

The Sima de los Huesos cervical spine

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Abstract

Information regarding the evolution of the neck in genus *Homo* is hampered owing to a limited fossil record. Neandertals display significant metric and/or morphological differences in all the cervical vertebrae, when compared to *Homo sapiens*. Thus, the important fossil record from the Middle Pleistocene site of Sima de los Huesos (SH) not only offers important information about the evolution of this anatomical region within the Neandertal lineage, but also provides important clues to understand the evolution of this region at the genus level. We present the current knowledge of the anatomy of the cervical spine of the hominins found in SH compared to that of Neandertals and modern humans, and, when possible, to *Homo erectus* and *Homo antecessor*. The current SH fossil record comprises 172 cervical specimens (after refittings) belonging to a minimum of 11 atlases, 13 axes, and 52 subaxial cervical vertebrae. The SH hominins exhibit a morphological pattern in their cervical spine more similar to that of Neandertals than that of *H. sapiens*, which is consistent with the phylogenetic position of these hominins. However, there are some differences between the SH hominins and Neandertals in this anatomical region, primarily in the length and robusticity, and to a lesser extent in the orientation of the spinous processes of the lowermost cervical vertebrae. We hypothesize that these differences in the lowermost subaxial cervical vertebrae could be related to the increase in the brain size and/or changes in the morphology of the skull that occurred in the Neandertal lineage.

KEYWORDS

cervical vertebrae, evolution, morphology, neck

1 | INTRODUCTION

The cervical spine is an important anatomical region: it connects the head to the trunk, protects the spinal cord, and provides attachment for muscles related to the movement of the head, trunk, and the upper limbs (Kapandji, 1974). Extant hominoids display significant differences in their cervical vertebral morphology (e.g., Arlegi et al.,

2017); Schultz, 1961). Arlegi et al. (2017) studied the orientation of the upper articular facets and the morphology of the mid-sagittal morphology of the subaxial cervical spine (i.e., from the third —C3— to the seventh —C7— cervical vertebrae) and found that these morphological differences are related to differences in their allometric pattern, locomotion, and neck posture. Despite the cervical column being highly integrated with the

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cranial base (Villamil, 2018), Arlegi et al. (2022) found that the upper cervical vertebrae (the atlas, C1; and the axis, C2) exhibit the lowest covariation with the cranium in hominids. Moreover, *Homo sapiens* displays, especially in the variables related to the head balance, a relatively different pattern of cranio-cervical correlation compared to its closer living relatives, *Pan troglodytes* and *Gorilla gorilla* (Arlegi et al., 2022). Thus, size, the form of locomotion, and posture, all affect the cervical morphology in extant hominids, and therefore, are important factors to be considered in the study of the evolution of the hominin neck.

Vertebrae are fragile and metameric elements. Therefore, their fossil record is relatively scarce, especially when compared with other anatomical regions such as teeth or mandibles. Additionally, the morphological similarity of the vertebrae of the subaxial cervical spine (C3–C7) makes their anatomical determination and comparative study difficult. Finally, it is often difficult to amass reasonable comparative samples in the museum collections, especially when compared with other anatomical regions, such as the cranium. Thus, traditionally, the study of the vertebral elements of important fossil hominins, when present, is smaller chapters within large monographs (e.g., Heim, 1976; Trinkaus, 1983). In the last 40 years, the fossil record has increased and fossils from Europe, Asia, and Africa are providing new insights into the evolution of this anatomical region (e.g., Arlegi et al., 2017; Gómez-Olivencia, Been, et al., 2013; Meyer, 2005; Williams et al., 2013).

Many anatomical features in the postcranium are different between the genus *Australopithecus s.l.* and the genus *Homo* and this is also the case for the cervical spine (see Gómez-Olivencia and Been (2019), Meyer and Williams (2019), and Williams and Meyer (2019) and references therein). Bramble and Lieberman (2004) suggested that the decoupling of the head and pectoral girdles could have occurred with *Homo erectus* and the presence of the nuchal ligament and a more balanced head was already present in *Homo habilis*. In fact, despite a relatively small fossil record, it is possible to observe morphological differences between these two genera. However, when focusing on genus *Homo*, it is also possible to observe significant differences within this genus. For example, the cervical spine of the Neandertals—the extinct species that is preserved in the most abundant fossil record—displays significant differences in all the cervical vertebrae when compared to recent *H. sapiens* (Gómez-Olivencia, Been, et al., 2013). The first cervical vertebra (C1; also called atlas) exhibits a dorso-ventrally long vertebral foramen, which is likely related to the dorso-ventrally long foramen magnum (Gómez-Olivencia et al., 2007; Gómez-Olivencia, Been,

et al., 2013). The Neandertal C1s display non-projecting tubercles for the insertion of the transverse ligament in a high proportion. Additionally, their posterior arch is less robust than that of *H. sapiens* (Gómez-Olivencia, Couture-Veschambre, et al., 2013). Palancar et al. (2020) performed a geometric morphometric study of the El Sidrón atlases which suggests that Neandertals display a relatively lower height of the lateral masses and flatter more horizontally oriented articular facets. The Neandertal second cervical vertebrae (C2; also called axis) are low and wide when compared to *H. sapiens*. However, owing to the dearth of axes in the fossil record, the polarity of this trait is unknown (Gómez-Olivencia et al., 2007; Gómez-Olivencia, Couture-Veschambre, et al., 2013). The Neandertal lower cervical spine (i.e., C3–C7), displays articular pillars that are further apart from each other, which result in wider vertebrae and wider vertebral foramina. In C5–C7, when compared to recent *H. sapiens*, Neandertals have longer and more horizontal spinous processes. The largest differences can be observed in C5 and the differences in the length of the spinous process decrease as we move caudally toward C7 (Arlegi et al., 2017; Gómez-Olivencia, Been, et al., 2013). In recent *H. sapiens*, it has been possible to determine the relationship between the orientation of the foramen magnum and the cervical lordosis (Been et al., 2014). Applying these regression formula to Neandertals, the average cervical lordosis for adult Neandertals is $25.8^\circ \pm 3.7$, which is significantly lower than both the lordosis measured in 74 standing contemporary *H. sapiens* ($37.3^\circ \pm 9.8$; $p < .0005$), and from the estimated lordosis of 7 *H. sapiens* skulls (Been et al., 2017).

In this scenario, the Middle Pleistocene site of Sima de los Huesos (SH), with a chronology of approximately 430 thousand years, has yielded a large collection of fossil hominin remains, including elements of the cervical spine (Arsuaga et al., 2014, 2015). The cervical vertebrae found at this site provides the opportunity to understand: (a) the evolution of the cervical spine within the Neandertal lineage, owing to their phylogenetic affinities between Neandertals and the SH hominins (Arsuaga et al., 2014, 2015; Martínez & Arsuaga, 1997; Meyer et al., 2016); and (b) the evolution of this anatomical region within genus *Homo*, owing to the general paucity of Middle and Lower Pleistocene fossil remains.

This study aims to present the current knowledge of the anatomy of the cervical spine of the hominins found in SH compared to that of Neandertals and *H. sapiens*, and, when possible, to selected earlier members of genus *Homo* (*Homo erectus s.l.* and *Homo antecessor*). The perceived differences will be discussed within an evolutionary and biomechanical framework.

1.1 | The cervical spine fossil record in genus *Homo* in the Lower and Middle Pleistocene

To fully understand the morphological features of the cervical spine of the SH hominins, we provide a selected account of other fossil hominins from the Lower and Middle Pleistocene.

For genus *Homo*, the oldest cervical fossil remains are the *H. erectus* remains found in Dmanisi (Georgia) with a chronology of c. 1.8 million years (Ma) (Lordkipanidze et al., 2007; Meyer, 2005; Meyer & Williams, 2019; and references therein). From the five vertebrae, associated with the adolescent cranium D2700, two of them are cervical vertebrae: the axis D2673 and the C3 D2674. Both specimens, but particularly the axis, show long spinous processes, which could be related to the facial prognathism and its consequences in the static equilibrium of the head, as well as in the dynamic equilibrium during running or paramasticatory activities (Meyer, 2005).

The famous 1.5 Ma KNM-WT 15000 *H. erectus/ergaster* skeleton also preserves a cervical vertebra: the C7 (Brown et al., 1985; Latimer & Ward, 1993). This vertebra displays a small vertebral canal when compared to *H. sapiens* (MacLarnon, 1993), which was first thought to be related to pathology but has later been interpreted as *H. erectus* having slightly narrower spinal canals than *H. sapiens* (Meyer & Haeusler, 2015; see Haeusler, 2019 for a review). There are however, two additional features that are noteworthy: the horizontal orientation of the spinous process and the more dorsal orientation of the upper articular facets (Arlegi et al., 2017; Carretero et al., 1999).

The TD6 level of Gran Dolina (Sierra de Atapuerca, Burgos, Spain), with an age between 780 and 949 ka (*kilo anne* = 10^3 years), has yielded an important human fossil record that was used to define a new human species: *H. antecessor* (Carbonell et al., 1995; Duval et al., 2018; Parés & Pérez-González, 1995, 1999). This species was first proposed to be ancestral to Neandertals and *H. sapiens* (Bermúdez de Castro et al., 1997) however, it was possibly already within the Neandertal lineage based on the morphology of the upper first molar (Gómez-Robles et al., 2007, 2013). Currently, the cervical fossil record in this site includes six cervical remains from individuals with different ages-at-death (Gómez-Olivencia et al., 2017). The nearly complete atlas ATD6-90, probably belonged to a female individual based on its small size (Carretero et al., 1999) and displays a caudally projecting anterior tubercle of the anterior arch and protruding (large) tubercles for the attachment of the transverse ligament (Gómez-Olivencia et al., 2007). The most complete subaxial cervical vertebrae, such as ATD6-51, display a very horizontally oriented spinous process.

The Zhoukoudian Locality 1 (Dragon Hill, Northern China) has provided a fragmentary *H. erectus* atlas, which displays damage produced by hyaenids at the right transverse process (Boaz et al., 2004). This atlas, found in 1936 in Locus I (level 22) has been associated with Skull VI based on spatial, stratigraphical, and morphological criteria. Therefore, it is considered part of the II (“eye-one”) individual, older than 600 ka before present (BP) (Boaz et al., 2004; Shen et al., 2001). To our notice, this fossil remain has not been described in detail.

Among the 152 human remains found in the Caune de l’Arago (Tautavel, Roussillon, France) assigned to *H. erectus tautavelensis*, only two belong to the spine: an atlas and axis from sublevel Gm (level G; Middle stratigraphic assemblage; c. 450 ka; Moigne et al., 2006; de Lumley, 2022). These two fragmentary fossils were found close to the cranium Arago 21 (de Lumley, 2015) and have been recently described in detail (Chevalier & de Lumley, 2022).

In this work, the cervical fossil remains from *Homo naledi* (Hawks et al., 2017; Williams et al., 2017) and *Homo floresiensis* (Morwood et al., 2005) have not been considered owing to their general differences in size with SH and that they are not closely related phylogenetically.

2 | THE SH CERVICAL SPINE

Carretero et al. (1999) published an atlas and two subaxial cervical vertebrae from SH as comparative sample for the Gran Dolina-TD6 vertebral remains. Afterward, the most complete adult atlases and axes were published by Gómez-Olivencia et al. (2007) and certain additional morphometric aspects of the subaxial cervical spine were published by Arsuaga et al. (2015). The current SH fossil record comprises 172 cervical specimens (after refittings). Regarding the first cervical vertebra (the atlas), the SH has yielded 30 fragments (after refittings) representing 11 atlases based on the repetition of the left lateral mass. Regarding the second cervical vertebra (the axis), the SH has yielded 22 fragments (after refittings) representing 13 axes based on the repetition of the odontoid process. Regarding the subaxial cervical spine, there are currently 120 fragments after refittings that represent a minimum of 52 subaxial cervical vertebrae based on the repetition of the right articular pillar. The most complete adult cervical vertebrae are listed in Table 1 and a selection of the most complete vertebrae is presented in Figures 1 and 2.

The labeling of the SH vertebrae is somehow different from that used for other skeletal remains from the same site (see Appendix 1 by Gómez-Olivencia et al., 2007). Apart from one or multiple “AT-” + inventory number, which is the field label, the most complete vertebrae also

TABLE 1 Inventory of the most complete cervical vertebrae from Sima de los Huesos.

Anatomical position	Label	Field label	Age-at-death	Description	Figure
C1	VC3	AT-1554	Young adult	Complete atlas	Figure 1
C1	VC7	AT-3339 + AT-3340 + AT-3341 + AT-3688	Adult	Nearly complete atlas that lacks the transverse processes	Figure 1
C1	VC16	AT-1140 + AT-2201	Adult	Lateral masses and the posterior arch. The anterior arc (AT-2852) likely belongs to this atlas	Figure 1
C2	VC4	AT-1555	Young adult	Complete Axis	Figure 1
C2	VC2	AT-2465	Adult	Nearly complete axis that lacks the transverse processes	Figure 1
C2	VC8	AT-3680 + AT-3840	Adult	Nearly complete axis that lacks the transverse processes	Figure 1
C2	VC28	AT-4634 + AT-4643	Adolescent/Young adult	Nearly complete axis that lacks the right transverse process	Figure 1
C3	VC5	AT-1557	Young adult	Nearly complete vertebra that lacks the transverse processes and the tip of the spinous process	Figure 2
C3	VC9	AT-3326 + AT-4673	Adult	Nearly complete vertebra that lacks the transverse processes and the spinous process	Figure 2
C4	VC6	AT-3681 + AT-3682	Adult	Nearly complete vertebra that lacks the transverse processes	Figure 2
C5	VC15	AT-2582	Adult	Nearly complete vertebra that lacks the transverse processes and the spinous process	Figure 2
C5	VC11	AT-3325	Adult	Nearly complete vertebra that lacks the right transverse process and the tip of the spinous process	Figure 2
C6	VC12	AT-3349 + AT-3372 + AT-3373	Adult	Nearly complete vertebra that lacks the transverse processes	Figure 2
C6	VC14	AT-315 + AT-325a + AT-325b	Adolescent/Young adult	Nearly complete vertebra that lacks the transverse processes and the left half of the tip of the spinous process	Figure 2
C7	VC1	AT-321 + AT-1556 + AT-1569 + AT-1609	Adolescent/ Young adult	Nearly complete vertebra that lacks the transverse process from the right side and the tip of the left transverse process	Figure 2
C7	VC13	AT-3038 + AT-3049	Adult	Very complete vertebra that lacks both transverse processes, the right pedicle and the spinous process	Figure 2

have another label. They are labeled with a “V” (for vertebra) and in this case, “C” for cervical and an Arabic number which indicates the inventory number. As this might be confusing with the anatomical position, the latter can be included between parentheses afterward. For example, the most complete atlases are labeled VC3, VC7, and VC16 (Gómez-Olivencia et al., 2007) and VC1 (C7) refers to a complete seventh cervical vertebra of a late adolescent/young adult, first published by Carretero et al. (1999).

2.1 | The atlas (C1)

Similar to Neandertals, the vertebral foramen of the SH atlas is dorso-ventrally longer than that in *H. sapiens*, which has been related to a dorso-ventrally long foramen magnum (Gómez-Olivencia et al., 2007 and references therein). The anterior arch of the SH atlases displays an anterior tubercle with a caudal projection in all the individuals, which is the usual condition in all the extinct *Homo* species for which we have information, however, it

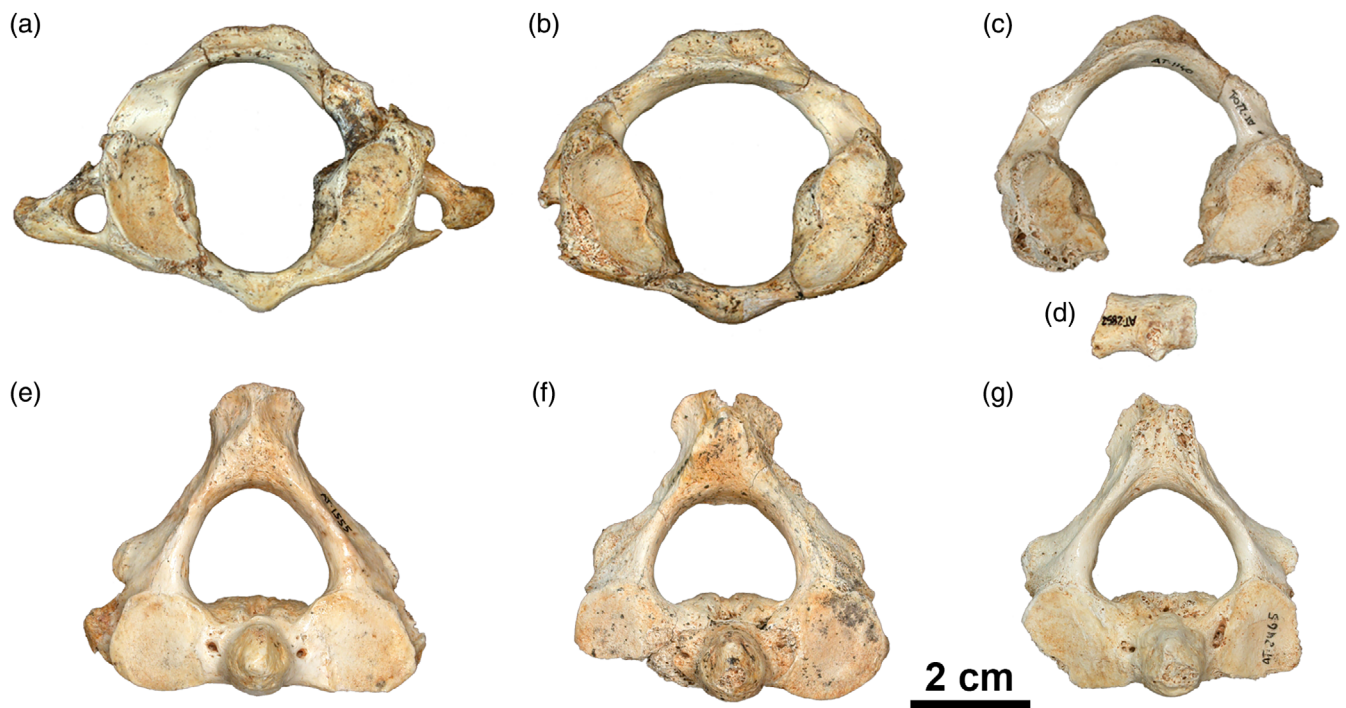


FIGURE 1 Most complete adult upper cervical vertebrae: atlases (a–d) and axes (e–g) from Sima de los Huesos in cranial view. (a) VC3 (C1); (b) VC7(C1); (c) VC16(C1); (d) the anterior arc AT-2852, which possibly belonged to VC16(C1), in ventral view; (e) VC4(C2); (f) VC8 (C2); and (g) VC2(C2).

is only present in some of *H. sapiens* (Table 2). This projection could be related to general robusticity as in the anterior tubercle is the attachment of the *Longus colli* muscle and the anterior longitudinal ligament (Figure 3). The *Longus colli* is a paired muscle that flexes the neck and rotates the cervical spine, when only one side is in action.

The lateral masses of the atlas present the transverse ligament tubercles on their medial aspect. The size of these tubercles differs within and across genus *Homo* species (Figure 4). In the only atlas specimen of *H. antecessor* these tubercles are large, similar to those in most of the *H. sapiens* individuals (Table 3). However, in Neandertals most of these tubercles are small (Table 3; Gómez-Olivencia et al., 2007; Gómez-Olivencia, Been, et al., 2013; Palancar et al., 2020). In the case of the SH hominins the percentage of small tubercles is higher than in *H. sapiens* but smaller than in Neandertals.

The posterior tubercle of the posterior arch of the SH C1s has been characterized as metrically close to the recent *H. sapiens* mean which is also the case for the *H. antecessor* ATD6-90 C1 (Carretero et al., 1999; Gómez-Olivencia et al., 2007). This is in contrast with the small size of the posterior arch of the Neandertal, which is more slender (Gómez-Olivencia, Been, et al., 2013; Palancar et al., 2020).

2.2 | The SH axes

The most remarkable anatomical feature of both the Neandertal and the SH axes is that they are craniocaudally low and mediolaterally wide when compared to *H. sapiens* (Figure 5; Gómez-Olivencia et al., 2007; Gómez-Olivencia, Been, et al., 2013). Additionally, the spinous processes of the SH axes have been described as robust when compared to recent *H. sapiens*. Gómez-Olivencia et al. (2007) described these spinous processes as possessing vertically oriented lateral walls, with a more trapezoidal and massive appearance, similar to other fossil hominins, including Neandertals (e.g., La Ferrassie 1 and Krapina 104; Radović et al., 1988) and Pleistocene *H. sapiens* (Tafaralt III; and Dolní Věstonice 15; Holliday, 2006).

2.3 | The SH subaxial cervical spine (C3–C7)

The detailed study of the Neandertal cervical subaxial spine has revealed some differences when compared to recent *H. sapiens*, at least between the male (or male-sized) individuals of these human groups (Gómez-Olivencia, Been, et al., 2013): dorsoventrally longer vertebrae (C4–C7), in some cases probably related to the longer spinous processes (C5–C7) and at least in C6 and C7 probably

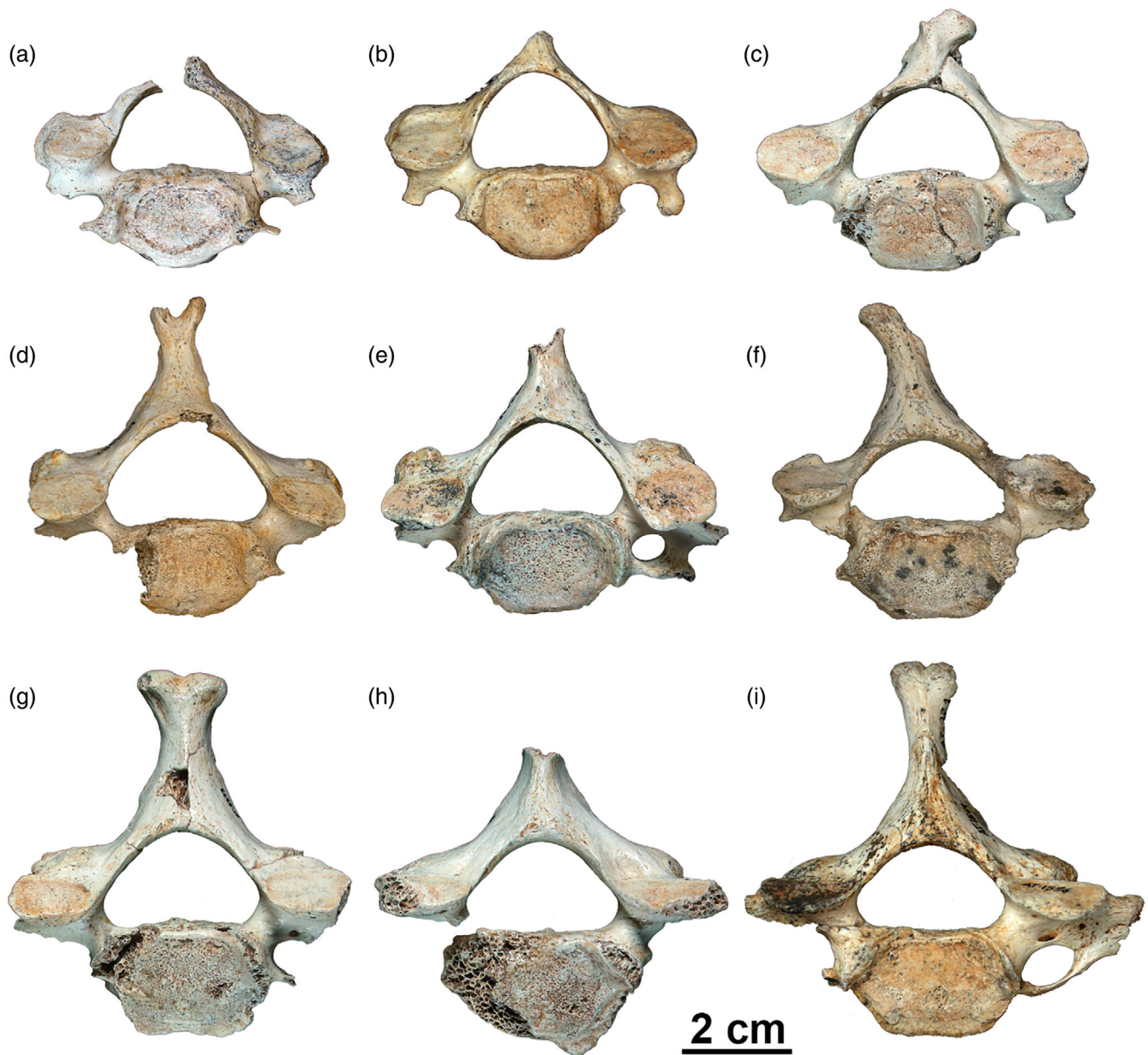


FIGURE 2 Most complete adult subaxial cervical vertebrae from Sima de los Huesos in cranial view. (a) VC9(C3); (b) VC5(C3); (c) VC6(C4); (d) VC15(C5); (e) VC11(C5); (f) VC14(C6); (g) VC12(C6); (h) VC13(C7); and (i) VC1(C7).

related to the more horizontal spinous processes; wider distance between upper articular facets (C3–C7), probably related to a wider vertebral canal (C3–C7), craniocaudally smaller vertebral bodies (C3–C7), craniocaudally shorter laminae in the C3, thicker laminae (C5 and C6 and probably in the C7). The extent of the differences is not always the same in the different vertebrae, and for example, there is a gradient of difference between the lengths of the spinous process in the C5–C7 segment. While Neandertals display longer spinous processes than recent *H. sapiens* in all these vertebrae, the largest differences are in the C5, and there is an increasing overlap toward the C7.

In the case of the SH, while the number of recovered cervical remains have increased there are not so many

complete adult cervical remains. However, despite the restricted number of available fossil remains, the morphological pattern of the SH subaxial cervical spine does not totally conform to the Neandertal pattern. The incomplete fifth cervical vertebra VC11(C5) from SH, which lacks the tip of the spinous process, displays a preserved dorso-ventral diameter (51 mm; Gómez-Olivencia, 2009) that is already 2.12 standard deviations above a recent *H. sapiens* male sample mean (45.9 ± 2.4 mm; Gómez-Olivencia, Been, et al., 2013). Contrarily, the spinous processes of the SH C6 and C7 are close to the recent *H. sapiens* mean and shorter than the Neandertal comparative samples; however, they are more robust than the more slender Neandertal spinous

TABLE 2 Frequency of presence of caudal projection of the anterior tubercle of the anterior arch of the atlas in the Sima de los Huesos hominins compared to other fossil and recent samples.

Individual/sample	Species/chronology	Projection	n	References
Sima de los Huesos	Middle Pleistocene	100%	6	(Gómez-Olivencia et al., 2007)
ATD6-90	<i>Homo antecessor</i> /Lower Pleistocene	100%	1	(Carretero et al., 1999; Gómez-Olivencia et al., 2007)
-	<i>Homo neanderthalensis</i> (Late Pleistocene)	100%	7	(Arensburg, 1991; Boule, 1911–1913; Gómez-Olivencia, Been, et al., 2013; Heim, 1976; Martin, 1923; Palancar et al., 2020)
-	Fossil <i>Homo sapiens</i> (Late Pleistocene)	25%	4	(McCown & Keith, 1939; Grine et al., 1998; this study)
European males ^a	Recent <i>Homo sapiens</i>	48.6%	37	(Gómez-Olivencia, 2009)
Euroamerican females ^b	Recent <i>Homo sapiens</i>	36.3%	33	(Gómez-Olivencia, 2009)
Euroamerican males ^b	Recent <i>Homo sapiens</i>	25%	28	(Gómez-Olivencia, 2009)

^aThe Burgos sample comprises 40 contemporary adult (estimated age at death is 20–45 years) male individuals from Burgos, Spain (Gómez-Olivencia, 2009; Gómez-Olivencia et al., 2007).

^bThe Euroamerican sample derives from the Hamann–Todd Osteological Collection (Cleveland Museum of Natural History; Gómez-Olivencia, 2009).

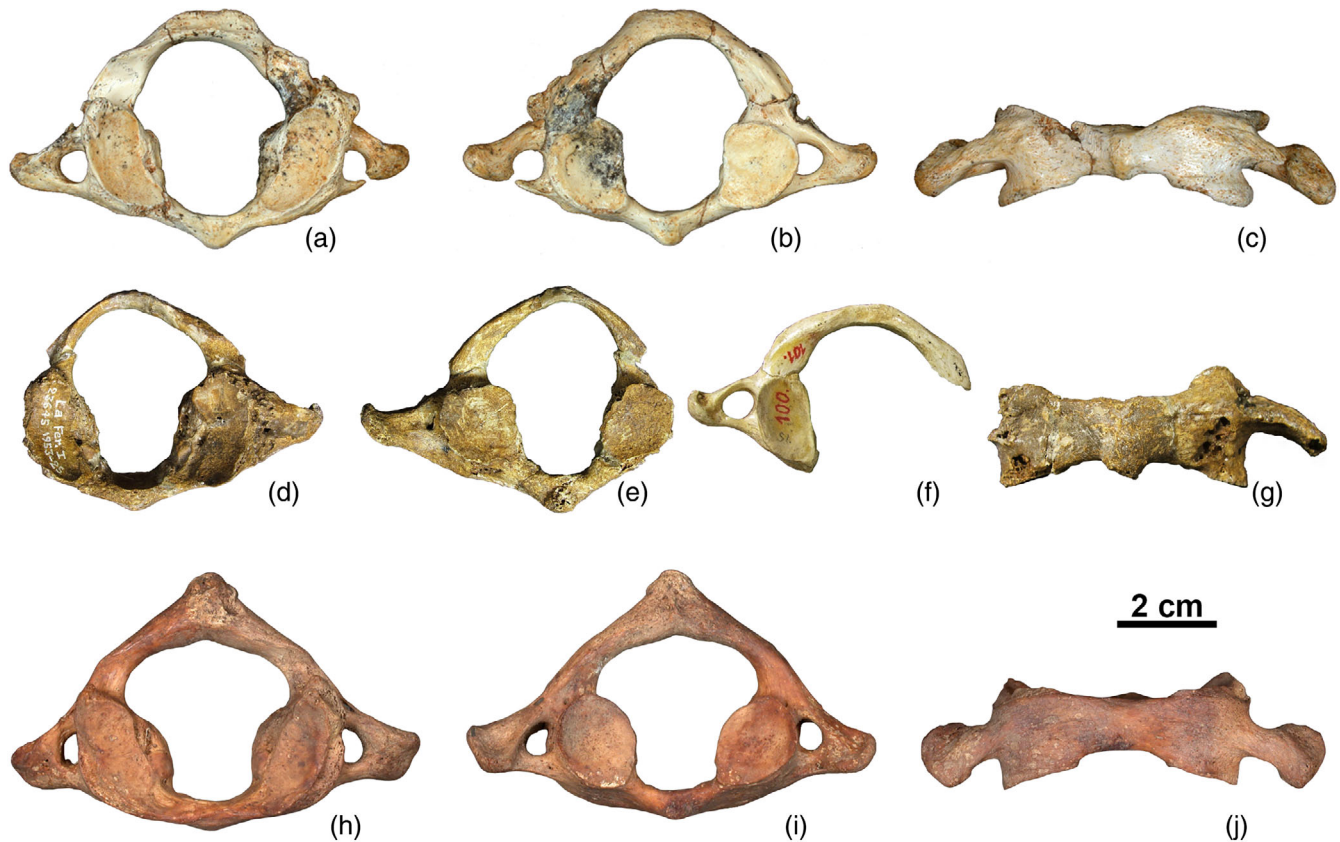


FIGURE 3 The SH atlas compared to other hominin atlases. Cranial (a), caudal (b), and ventral (c) views of the VC3(C1) atlas from Sima de los Huesos. Cranial (d), caudal (e), and ventral (g) views of the La Ferrassie 1 atlas. Caudal (f) view of the Krapina 100 + 101 atlas. Cranial (h), caudal (i), and ventral (j) views of a recent *H. sapiens* atlas.

processes (Arsuaga et al., 2015; Carretero et al., 1999; Gómez-Olivencia et al., 2011). The angle of the spinous processes of the SH C6 and C7 are below the recent *H. sapiens* mean, however, in general not as small as in

the Neandertals (Figure 6; Arsuaga et al., 2015). Finally, the width of the vertebral foramen of the subaxial cervical vertebrae of the SH published by Carretero et al. (1999) is close to the mean of recent

H. sapiens males and below Neandertals (Gómez-Olivencia, Been, et al., 2013).

Recent *H. sapiens* display different percentages of bituberculosis of the tip of the spinous process. Its presence increases from 73.91% in the C3 to a maximum of 92.65% in C5 and thereafter, decreases to 58.82% in the C6 and 0% in the C7. Some of the vertebrae (including the C7) might exhibit a partial bituberculosis (Gómez-Olivencia, Been, et al., 2013). In the case of Neandertals, there is evidence of the presence of bituberculosis in the C3–C5 segment in some individuals, though the percentage of presence is smaller than in recent *H. sapiens* and one C6 (out the five specimens available) displays a partial bituberculosis of the tip (Gómez-Olivencia, Been, et al., 2013). In the case of SH, VC15 (C5; Figure 7) displays a clear bituberculosis of the tip of the spinous

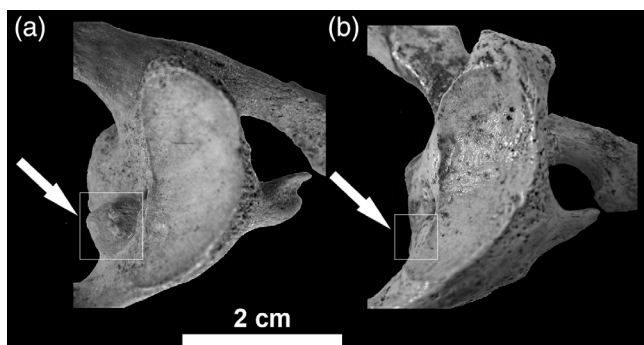


FIGURE 4 Cranial view of the lateral mass of the atlas. Left: a recent *H. sapiens* which displays a well-developed transverse ligament tubercle, a condition also present in the *H. antecessor* atlas ATD6-90. Right: VC3 from SH displays a flat surface, instead of a tubercle which is the most common feature found in both SH and Neandertals. Modified from Gómez-Olivencia et al. (2007).

process. The very robust spinous process of the SH vertebra VC12 (C6; Figure 6) displays a partial bituberculosis of the tip of the spinous process.

2.4 | The neck as a whole: Neck length

The supralaryngeal vocal tract (SVT) proportions, that is, the proportions between its vertical segment (SVTv; the pharynx) and its horizontal segment (SVTh; the oral cavity) has attracted the interest of scholars owing to its relationship with the spoken language (Böe et al., 2002; Martínez et al., 2013, and references therein). The presence of a complete cervical spine in the SH associated to Cranium 5 has allowed the reconstruction of the vocal tract proportions of a Middle Pleistocene individual for the first time (Arsuaga et al., 2014; Gómez-Olivencia, 2009; Gómez-Olivencia et al., 2011; Martínez et al., 2013). The neck length (based on the summed heights of the individual vertebrae: C2–C7) of the SH individual is slightly shorter than that of the La Ferrassie 1 Neandertal male individual, and these two individuals are slightly below the recent *H. sapiens* male mean (Martínez et al., 2013). The vocal tract proportions (SVTv:SVTh) are also similar for the SH Cranium 5 individuals (ratio = 0.81) and the La Ferrassie 1 individual (ratio = 0.79), which has been suggested to have similar capabilities regarding the production of the full range of sounds emitted during the modern human spoken language (Böe et al., 2002; Martínez et al., 2013). These two fossil hominin SVTv:SVTh ratios are below the recent *H. sapiens* adult male mean basically owing to their longer horizontal segment (Martínez et al., 2013).

TABLE 3 Frequency of the different sizes of the transverse ligament tubercles of the atlas of the Sima de los Huesos sample, compared to other fossil and recent samples (Gómez-Olivencia et al., 2007; Gómez-Olivencia, Been, et al., 2013; Palancar et al., 2020).

Species and/or chronology	Sample (n)	Sex	Large tubercle (%)	Asymmetry ^a (%)	Small tubercle (%)
Middle Pleistocene	Sima de los Huesos (n = 6)	Males (n = 3), indeterminate (n = 3)	33.3	0	66.7
<i>Homo antecessor</i> (Lower Pleistocene)	Gran Dolina-ATD6-90	Female?	100	0	0
<i>H. neanderthalensis</i> (Late Pleistocene)	n = 12	Pooled sex	0	9.1	90.9
<i>H. sapiens</i> (Recent)	European (n = 39) ^b	Males	74.4	10.2	15.4
<i>H. sapiens</i> (Recent)	Euroamerican (n = 29) ^b	Males	96.6	0	3.4
<i>H. sapiens</i> (Recent)	Euroamerican (n = 33) ^b	Females	75.75	15.15	9.10

^aAsymmetry refers to the presence of a large transverse ligament tubercle in one of the lateral masses and a small tubercle in the other lateral mass, within the same atlas.

^bSee Table 1 for the provenance of the comparative samples.

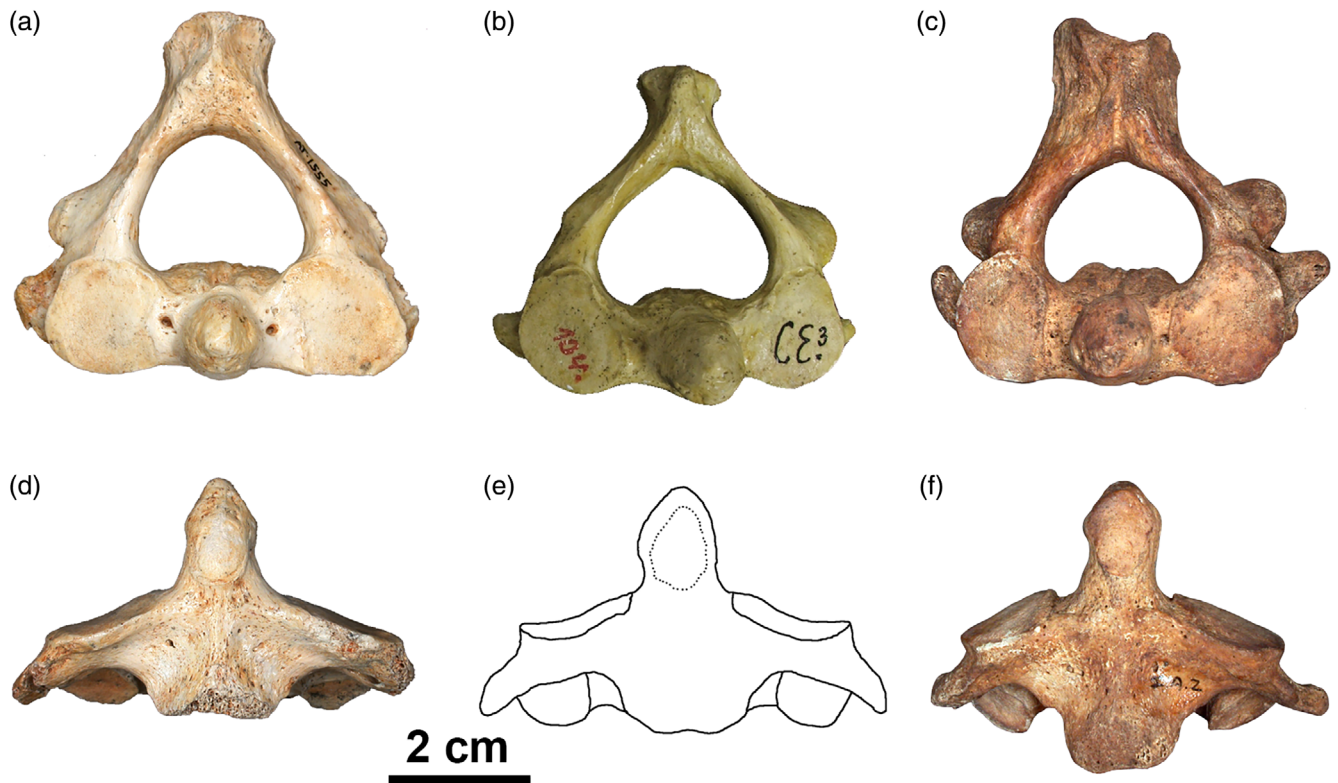


FIGURE 5 The SH axis compared to other hominin atlases. Cranial (a) and ventral (d) views of the VC4 atlas from Sima de los Huesos. Cranial (b) view of the Neandertal axis 104 from Krapina. Cranial (c) and ventral (f) views of a recent *H. sapiens* atlas. Ventral (e) view of the Neandertal Regourdou axis as was drawn by Piveteau (1966); see also Gómez-Olivencia, Couture-Veschambre, et al. (2013).

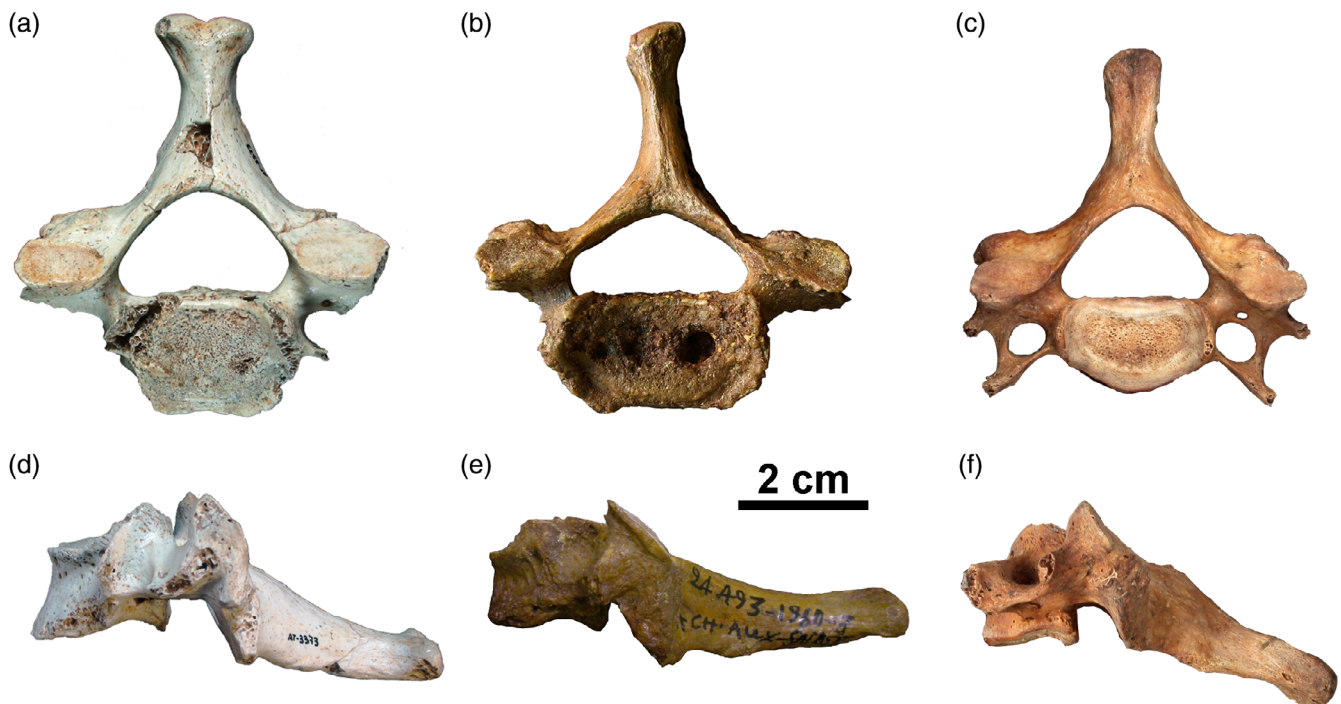


FIGURE 6 Comparison of the SH C6 to other hominin C6s. Cranial (a) and lateral (d) views of the VC12 from Sima de los Huesos. Cranial (b) and lateral (e) views of the La Chapelle-aux-Saints 1 C6. Cranial (c) and lateral (f) views of a recent *H. sapiens* C6.

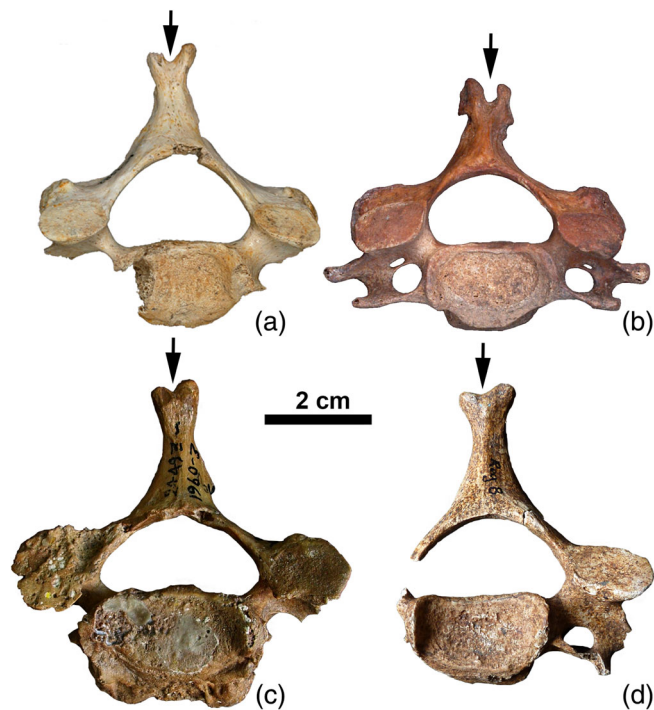


FIGURE 7 Comparison of the bituberculosity in the fifth cervical vertebra. (a) VC15 from the Sima de los Huesos; (b) recent *H. sapiens*; (c) the C5 of the La Chapelle-aux-Saints 1 Neandertal; (d) the C5 of the Regourdou 1 Neandertal. Note also the longer spinous process of both the SH and the Neandertal C5 compared to the shorter *Homo sapiens* spinous process.

3 | DISCUSSION AND CONCLUSIONS

Cautiously considering owing to the restricted fossil record, the cervical morphology of the SH hominins does not fully conform to the morphology present in Neandertals or in *H. sapiens*. Additionally, it also presents morphological differences with the restricted *H. erectus* and *H. antecessor* fossil record. Table 4 presents a summary of the morphological features of the SH hominins compared to other species of the genus *Homo*.

First, when compared to the vertebral remains from Dmanisi, the SH vertebrae are larger and the axis does not exhibit such relatively long spinous process. Second, when compared to the KNM-WT 15000 C7, the orientation of upper articular facets of the SH hominins are more transversally oriented, similar to the configuration present in Neandertals and *H. sapiens*. This latter orientation is also present in the immature *H. antecessor* C7 ATD6-75 (anatomical position corrected by Gómez-Olivencia, 2009 based on the degree of superposition of the articular facets and the morphology of the transverse process). Thus, assuming that the orientation of the upper facets present in the KNM-WT 15000 C7 is the typical for *H. erectus* (i.e., slightly medially oriented) and

that the facet orientation of ATD6-75 is also typical for *H. antecessor* (transversally oriented), it can be hypothesized that there was a slight change of orientation in the upper articular processes in between these two species. In both the cases of *H. erectus* and *H. antecessor*, the fossil record for these two species is very limited and the range of morphological variation of these two species is still not well known. Thus this comparison should be considered with caution until new fossil remains are found.

Second, the size of the vertebral canal in the SH hominins is similar to that of recent *H. sapiens* and above that present in *H. erectus* and *H. antecessor*. It should be noted that the cranial capacity of the SH hominins is above that estimated for *H. antecessor* and *H. erectus* s.l. (Arsuaga et al., 1997, 1999, 2014). The Neandertal male individuals studied by Gómez-Olivencia, Been, et al. (2013) display a mediolaterally larger vertebral canal, which could be considered an apomorphic feature of this latter group. However, the female Neandertal cervical record is very scarce to assess this feature.

Third, all the lowermost cervical vertebrae of fossil *Homo* exhibit very horizontal spinous processes (Arlegi et al., 2017; Carretero et al., 1999; Gómez-Olivencia, 2009; Gómez-Olivencia, Been, et al., 2013). This feature should be considered as a plesiomorphy within the genus *Homo* and therefore, the orientation present in *H. sapiens* should be considered as apomorphic, and we hypothesize that could be (at least, partially) related to rotation of the nuchal plane that occurred in *H. sapiens*, and all the related changes in the muscular and ligament insertions. Additionally, the SH hominins share with Neandertals a higher presence of small transverse ligament tubercles in the C1, a low and mediolaterally wide axis, and a long spinous process of C5. The polarity of these traits is still unknown owing to the restricted *H. erectus* and *H. antecessor* fossil record for these anatomical regions. Contrarily, when compared to Neandertals, the spinous processes of the lowermost cervical vertebrae of the SH hominins are shorter and more robust (Gómez-Olivencia et al., 2011). There is an increase in the cranial capacity from the Middle Pleistocene European populations, such as the SH, to the Upper Pleistocene Neandertal populations, and also differences in the cranial morphology between these two groups (Arsuaga et al., 1999, 2014), which could have altered the equilibrium of the head. Considering the relationship between the cervical and cranial morphology in extant humans and nonhuman great apes (Arlegi et al., 2022), it can be hypothesized that some of the differences of the SH hominins with Neandertals could be related to differences in size and shape of the cranium.

There are other features that are present in the SH cervical spine and, although they are absent in the recent

TABLE 4 The Sima de los Huesos cervical vertebrae: summary of metrical and morphological traits^a.

Bone	Trait	<i>Homo erectus</i>	<i>Homo antecessor</i>	Sima de los Huesos	Neandertals	<i>Homo sapiens</i>	References
Atlas (C1)	Vertebral canal dorsoventral diameter	?	Short (female individual)	Long	Very long	Short	(Gómez-Olivencia et al., 2007)
	Caudal projection of the anterior tubercle	?	100%	100%	100%	48.6%	(Carretero et al., 1999; Gómez-Olivencia et al., 2007; Palancar et al., 2020)
	Size of the tubercles for the insertion of the transverse ligament		Large	Small (66.7%)	Small (90.9%)	Large (74.4%)	(Gómez-Olivencia et al., 2007; Palancar et al., 2020)
	Size of the posterior arch		Large	Large	Small	Large	(Gómez-Olivencia et al., 2007; Gómez-Olivencia, Been, et al., 2013; Palancar et al., 2020)
Axis	Morphology	?	?	Low and wide	Low and wide	Tall and narrow	(Gómez-Olivencia et al., 2007; Gómez-Olivencia, Been, et al., 2013)
Lower cervical spine	C5 spinous process length	?	?	Long	Long	Short	(Gómez-Olivencia, Been, et al., 2013; This study)
	C6-C7 spinous process length		?	Short	Long	Short	(Arsuaga et al., 2015; Gómez-Olivencia, Been, et al., 2013)
	C6-C7 spinous process orientation	More horizontal	More horizontal	More horizontal	More horizontal	More vertical	(Arsuaga et al., 2015; Carretero et al., 1999; Gómez-Olivencia, Been, et al., 2013)
	Width of the vertebral canal	Very narrow	Narrow	Narrow	Wide	Narrow	(Carretero et al., 1999; Gómez-Olivencia, Been, et al., 2013)

^aThis table updates the information provided by Arsuaga et al. (2015).

H. sapiens, they are present in the Paleolithic *H. sapiens* fossils. This is the case of the morphology of spinous process of the axis, whose morphology would be more related to the strong development of the nuchal muscles *M. rectus capitis posterior major* and *M. obliquus capitis inferior* (Gómez-Olivencia et al., 2007 and references therein). These muscles appear to have been more developed in the Paleolithic hunter-gatherers (irrespective of their taxonomical attribution) than in the modern industrial populations. In the case of the caudal projection of the anterior tubercle of the anterior arch of the atlas, which is the insertion point of ligaments and muscles, the caudal development of this feature could be related to robusticity and thus, it can be hypothesized that the Upper Paleolithic possibly exhibited more dorsal projections of the anterior tubercle than the recent industrial populations. However, the study of a large Upper Paleolithic *H. sapiens* sample would be necessary to test this hypothesis.

In summary, the SH hominins display a morphological pattern in their cervical spine more similar to that of Neandertals than to recent (and fossil) *H. sapiens* populations, which is consistent with the phylogenetic position of these hominins. However, there are, some differences between the SH hominins and Neandertals in this anatomical region, primarily in the length and robusticity, and to a lesser extent in the orientation of the spinous processes of the lowermost cervical vertebrae. We hypothesize that these differences could be owing to the encephalization that occurred in the Neandertal lineage, which altered the size and shape of the cranium and therefore probably altered the static and dynamic equilibrium of the head. To fully comprehend the evolution of this anatomical region in the genus *Homo*, apart from new fossil remains, additional studies are necessary to understand the morphological integration of the individual vertebrae, and their covariation with adjacent anatomical regions.

AUTHOR CONTRIBUTIONS

Asier Gómez-Olivencia: Conceptualization; formal analysis; investigation; methodology; supervision; writing – original draft; writing – review and editing. **Juan Luis Arsuaga:** Conceptualization; funding acquisition; project administration; supervision; writing – review and editing.

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REFERENCES

- Arensburg, B. (1991). The vertebral column, thoracic cage and hyoid bone. In O. Bar-Yosef & B. Vandermeersch (Eds.), *Le squelette moustérien de Kébara 2* (pp. 113–147). Éditions du CNRS.
- Arlegi, M., Gómez-Olivencia, A., Albessard, L., Martínez, I., Balzeau, A., Arsuaga, J. L., & Been, E. (2017). The role of allometry and posture in the evolution of the hominin subaxial cervical spine. *Journal of Human Evolution*, *104*, 80–99.
- Arlegi, M., Pantoja-Pérez, A., Veschambre-Couture, C., & Gómez-Olivencia, A. (2022). Covariation between the cranium and the cervical vertebrae in hominids. *Journal of Human Evolution*, *162*, 103112.
- Arsuaga, J. L., Carretero, J.-M., Lorenzo, C., Gómez-Olivencia, A., Pablos, A., Rodríguez, L., García-González, R., Bonmatí, A., Quam, R. M., Pantoja-Pérez, A., Martínez, I., Aranburu, A., Gracia-Téllez, A., Poza-Rey, E., Sala, N., García, N., Alcázar de Velasco, A., Cuenca-Bescós, G., Bermúdez de Castro, J. M., & Carbonell, E. (2015). Postcranial morphology of the Middle Pleistocene humans from Sima de los Huesos, Spain. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 11524–11529.
- Arsuaga, J. L., Martínez, I., Arnold, L. J., Aranburu, A., Gracia-Téllez, A., Sharp, W. D., Quam, R. M., Falguères, C., Pantoja-Pérez, A., Bischoff, J., Poza-Rey, E., Parés, J. M., Carretero, J. M., Demuro, M., Lorenzo, C., Sala, N., Martínón-Torres, M., García, N., Alcázar de Velasco, A., ... Carbonell, E. (2014). Neandertal roots: Cranial and chronological evidence from Sima de los Huesos. *Science*, *344*, 1358–1363.
- Arsuaga, J. L., Martínez, I., Gracia, A., Carretero, J. M., Lorenzo, C., García, N., & Ortega, A. I. (1997). Sima de los Huesos (Sierra de Atapuerca, Spain). The site. *Journal of Human Evolution*, *33*, 109–127.
- Arsuaga, J. L., Martínez, I., Lorenzo, C., Gracia, A., Muñoz, A., Alonso, O., & Gallego, J. (1999). The human cranial remains from Gran Dolina Lower Pleistocene site (Sierra de Atapuerca, Spain). *Journal of Human Evolution*, *37*, 431–457.
- Been, E., Gómez-Olivencia, A., Shefi, S., Soudack, M., Bastir, M., & Barash, A. (2017). Evolution of spinopelvic alignment in hominins. *The Anatomical Record*, *300*, 900–911.

- Been, E., Shefi, S., Zilka, L. R., & Soudack, M. (2014). Foramen magnum orientation and its association with cervical lordosis: A model for reconstructing cervical curvature in archeological and extinct hominin specimens. *Advances in Anthropology*, 4, 133–140.
- Bermúdez de Castro, J. M., Arsuaga, J. L., Carbonell, E., Rosas, A., Martínez, I., & Mosquera, M. (1997). A hominid from the Lower Pleistocene of Atapuerca, Spain: Possible ancestor to neandertals and modern humans. *Science*, 276, 1392–1395.
- Boaz, N. T., Ciochon, R. L., Xu, Q., & Liu, J. (2004). Mapping and taphonomic analysis of the *Homo erectus* loci at Locality 1 Zhoukoudian, China. *Journal of Human Evolution*, 46, 519–549.
- Boë, L.-J., Heim, J.-L., Honda, K., & Maeda, S. (2002). The potential Neandertal vowel space was as large as that of modern humans. *Journal of Phonetics*, 30, 465–484.
- Boule, M. (1911–1913). L'homme fossile de la Chapelle-aux-Saints. *Ann de Paléontologie*, 6, 111–172 7, 21–56, 85–192; 8, 1–70.
- Bramble, D. M., & Lieberman, D. E. (2004). Endurance running and the evolution of *Homo*. *Nature*, 432, 345–352.
- Brown, F. H., Harris, J., Leakey, R., & Walker, A. (1985). Early *Homo erectus* skeleton from West Lake Turkana, Kenya. *Nature*, 316, 788–792.
- Carbonell, E., Bermúdez de Castro, J. M., Arsuaga, J. L., Díez, J. C., Rosas, A., Cuenca-Bescós, G., Sala, R., Mosquera, M., & Rodríguez, X. P. (1995). Lower Pleistocene hominids and artifacts from Atapuerca-TD6 (Spain). *Science*, 269, 826–830.
- Carretero, J. M., Lorenzo, C., & Arsuaga, J. L. (1999). Axial and appendicular skeleton of *Homo antecessor*. *Journal of Human Evolution*, 37, 459–499.
- Chevalier, T., de Lumley, M.-A. (2022). Les vertèbres de l'Homme de la caune de l'Arago: L'atlas (A122) et l'axis (A123). In M.-A. de Lumley (Ed.), *Caune de l'Arago. Tautavel-en-Roussillon, Pyrénées-Orientales, France. Tome IX. Les restes humains du Pléistocène moyen de la Caune de l'Arago* (pp. 437–450). CNRS Éditions.
- de Lumley, M.-A. (2015). L'homme de Tautavel. Un *Homo erectus* européen évolué. *Homo erectus tautavelensis*. *L'Anthropologie*, 119, 303–348.
- de Lumley, M.-A. (2022). Inventaire. Répartition stratigraphique. Représentation anatomique. In M.-A. de Lumley (Ed.), *Caune de l'Arago. Tautavel-en-Roussillon, Pyrénées-Orientales, France. Tome IX. Les restes humains du Pléistocène moyen de la Caune de l'Arago* (pp. 21–46). CNRS Éditions.
- Duval, M., Grün, R., Parés, J. M., Martín-Francés, L., Campaña, I., Rosell, J., Shao, Q., Arsuaga, J. L., Carbonell, E., & Bermúdez de Castro, J. M. (2018). The first direct ESR dating of a hominin tooth from Atapuerca Gran Dolina TD-6 (Spain) supports the antiquity of *Homo antecessor*. *Quaternary Geochronology*, 47, 120–137.
- Gómez-Olivencia, A. (2009). *Estudios paleobiológicos sobre la columna vertebral y la caja torácica de los humanos fósiles del Pleistoceno, con especial referencia a los fósiles de la Sierra de Atapuerca*. In: Departamento de Ciencias Históricas y Geografía. Burgos: Universidad de Burgos. p. 553.
- Gómez-Olivencia, A., Arsuaga, J. L., Bermúdez de Castro, J. M., & Carbonell, E. (2017). The vertebral column of the Gran Dolina-TD6 and Sima de los Huesos hominins: New remains and new results. *American Journal of Physical Anthropology*, 162, 197.
- Gómez-Olivencia, A., Arsuaga, J. L., Carretero, J. M., Gracia, A., & Martínez, I. (2011). *A complete neck from Sima de los Huesos and the evolution of the cervical spine in Neandertal lineage*. Proceedings of the First Annual Meeting, European Society for the study of Human Evolution. p. 41.
- Gómez-Olivencia, A., & Been, E. (2019). The spine of late *Homo*. In E. Been, A. Gómez-Olivencia, & P. A. Kramer (Eds.), *Spinal evolution: Morphology, function, and pathology of the spine in hominoid evolution* (pp. 185–211). Springer.
- Gómez-Olivencia, A., Been, E., Arsuaga, J. L., & Stock, J. T. (2013). The Neandertal vertebral column 1: The cervical spine. *Journal of Human Evolution*, 64, 608–630.
- Gómez-Olivencia, A., Carretero, J. M., Arsuaga, J. L., Rodríguez-García, L., García-González, R., & Martínez, I. (2007). Metric and morphological study of the upper cervical spine from the Sima de los Huesos site (Sierra de Atapuerca, Burgos, Spain). *Journal of Human Evolution*, 53, 6–25.
- Gómez-Olivencia, A., Couture-Veschambre, C., Madelaine, S., & Maureille, B. (2013). The vertebral column of the Regourdou 1 Neandertal. *Journal of Human Evolution*, 64, 582–607.
- Gómez-Robles, A., Bermúdez de Castro, J. M., Arsuaga, J.-L., Carbonell, E., & Polly, P. D. (2013). No known hominin species matches the expected dental morphology of the last common ancestor of Neanderthals and modern humans. *Proceedings of the National Academy of Sciences*, 110, 18196–18201.
- Gómez-Robles, A., Martínón-Torres, M., Bermúdez de Castro, J. M., Margvelashvili, A., Bastir, M., Arsuaga, J. L., Pérez-Pérez, A., Estebarez, F., & Martínez, L. M. (2007). A geometric morphometric analysis of hominin upper first molar shape. *Journal of Human Evolution*, 53, 272–285.
- Grine, F. E., Pearson, O. M., Klein, R. G., & Rightmire, G. P. (1998). Additional human fossils from Klasies River Mouth, South Africa. *Journal of Human Evolution*, 35, 95–107.
- Haeusler, M. (2019). Spinal pathologies in fossil hominins. In E. Been, A. Gómez-Olivencia, & P. A. Kramer (Eds.), *Spinal evolution: Morphology, function, and pathology of the spine in hominoid evolution* (pp. 213–245). Springer.
- Hawks, J., Elliott, M., Schmid, P., Churchill, S. E., Ruitter, D. J., Roberts, E. M., Hilbert-Wolf, H., Garvin, H. M., Williams, S. A., Delezene, L. K., Feuerriegel, E. M., Randolph-Quinney, P., Kivell, T. L., Laird, M. F., Tawane, G., DeSilva, J. M., Bailey, S. E., Brophy, J. K., Meyer, M. R., ... Berger, L. R. (2017). New fossil remains of *Homo naledi* from the Lesedi Chamber, South Africa. *eLife*, 6, e24232.
- Heim, J.-L. (1976). *Les Hommes fossiles de la Ferrassie. I. Le gisement. Les squelettes adultes (crâne et squelette du tronc)*. Masson.
- Holliday, T. W. (2006). The vertebral columns. In E. Modern (Ed.), *Trinkaus E, Svoboda J* (pp. 242–294). Oxford University Press.
- Kapandji, I. A. (1974). The physiology of the joints. In *The trunk and vertebral column* (Vol. 3). Churchill Livingstone.
- Latimer, B., & Ward, C. V. (1993). The thoracic and lumbar vertebrae. In A. Walker & R. Leakey (Eds.), *The Nariokotome Homo erectus skeleton* (pp. 266–293). Springer.
- Lordkipanidze, D., Jashashvili, T., Vekua, A., de León, M. S. P., Zollikofer, C. P. E., Rightmire, G. P., Pontzer, H., Ferring, R., Oms, O., Tappen, M., Bukhsianidze, M., Agusti, J., Kahlke, R., Kiladze, G., Martínez-Navarro, B., Mouskhelishvili, A., Nioradze, M., & Rook, L. (2007). Postcranial evidence from early *Homo* from Dmanisi, Georgia. *Nature*, 449, 305–310.
- MacLarnon, A. M. (1993). The vertebral canal. In A. Walker & R. Leakey (Eds.), *The Nariokotome Homo erectus skeleton* (pp. 359–390). Springer.
- Martin, H. (1923). *L'Homme fossile de la Quina*. Librairie Octave Doin.

- Martínez, I., & Arsuaga, J. L. (1997). The temporal bones from Sima de los Huesos Middle Pleistocene site (Sierra de Atapuerca, Spain). A phylogenetic approach. *Journal of Human Evolution*, 33, 283–318.
- Martínez, I., Rosa, M., Quam, R., Jarabo, P., Lorenzo, C., Bonmatí, A., Gómez-Olivencia, A., Gracia, A., & Arsuaga, J. L. (2013). Communicative capacities in Middle Pleistocene humans from the Sierra de Atapuerca in Spain. *Quaternary International*, 295, 94–101.
- McCown, T. D., & Keith, A. (1939). *The stone age of Mount Carmel. The fossil human remains from the levalloiso-mousterian*. Clarendon press.
- Meyer, M., Arsuaga, J.-L., de Filippo, C., Nagel, S., Aximu-Petri, A., Nickel, B., Martínez, I., Gracia, A., Bermúdez de Castro, J. M., Carbonell, E., Viola, B., Kelso, J., Prüfer, K., & Pääbo, S. (2016). Nuclear DNA sequences from the Middle Pleistocene Sima de los Huesos hominins. *Nature*, 531, 504–507.
- Meyer, M. R. (2005). *Functional biology of the Homo erectus axial skeleton from Dmanisi*. University of Pennsylvania.
- Meyer, M. R., & Haeusler, M. (2015). Spinal cord evolution in early *Homo*. *Journal of Human Evolution*, 88, 43–53.
- Meyer, M. R., & Williams, S. A. (2019). The spine of early Pleistocene *Homo*. In E. Been, A. Gómez-Olivencia, & P. A. Kramer (Eds.), *Spinal evolution: Morphology, function, and pathology of the spine in hominoid evolution* (pp. 153–183). Springer.
- Moigne, A.-M., Palombo, M. R., Belda, V., Heriech-Briki, D., Kacimi, S., Lacombat, F., de Lumley, M.-A., Moutoussamy, J., Rivals, F., Quilès, J., & Testu, A. (2006). Les faunes de grands mammifères de la Caune de l'Arago (Tautavel) dans le cadre biochronologique des faunes du Pléistocène moyen Italien. *L'Anthropologie*, 110, 788–831.
- Morwood, M. J., Brown, P., Jatmiko, S. T., Wahyu Saptomo, E., Westaway, K. E., Awe Due, R., Roberts, R. G., Maeda, T., Wasisto, S., & Djubiantono, T. (2005). Further evidence for small-bodied hominins from the Late Pleistocene of Flores, Indonesia. *Nature*, 437, 1012–1017.
- Palancar, C. A., Torres-Tamayo, N., García-Martínez, D., García-Taberner, A., Rosas, A., & Bastir, M. (2020). Comparative anatomy and 3D geometric morphometrics of the El Sidrón atlases (C1). *Journal of Human Evolution*, 149, 102897.
- Parés, J. M., & Pérez-González, A. (1995). Paleomagnetic age for hominid fossils at Atapuerca archaeological site, Spain. *Science*, 269, 830–832.
- Parés, J. M., & Pérez-González, A. (1999). Magnetochronology and stratigraphy at Gran Dolina section, Atapuerca (Burgos, Spain). *Journal of Human Evolution*, 37, 325–342.
- Piveteau, J. (1966). La grotte de Regourdou (Dordogne): Paléontologie Humaine. *Annales de Paléontologie (Vertébrés)*, 52, 163–194.
- Radović, J., Smith, F. H., Trinkaus, E., & Wolpoff, M. H. (1988). *The Krapina hominids. An illustrated catalog of skeletal collection*. Croatian Natural History Museum.
- Schultz, A. H. (1961). *Primatologia. Handbuch der primatenkunde*. S. Karger.
- Shen, G., Ku, T.-L., Cheng, H., Edwards, R. L., Yuan, Z., & Wang, Q. (2001). High-precision U-series dating of locality 1 at Zhoukoudian, China. *Journal of Human Evolution*, 41, 679–688.
- Trinkaus, E. (1983). *The Shanidar Neandertals*. Academic Press.
- Villamil, C. I. (2018). Phenotypic integration of the cervical vertebrae in the Hominoidea (primates). *Evolution*, 72, 490–517.
- Williams, S. A., García-Martínez, D., Bastir, M., Meyer, M. R., Nalla, S., Hawks, J., Schmid, P., Churchill, S. E., & Berger, L. R. (2017). The vertebrae and ribs of *Homo naledi*. *Journal of Human Evolution*, 104, 136–154.
- Williams, S. A., & Meyer, M. R. (2019). The spine of *Australopithecus*. In E. Been, A. Gómez-Olivencia, & P. A. Kramer (Eds.), *Spinal evolution: Morphology, function, and pathology of the spine in hominoid evolution* (pp. 125–151). Springer.
- Williams, S. A., Ostrofsky, K. R., Frater, N., Churchill, S. E., Schmid, P., & Berger, L. R. (2013). The vertebral column of *Australopithecus sediba*. *Science*, 340, 1232996.

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