

Chapter 2

The Hominoid Cranial Base in Relation to Posture and Locomotion



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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

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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

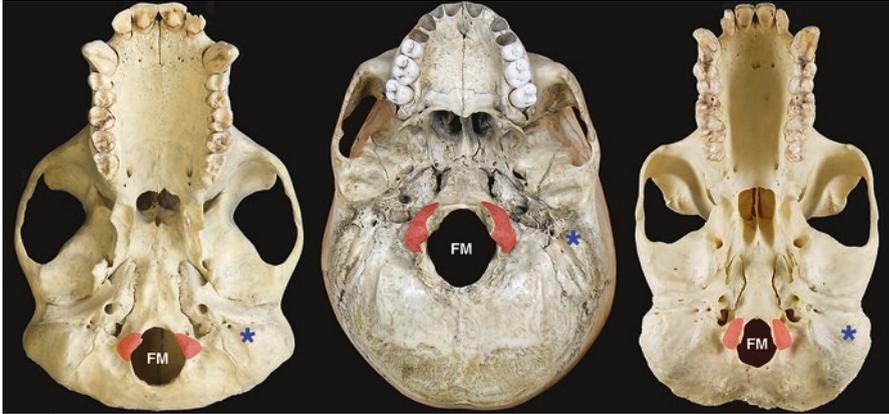


Fig. 2.1 Inferior views of the crania of *Pan troglodytes* (left, FMNH 18406), *Homo sapiens* (middle), and *Gorilla gorilla* (right, AMNH 167236). Occipital condyles highlighted in red; FM = foramen magnum; blue asterisk = tip of mastoid process. Specimens oriented in the Frankfort horizontal and scaled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

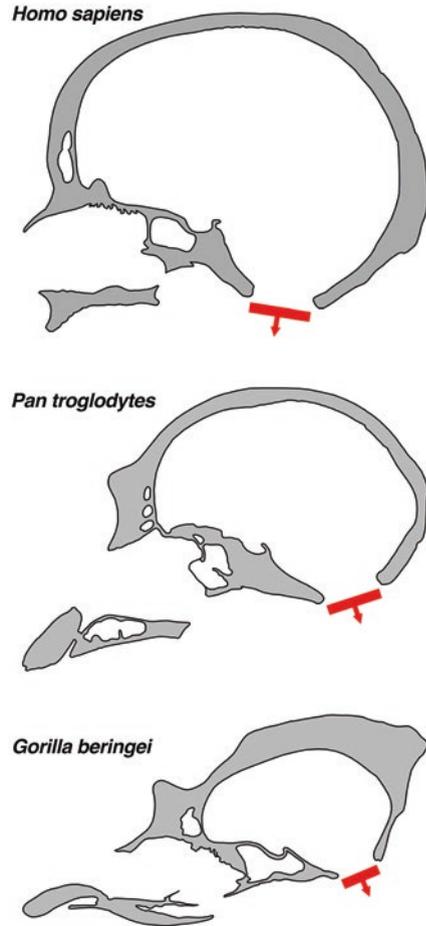
(i.e., maintains equilibrium) (Şenyürek 1938; Schultz 1942; Adams and Moore 1975). Because the heads of great apes have more mass located anterior to the occipital condyles than posterior to the occipital condyles (i.e., greater resistance and longer resistance arm), a large amount of effort from the 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 biauricular 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 spheno-occipital 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

great apes reveal that *Pongo* does not have a more anteriorly inclined foramen magnum (or occipital condyles) than the African apes, despite its greater reliance on orthograde trunk postures (Moore et al. 1973).

While differences in foramen magnum position and orientation between humans and other extant hominoids are readily apparent, the relationship, if any, between these two aspects of foramen magnum morphology is not clear, particularly when comparative samples are expanded to include other extant primates and mammals. Bolk (1909, 1910) speculated that foramen magnum position and orientation are linked, and some researchers have even employed foramen magnum orientation as a proxy for foramen magnum position (Ruth et al. 2016). However, a direct analysis of the relationship between these two variables in hominoids and various other mammalian clades demonstrates that foramen magnum orientation is at most only weakly correlated with foramen magnum position (Russo and Kirk 2017). Furthermore, reports that some *Australopithecus* specimens appear to exhibit human-like foramen magnum positions but more chimpanzee-like foramen magnum orientations (Kimbel and Rak 2010) indicate that foramen magnum position and orientation are not tightly coupled and may have been influenced by different selective forces during the course of hominin evolution.

Finally, as mentioned above, both foramen magnum position and orientation are likely influenced by factors other than posture and locomotion. Compared to other hominoids, humans exhibit a number of derived cephalic features (e.g., an enormously enlarged brain and neurocranium, a shortened rostrum, and a reduced size of the masticatory apparatus) that have been suggested to play a role in determining basicranial morphology. Indeed, a probable influence of brain size on foramen magnum morphology in hominoids has been recognized for nearly as long as foramen magnum morphology has been invoked to predict posture and locomotion (e.g., Bolk 1909; Le Gros Clark 1934; Weidenreich 1941; Ashton 1957; Biegert 1957, 1963). These early researchers hypothesized that increased encephalization was responsible for the pronounced basicranial flexion that distinguishes modern humans from other extant hominoids. In this evolutionary scenario, increases in brain size in hominins caused a downward rotation of the posterior cranial base relative to the facial skeleton, resulting in increased cranial base flexion (Fig. 2.2). As the cranial base became more flexed in hominins, the nuchal region deflected from a more vertical to a more horizontal orientation and the position of the foramen magnum shifted anteriorly (Biegert 1957, 1963; see also Bastir et al. 2010). Ontogenetic studies have demonstrated that the foramen magnum and occipital condyles migrate posteriorly in great apes but remain more anteriorly situated in humans during growth (Ashton and Zuckerman 1952; Schultz 1955; Ashton and Zuckerman 1956). These observations may support a link between increased basicranial flexion and increased encephalization if ontogenetic increases in brain size prevent posterior migration of the foramen magnum in humans (Ashton and Zuckerman 1952, 1956; Schultz 1955). However, other researchers have speculated that it is the acquisition of bipedal posture and locomotion that prevents posterior migration of the foramen magnum in humans (Bolk 1915). By the same token, the formation of a well-developed nuchal plane of the occipital bone as an insertion site

for the nuchal musculature during ontogeny may be tied to the more posteriorly facing foramina magna of great apes and possibly *Australopithecus* (Kimbel et al. 2004). Interspecific studies of primates and other mammals reveal that some metrics of brain size (i.e., encephalization ratio, index of relative encephalization) appear related to foramen magnum orientation (Spoor 1997; Ruth et al. 2016), while other metrics of brain size (i.e., encephalization quotient) have either a weak or nonexistent relationship with foramen magnum orientation (Russo and Kirk 2017). Although such disparate results may be attributable to a number of factors (e.g., the use or lack of phylogenetic methods), it is clear that the choice of metrics for quantifying (1) relative brain size, (2) foramen magnum orientation, and (3) foramen magnum position has a major impact on the outcome of any analysis (Russo and Kirk 2017). A similar conclusion applies to the proposed relationship between brain size and basicranial flexion, which differs according to the primate clade being considered and the metrics used to quantify basicranial flexion and relative brain size (Ross and Ravosa 1993; Ross and Henneberg 1995; Spoor 1997; Strait and Ross 1999; Lieberman et al. 2000; McCarthy 2001). Facial size either alone or considered in conjunction with brain size has also been suggested to influence basicranial anatomy in primates and other mammals (e.g., Huxley 1863; Weidenreich 1941; Biegert 1963; Ross and Ravosa 1993; Bastir et al. 2010; Ruth et al. 2016; Russo and Kirk 2017; Villamil 2017). In this scenario, smaller faces are presumably linked with more flexed basicrania and thus more anteriorly shifted cranial base structures including the foramen magnum (e.g., as in humans), whereas larger faces are linked with less flexed basicranial and thus more posteriorly shifted cranial base structures (e.g., as in great apes). However, like brain size, the results of any analysis of the relationship between foramen magnum morphology and facial size will be strongly influenced by metric choice and comparative sample composition (e.g., see results for marsupials by Russo and Kirk (2017) and Villamil (2017)).

2.4 Occipital Condyles

The occipital condyles represent the sole bony connection between the head and the rest of the axial skeleton. As noted above, the occipital condyles are paired structures located on either side of the foramen magnum that articulate with the prezygapophyses of the atlas and form the fulcrum of the atlanto-occipital joint (Schultz 1942, 1955) (Fig. 2.1). Early observations of the cranio-cervical interface recognized the utility of the occipital condyles as landmarks for determining how the head is “balanced” on the torso (e.g., Bolk 1909; Schultz 1917, 1942, 1955; Broom 1938; Şenyürek 1938; ; Le Gros Clark 1950; Moore et al. 1973). As a result, many of these papers devised methods for measuring the relative lengths and sizes of pre- and post- condylar head “segments” using indices in order to model the atlanto-occipital lever system. For example, Şenyürek (1938) divided the distance between a point in the middle of the occipital condyle articular surface and prosthion by the prosthion-opisthocranium chord in his calculation of a “cranial equilibrium index.”

He concluded that the lower index observed for humans compared to other primates meant the condyles were more anteriorly situated, providing enhanced mechanical advantage in bipedal postures. Schultz (1942) (see also Schultz 1917) expanded on this work by operationalizing the head-neck lever system using an apparatus that allowed him to calculate the actual weights of the pre- and post-condylar segments¹ of the head from cadaveric specimens. Schultz (1942) concluded that modern humans exert considerably less muscular force (~16% of head weight) to “balance” the head atop the neck compared to other primates (~37% of head weight on average). These early comparative studies of extant primates generally agree that the more anteriorly positioned occipital condyles in modern humans confer an advantage compared to other primates for “balancing” the head atop an upright spine.

Researchers focused on interpreting hominin basicranial anatomy have expanded on these analyses and invoked the position of the occipital condyles as an indication of head and neck posture in extinct hominins. Le Gros Clark (1950) calculated a “condylar position index” as the distance from the center of the occipital condyle to the posterior cranial vault, divided by the distance from the center of the occipital condyle to prosthion $\times 100$. Using this metric, he found that *Au. africanus* (represented by the adult specimen STS 5) exhibited occipital condyles more similar to modern humans and other extinct hominins than to most extant nonhuman hominoids. Le Gros Clark (1950) therefore concluded that the “bodily posture” of *Au. africanus* was similar to bipedal hominins (246). However, other studies of the STS 5 cranium using the same metric and expanded anthropoid samples found that occipital condyle position in *Au. africanus* is either more similar to African apes than to modern humans or is intermediate between the two groups (Ashton and Zuckerman 1951; Adams and Moore 1975). This later research therefore suggests that skull “balance” in *Au. africanus* was unlike modern humans despite the shared adoption of bipedal postures and locomotion. Such a finding seems consistent with the clear differences in cranial architecture between *Homo* and *Australopithecus* that would be expected to influence the biomechanics of the atlanto-occipital joint, including facial size and robusticity, rostral length, masticatory apparatus size, and brain size (Kimbel et al. 2004).

In addition to investigations of the anteroposterior position of the occipital condyles along the cranial base, the angle of condylar articular surfaces and the inferior projection of the occipital condyles have also been examined for their utility in assessing the head postures of extant hominoids and fossil hominins (Moore et al. 1973; Adams and Moore 1975; Kimbel et al. 2004). The angle of condylar articular surfaces, measured as a chord connecting the anterior- and posterior-most points on the articular surface, is generally quantified relative to the Frankfort horizontal. This metric (“condylar angle”) has been presumed to reflect the orientation of the cervical vertebral column and direction of associated muscular forces relative to the cranial base (Moore et al. 1973; Demes 1985). Like the anteroposterior position of the occipital condyles, condylar angle distinguishes modern humans from other extant

¹Schultz’s (1942) study differed from that of Şenyürek (1938) by substituting the inferior-most point on the condyle for the middle of the condyle and by substituting inion for opisthocranium.

hominoids (Knese 1948 as cited in Demes 1985; Moore et al. 1973; Adams and Moore 1975). In modern humans, the articular surfaces of the occipital condyles face more ventrally than in great apes. As a result, for the presumed head/neck postures most often adopted by hominoids (i.e., more vertical in modern humans and more horizontal in great apes), reaction forces occur perpendicular to the joint surfaces (Demes 1982, 1985). These observations may also be extended to *Australopithecus*, which can be readily discriminated from African apes by its more human-like condylar angle (Moore et al. 1973; Adams and Moore 1975). This observation for condylar angle is interesting given that foramen magnum orientation, which would seemingly be linked with condylar angle, does not distinguish *Australopithecus* from African apes to the same extent (Kimbel and Rak 2010). In addition to occipital condyle angle, Kimbel et al. (2004:101) noted that, when viewed posteriorly, the occipital condyles and supramastoid crest of *Pan* form a “continuous arched outline” such that the occipital condyles project more inferiorly relative to more lateral structures in the basicranium. In *Au. afarensis*, by comparison, the mastoid region is more clearly delineated from the occipital condyles (which are invaginated into the cranial base) and the rest of the cranial base by the mastoid processes (Kimbel et al. 2004). The functional implications (if any) of this configuration are poorly understood but might be related to differing patterns of pneumatization of the temporal bone (see below).

Other than their general topographic position, little is known about the morphology of the occipital condylar articular surfaces themselves. At least one worker has noted the concordance between the areas of the occipital condyle articular surfaces and body size (Martin 1980). Much more is likely to be learned from detailed analyses of the size and shape of the occipital condyles (Coroner and Latimer 1991; Nishimura et al. 2017) and/or their inferred morphology as mirrored in the subjacent prezygapophyses of the atlas (Gommery 1996; Manfreda et al. 2006; Nalley and Grider-Potter 2017). Because the occipital condyles articulate directly with the prezygapophyses of the atlas, researchers have focused on what might be revealed from investigations of occipital condyle shape in relation to potential movements at the atlanto-occipital joint. The primary movements at this joint are sagittal plane flexion and extension (i.e., pitch) (Lopez et al. 2015). However, the articulation between the atlas and subjacent second cervical vertebra (the axis) also allows for rotational movements (i.e., yaw) such that, together, a great deal of mobility can be achieved at this bony junction of the cranio-cervical interface. Coroner and Latimer (1991) collected direct tracings of both the occipital condyles and the reciprocal facets of the atlas and determined that the atlanto-occipital joint could be modeled as two curves—an anterior curve and a posterior curve—with great apes exhibiting more acutely angled articular profiles compared to modern humans. Gommery (1996) identified distinct aspects of the prezygapophyseal articular surfaces of C1 that correspond to the occipital condyles, noting the greatest variation among a sample of strepsirrhines, platyrrhines, cercopithecoids, and hominoids in the retroglenoid tubercle,² which could hypothetically serve to restrict or permit movements

²Gommery (1996) refers to the prezygapophyses of the atlas as the “glenoid cavities,” so in this sense, a retroglenoid tubercle is a bony extension of the dorsal curve of the atlas’ prezygapophysis.

at the atlanto-occipital joint. With respect to the curvature of the articular surfaces, a number of workers have noted that modern humans exhibit flatter prezygapophyses of the first cervical vertebra compared to other hominoids, which exhibit more deeply dorsoventrally concave prezygapophyses (Dickman et al. 1994; Manfreda et al. 2006; Nalley and Grider-Potter 2017). A relationship between occipital condyle morphology and locomotion in an expanded primate sample has been documented by Nishimura et al. (2017), who noted subtle differences in occipital condylar morphology among suspensory and arboreal and terrestrial quadrupeds. Together, the singular and more gently curved articular profile shapes and flatter articular surfaces of the occipital condyles in modern humans are interpreted to permit movement in a greater number of directions at the atlanto-occipital joint (Coroner and Latimer 1991). In contrast, the more acutely curved articular profile shapes and dorsoventrally deeper condylar articular surfaces of hominoids and many other primates (e.g., baboons) are interpreted to provide resistance to ventral translation of the head on the neck. This configuration may be necessitated by the fact that quadrupeds typically hold their heads (which have a center of gravity that sits below the occipital condyles; Demes 1985) in front of a more horizontally oriented torso. The relationship between neck posture and occipital condyle curvature is also supported by research showing that occipital condyle curvature increases as neck inclination angle (Ross and Ravosa 1993) increases (i.e., as necks become increasingly horizontal) (Nalley and Grider-Potter 2017).

2.5 Additional Structures of the Cranio-cervical Interface

Immediately adjacent to the foramen magnum and occipital condyles on the posterior cranial base are the insertion sites of the muscles that move the head relative to the rest of the body. The anterior migration of the foramen magnum/occipital condyles and attendant shortening of the basioccipital noted above for modern humans has important consequences for the insertion sites of the prevertebral muscles (Dean 1984, 1985). In great apes, the *mm. rectus capitis anterior*, which originate from C1 and C2, insert on the basioccipital immediately anterior to the foramen magnum and are closely approximated near the midline (Dean 1985). In humans however, the *mm. rectus capitis anterior* have more laterally positioned insertion sites immediately anterior to the occipital condyles, with a large space intervening between their medial borders (Dean 1984; Standring 2016). Perhaps of greater functional consequence is the fact that the *m. longus capitis*, which originates on C3–C6 and inserts on the basioccipital anterior to the *m. rectus capitis anterior*, has a much smaller and anteroposteriorly shortened insertion site in humans compared to great apes (Dean 1985). This difference could conceivably be the simple consequence of basioccipital shortening in humans and an associated decrease in the area available for muscular attachment. However, because the *m. longus capitis* is a powerful head flexor,

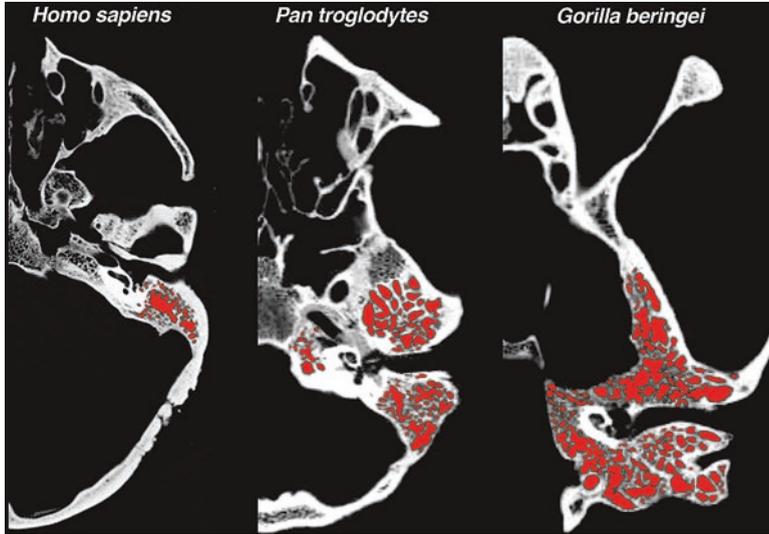


Fig. 2.3 Transverse sections through the crania of *Homo sapiens* (left), *Pan troglodytes* (middle, USNM 395820), and *Gorilla beringei* (right, USNM 395636). Pneumatic spaces of the temporal bone are shown in red. Images scaled to the same approximate anteroposterior length. The plane of each section intersects the cochlear labyrinth and external acoustic meatus, but note that the plane of sectioning for *Gorilla* is more obliquely inclined

it also seems likely that differences between great apes and humans in the size and mechanical advantage of the m. longus capitis could also be related to differences in the use of the canine teeth (sensu Dean 1984). In great apes, the canines are large and projecting and are frequently used in contests between individuals over access to mates and resources (Plavcan et al. 2012). Fighting with canines would seem to require, inter alia, the ability to powerfully flex the head in order to drive the projecting maxillary canines into the body of an opponent.³ Modern humans, which possess incisiform canines, may be less reliant than great apes on having a large m. longus capitis because humans no longer rely on large canines for exchanging visually mediated threats or for fighting.

The bony structure of the posterior basicranium lateral to the foramen magnum and occipital condyles also differs substantially between humans and great apes. These differences partly reflect the degree of temporal bone pneumatization, which is far more extensive in African apes than in humans (Fig. 2.3; Sherwood 1999). In all great apes, the mastoid region of the temporal bone has a mastoid process that projects only a modest distance inferiorly (Lockwood et al. 2002) and lacks a groove for the origin of the posterior belly of the digastric on its medial surface (Dean 1984). Lateral to the apex of the mastoid process is a large roughened entheses marking the

³ Indeed, as noted by Dean (1984) saber toothed cats may require large m. longus capitis in order to employ their maxillary canines during predation.

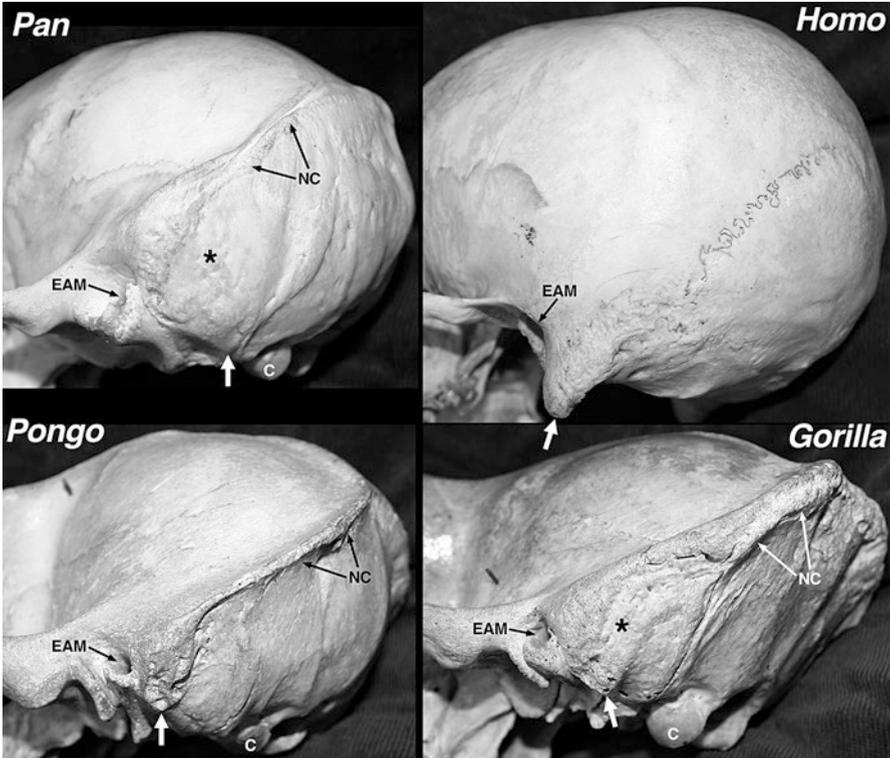


Fig. 2.4 Crania of great apes and humans in posterolateral view. Large white arrow = apex of mastoid process; asterisk = laterally projecting and extensively pneumatized mastoid region of African apes; C = occipital condyle; EAM = external acoustic meatus; NC = nuchal crest. Images not to scale. Occipital condyles of *Homo* not visible in this view due to their anteriorly shifted position. The prominent roughened entheses adjacent to the asterisks in *Pan* and *Gorilla* include the sites of origin of the m. sternocleidomastoid and m. splenius capitis (Dean 1984)

site of origin for the m. sternocleidomastoid (Fig. 2.4). This enthesis terminates superiorly at the nuchal crest,⁴ immediately posterior to the external acoustic meatus. Although the mastoid process does not project far inferiorly, the entire mastoid region of great apes projects further laterally than in modern humans (Figs. 2.1, 2.4, 2.5). This extensive lateral projection of the mastoid region and anterior nuchal crest in great apes is the direct result of pneumatization of the posterolateral temporal bone (Fig. 2.5). Medial to the m. sternocleidomastoid, muscles originating from the pneumatized mastoid region of African apes include the anterior portion of the m. splenius capitis, the m. longissimus capitis, and the posterior belly of the m. digastric (Dean 1984).

⁴Note that the nuchal and supramastoid crests are confluent structures in extant great apes.

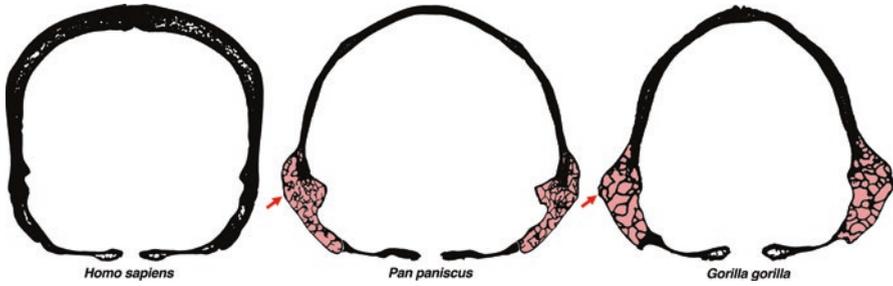


Fig. 2.5 Coronal sections through the neurocrania of *Homo sapiens* (left), *Pan paniscus* (middle, MCZ 38019), and *Gorilla gorilla* (right, MCZ 14750). The plane of each section intersects the posterior-most foramen magnum, immediately anterior to opisthion. Posterior pneumatic spaces of the temporal bone in apes are shown in pink. Specimens scaled to the same approximate supero-inferior height. Red arrows unilaterally mark the inferior margin of the nuchal crest in apes. The muscles originating from the pneumatized portions of the mastoid shown in these sections include the m. sternocleidomastoid and the m. splenius capitis (Dean 1984)

In modern humans, the mastoid process projects further inferiorly than in great apes (Lockwood et al. 2002; Fig. 2.4), and the posterior belly of the m. digastric originates from a bony groove adjacent to the medial surface of the process (Dean 1984). As in great apes, the human m. rectus capitis lateralis lies immediately lateral to the occipital condyles, suggesting that the site of origin for this muscle has migrated anteriorly with the condyles and foramen magnum. As a result, the human m. rectus capitis lateralis is positioned anteromedial to the origin of the m. digastric rather than medially adjacent to the m. digastric as in apes. The projecting mastoid process of humans is typically pneumatized (Strandring 2016) but modern humans lack the extensive pneumatization of the posterolateral temporal bone seen in great apes (Figs. 2.3 and 2.5).

It is currently unclear to what extent the derived confinement of the m. digastric origin to a mediolaterally narrow digastric groove in modern humans could be related to the evolution of a more projecting mastoid process. However, the evolution of a more inferiorly projecting mastoid process in modern humans may ultimately be tied to differences in the function of the m. sternocleidomastoid, which inserts on the mastoid process. In both apes and humans, the m. sternocleidomastoid plays a key role in rotating the head from side to side (i.e., yaw rotations; Aiello and Dean 1990). However, in apes, which resemble other primate quadrupeds in having more inclined (i.e., obliquely oriented) necks than modern humans (Strait and Ross 1999), the m. sternocleidomastoid runs posteroinferiorly from origin to insertion and passes posterior to the axis of rotation of the atlanto-occipital joint (Aiello and Dean 1990). Accordingly, the ape m. sternocleidomastoid plays a role similar to the nuchal muscles in helping to keep the head elevated. This configuration differs from modern humans, in which the neck is more vertically oriented during bipedal postures (Strait and Ross 1999) and the head is positioned above the torso, so that the m. sternocleidomastoid runs inferiorly and slightly anteriorly and medially from origin to insertion. The human m. sternocleidomastoid thus plays no role in keeping

the head elevated (i.e., head extension), but modern humans presumably require little muscular effort to prevent passive flexion of the head given their smaller more gracile faces and the habitual position of the head above the torso. Inferior projection of the mastoid process may allow the *m. sternocleidomastoid* to play a role in returning the head to a neutral resting position (i.e., head flexion) when the head is already extended (Krantz 1963). This novel ability of the *m. sternocleidomastoid* to flex the head in humans may have been rendered more important by the evident decrease in the importance of the *m. rectus capitis anterior* as a head flexor (Dean 1985).

Posterior to the foramen magnum, the most salient osteological difference between modern humans and great apes concerns the development of the nuchal crest. The prominent nuchal crests of great apes (Fig. 2.4) probably increase the surface area available for the sites of insertion of the nuchal muscles. The nuchal muscles of great apes are massive, and this large size may be necessitated by the relatively posterior position of the occipital condyles and the need to hold up a large and projecting face (Schultz 1942; Adams and Moore 1975; Demes 1985; Aiello and Dean 1990). Both factors increase the load at the atlanto-occipital joint and increase downward torques that would passively flex the head if not compensated by muscular action (Schultz 1942; Lieberman et al. 2000; Demes 1985). Indeed, at least one electromyography study has shown that, in trained macaques, head and neck extensor musculature is more active during quadrupedal and horizontal neck postures than during seated upright and vertical neck postures, presumably in response to gravitational forces that would otherwise flex the head at the atlanto-occipital joint (Choi et al. 2003). Due to expansion of the neurocranium in modern humans, there is evidently ample room available for nuchal muscles to insert on the occipital squama (Dean 1984, 1985; Aiello and Dean 1990). Reduction in the size and anterior projection of the facial skeleton and changes in head and neck posture have also diminished the need for powerful head extensors to hold the head level. As a result, modern humans do not require the large and projecting nuchal crests that are shared by other great apes.

2.6 Summary

Comparative observations of primate basicranial anatomy indicate that evolutionary changes in head, neck, and body posture are associated with corresponding changes in the morphology of the cranio-cervical interface. Within the Hominoidea, modern humans demonstrate a profound reorganization of the cranio-cervical interface that distinguishes them from living apes. This reorganization includes a shift to a more anteriorly positioned and anteroinferiorly oriented foramen magnum, a shift to more anteriorly positioned occipital condyles with flattened articular surfaces, and a reconfiguration of the muscles that move the head relative to the neck and torso. The most significant changes in myology of the cranio-cervical interface include

reductions in the capacity of the *m. longus capitis* and *m. sternocleidomastoid* to flex and extend the head, respectively, and reductions in the size of the nuchal musculature. Shifts in the myology of the cranio-cervical interface are reflected in the bony anatomy of the region, including the evolution of a more inferiorly projecting mastoid process and diminution of the nuchal crest. Comparative and experimental studies suggest that many of these features distinguishing modern humans from living apes are the result of habitual adoption of more orthograde postures associated with bipedal locomotion. As a result, some of the derived features of the human cranial base (e.g., forward shift of the foramen magnum and shortening of the basioccipital) also characterize a variety of fossil hominin taxa.

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