistance/load or out-force) of the facial skeleton are thus offset by the posterior projection of the neurocranium (i.e., force/effort arm or in-lever), and the force of the nuchal musculature (i.e., muscular effort or in-force) preserves neutral head posture

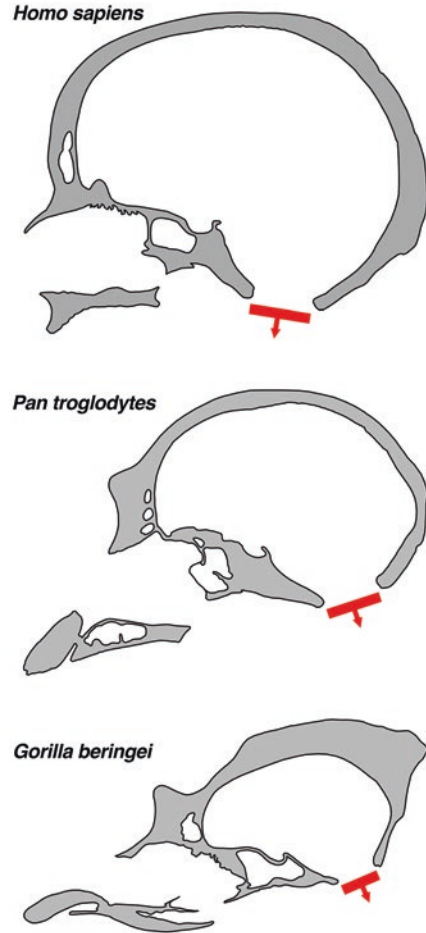
(i.e., maintains equilibrium) (Şenyürek 1938; Schultz 1942; Adams and Moore 1975). Because the heads of great apes have more mass located anterior to the occipital condyles than posterior to the occipital condyles (i.e., greater resistance and longer resistance arm), a large amount of effort from the neck muscles and/or bony modifications that affect the length of their force arm (e.g., spinous processes) are required to keep the head upright and level (Schultz 1942). In contrast to great apes, modern humans have a relatively smaller face (i.e., less resistance) and a more centrally located atlanto-occipital joint (i.e., shorter resistance arm), and thus less muscular effort is required to keep the head upright and level.

2.3 Foramen Magnum

The foramen magnum is the “great hole” of the occipital bone through which (1) the spinal cord exits the braincase and passes into the vertebral canal and (2) the vertebral arteries enter the braincase. The foramen magnum, along with the occipital condyles, provides a direct osteological marker of where (and to some extent how) the cervical vertebral column articulates with the head. In anatomical position, the human head is positioned superior to the torso and the head’s rostro-caudal axis is essentially perpendicular to the long axis of the vertebral column. By contrast, when standing quadrupedally, the head of a chimpanzee or gorilla is positioned anterior to the torso as in most other mammals. Accordingly, a more anterior position of the foramen magnum along the midline axis of the cranial base has traditionally been linked to habitual postures in which the head is located superior to the trunk, whereas a more posterior position of the foramen magnum on the cranial base has been thought to reflect habitual postures in which the head is located more anteriorly relative to the trunk. That humans have a more anteriorly positioned foramen magnum than African apes (Figs. 2.1 and 2.2) is a distinction first observed in the mid-eighteenth century (Daubenton 1764). Most comparative research published since that time overwhelmingly favors the conclusion that the foramen magnum is more anteriorly positioned in humans than in any other living primate species (Broca 1872; Topinard 1890; Bolk 1909; Dart 1925; Dean and Wood 1981, 1982; Luboga and Wood 1990; Schaefer 1999; Ahern 2005; Russo and Kirk 2013, 2017; Russo et al. 2016; Neaux et al. 2017).

Foramen magnum position has been quantified as the anteroposterior position of basion (the anterior-most margin of the foramen magnum at midline) relative to select cranial dimensions, such as cranial length (Dart 1925). Basion position has also been assessed relative to a variety of more anteriorly placed cranial landmarks or their derivatives, including the bicarotid chord (White et al. 1994; Schaefer 1999; Ahern 2005; Suwa et al. 2009; Kimbel et al. 2014), the bitympanic and bicauricular chords (Dean and Wood 1981, 1982), the biporion chord (Ahern 2005), foramen cecum, subnasale, and glabella (Luboga and Wood 1990), and the distal-most molar, posterior hard palate, anterior margin of the temporal fossa, and sphenoccipital sychondrosis (Russo and Kirk 2013, 2017; Neaux et al. 2017). Several studies

Fig. 2.2 Sagittal sections through the crania of *Homo sapiens* (top), *Pan troglodytes* (middle, USNM 395820), and *Gorilla beringei* (bottom, USNM 395636). Position and orientation of the foramen magnum indicated for each specimen by a red bar and arrow. Specimens oriented in the Frankfort horizontal and scaled to the same approximate anteroposterior length



(e.g., Weidenreich 1943; Kimbel et al. 2004; see also Russo and Kirk 2017) defined the position of the foramen magnum using opisthion (the posterior-most point on the margin of the foramen magnum at midline) rather than basion, quantifying foramen magnum position as the distance from opisthion to the posterior-most extent of the cranial vault divided by cranial length (i.e., the “Weidenreich index”; Kimbel et al. 2004). Analyses using anteriorly located landmarks as reference points for quantifying basion position have generated mixed results with varying degrees of success in distinguishing between bipedal humans and non-bipedal primates (see Russo and Kirk 2013 for a review). For example, the utility of the biporion chord for assessing relative basion position has been questioned due to its poor performance in discriminating among extant or extinct hominoids (Dean and Wood 1981; Luboga and Wood 1990; Ahern 2005). By comparison, the position of basion relative to the bicarotid chord has been used more widely and generally indicates a more forward

position of the foramen magnum in modern humans and extinct hominins compared to African apes (Schaefer 1999; Ahern 2005; Kimbel et al. 2014). The position of basion relative to the distal-most molar, the posterior edge of the bony palate at midline, the anterior-most margin of the temporal fossa, and the spheno-occipital synchondrosis also distinguishes humans from other extant hominoids (Russo and Kirk 2013, 2017; Neaux et al. 2017). However, it should be noted that the use of the spheno-occipital synchondrosis as a reference point for assessing basion position also reflects basioccipital length (the distance from basion to sphenobasion; Russo and Kirk 2017). By the same token, the use of the distal-most molars, posterior hard palate, and anterior temporal fossae to quantify relative basion position may be complicated by selection acting on the morphology of the facial skeleton and masticatory apparatus (Ruth et al. 2016; Russo and Kirk 2013, 2017; Neaux et al. 2017). Similarly, analyses that rely on the use of landmarks posterior to opisthion are evidently strongly influenced by the differences between modern humans and other extant hominoids in the posterior projection of the braincase as a result of neurocranial expansion in humans (Kimbel et al. 2004; Russo and Kirk 2017) (see below for further discussion).

While most researchers have linked the distinctive position of the foramen magnum in modern humans to habitual bipedalism, an anteriorly positioned foramen magnum has also been suggested to reflect upright (i.e., orthograde) trunk posture more generally (Kimbel and Rak 2010). In either scenario, the commonly accepted functional explanation is that a more anteroposteriorly “centered” foramen magnum along the cranial base midline in modern humans permits the head to sit atop an upright spine with minimal muscular effort (Şenyürek 1938; Schultz 1942, 1955). The relationship between an anteriorly positioned foramen magnum and bipedal locomotion receives support from comparative research demonstrating that bipedal marsupials and rodents resemble humans in possessing more anteriorly positioned foramina magna and shorter basioccipitals than their quadrupedal close relatives (Russo and Kirk 2013, 2017). In fact, the available comparative evidence indicates that anterior migration of the foramen magnum has evolved in concert with bipedalism (both striding and saltatory) in at least five mammalian clades: the Homiinae, Macropodidae, Dipodidae, Heteromyidae, and Pedetidae (Russo and Kirk 2013, 2017). The hypothesis that orthograde trunk posture (rather than bipedal locomotion per se) influences foramen magnum position (Kimbel and Rak 2010) also receives some support because strepsirrhine primates known to employ orthograde positional behaviors (e.g., vertical clingers and leapers like *Propithecus* and *Lepilemur*) exhibit more anteriorly positioned foramina magna than non-orthograde strepsirrhine primates (Russo and Kirk 2013).

The apparent relationship between an anteriorly positioned foramen magnum and bipedal locomotion in extant hominoids has been used by paleoanthropologists as a basis for inferring bipedalism, and thus hominin status, in the human fossil record. The utility of the foramen magnum as an indicator of upright posture and bipedalism in fossil hominins was initially noted by Raymond Dart (1925) in his description of the “Taung child,” the juvenile holotype specimen of *Australopithecus africanus*. Dart (1925) surmised that the anteriorly shifted foramen magnum of *Au.*

africanus (in comparison to a sample of baboons, chimpanzees, and modern humans) “points to the assumption by this fossil group of an attitude appreciably more erect...The improved poise of the head, and the better posture of the whole-body framework which accompanied this alteration in the angle at which its dominant member was supported, is of great significance. It means that a greater reliance was being placed by this group on the feet as organs of progression” (197). Since this report, the anterior position of the foramen magnum has been cited numerous times as morphological evidence of bipedal locomotion in putative hominins, including the Mio-Pliocene genera *Sahelanthropus* and *Ardipithecus* (e.g., Le Gros Clark 1954; Dean and Wood 1982; White et al. 1994; Brunet et al. 2002; Guy et al. 2005; Suwa et al. 2009; White et al. 2009). As a result, an anteriorly positioned foramen magnum is a commonly cited synapomorphy of hominins (e.g., White et al. 1994; Guy et al. 2005; Zollikofer et al. 2005; Kimbel et al. 2014).

In addition to differences in the anteroposterior *position* of the foramen magnum, extant hominoids also differ in the anteroinferior *inclination* of the foramen magnum (Fig. 2.2). This latter aspect of foramen magnum morphology is variously referred to as “foramen magnum orientation” (Kimbel et al. 2004; Pickford 2005; Been et al. 2014; Russo and Kirk 2017), “foramen magnum angle” (Ruth et al. 2016), “foramen magnum – orbital plane angle” (Strait and Ross 1999; Wolpoff et al. 2002; Zollikofer and Ponce de León 2005), and “inclination of occipital foramen” (Weidenreich 1943), depending on the authors and/or their choice of reference planes. The plane of the foramen magnum is defined by a chord connecting basion and opisthion. Foramen magnum orientation is typically quantified as the angle between this basion-opisthion chord and a reference plane projected into the midsagittal plane, such as the Frankfort horizontal (drawn through orbitale and porion when the cranium is viewed in *norma lateralis*) (but see Strait and Ross 1999). Previous analyses have shown that the modern human foramen magnum is distinctly anteroinferiorly oriented rather than posteroinferiorly oriented as in great apes (Daubenton 1764; Broca 1877; Bolk 1910; Luboga and Wood 1990; Pickford 2005; Zollikofer et al. 2005; Russo and Kirk 2017). In other words, although all hominoids possess foramina magna that face inferiorly to some extent, the foramina of humans are more anteriorly facing, while those of apes (and many other mammals) are more posteriorly facing (Fig. 2.2). A link between this derived foramen magnum orientation in humans and more vertical human-like neck and trunk postures is intuitively appealing and is also supported by research demonstrating a relationship between foramen magnum orientation and total cervical lordosis in intraspecific samples of modern humans (Been et al. 2014). However, the orientation of the foramen magnum relative to the orbital axis (an alternative reference plane to the Frankfort horizontal [Strait and Ross 1999]) in humans is similar to that of a wide range of other anthropoid taxa with very different neck postures (Lieberman et al. 2000). Foramen magnum orientation is also not correlated with measures of neck posture among non-human primates (Lieberman et al. 2000), suggesting that the orientation of the foramen magnum is a poor indicator of the orientation of the cervical vertebral column in interspecific samples. By extension, foramen magnum orientation is probably also a poor indicator of trunk posture. Comparisons among