



## The role of allometry and posture in the evolution of the hominin subaxial cervical spine



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### ABSTRACT

Cervical vertebrae not only protect the spinal cord but also are the insertion and origin points for muscles related to the movement of the head, upper limb, and trunk, among others, and are thus important elements in primate evolution. While previous work has been undertaken on the first two cervical vertebrae, there is a dearth of studies on the subaxial cervical spine in hominines. In this paper, we provide detailed morphological information on two important aspects of the subaxial cervical vertebrae (C3 – C7): mid-sagittal morphology and superior facet orientation. We studied large samples of African apes including modern humans and the most complete fossil hominin subaxial cervical vertebrae using both traditional and geometric morphometrics. There are significant differences between extant hominoids related to the relative length and orientation of the spinous process as well as to the orientation of the articular facets, which are related to size, locomotion, and neck posture. In fact, fossil hominins do not completely conform to any of the extant groups. Our assessment of mid-sagittal morphology and superior articular facet orientation shows that australopiths have more *Homo*-like upper subaxial cervical vertebrae coupled with more “primitive” lower cervical vertebrae. Based on these results, we hypothesize that those changes, maybe related to postural changes derived from bipedalism, did not affect the entire subaxial cervical spine at once. From a methodological point of view, the combination of traditional and geometric morphometric data provides a more integrative perspective of morphological change and evolution, which is certainly useful in human evolutionary studies.

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### 1. Introduction

Cervical vertebrae not only protect the spinal cord but also are the attachment sites of muscles related to the movement of the head, upper limb, and trunk. Thus, cervical morphology can potentially provide important information regarding body posture

and locomotion in both extant and fossil primates. Surprisingly, while body posture and locomotion are major subjects of interest in primate evolution (Ankel, 1972; Gebo, 1996; Nakatsukasa et al., 2004; Preuschoft, 2004), the analysis of the postcranial axial skeleton has received less attention than other anatomical parts, such as the long bones. In the last decade, there has been growing interest in the morphology and biomechanics of the primate spine, especially in the lumbar area, with particular interest arising from the study of new fossil hominoid remains (Gommery, 1997, 1998; Ishida et al., 2004; Shapiro et al., 2005; Nakatsukasa et al., 2007; Nakatsukasa, 2008; Kikuchi et al., 2012, 2015; Russo and Shapiro,

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2013). This renewed interest includes new studies on the evolution of the numbers of vertebrae (Haeusler et al., 2002; Pilbeam, 2004; McCollum et al., 2010; Williams, 2012a, b; Williams et al., 2016) and morphological studies on fossil and recent human collections that are improving our knowledge of the evolution of this anatomical region (Been, 2005; Meyer, 2005, 2016; Gómez-Olivencia et al., 2007, 2013a, b; Gómez-Olivencia, 2009, 2013a, b; Been et al., 2010, 2012, 2014a; Bonmatí et al., 2010; Williams et al., 2013; Arsuaga et al., 2015; Meyer and Haeusler, 2015). However, there remains a dearth of data regarding several aspects of the spine, including the cervical spine of the subfamily Homininae<sup>1</sup> (*Gorilla*, *Pan*, and *Homo*). The knowledge of this region is still based largely on the seminal work by Schultz (1961) and recent work by Manfreda et al. (2006), Nalley and Grider-Potter (2015), and Meyer (2016).

### 1.1. The Homininae neck

Schultz (1961) described the primate axial skeleton extensively, tackling several problems such as vertebral formula (Schultz and Straus, 1945) and morphology and weight of the different spinal regions, among others. He categorized different patterns of mid-sagittal cervical vertebrae morphology in apes, arguing that these differences were mainly due to the pronounced spinous process of African apes (*Gorilla* and *Pan*; Schultz, 1961). He also considered the long spinous process present in *Gorilla*, *Pan*, pottos, and a few New World monkeys to be derived, and that the shorter dorso-ventral cervical vertebrae in modern humans are not related to their reduced nuchal musculature mass and the reduced numbers of muscles in this area compared to the rest of the great apes, but were a feature seen in the majority of primates (Schultz, 1961). In the subaxial cervical spine, the relative dorsoventral length of the cervical vertebrae changes following a pattern that differs depending on the taxon: unlike humans and gibbons, in which the seventh cervical vertebra bears the longest spinous process, in the rest of the apes this maximum length is present in the fifth or sixth cervical vertebra (Schultz, 1961). The drawback of Schultz's (1961) work is that it is based on a very low number of individuals (i.e., the relative length of the spinous process is based on one specimen for most primates, and two for *Hylobates*, *Pongo*, *Pan*, *Gorilla*, and *Homo*). Manfreda et al. (2006) performed an in-depth geometric morphometric study of the atlas in nine primate taxa, five of which were hominoids. The three main conclusions of their study were that the studied taxa differed in atlas morphology, that *Homo sapiens* showed an allometric shape change different from the rest of the primates, and that it was possible to identify morphological features related to locomotion (Manfreda et al., 2006). A more recent study by Nalley and Grider-Potter (2015) on the subaxial cervical spine (C3–C7) also provided evidence for a link between function and form between the cervical morphology and postural behaviors in primates. These authors showed that primates with more pronograde heads and necks showed longer spinous processes. However, there is still a large gap in our knowledge regarding subaxial spine evolution in hominines (i.e., subfamily Homininae: *Gorilla*, *Pan*, and *Homo*) and other hominoids (Hylobatidae, Ponginae, and Homininae). Moreover, to what extent (if any) size, locomotion, and head posture influence cervical morphology is not fully understood.

<sup>1</sup> We follow the taxonomy proposed by Mittermeier et al. (2013) for extant primates: the superfamily Hominoidea is divided into the families Hylobatidae (gibbons) and Hominidae (great apes), the latter of which includes two subfamilies: Ponginae (genus *Pongo*) and Homininae (three genera: *Gorilla*, *Pan*, and *Homo*). The term "great apes" includes humans and the term "African apes" is a paraphyletic way to refer to two genera: *Gorilla* and *Pan*.

Additionally, there is a dearth of quantitative studies testing whether differences in cervical morphology are related to (or by-products of) adjacent anatomical regions.

This work has three main objectives. The first is to provide detailed morphological information on two important aspects of subaxial cervical (C3–C7) morphology, mid-sagittal morphology and the superior articular facet orientation, in a large sample of hominines using both traditional and geometric morphometrics. The second is to investigate the morphological changes of these two areas in human evolution. The third is to understand the influence of allometry in the morphology of the subaxial cervical spine and the correlation of this with posture and locomotion in Homininae.

## 2. Materials

The sample studied here comprises both extant and extinct hominoids. The extant hominoid sample is basically composed of individuals from the subfamily Homininae with a few additional *Pongo* and hylobatid specimens. The fossil sample includes extinct members of *Australopithecus* and *Homo*.

### 2.1. Extant hominoid sample

The subaxial cervical spine (i.e., C3–C7) of 127 adult individuals of the subfamily Homininae from five extant species (*H. sapiens*, *Gorilla gorilla*, *Gorilla beringei*, *Pan troglodytes*, and *Pan paniscus*) pooled in three genera (i.e., *Homo*, *Gorilla*, *Pan*) were studied. Twelve additional individuals, seven members of *Pongo* (*Pongo pygmaeus*,  $n = 6$ ; *Pongo* sp.,  $n = 1$ ) and five hylobatids (*Hylobates lar*,  $n = 2$ ; *Hylobates pileatus*,  $n = 1$ ; *Nomascus concolor*,  $n = 1$ ; *Nomascus gabriellae*,  $n = 1$ ) were also included (Table 1). Only individuals with at least three complete subaxial cervical vertebrae were included. Damaged vertebrae or pathological individuals were not included. Individuals were considered adults when the annular epiphyses were fused to the vertebral body and the secondary center of ossification of the tip of the spinous process was completely fused. In order to represent a wide range of variability, the sample included both extant species of the genus *Gorilla* (i.e., *G. gorilla* and *G. beringei*, the latter of which includes both subspecies), both species of the genus *Pan* (*P. troglodytes* and *P. paniscus*), and a large and heterogeneous sample of modern human populations from South America, Asia, Europe, and Africa, including small-bodied populations such as African Bubi and Philippine Negritos. The diverse modern human sample was purposefully selected to increase its variation and attempt to compensate for the variation in the *Gorilla* and *Pan* genera, which were composed of more than one species. As there were two immature specimens (the C7s of KNM-WT 15000 and U.W. 88-09, see below) in the fossil sample, a group of 15 immature *H. sapiens* and six *Pan* (five *P. troglodytes* and one *P. paniscus*) were included in the analysis in order to assess whether ontogenetic morphological changes could affect our results.

### 2.2. Fossil hominin sample

The fossil sample includes eight well preserved subaxial cervical vertebrae (Table 2). This material belongs to four extinct species: *Homo neanderthalensis*, *Homo ergaster*, *Australopithecus afarensis*, and *Australopithecus sediba*. In order to include as many fossil individuals as possible, cervical vertebra belonging to each of two subadult individuals (KNM-WT 15000, *H. ergaster* and U.W. 88-09, *A. sediba*) were included in the sample. The fossil data used in this study was derived from CT or micro-CT scans of the original material and high quality casts or surface scans based on

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