



The Neanderthal cervical spine revisited

Carlos A. Palancar^{a,*}, Daniel García-Martínez^{b,c}, Markus Bastir^a

^a Group of Paleoanthropology, Department of Paleobiology, Museo Nacional de Ciencias Naturales (CSIC), 28006, Madrid, Spain

^b Physical Anthropology Unit, Biodiversity, Ecology and Evolution Department, Universidad Complutense de Madrid, 28040, Madrid, Spain

^c Laboratory of Forensic Anthropology, Centre for Functional Ecology, Department of Life Sciences, Universidade de Coimbra, 3000-456, Coimbra, Portugal



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ABSTRACT

Recent studies have challenged the long-held notion that Neanderthals possessed a more stable and less lordotic cervical spine than modern humans. To investigate this hypothesis further, we conducted the first three-dimensional geometric morphometric analysis focused on the Neanderthal cervical spine, examining 43 classic *Homo neanderthalensis* cervical vertebrae alongside 243 *Homo sapiens* cervical vertebrae from diverse populations, including the whole cervical spine (C1–C7). The Neanderthal sample comprises specimens from well-known individuals such as La Ferrassie 1, La Chapelle-aux-Saints 1, Kebara 2, Shanidar 2, Regourdou 1, and the Krapina group, ensuring completeness for a detailed analysis. Our results reveal a distinct morphological difference—that is greater in the lower levels—in the Neanderthal cervical spine, including a craniocaudally shorter and mediolaterally wider shape, longer spinous processes, and horizontally oriented articular facets. Contrary to earlier hypotheses, the study challenges the notion of reduced cervical lordosis in Neanderthals, proposing instead a potentially greater lordotic curvature than in modern humans, as evidenced by articulated mean forms and Cobb angle measurements. These findings suggest robust neck musculature adaptations in Neanderthals, potentially reflecting biomechanical responses to support the head and inhibit joint displacement. The study also highlights implications for respiratory biomechanics, with differences in the orientation of transverse processes (attachment site of the scalene muscle) potentially influencing neck muscle length and function, which could affect respiratory capacity in Neanderthals. In summary, our comprehensive examination sheds new light on the morphology and functional implications of the Neanderthal cervical spine, offering valuable insights into the intricate adaptations of Neanderthals and their implications for functional morphology and evolutionary biology.

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1. Introduction

The Neanderthal vertebral column has been a subject of interest since Boule's (1911–1913) initial descriptions, which, although now revised, provided the first comprehensive skeletal analysis of Neanderthals. Subsequent studies challenged Boule's interpretation, such as Straus and Cave (1957), who re-evaluated the posture and morphology of Neanderthal vertebrae, and Trinkaus (1983, 1985), who expanded on Neanderthal-modern human vertebral comparisons. Arambourg (1955) and Toerien (1955) contributed further to our understanding of Neanderthal cervical morphology examining vertebral adaptations in different Neanderthal specimens. More

recent works (Gómez-Olivencia et al., 2013a, 2013b; Meyer and Haeusler, 2015; Nalley and Grider-Potter, 2015, 2017; Meyer, 2016; Arlegi et al., 2017; Meyer et al., 2018; Haeusler et al., 2019; Beaudet et al., 2020) provide updated perspectives on the spinal morphology of Neanderthals, early hominins, and primates, with an emphasis on functional implications and methodological approaches for vertebral analysis. Together, these studies underscore the evolution of thought on Neanderthal spinal anatomy, setting a framework for current research.

Additionally, research shows that the Neanderthal axial skeleton provides valuable insights into various aspects such as neck kinematics (Palancar et al., 2024), paleoecology (Bastir et al., 2020), physiology (García-Martínez et al., 2014, 2018; Gómez-Olivencia et al., 2018), and even social behavior, including inbreeding (Ríos et al., 2019; Palancar et al., 2020b). While Neanderthal thoracic vertebrae and the entire ribcage have been studied using geometric

* Corresponding author.

E-mail address: palancar.carlos@gmail.com (C.A. Palancar).

morphometrics (Bastir et al., 2015, 2017), revealing new insights into the spatial arrangement of anatomical features, these recent methods for three-dimensional (3D) analysis have yet to be applied to the Neanderthal cervical spine.

1.1. Neanderthal cervical spine

More than 10 years ago, Gómez-Olivencia et al. (2013a) conducted the most exhaustive study to date focused on the Neanderthal cervical spine, analyzing several traditional measurements. In that work, the authors highlighted several differences in the Neanderthal cervical morphology, compared to modern humans, at all cervical levels.

Gómez-Olivencia et al. (2013a) measured 20 variables in the atlas vertebrae. In comparison to modern humans, the Neanderthal atlas exhibited several distinct features: a dorsoventrally elongated canal, a mediolaterally larger atlantoaxial joint, an anteroposteriorly larger lower articular facet, a smaller posterior tubercle, smaller tubercles for transverse ligament insertion, and an anterior tubercle projecting caudally. However, among these differences, only four characteristics (canal dorsoventral diameter, anterior tubercle thickness, transverse diameter of the fovea dentis, and posterior tubercle thickness) significantly differed from the means for modern humans and not in all studied atlases (i.e., the atlas of Regourdou does not present any dimension significantly different from modern humans).

Gómez-Olivencia et al. (2013a) measured 18 variables in the axis vertebrae. Compared to modern humans, the Neanderthal axis had a mediolaterally larger atlantoaxial joint, wider vertebral canal, smaller total height, smaller height of the dens, and a dorsoventrally and mediolaterally wider vertebral body in the inferior view. Those differences were out of the range of modern humans only in one (two maximum) Neanderthal axis.

Gómez-Olivencia et al. (2013a) measured 27 variables in the lower cervical vertebrae (C3–C7). Compared to modern humans, Neanderthal subaxial cervical vertebrae were mediolaterally wider in absolute and relative (vs. canal width) terms and dorsoventrally longer, with craniocaudally shorter vertebral bodies and longer and more horizontally oriented spinous processes. As in the upper cervical vertebrae, those measures were out of the range of modern humans in at least one Neanderthal but not in all of them.

Gómez-Olivencia et al. (2013a) concluded that Neanderthal vertebrae are mediolaterally wider and dorsoventrally longer than those of modern humans, partly due to their longer, more horizontally oriented spinous processes. As a result, the Neanderthal neck would have been more stable in both the mid-sagittal and coronal planes. More recently, Been et al. (2017) analyzed the spinopelvic alignment within hominins, estimating a reduced cervical lordosis in Neanderthals. Been and Bailey (2019) further described several morphological characteristics found in Neanderthals that are also present in modern humans with cervical hypolordosis and reduced mobility of the neck. However, Palancar et al. (2024) recently demonstrated that the hypothesis of limited Neanderthal neck mobility is unfounded when experimental methods (applied to modern humans and extrapolated to Neanderthals) are used. Indeed, they found that Neanderthals would likely have had a similar range of motion in the upper cervical spine. Haeusler et al. (2019) studied the Neanderthal of La Chapelle-aux-Saints 1, proposing a “usual human (...) neck curvature” for this individual (Haeusler et al., 2019: 4923). Taking into account that the previously hypothesized reduced lordosis has been measured in a few—and mostly incomplete—Neanderthals (La Chapelle-aux-Saints 1, Shanidar 1, La Ferrassie 1, Gibraltar, Tabun 1 [Been et al., 2017]) or assumed by extrapolating from modern human condition (Been and Bailey, 2019), analyzing variation in more complete

Neanderthal individuals and the Neanderthal mean condition via 3D geometric morphometrics could contribute to a better understanding of Neanderthal cervical morphology.

Objectives Thus, applying 3D modeling methods in this context is expected to yield working hypotheses and reference samples that can be used for comparison with new material, such as Simanya (Morales et al., 2023). To the best of our knowledge, we present the first virtual anthropology analysis of the Neanderthal cervical spine, using 3D methods to achieve two specific goals.

- 1) Study morphological differences in cervical vertebrae: To investigate whether Neanderthals exhibit distinct cervical vertebrae form compared to modern humans, exploring potential functional or biomechanical implications of these differences.
- 2) Assess cervical lordosis differences: To assess whether Neanderthals had a reduced cervical lordosis compared to modern humans, evaluating potential differences in spinal curvature that could have influenced posture, biomechanics, or respiratory function.

2. Material and methods

2.1. Material

The Neanderthal sample (Table 1) includes the cervical vertebrae ($n = 43$) of several of the best-known, most complete, and most extensively studied Neanderthals: La Ferrassie 1 and La Chapelle-aux-Saints 1 housed at the Musée de l'Homme (Paris, France), Kebara 2 and Shanidar 2 casts from the Musée National de Préhistoire (Les Eyzies, France), Regourdou 1 casts housed at the Musée d'art et d'archéologie du Périgord (Perigueux, France), and Krapina individuals from Croatian Natural History Museum (Zagreb, Croatia). Since the original fossils of La Quina 5 and Shanidar (except for Shanidar 3) are lost, the sample examined here represents most of the original material available for study. While the sample used by Been et al. (2017) (La Chapelle-aux-Saints 1, Shanidar 1, La Ferrassie 1, Gibraltar, and Tabun 1) provided valuable insights, our sample includes a greater number of more complete individuals (three vs. one). This is particularly advantageous when aiming to reconstruct and articulate the entire cervical spine, as well as to measure lordosis.

Neanderthal pathologies Several Neanderthal individuals in this study exhibit pathologies affecting the cervical vertebrae morphology. Regourdou 1 C3 shows small grooves for the accommodation of the posterior lamina of the transverse processes of C2 (Gómez-Olivencia et al., 2013b). La Ferrassie 1 cervical spine shows osteophytic growth in almost all articular facets—unciform joints of C3 deformed and an exostosis in the C1 left transverse foramen (Gómez-Olivencia, 2013a). La Chapelle-aux-Saints 1 presents exostosis and bone degeneration in several cervical levels, especially in the inferior ones (Trinkaus, 1985). Half of the Krapina cervical vertebrae show osteophytes in both the vertebral bodies and the left articular facets (Trinkaus, 2016). To avoid issues in quantifying vertebral morphology in specimens with pathology, we implemented the following precautions: 1) not measuring poorly preserved regions or those with common pathologies, such as the transverse foramen; 2) avoiding the measurement of osteophytic rims on vertebral bodies or articular facets (measuring only up to the point where the exostosis begins, as shown in Supplementary Online Material [SOM] Fig. S1); and 3) estimating the geometry of the affected region when the previous options were not feasible, as was the case, for example, with some uncinate processes or lacking structures (estimation protocol is explained in detail below).

For the modern human sample, a total of 243 cervical vertebrae from 35 individuals were measured from various osteological

Table 1
Sample composition.

Species	Population/site	Sex	Osteological collection	C1	C2	C3	C4	C5	C6	C7	Total
Modern humans	Europeans	Male	Madrid, Spain ^a	12	12	13	13	13	13	13	89
		Female	Madrid, Spain ^a	5	4	5	5	5	5	5	34
	Africans	Male	Coimbra, Portugal ^b	4	5	4	5	5	5	5	33
		Female	Coimbra, Portugal ^b	4	5	5	5	5	5	5	34
	Inuits	Male	New York, USA ^c	4	4	4	4	4	4	4	28
			Copenhagen, Denmark ^d	4	4	3	3	3	3	2	22
		Female	New York, USA ^c	4	4	3	4	4	4	4	27
			Copenhagen, Denmark ^d	4	4	4	4	4	4	4	28
	Total	Unknown	Copenhagen, Denmark ^d	3	3	3	3	3	3	3	21
			Male	24	25	24	25	25	24	172	
		Female	17	17	17	18	18	18	123		
		Unknown	3	3	3	3	3	3	21		
Total		44	45	44	46	46	46	45	316		
Neanderthals	Krapina ⁱ	Original	Zagreb, Croatia ^e	2	3	2	1	2	1		11
	La Ferrassie 1 ^j	Original	Paris, France ^f	1	1	1	1	1	1	7	
	La Chapelle-aux-Saints 1 ^k	Original	Paris, France ^f	1	1		1	1	1	6	
	Regourdou 1 ^l	Cast	Perigieux, France ^g			1	1	1	1	5	
	Shanidar 2 ^m	Cast	Les Eyzies, France ^h	1	1	1	1	1	1	7	
	Kebara 2 ⁿ	Cast	Les Eyzies, France ^h	1	1	1	1	1	1	7	
	Total			6	7	6	6	7	6	5	43

Detailed fossil descriptions and images can be found at:

^a Universidad Complutense de Madrid, Madrid (Spain).

^b Dryas Octopetala, Coimbra (Portugal).

^c American Museum of Natural History, New York (USA).

^d University of Copenhagen, Copenhagen (Denmark).

^e Croatian Natural History Museum, Zagreb (Croatia).

^f Musée de l'Homme, Paris (France).

^g Musée d'art et d'archéologie du Périgord, Perigieux (France).

^h Musée National de Préhistoire, Les Eyzies (France).

ⁱ Trinkaus (2016).

^j Gómez-Olivencia (2013a).

^k Gómez-Olivencia (2013b).

^l Gómez-Olivencia et al. (2013b).

^m Trinkaus (1983).

ⁿ Arensburg (1991).

collections (Europeans, Africans, and Inuit). The European sample was obtained from the osteological collection of the Escuela de Medicina Legal (Universidad Complutense de Madrid, Spain). The African sample is an archaeological sample (15th–17th centuries) of enslaved individuals, most likely from the Gulf of Guinea region, exhumed from the Valle da Gafaria site (Lagos, Portugal) (Wasterlain et al., 2016; Ferreira et al., 2019) that is housed at Dryas Octopetala (Coimbra, Portugal). The Inuit sample was obtained from two different collections: Greenland Inuit housed at the Panum Institute (Faculty of Health Sciences, University of Copenhagen, Denmark) and Alaskan Inuit housed at the American Museum of Natural History (New York, USA). Information on age at death and sex was recorded for all individuals. To achieve a balanced sample, we ensured that vertebrae per level, sex, and population were as evenly represented as possible (Table 1). None of the vertebrae used in this study presented any pathological condition affecting its morphology. The difficulty of determining the level of isolated subaxial cervical vertebrae is high. However, individuals analyzed in this study preserved the entire cervical spine or were missing only one vertebra in the series, allowing us to determine cervical levels by manually assembling the cervical vertebrae through their interarticular facet fit.

Data collection followed the standard workflows for virtual morphological methods described by Bastir et al. (2019). All vertebrae were scanned with a high-resolution (0.05 mm) Artec Space Spider 3D surface scanner based on blue-light technology (Artec Spider, Artec Group, Luxembourg). Postprocessing of the scans (cleaning, smoothing, and aligning) was performed in Artec Studio v. 12 software.

2.2. Geometric morphometrics

Each 3D vertebral model was measured separately using a previously tested template of digitization, employing both landmarks and curved semilandmarks in Viewbox v. 4.0 (Kifisia, Greece). Atlas shape was measured with 107, axis with 66, and subaxial cervical vertebrae with 81 (semi)landmarks (Fig. 1).

Because most fossil vertebrae lacked at least one landmark or semilandmark, missing data estimation was necessary. For this purpose, we used the function 'estimate.missing' in geomorph v. 4.0.5 (Adams et al., 2017). The selected method thin-plate spline interpolates landmarks by deforming the mean of the reference sample to estimate the locations of missing landmarks and semilandmarks on a target specimen (Gunz et al., 2009). Missing data estimation was performed using as reference the same cervical level as the target vertebra (i.e., the estimation of missing landmarks of the fourth cervical vertebra of Kebara 2 was performed using all Neanderthals C4 as the reference sample). Information on all landmarks that needed estimation can be found in SOM Tables S1–S3. Shape coordinates of all analyzed vertebrae were uploaded to Mendeley Data (<https://doi.org/10.17632/xm475r894v.1>).

Semilandmarks were reslid along tangents to their respective curves, following a protocol that minimizes bending energy between the mean shape and each vertebra's shape (Gunz et al., 2005; Gunz and Mitteroecker, 2013), using the 'RelaxLM' function within package Morpho v. 2.11 (Schlager, 2017).

Landmark and semilandmark configurations were iteratively translated to a common origin, isometrically scaled to unit centroid

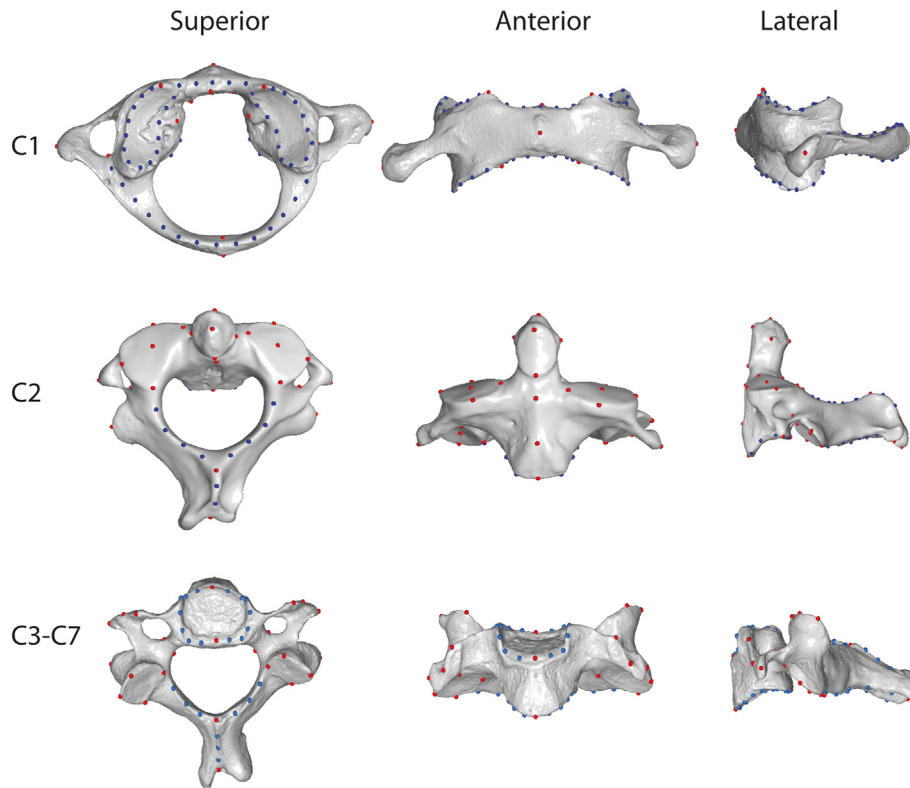


Figure 1. Digitization template of C1, C2, and subaxial cervical modern human vertebrae. Landmarks are shown in red and curve semilandmarks in blue. Modified from Palancar et al. (2021). Note that the subaxial cervical vertebrae are measured with a template that allows digitization of both bifid and nonbifid spinous processes, measuring the most posterior end in the mid-sagittal plane and also left and right margins of the process in the inferior view. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

size, and rotated to minimize the Procrustes distance between homologous landmarks, following generalized Procrustes analysis (Gower, 1975). Procrustes analysis was performed with the function 'procSym' in Morpho v. 2.11 (Schlager, 2017). This analysis yielded Procrustes shape coordinates, which do not contain size information. To include size information in the analysis of shape—defined as form—Procrustes analysis is performed without the scaling step (Mitteroecker et al., 2013), also with the function 'procSym' in Morpho v. 2.11 (Schlager, 2017), and yielded form coordinates.

Shape or form differences between species were assessed through Procrustes distances. Procrustes distance (i.e., the Euclidean distance between the two sets of landmarks in shape/form coordinates) is a measure of shape difference between two objects: it is zero only when two objects have the same shape (O'Higgins, 2000; Gunz et al., 2009; Mitteroecker and Gunz, 2009; Gunz and Mitteroecker, 2013). Mean shape/form comparisons were conducted between Neanderthals and modern humans at each cervical level. The statistical significance ($p < 0.05$) of these mean shape/form comparisons was based on permutation tests of Procrustes distances between means carried out in RStudio using the function 'permudist' in Morpho v. 2.11 (Schlager, 2017).

To assess serial shape and form differences, a principal component analysis was conducted on both shape and form Procrustes coordinates using the function 'gm.prcmp' in geomorph v. 4.0.5 (Adams et al., 2017).

2.3. Cervical lordosis

To analyze cervical lordosis, we obtained the mean form of every cervical level separately for Neanderthals and modern humans.

Once we have the mean cervical vertebrae of each species, we articulate them looking for the osteologically neutral posture (ONP): two vertebrae are in ONP if their faces are parallel and the zygapophyses overlap fully. This method was described by Mallison (2010), applied in modern humans by Bastir et al. (2019), and validated in the human thoracic spine by Bastir et al. (2020) and López-Rey et al. (2024). Specifically, starting from C7, articulation of C6 was performed looking for the maximum overlap of the zygapophyses and the most possible parallelism between the superior endplate of C7 and the inferior endplate of C6. Then, C6 is articulated with C5, and so on. Articulation of the atlas and axis—as there is no vertebral body in the atlas—was performed looking for the parallelism of the posterior arch of the atlas and the spinous process of the axis.

Posteriorly, cervical lordosis was measured following Been et al. (2014): Cobb angle was measured between the line parallel to the foramen magnum (FM) and the line parallel to the inferior endplate of the last cervical vertebra (C7). Since the FM is not studied here, we used a line parallel to the superior articular facets (SAFs) of the atlas as a proxy.

3. Results

3.1. Mean form comparison

The mean form was compared between Neanderthals and modern humans for the atlas, axis, and C3–C7 cervical levels (Fig. 2).

Atlas (C1) Compared to modern humans, the Neanderthal atlas shows a greater anteroposterior dimension in both the entire

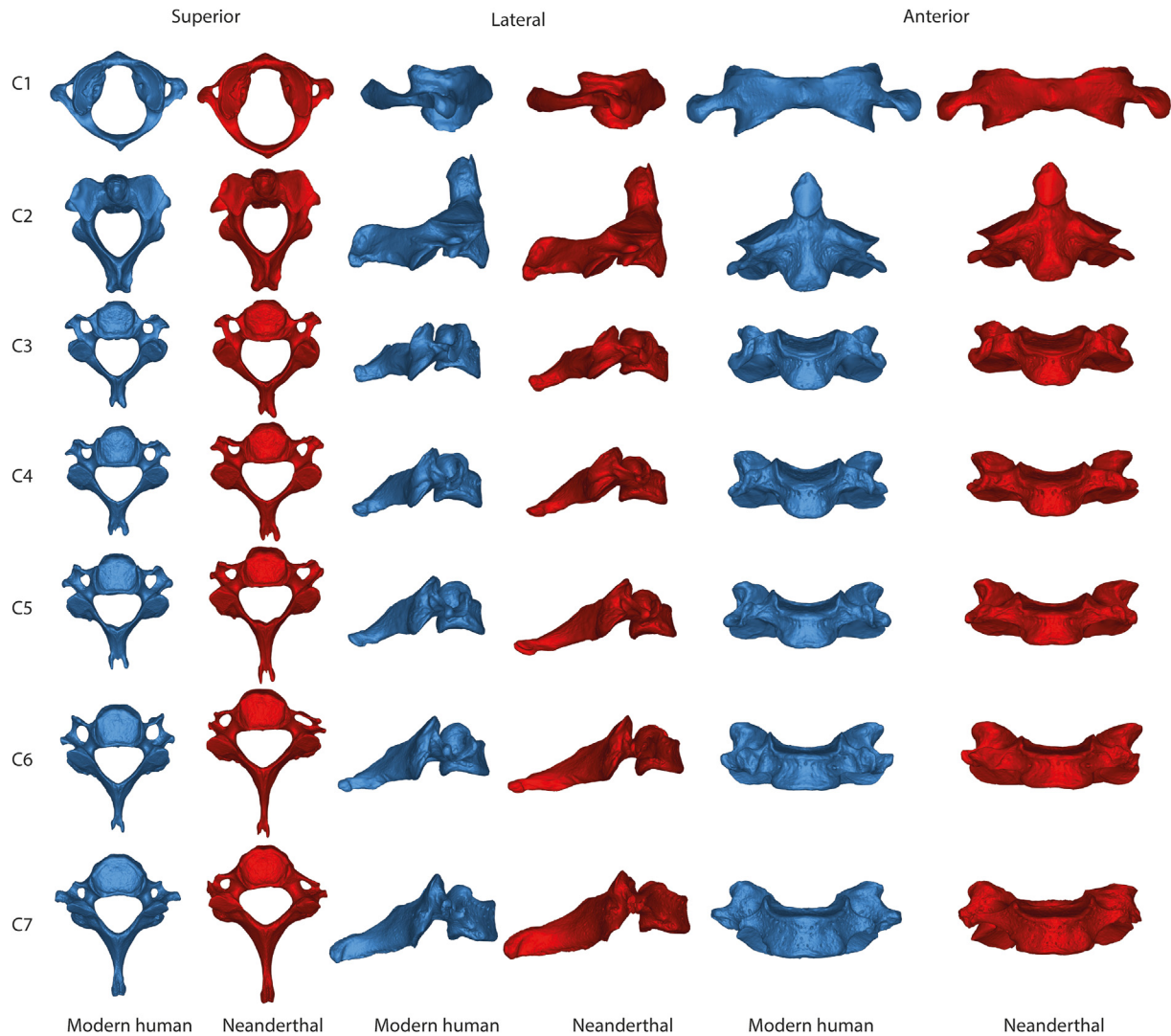


Figure 2. Mean form of each cervical level by species. Neanderthal specimens are shown in the left, in red and modern humans in the right, in blue. Note that, even if they seem to be bifid, spinous processes are not digitized to compare the presence of bifid and nonbifid individuals. None of the Neanderthal lower cervical vertebrae are bifid. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

vertebra and the neural canal. The posterior tubercle is reduced in Neanderthals, and the anterior tubercle projects inferiorly. In addition, the SAFs are longer and flatter. The lateral masses are craniocaudally shorter. Mean differences are statistically significant for both shape and form spaces (Table 2).

Axis (C2) Compared to modern humans, the Neanderthal axis displays an odontoid process oriented anteriorly and a spinous process oriented more horizontally. The vertebral body is reduced both mediolaterally and anteroposteriorly and is less curved. The neural canal is mediolaterally wider. Mean differences were statistically significant in both shape and form spaces (Table 2).

Lower cervical vertebrae (C3–C7) All Neanderthal subaxial cervical vertebrae, compared to modern humans, have craniocaudally shorter vertebral bodies, shorter uncinat processes, a larger neural canal, and longer, more horizontally oriented spinous processes (though this last feature is less evident in C3 and C4). Upper articular facets are more horizontally oriented, except in C7. Regarding the mediolateral orientation, Neanderthal vertebrae's SAFs are more medially oriented at all levels, although the greatest difference compared to modern humans is found on the C7. Lateral

processes from C3 to C5 are more anteriorly oriented in Neanderthals, while in C6 and C7, they are more posteriorly oriented.

The observed morphological differences are not statistically significant across all cervical levels (Table 2). As shown by Procrustes distance comparisons, Neanderthal upper subaxial cervical

Table 2

Procrustes distances (PDs) between Neanderthal and modern human cervical vertebrae by vertebral level and results of tests of significance (permutation tests) between species.

Vertebral level	Shape		Form	
	PD	<i>p</i> value	PD	<i>p</i> value
C1	0.068	0.009	18.31	0.039
C2	0.064	0.008	10.34	0.045
C3	0.081	0.155	16.52	0.135
C4	0.087	0.102	15.95	0.164
C5	0.101	0.053	23.34	0.047
C6	0.133	0.008	28.49	0.009
C7	0.115	0.051	25.18	0.058

levels (C3 and C4) together with the seventh are not significantly different from those of modern humans (SOM Fig. S2; Table 2). However, significant morphological differences are present at the fifth and sixth cervical vertebral levels (Table 2).

3.2. Cervical lordosis comparison

The mean forms of each cervical level were articulated using the ONP method for each species (Fig. 3). Compared to modern humans, the Neanderthal cervical spine is craniocaudally shorter, mediolaterally wider, and anteroposteriorly longer. After articulating the mean cervical spines, the Cobb angle for cervical lordosis was measured as 40° in modern humans and 48° in Neanderthals (Fig. 4).

As shown in the first principal component plots, differences between modern humans and Neanderthals are evident in the shape (Fig. 5B), but not in the form (Fig. 5A), of the cervical spine. These results highlight the importance of 3D shape analysis. While both trajectories are similar in form space, a differentiation beginning at C5 is apparent in shape space. Centroid size analysis reveals a similar pattern (Fig. 6), with no significant differences in size progression between Neanderthals and modern humans.

4. Discussion

4.1. Mean form comparison

Upper cervical spine As previously found by Palancar et al. (2020a), the Neanderthal atlas displays a flatter C1 SAF. Nalley and Grider-

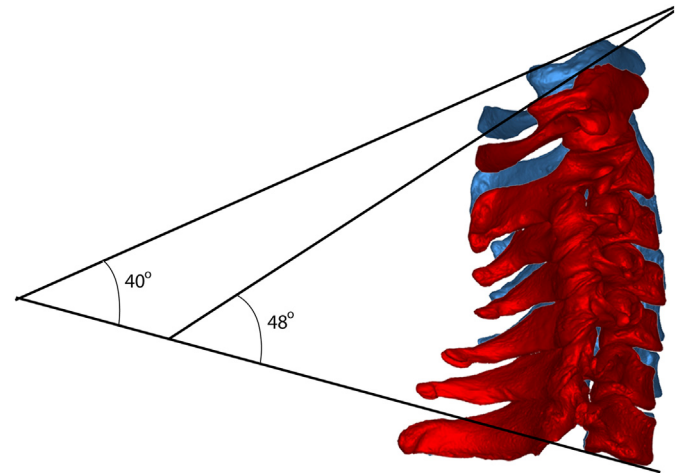


Figure 4. Cervical lordosis Cobb angle measurement of both Neanderthal (red) and modern human (blue) mean cervical spine. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Potter (2017) identified a significant relationship between the concavity of the C1 SAF and the horizontal orientation of the neck in hominoids. A greater concavity of the C1 SAF has been interpreted as providing greater joint stability and limiting joint displacement (Demes, 1985; Strait and Ross, 1999; Gommery, 2006; Levangie and Norkin, 2011). However, the lower concavity of C1 SAF in

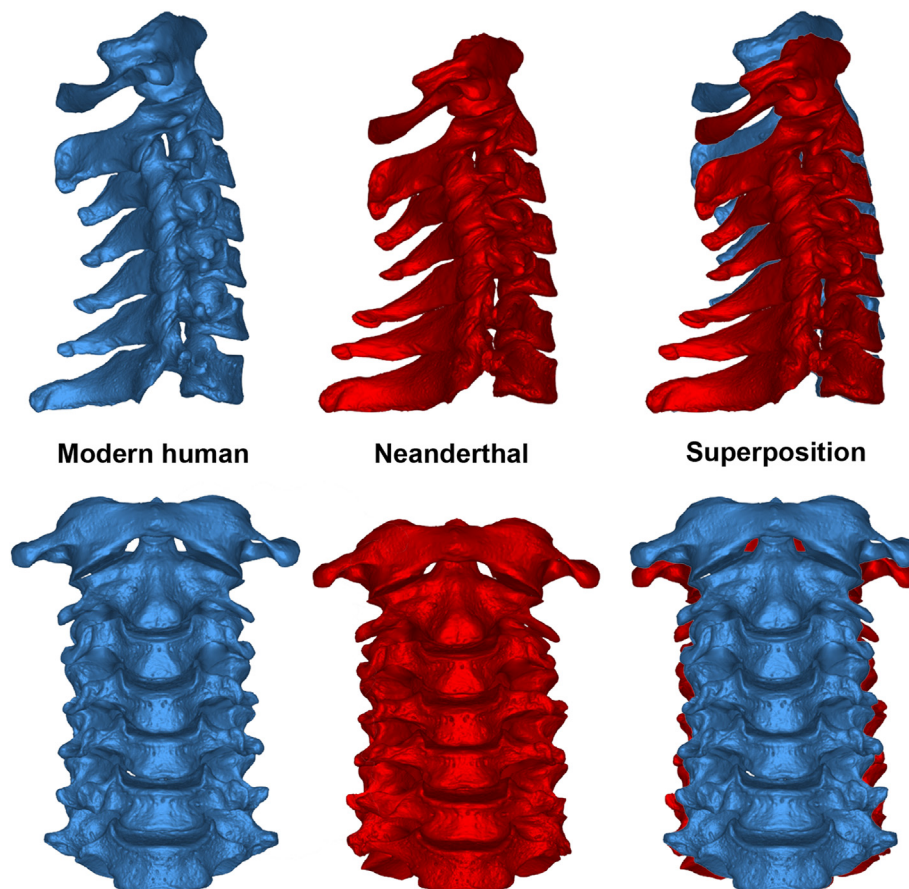


Figure 3. Articulated mean cervical spines by species in lateral (top) and anterior (bottom) views. The third view is the superposition of Neanderthals (red) and modern humans (blue) to facilitate visualization of differences. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

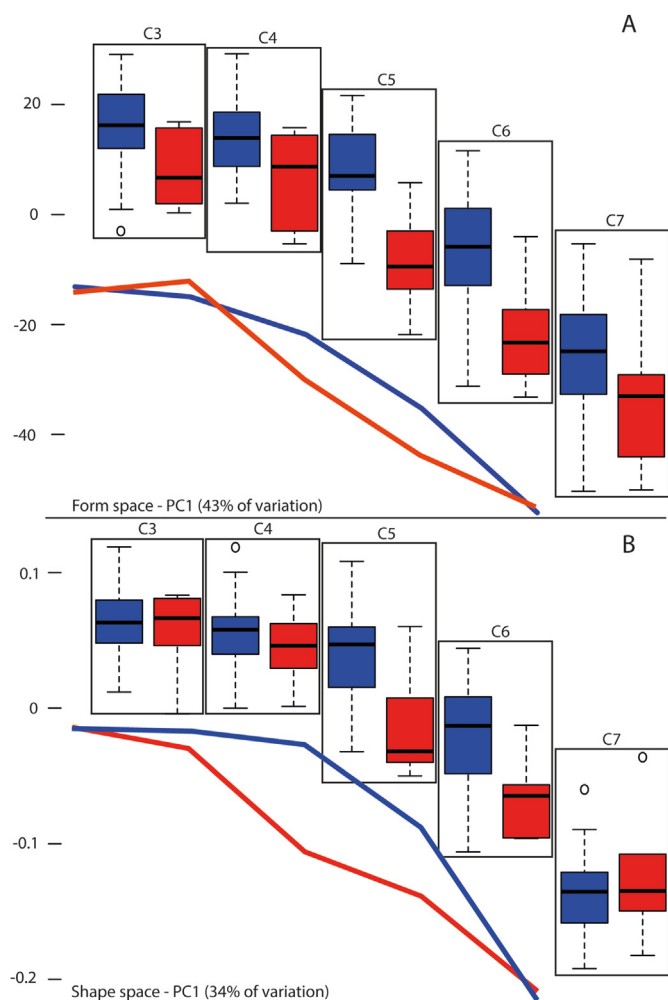


Figure 5. First principal component (PC) box and jitter plots in form (A) and shape (B) spaces. Principal component 1 accounts for 34% of total variation in shape space and 43% in form space. The lines represent the change in the PC scores by level in each species. Note that the difference between the trajectories of the lines is greater in shape space and starts at C5. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

Neanderthals does not provoke differences in joint stability compared to modern humans, as recently tested by Palancar et al. (2024).

To the best of our knowledge, this study is the first to demonstrate that the odontoid process of Neanderthals is more anteriorly oriented (i.e., more vertical) than in modern humans. The orientation of the odontoid process has been widely analyzed in hominoids, with studies indicating that species with a more vertical neck posture have anteriorly oriented odontoid processes (Aiello and Dean, 2002; Gommery, 2006; Meyer, 2016; Nalley and Grider-Potter, 2017). This has been attributed to a biomechanical response to lower energetic requirements of the nuchal musculature by positioning the weight of the skull to be better supported by the entire cervical column (Nalley and Grider-Potter, 2017). However, it is important to recognize that the orientation of the odontoid process is not solely indicative of postural differences between Neanderthals and modern humans. Instead, it is part of a complex anatomical system that integrates with cervical lordosis and the cranial base. The odontoid angle is influenced by the morphology of the sphenoid-occipital clivus and the orientation of the FM, with a shorter clivus leading to a ventroflexed FM and a more vertical orientation of the odontoid process (Meyer and Williams, 2019).

This relationship is particularly significant in primates with a dorsally oriented FM, where retroflexion of the FM is often accompanied by retroflexion of the odontoid process (Kimbel and Rak, 2010; Meyer and Williams, 2019). Additionally, clinical studies on conditions like platybasia (basion is not above the plane of opisthion) have demonstrated an association with odontoid retroflexion (McKenna et al., 2006). Therefore, it may be premature to suggest that differences in odontoid orientation directly reflect differing postural regimes without considering these integrated anatomical patterns in the cranial base and upper cervical spine (Villamil, 2018).

Lower cervical spine There are several differences between Neanderthals and modern humans at the subaxial vertebral levels that are also relevant for posture.

A significant difference is the orientation of the SAFs, which are more horizontally and medially oriented in Neanderthals than in modern humans. Regarding the mediolateral orientation, our findings differ from those of Arlegi et al. (2017), who reported that at the lowest cervical levels (C6 and C7), the SAFs of Neanderthals were more laterally oriented than in modern humans (but not at C5). They suggested that this feature could be linked to the lateral positioning of the articular pillars in Neanderthals and associated with wider vertebral canals. While we also observe these two latter characteristics in Neanderthal vertebrae, our findings on lateral orientation require further investigation. Arlegi et al. (2017) found a notable difference in mediolateral orientation between C5 and the lower levels (C6 and C7), with the fifth cervical vertebra being more medially oriented and the sixth and seventh more laterally oriented (than in modern humans). However, as their study was based on four Neanderthal vertebrae, a more comprehensive analysis is needed.

Regarding the craniocaudal orientation, Nalley and Grider-Potter (2015) detected a relation between the facet angle and neck posture in humans and other Primates. As a coronally oriented articular facet provides stability, it is present in the necks of prognathic species. Thus, the horizontally oriented articular facets of Neanderthals would make the cervical vertebrae more unstable than in modern humans as the coronally oriented articular facets are related to a greater resistance to ventral displacement in Primates, limiting flexion and extension (Nalley and Grider-Potter, 2015).

The uncinat process height and shape were recently studied in several human and nonhuman primates by Meyer et al. (2018). They found a relationship between the uncinat process and locomotor pattern, with arboreal taxa displaying a greater height of the uncinat process, possibly linked to increased stability of the cervical spine. Nonarboreal hominins (such as *Homo erectus*) exhibit a reduced uncinat process, favoring mobility over stability (Meyer et al., 2018). Neanderthals also exhibit a reduced uncinat process, expected for nonarboreal locomotion patterns, and it is even more reduced than in modern humans. This could also be a consequence of more generalized less vertical development within the spine in this species.

These last two features (uncinac process height and horizontally oriented articular facets) could be related to the greater length of the Neanderthal spinous processes. As these characteristics, together with the flatness of the C1 SAFs of the atlas, confer a greater instability to the Neanderthal cervical spine, neck muscles need to be stronger to avoid joint displacement and cervical whiplash, leading to a greater spinous process length, similar to what is observed in great apes (Nalley and Grider-Potter, 2015). Additionally, previous literature suggests that the length of cervical spinous processes may be related to facial prognathism as prognathic faces tend to result in an extended head posture, which in turn increases loading at the spinous processes (Motoyoshi et al.,

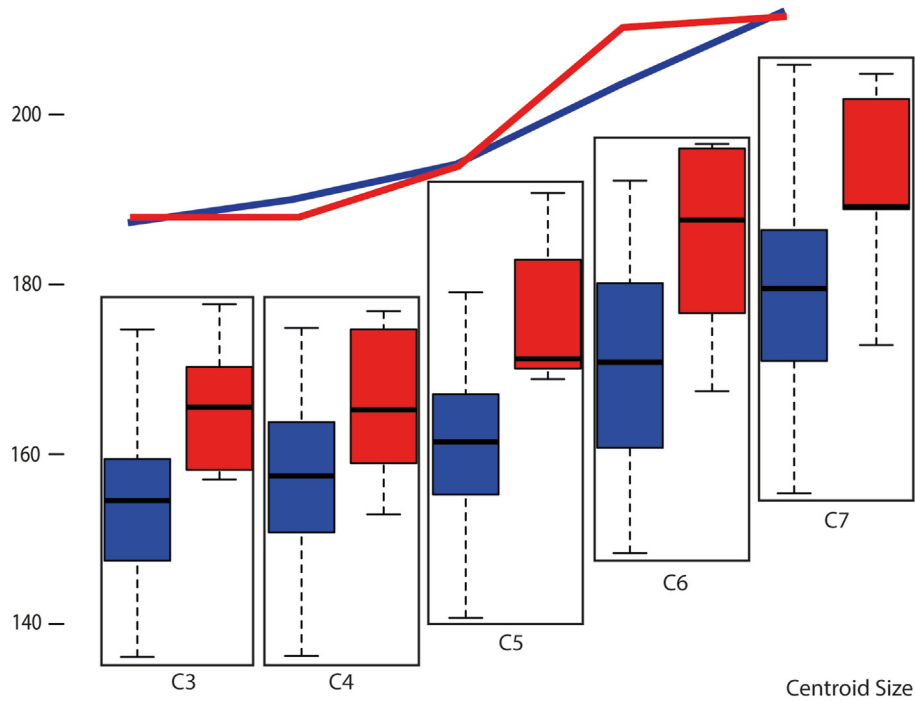


Figure 6. Centroid size (CS) box and jitter plot. The lines represent the change in CS by cervical vertebral level in each species. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

2002; Solow and Sandham, 2002). This loading is partly due to the large anterior moment arm caused by prognathism, which necessitates counterbalancing moments posterior to the head's center of gravity (Graf et al., 1995; Meyer, 2005, 2016). Furthermore, the large C2 spinous process in Neanderthals has been interpreted as a potential adaptation to ventral loading incurred during parmastication (Trinkaus, 1987).

Shorter vertebral bodies, as observed in Neanderthals, may also reduce the bending moments around the apophyseal joints (Graf et al., 1995; Meyer, 2005), contributing to improved head balance over the spinal column, as shorter and wider vertebrae present less movement around their vertical axis. The reduced vertebral body height is also found in the thoracic (Bastir et al., 2017) and lumbar (Gómez-Olivencia et al., 2017) vertebrae of Neanderthals. It seems like the cervical spine also shares the general bauplan of Neanderthals, with wide, short, and massive bodies (Churchill, 2006). Indeed, except for the atlas, modern human cervical vertebrae show high integration values (Arlegi et al., 2018). Even so, the integration of the spine should be studied taking into account more species of *Homo*.

The orientation of the transverse processes is also different, with a more anterior positioning in Neanderthals (C2–C5). The cervical transverse processes are variable across primates, specifically referring to length and orientation (Schultz, 1942), and recently, Nalley and Grider-Potter (2015) did not find a clear relation between transverse process angle and neck posture. However, this different orientation in Neanderthals could induce differences in cervical biomechanics and will be discussed below. A better understanding of these biomechanical factors is essential to fully appreciate the functional implications of Neanderthal cervical spine morphology.

4.2. Cervical lordosis comparison

Contrary to previous hypotheses, Neanderthals may not have a reduced lordosis. Cervical lordosis in modern humans (40°) is

consistent with findings from previous studies performed on adults, measuring Cobb angles 37.3° (Been et al., 2014) and 38° (Been et al., 2017). However, here we propose a greater Neanderthal cervical lordosis (48°). Our results are in line with the work of Haeusler et al. (2019), who found a cervical and lumbar lordosis similar to that of modern humans for La Chapelle-aux-Saints 1 Neanderthal. The proposed reduced Neanderthal cervical lordosis of 26° estimated by Been et al. (2017) was based on five individuals: La Chapelle-aux-Saints 1, Shanidar 1, La Ferrassie 1, Gibraltar, and Tabun 1. Although these authors measured cervical lordosis following the same method used here, there is no clear explanation of the method they used to articulate the cervical vertebrae of those fossil individuals. Besides, various individuals have incomplete cervical spines, making the articulation and measuring of cervical lordosis difficult. In addition, they measured modern human cervical lordosis on spinal radiographs of living humans in a standing upright position. So, taking into account that in the present work, both cervical spines (modern humans and Neanderthals) were articulated and measured using the same methods and that the Neanderthal sample constitutes a larger amount of both isolated elements and complete individuals, the greater estimate of cervical lordosis of Neanderthals would gain support.

It is important to mention that it is the shape and not the size that is driving this cervical lordosis difference. As shown by the first principal component in shape space (Fig. 5B), the trajectory of the cervical vertebrae differs at C5 and C6 levels. Contrary, in form space (Fig. 5A) and centroid size trajectories (Fig. 6), there are no such differences between modern humans and Neanderthals. Thus, it is in the shape—and more specifically, the shape of C5, C6, and C7 (SOM Fig. S2)—where cervical lordosis differences reside. Indeed, in mean form comparison (Fig. 2), no great differences are appreciated at C3 and C4 levels between Neanderthals and modern humans.

Biomechanics Differences in the orientation of the transverse processes and the height of the cervical spine affect the neck musculature orientation and length. For example, the anterior scalene

muscle is inserted in the transverse process of the C2–C6 vertebrae (origin) and the superior aspect of the sternal extreme of the first rib. It intervenes directly in the elevation of the rib cage during inspiration (Legrand et al., 2003). As the transverse processes of the cervical vertebrae are more anteriorly oriented and the total height is lower in Neanderthals than in modern humans, the anterior scalene would also be shorter and more horizontally oriented. The shortening and different orientation of this muscle of the Neanderthal neck and the lesser axial curvatures of the first ribs (Bastir et al., 2015) could affect the respiratory motion and should be the focus of future analyses.

In addition, recent work (Palancar et al., 2024) has suggested on experimental data that the Neanderthal upper cervical spine could be more mobile than previously hypothesized. These new data on the entire and articulated cervical spine should be also studied in terms of mobility to test whether Neanderthals' neck is more stable and less mobile than that of modern humans. Several features such as the reduced uncinat process or the horizontally oriented articular facets suggest that the mobility could be greater in Neanderthals (Clausen et al., 1997; Nalley and Grider-Potter, 2015).

4.3. Study limitations

Neanderthal pathologies are a crucial limitation of the present work. As stated before, several Krapina vertebrae, La Ferrassie 1, La Chapelle-aux-Saints 1, and Regourdou 1 show at least one pathological condition. However, previous works analyzing the spine curvature in Neanderthals also used some of these individuals: La Ferrassie 1 and La Chapelle-aux-Saints 1 (Been et al., 2017; Haeusler et al., 2019). One advantage of the methodology used in the present study is that it avoids or estimates pathology-affected regions and reconstructs average cervical vertebrae. To avoid regions affected by pathology, landmarks influenced by factors such as osteophytic growth on the edge of the articular facet can be manually placed at the beginning of the exostosis (the true edge of the articular facet). An example is provided in SOM Figure S1. The estimation approach (thin-plate spline interpolation, explained in Section 2.2) minimizes the influence of conditions affecting isolated vertebrae, allowing for a more accurate assessment of 'normal' and average morphologies. Moreover, considering the high number of anomalies and pathologies present in Pleistocene populations (Trinkaus, 2018), this issue is consistently encountered in human evolution studies as there are few perfectly healthy specimens available for analysis. The only possible solution is to use more comprehensive techniques to address this problem and avoid the study of isolated cases, allowing for the examination of average morphologies. Even so, pathological specimens or vertebrae could be modifying the alignment of articular facets and misrepresenting the original Neanderthal curvature in the present study.

Regarding sample size, the Neanderthal sample includes only three individuals (La Ferrassie 1, Shanidar 2, and Kebara 2) that have all the cervical vertebrae preserved. Even so, among the samples used by Been et al. (2017), only one individual was complete (La Ferrassie 1) and Haeusler et al. (2019) studied a single (incomplete) individual (La Chapelle-aux-Saints 1). Even if the number of complete individuals is not high, it is higher than in previous studies and it is complemented by a great number of incomplete individuals from Krapina, Regourdou, and La Chapelle. Moreover, the fossil sample is always a problem in paleoanthropology that we only can address using the most comprehensive techniques and estimations as we have performed here.

Another primary limitation of this study is the challenge of accurately reconstructing cervical lordosis from fossil vertebrae. Cervical lordosis is not exclusive to humans but is present across all amniotes, including mammals, where the head is typically

maximally extended in static postures (Vidal et al., 1986; Taylor et al., 2009; Meyer and Williams, 2017, 2019). In humans and apes, the wedging angles of cervical vertebral bodies, except for the C7 vertebra, are kyphotic (Meyer, 2016). The physiological lordosis of the cervical spine is achieved primarily through the lordotic curvature of the intervertebral discs (Johnson, 1998), which are not preserved in fossil records. Therefore, estimating a specific value of Neanderthal cervical lordosis, such as the 48° Cobb angle reported in this study, is inherently uncertain without direct knowledge of the wedging angles of the cervical intervertebral discs. This contrasts with the lumbar region, where the intervertebral discs, except for the lumbosacral joint, have less influence on the wedging angles (Gogen et al., 2007). While we suggest that Neanderthals had a degree of cervical lordosis consistent with a healthy curvature, this estimation must be interpreted with caution given the absence of data on intervertebral disc morphology and its impact on cervical curvature.

5. Conclusions

In this study, 3D geometric morphometrics and virtual anthropology techniques for reconstructing neck posture have been applied to the study of the cervical vertebrae of Neanderthals and modern humans. By employing these techniques and incorporating samples that belong to more complete individuals, new and important features of Neanderthal cervical spine are discovered. Contrary to previous hypotheses, the cervical lordosis of Neanderthals may not be smaller than that of modern humans. In addition, a different orientation of the odontoid process of the axis is detected, being more anteriorly oriented in Neanderthals. That and other morphological characteristics of Neanderthals—such as the flatness of the SAFs of the atlas or the reduced uncinat process—suggest that the needs of the neck muscles to inhibit joint displacement and support the head might have been greater.

Declaration of competing interest

The authors have no conflicts of interest to declare.

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Author contributions

Carlos A. Palancar: Writing – original draft, Investigation, Formal analysis, Conceptualization. **Daniel García-Martínez:** Writing – review & editing, Supervision, Investigation, Data curation. **Markus Bastir:** Writing – review & editing, Funding acquisition.

Supplementary Online Material

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