JASs Journal of Anthropological Sciences Open Access
Research articles Vol. 99 (2021), pp. 97 - 116 doi.10.4436/jass.99015

Geometric Morphometrics of the human cervical vertebrae: sexual and population variations

Carlos A. Palancar[1,2], Daniel García-Martínez[3,4,5], David Cáceres-Monllor[6], Bernardo Perea-Pérez[6], Maria Teresa Ferreira[5] & Markus Bastir[1]

1) *1Museo Nacional de Ciencias Naturales (CSIC), Department of Paleobiology, Paleoanthropology Group. Madrid, Spain*
e-mail: palancar.carlos@gmail.com

2) *Universidad Autónoma de Madrid, Faculty of Sciences, Department of Biology. Madrid, Spain*

3) *Universidad Complutense de Madrid, Faculty of Biological Sciences, Department of Biodiversity, Ecology, and Evolution, Physical Anthropology Unit. Madrid, Spain*

4) *Centro Nacional de Investigación sobre la Evolución Humana, Burgos, Spain*

5) *University of Coimbra, Centre for Functional Ecology, Laboratory of Forensic Anthropology, Department of Life Sciences. Coimbra, Portugal*

6) *Universidad Complutense de Madrid, Faculty of Medicine, Department of Toxicology and Health Legislation, Madrid, Spain*

Summary - *This study aims to carry out the first geometric morphometric analysis of the 3D size and shape of the full series of cervical vertebrae delving into variability related to sex and population background. For this reason, we analyzed the cervical vertebrae of both males and females belonging to Europeans, Africans, and Greenland Inuit. We 3D-scanned a total of 219 cervical vertebrae of males and females of three different modern human populations (European, African, and Inuit). A minimum of 72 landmarks and curve semilandmarks were positioned in each of the 3D vertebral models. Landmark configurations were analyzed following the standards of 3D Geometric Morphometrics to test for size and shape differences related to sex or population variation. Results show that male cervical vertebrae are consistently larger than in females while no regular shape differences are observed between males and females in any of the populations. Sex differences in cervical lordosis are thus not supported at the skeletal level of the 3D shape. On the other hand, there is no evidence for population-specific differences in size while shape does vary considerably, possibly also in relation to eco-geographic factors of overall trunk shape. Cervical vertebrae in cold-adapted Inuit were consistently shorter than in Europeans and Africans. The cervical spine may show a different pattern than the thoracic and lumbar spine, which might be related to stronger integration with the cranium, head mobility, and soft-tissue dependence. Our findings suggest that morpho-functional interpretations of the cervical spine based on vertebral skeletal morphology requires caution.*

Keywords - *Atlas, Axis, Subaxial, European, African, Inuit.*

Introduction

The cervical spine connects the cranium with the postcranial skeleton and thus, it is an important anatomical region of the human body, being responsible for maintaining the visual field and its integration with the head and body posture (Strait and Ross 1999). Besides, several muscles of the neck, upper limbs, and trunk are attached to the cervical spine (Netter 2008). Despite this importance of the cervical vertebrae, its morphological 3D variation within modern humans is not well known. While recently several studies have been focused on the variability of the cervical vertebrae within fossil hominins and non-human primates (Arlegi et al. 2017; Beaudet et al. 2020; Gómez-Olivencia et al. 2013; Grider-Potter et al. 2020; Meyer 2016; Nalley and Grider-Potter 2015, 2017; Palancar et al. 2020a,b), and even some limited 2D geometric morphometric analyses have explored shape variation of the cervical uncinate processes (Meyer et al. 2017, 2018), the 3D shape variation of the extant human cervical vertebrae remains uncertain. A recent study (Palancar et al. 2020b) has identified differences in the orientation of the articular facets in Neandertals and modern humans, yet without knowledge about ranges of variation in different modern human populations, the functional interpretation of fossil evidence is difficult. Thus, better knowledge about the 3D variability in extant humans is important for the interpretation of the cervical morphology of fossil hominins. In this context, primary biological factors of variation such as geographic origin or sexual dimorphism are relatively unknown and no study has yet addressed the 3D features of cervical subaxial variation in this respect. For this reason, the main objective of this study is to increase our knowledge about the human cervical vertebrae 3D variability, taking into account sexual dimorphism and population variations.

Few studies have analyzed variation in cervical vertebrae morphology within *H. sapiens*. Regarding the sexual dimorphism, several authors performed statistical analyses to determine the sex of an individual through cervical vertebrae linear measurements (Reverte-Coma 1999; Marino,1995; Del Río and Sánchez 1997; Del Río et al. 2000; Wescott 2000; Medina et al. 2011; Gama et al. 2015). These studies have shown that size is a good sex discriminator but no shape differences were studied. However, more recently, Been et al. (2017) measured the lordosis of the entire cervical spine in radiographs of both males and females and concluded that the internal architecture of the cervical spine varies within sexes, with males showing a smaller upper (C1-C3) and higher lower cervical lordosis than females. This likely implies differences in the 3D structures of cervical vertebrae or suggest at least differences in the intervertebral disc morphology. In addition, Pan et al. (2018) found kinematic differences between males and females in the cervical region; specifically, they found that the range of motion of females was greater, although the difference in ranges between sexes varied with the age. For example, males and females in their 20s did not present differences in the range of motion, while females in their 30ies and 40ies presented a greater range of motion for flexo-extension and rotation movements than males of the same age group (Pan et al. 2018). Contrary to Pan et al.'s results, Lind et al. (1989) found that males had more extension, lateral bending, and rotation than females. The possible differences in the ranges of motion between sexes remain unclear. All these studies reveal the necessity of analyzing the sexual dimorphism of 3D size and shape in vertebral morphology, because the skeletal morphology, musculature, and ranges of motion are supposed to be highly related to each other (Bogduk and Mercer 2000; Mercer and Bogduk 2001).

However, all of these studies were based on linear measurements or ranges of motion and did not quantify the 3D shape of the cervical vertebrae morphology and thus, the sexual dimorphism in 3D shape and size is not clear. Nonetheless, in both the thoracic and the lumbar vertebrae the entire 3D shape variation has been analyzed concerning sex (Bastiret al. 2014; Lois-Zlolniski et al. 2019). Thoracic vertebrae of males show more dorsally oriented transverse processes, relatively larger vertebral bodies, and caudally oriented spinous processes than females, although this pattern is not equal in every thoracic level (Bastir et al. 2014). Regarding the lumbar spines, they are relatively narrower and craniocaudally elongated in females (Lois-Zlolniski et al. 2019). The spine, as the principal axis of the axial skeleton, is also the central pillar of the torso (thorax, lumbar spine, and pelvis), which connects the spine with ribs and pelvis. As an anatomical complex, the torso shows sexual dimorphism in 3D size and shape with larger males than females and with females having narrower thoraces and wider pelvis than the males (Torres-Tamayo et al. 2018a). Regarding the ribcage morphology, García-Martínez et al. (2016) also found statistical differences between sexes when analyzing the 3D shape with males showing wider, lower ribcages than females. Fischer and Mitteroecker (2017) analyzed more recently with 3D geometric morphometric the human pelvis shape variation in relation to sex and found a clear differentiation between sexes in the 3D morphology. All this evidence indicates that the cervical spine is the only anatomical region of the axial skeleton and related regions (the torso) that have not yet been analyzed under the focus of sexual dimorphism in a 3D perspective. One aim of this study is to fill this gap of knowledge.

We also investigate 3D shape variation related to potential differences between populations, a factor that to the best of our knowledge has not at all been addressed in cervical vertebrae. To date, only the prevalence of bifid spinous processes in subaxial cervical vertebrae (Duray et al. 1999; Asvat 2012) and eight metric distances of the atlas (Marino 1997; Swenson 2013) have been analyzed under the focus of population variability. Nevertheless, as occurring with sexual dimorphism, other anatomical structures related to the axial skeleton have been analyzed in this sense. Lois-Zlolniski et al. (2019) concluded that the population affects the morphology of the lumbar spine, with their Mediterranean sample being more lordotic than their South African sample. Geographic variation is very well studied in the craniofacial system. The entire cranium (Harvati and Weaver 2006; Galland and Friess 2016) the cranial base and mandible (Kuroe et al. 2004; Bastiret al. 2004), and the foramen magnum (Zdilla et al. 2017) show all different morphologies depending on the geographic and genetic origin of the individual. Taking this into account and the fact that craniofacial morphology, head posture, and cervical spine are highly related (Solow et al. 1984; Solow and Tallgren 1971, 1976; Tallgren and Solow 1987), it is likely that the cervical vertebrae of different populations will also show such significant patterns of variation. Preliminary analyses on C7 (Palancar et al. 2019) seem to support this hypothesis. However, no studies have yet been performed in detail and in the entire subaxial series to address this hypothesis. For this reason, we test here the possible differences of the cervical spine morphology between three different modern human populations: Africans, Europeans, and Inuit.

Besides the possible differences in the cervical spine due to population variations and genetic drift, a possible eco-geographic variability of this structure is also interesting. According to the classic rules postulated by Allen and Bergmann (Allen 1877; Bergmann 1847), the surface/volume ratio of the animals varies depending on the temperature of the habitat of endothermic mammals and their associated energetic demands. More recently, several studies have tested Allen's and Bergmann's rules for humans adapted to extreme climatic habitats (Foster and Collard 2013; Holliday 1997, 1999; Holliday and Hilton 2010; Holliday and Ruff 2001; Katzmarzyk and Leonard 1998; Pearson 2000; Roseman and Auerbach 2015; Ruff 1991, 1994, 2002; Ruff and Walker 1993; Ruff et al. 2005; Trinkaus 1981). For example, García-Martínez et al. (2018) concluded that the rib size and curvature are related to the latitude of the population, with ribs being longer in populations inhabiting high latitudes than the populations inhabiting areas near the equator. Longer and differently curved ribs could indicate a wider and deeper chest and a stockier body shape in Inuit. Adaptations are also observed at the level of the respiratory system function (Evteev et al. 2014) and overall body shape: tall, narrow bodies are better suited to heat dissipation than shorter and stockier (shorter and wider) bodies, which are better at heat retention (Ruff 1991, 1994, 2002). A relatively shorter spine (all segments) could be thus expected in cold-adapted humans in this eco-geographic context.

Even so, the above-mentioned works were focused on the limbs, the ribs, or the general bauplan and so the effect that this potential eco-geographic adaptation could have on the morphology of the cervical spine of modern humans remains unknown. Its possible adaptation, being the first segment of the postcranial skeleton and having a close relationship with the upper airways (Muto et al. 2002), has a great interest under the focus of breathing skills and energetic demands.

Objective and hypotheses

This study aims to carry out the first geometric morphometric analysis of the 3D size and shape of the full series of cervical vertebrae delving into variability related to sex and population background. For this reason, we analyzed the cervical vertebrae of both males and females belonging to three different populations: Europeans, Africans, and Greenland Inuit. Taking into account the aforementioned information, we are testing two main hypotheses here:

Hypothesis 1: both size and shape of the cervical vertebrae will differ between sexes. As several studies have demonstrated that it is possible to determine the sex of an individual through linear measurements taken in the cervical vertebrae (Reverte-Coma 1999; Marino 1995; Del Río and Sánchez 1997; Del Río et al. 2000; Wescott 2000; Medina et al. 2011; Gama 2012) we expect to find differences in the size between males and females. Regarding the shape, both the cervical lordosis and the range of motion varies between sexes (Been et al. 2017; Pan et al. 2018) and as far as these features are influenced by the bony morphology, sexual shape dimorphism can be expected.

Hypothesis 2: both size and shape of the cervical vertebrae will vary between populations (African, European, and Inuit). The cranium presents the size and shape variability within populations (Galland and Friess 2016; Kuroe et al. 2004; Zdilla et al. 2017) and thus, we expect to obtain similar results in the anatomical region supporting the cranium, highly related both functionally and developmentally. Besides, the eco-geographic adaptation of the Inuit population in the ribs (García-Martínez et al. 2018) together with the climatic adaptation that has been also found in the cranium (Harvati and Weaver 2006; Galland and Friess 2016) led us to hypothesize that the vertebrae of the cervical spine will be shorter in the Inuit population than in the African and European population. Regarding the two latter populations, differences between them are also expected as the entire torso showed a different morphology in Sub-Saharan African and Mediterranean populations studied by Torres-Tamayo et al. (2018b). The Mediterranean population was slenderer than the Sub-Saharan African population (Torres-Tamayo et al. 2018b). Due to the close anatomical relationship, the cervical spine could also present shape differences between these populations.

Methods

Sample composition

A total of 219 cervical vertebrae were measured from different osteological collections (Tab. 1). The European sample (N = 76) was obtained from the osteological collection of the Escuela de Medicina Legal (Universidad Complutense de Madrid, Spain). The African sample (N = 67) is an archaeological sample (15th-17th centuries) of enslaved individuals, most likely from the Gulf of Guinea region, exhumed from Valle da Gafaria site (Lagos, Portugal) (Ferreira et al. 2019; Wasterlain et al. 2016) that is housed at Dryas Octopetala (Coimbra, Portugal). The Inuit sample (N = 76) was obtained from two different collections: Greenland Inuit housed at the Panum Institute (Faculty of Health Sciences, University of Copenhaguen, Denmark) and Alaskan Inuit housed at the American Museum of Natural History (New York, USA). All the specimens were documented in terms of age-at-death and sex. To balance the sample, the number of vertebrae per level, sex, and the population is the most equal possible. 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, all the individuals analyzed in this study preserved the entire cervical spine (except 12 that only preserved the atlas) and thus, the determination of the cervical level was possible by manually assembling the cervical vertebrae using the fit of their interarticular facets.

Landmark templates of digitization

Both the atlas (C1) and the axis (C2) are atypical cervical vertebrae as they present unique

Tab. 1 - Sample composition.

POPULATION	SEX	OSTEOLOGICAL COLLECTION	C1	C2	C3	C4	C5	C6	C7	TOTAL
Europeans	Male	Madrid, Spain[1]	8	5	5	5	5	5	5	38
	Female	Madrid, Spain[1]	8	5	5	5	5	5	5	38
Africans	Male	Coimbra, Portugal[2]	4	5	4	5	5	5	5	33
	Female	Coimbra, Portugal[2]	4	5	5	5	5	5	5	34
Inuit	Male	New York, USA[3]	8	5	5	5	5	5	5	38
		Copenhagen, Denmark[4]								
	Female	New York, USA3	8	5	5	5	5	5	5	38
		Copenhagen, Denmark[4]								
Total	Male		20	15	14	15	15	15	15	109
	Female		20	15	15	15	15	15	15	110

[1] Universidad Complutense de Madrid.
[2] Dryas Octopetala.
[3] American Museum of Natural History.
[4] University of Copenhagen.

features and morphologies. The atlas lacks any vertebral body or spinous process and the axis possess the dens and thus, they are not usually analyzed together with the subaxial cervical vertebrae (C3-C7) (Gómez-Olivencia et al. 2013; Nalley and Grider-Potter 2015, 2017), which present homologous features (Kapandji 1974; White and Panjabi 1990). Due to this morphological variability within the cervical vertebrae, this study has been carried out through three different templates of digitization, depending on the analyzed vertebra (Fig. 1, Supplementary Material Tab. 1, 2, and 3). 119 landmarks and semilandmarks were taken in each atlas, while 72 in each axis and 89 in each subaxial cervical vertebra.

Data acquisition

All data were obtained following standard workflows in virtual morphological methods described by Bastir et al. (2019). Firstly, the vertebrae were scanned with a high-resolution Artec Space Spider 3D surface scanner based on blue light technology (Artec Spider, Artec Group, Luxembourg). Post-processing of the scans (cleaning, smoothing, and aligning) was performed in Artec Studio software version 12. Finally, the 3D surface models were imported into Viewbox software version 4.0 (dHAL, Kiffisia, Greece) to collect the coordinates of the landmarks and semilandmarks of the curve following the three different templates of digitization. Semilandmarks were re-slid along tangents to their corresponding curves, following a protocol that minimizes bending energy between the full mean shape and the shape of each vertebra (Gunz et al. 2005; Gunz and Mitteroecker 2013).

Landmark and semilandmark configurations were iteratively translated to a common origin, scaled to unit centroid size, and rotated to minimize the Procrustes distance between homologous

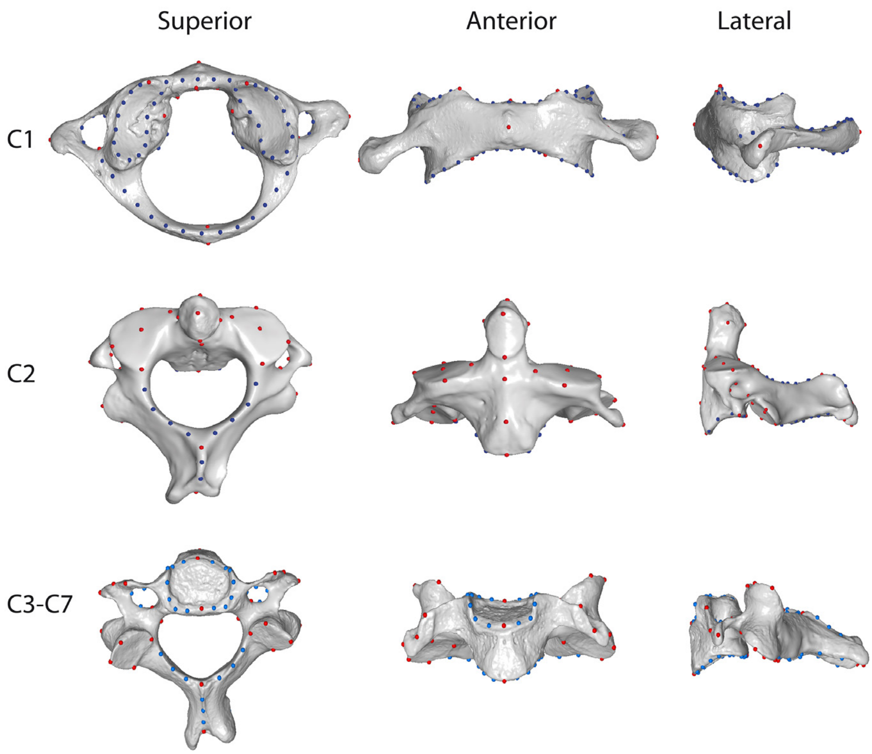

***Fig. 1** - Templates of digitization of atlas (up), axis (middle), and subaxial (bottom) vertebrae in left lateral view. Red: landmarks; Blue: curve semilandmarks.*

landmarks following the Generalized Procrustes analysis (GPA) (Gower 1975; Bookstein 1991). This analysis yielded Procrustes shape coordinates that were further analyzed by multivariate statistical shape analyses (O'Higgins 2000). Shape differences can be assessed using Procrustes distances, defined as the square root of the summed squared distances between Procrustes registered landmark configurations and their shape coordinates (O'Higgins 2000; Gunz et al. 2009; Mitteroecker and Gunz 2009).

Hypotheses testing

Hypothesis 1. Variation concerning sex several regression analyses using the sex of the individuals as a dummy variable (Hardy 1993) were carried out to determine possible differences in the vertebral shape and size between sexes and their amount of explained variance. Consequently, two types of regression were performed: Procrustes shape coordinates vs sex; and Centroid size vs sex. These regressions were performed in the entire sample, by population, and by levels of the cervical vertebrae to observe whether the possible morphological or size differences are general or specific of any population or level. Therefore, a total of 32 Dummy regressions were carried against the null hypothesis of no sexual dimorphism.

Hypothesis 2. Variation in relation to population. As the population variable has three different categories (African, European, and Inuit), it is not possible to perform dummy regressions (Hardy 1993). For this reason, to test the H2, a permutation test (1000 permutations) for pairwise

Procrustes distances among groups (Klingenberg and Monteiro 2005) was performed to observe whether there are differences in the vertebral shape between populations. To test the possible size differences between Africans, Europeans, and Inuit, an ANOVA or Kruskal-Wallis test (depending on the normality of the sample) was carried out. Both permutations and ANOVA tests were carried out in the entire sample and by levels of the cervical vertebrae to observe whether the possible morphological and size differences are general of the cervical spine or specific of any level. Therefore, a total of 24 permutation tests were made to quantify possible population variation.

Both dummy regressions (H1) and permutation tests (H2) were executed in MorphoJ software version 1.02 (Klingenberg 2011). ANOVA and Kruskal-Wallis tests (H2) were performed in Past version 3 (Hammer et al. 2001). To identify the possible morphological meaning of statistical differences, group mean shapes were generated by MorphoJ software and their 3D visualizations – based on Thin Plate Spline interpolation (Bookstein 1991) – were produced by Evan Toolkit software version 1.71www.evan-society.com.

Results

Variation in relation to sex

Table 2 shows that the relation between the vertebral morphology and the sex is weak, as only three out of 32 regressions are statistically significant. In fact, there is only statistical significance on the axis in the European populations and at the level of C5 in both the European and African populations. Figure 2 shows the mean shapes of the axis vertebrae of European males and females. Figure 3 shows the mean shapes of the C5 vertebrae of European and African males and females. Interestingly, the dimorphism pattern at the fifth cervical vertebra is different between populations. While in Africans the males present relatively shorter vertebral bodies, in Europeans the male bodies are relatively taller. In the European population, the spinous process is relatively shorter and more caudally oriented in the females, while in the African population, the females present a relatively longer and more cranially oriented spinous process than the males. The neural canal seems similarly relatively larger in females than in males in both populations.

Table 3 shows the results of the dummy regressions between the Centroid size and the sex variable. As shown, the relation between the Centroid size and the sex is strong (27 out of 32 are statistically significant). Taking into account all populations, sex affects size differences at all levels. However, splitting into populations, show that the European population shows fewer differences in size, like C3, C5, and C6 do not present statistical significance. Both Africans and Inuit show statistically significant differences at every level except one (C1 in Africans and C2 in Inuit).

Variation in relation to population

Regarding the relation between the vertebral shape and the differences between populations, we obtained very different results, as 23 out of 24 permutations tests were significant (Tab. 4). Significant differences were found between all populations taking into account all the cervical vertebrae and by levels, except for the case of C7, where no differences were found between African and European populations. Figures 4, 5, and 6 show the mean shapes of vertebrae of each population to clarify the differences. The atlas shows great variability in the posterior tubercle, being the most developed in Africans and only slightly visible in Inuit. The superior articular facets are also different between populations: Europeans have the most concave ones and the Africans the flattest. The maximum height of the atlas is not different between populations. Figure 2 shows the axis variability within populations: the spinous process of Europeans is the longest, while the Inuit have the shortest spinous process. The orientation of the dens of the axis is also different between populations, being more vertically oriented relative to the arch in Europeans and Inuit than in Africans. The vertebral body is more concave in Europeans and relatively flatter in Inuit. Regarding the population variability on the subaxial cervical vertebrae (Fig. 6), differences are mainly focused

***Tab. 2** - Predicted values of the Dummy regressions between the Procrustes shape coordinates and the sex.*

	C1	C2	C3	C4	C5	C6	C7	C3-C7
ALL POPULATIONS	2.38	3.8	5.47*	4.44	5.15*	3.51	3.19	1.42*
EUROPEANS	5.82	18.96***	17.57*	14.33	14.9**	10.66	12.53	3.70*
AFRICANS	9.92	7.14	12.71	13.68	20.06**	11.7	12.21	4.08*
INUIT	8.75	13	10.5	9.16	12.32	11.29	8.7	2.01

* = $p < 0.1$; ** = $p < 0.05$; *** = $p < 0.01$

***Tab. 3** - Predicted values of the Dummy regressions between the Centroid size and the sex.*

	C1	C2	C3	C4	C5	C6	C7	C3-C7
ALL POPULATIONS	39.57***	46.44***	50.46***	56.55***	53.91***	50.17***	58.74***	24.96***
EUROPEANS	49.10***	51.85**	31.94*	46.04**	39.17*	38.01*	57.81**	17.43***
AFRICANS	33.29	64.99**	68.94**	68.39**	65.19***	60.41***	68.81***	36.13***
INUIT	40.68***	34.46*	63.37**	64.87***	58.05**	52.73**	59.46**	22.16***

* = $p < 0.1$; ** = $p < 0.05$; *** = $p < 0.01$

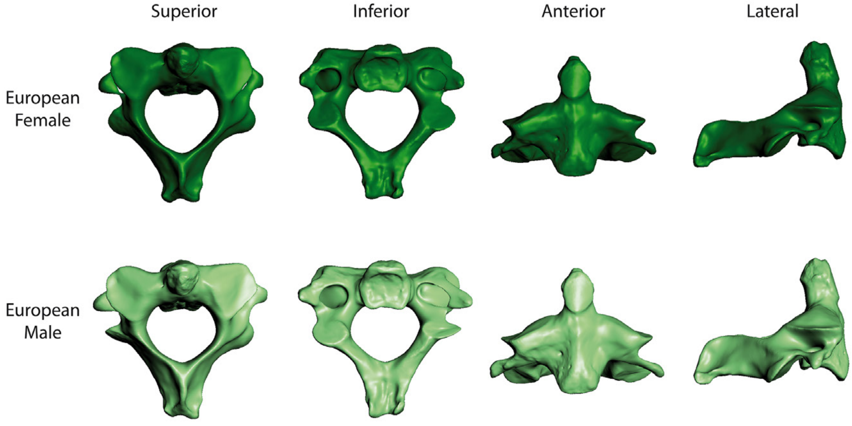

***Fig. 2** - Mean shape of the axis vertebra of both males and females of the European population. Differences are focused on the size of the vertebral canal (greater in males), the size of the vertebral body (greater in males), the length of the spinous process (greater in females), and the orientation of the inferior articular facets (more posteriorly oriented in males).*

Tab. 4 - Results of the Procrustes distance analyses between populations.

C1	African	European
European	0,0528***	
Inuit	0,0563***	0,0388***

C2	African	European
European	0,0663***	
Inuit	0,0681***	0,0683***

C3	African	European
European	0,0688***	
Inuit	0,0687***	0,0918***

C4	African	European
European	0,0777***	
Inuit	0,0597***	0,0927***

C5	African	European
European	0,0834***	
Inuit	0,074***	0,0947***

C6	African	European
European	0,0756***	
Inuit	0,0834***	0,0885***

C7	African	European
European	0,0509	
Inuit	0,0674***	0,072***

C3-C7	African	European
European	0,0593***	
Inuit	0,053***	0,0768***

*** = $p < 0.01$. The p-values are result of the permutation tests of pairwise Procrustes distances between groups.

on the relative vertebral body widths and length, the spinous process length and orientation, and the laminae height. The laminae height is highly related to the vertebral body height, and both present their maximum in the European population and its minimum in the Inuit population. The vertebral body in the coronal plane is the relatively widest in the Inuit population and the narrowest in the European one. The uncinate process of Europeans is the relatively highest and Inuit present the lowest. The spinous process is the longest and the most caudally oriented in the European population and the shortest and most cranially oriented in the Inuit one. This spinous process is the widest in Europeans and the narrowest in Africans. In addition, as Table 4 reveals, taking into account all the subaxial cervical vertebrae, the European population is the most different as indicated by the greatest Procrustes distances between the Europeans and the other two population means.

Regarding the ANOVA/Kruskal Wallis tests performed on the Centroid Size, none of the levels present differences in CS by populations (Tab. 5). The result is neither significant taking into account all the cervical vertebrae (C3-C7). Figure 7 shows the Centroid size distribution of the means in a box and jitter plot. The African population shows greater variability in size at every vertebral level except for the atlas and axis.

Discussion

To the best of our knowledge, this is the most comprehensive study delving into the 3D size and shape variability of the modern human cervical vertebrae. As shown by our results, the

Tab. 5 - Results of the ANOVA and Kruskal-Wallis tests to study the effect of the population on the size

	TEST	*P*	F	DF	H²
C1	ANOVA	0.29	1.273	2	---
C2	ANOVA	0.35	1.07	2	---
C3	ANOVA	0.74	0.3022	2	---
C4	ANOVA	0.94	0.05428	2	---
C5	ANOVA	0.95	0.05255	2	---
C6	Kruskal-Wallis	0.8	---	---	0.4439
C7	ANOVA	0.95	0.04515	2	---
C3-C7	Kruskal-Wallis	0.89	---	---	0.2287

shape variability of the human lower cervical spine is strongly related to the population factor, while the sexual dimorphism only affects the size of the vertebrae but not its 3D shape.

Variation in relation to sex

In both extant and extinct hominins, a common factor of variability between sexes is the size, being normally greater in males than in females both in craniofacial (Bastir et al. 2011; Bulygina et al. 2006; Garvin 2020; Hall 2005; Rosas and Bastir 2002; Rosas et al. 2002) and postcranial levels (Arsuaga and Carretero 1994; Bastir et al. 2014; Carlson et al. 2007; Gama et al. 2015; Kranioti and Michalodimitrakis 2009; Navega et al. 2015; Reno et al. 2003; Rosas et al. 2015; Ruff 1987; Stock 2020). The cervical spine is no exception in this sense: males have larger cervical vertebrae than the females at all studied levels (Tab. 3), as is also shown in previous studies of extant data (Reverte-Coma 1999; Marino 1995; Del Río and Sánchez 1997; Del Río et al. 2000; Wescott 2000; Medina et al. 2011; Gama 2012) and also in fossils: *Australopithecus afarensis* present sex differences in cervical vertebra size (KSD-VP-1/1 vs A.L. 333-106: Meyer, 2016). However, the shape factor does not follow the pattern observed in the axial and torso bones. Contrary to our expectations, cervical vertebrae do not present sexual shape dimorphism (Tab. 2, Supplementary Material Fig. 1), being the cervical spine the only region of the axial skeleton whose shape is not influenced by the sex (Bastir et al. 2014; Fischer and Mitteroecker 2017; García-Martínez et al. 2016; Scholtz et al. 2010; Lois-Zlolniski et al. 2019). The thoracic vertebrae and ribcage sexual dimorphism have been related to different factors related to trunk shape and breathing patterns (Bastir et al. 2014; García-Martínez et al. 2016, 2019; Torres-Tamayo et al. 2018a) while the lumbar spine and pelvic sexual dimorphism are related to obstetric factors (Fischer and Mitteroecker 2017; Lois-Zlolniski et al. 2019). Differences between sexes in the scapular girdle may be the result of differences in physical activity and muscle development (Scholtz et al. 2010). Although several muscles of the neck, trunk, and upper limbs are also attached at the cervical vertebrae, the different development of these muscles between sexes does not seem to modify the morphology of the cervical vertebrae to the point of being detected as sexual 3D shape dimorphism. Regarding the important function of the neck as the load bearer of the cranium, the relative weight of the cranium compared to the total body weight is the same in males and females (Williams 2002) and thus, the relative strength of the cervical spine is likely to be relatively equal in both the sexes. Besides, the cranial base does not present differences between sexes (Bigoni et al. 2010, but see Bruner and Ripani 2008) and developmentally, the cranial base and the cervical spine are highly related (Cunningham et al. 2016), with similar Hox genes expressions during their development (Carpenter 2002).

The result of the different sexual dimorphism patterns found in the fifth cervical vertebrae of Europeans and Africans (Fig. 3) supports the result of no general sexual dimorphism in all cervical vertebrae and populations. Whether both European and African populations had presented the same pattern in the fifth vertebrae, we could suggest that the sexual dimorphism is lower in the other levels and we have not perceived it. Conversely, African and European patterns of

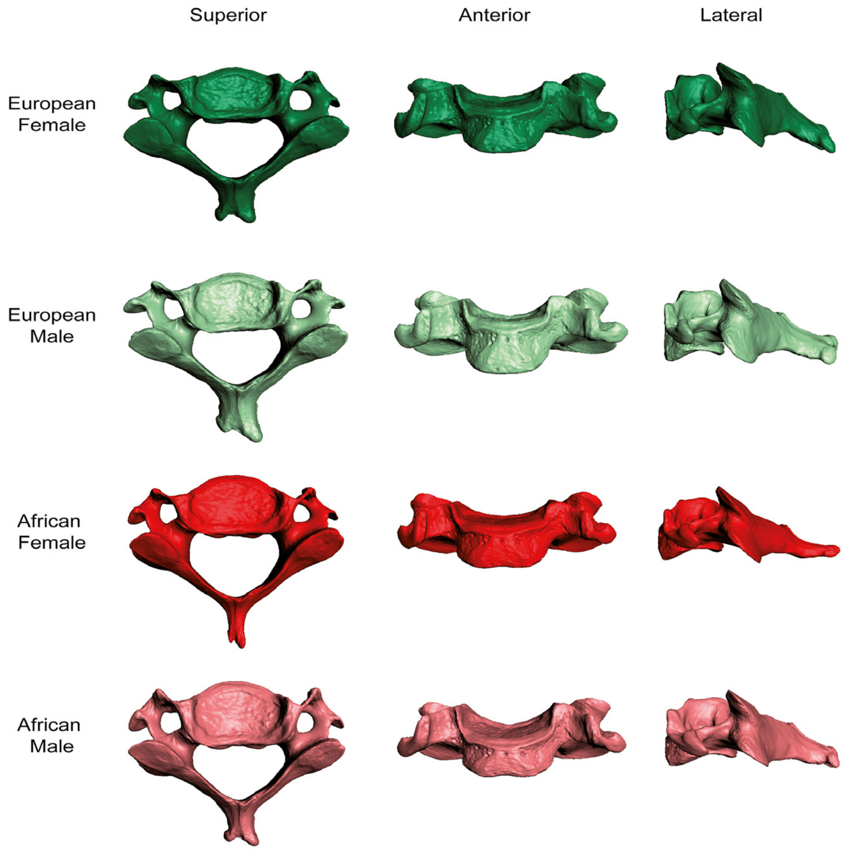

***Fig. 3** - Mean shape of the fifth cervical vertebra of both males and females of European and African populations. Differences are focused on the vertebral body height and width, neural canal area, uncinate process height, and the spinous process length and orientation.*

sexual dimorphism differ, which implies that the population and not the sex is the principal factor of shape variability in the cervical vertebrae.

Taking into account that previous studies have shown differences between sexes in the curvature and ranges of motion of the cervical region (Been et al. 2017; Pan et al. 2018), the absence of differences including body wedging (Supplementary Material Fig. 2) suggests that the soft tissues (and not the bony structure) relate the lordosis and mobility of the neck. This is in line with recent work performed in several Primates, which concluded that the relation between the bony morphology (linear dimensions) and the ranges of motion (unilinear movements) of the neck was extremely weak (Grider-Potter et al. 2020). These authors suggested that the ligaments rather than the bony morphology limited the mobility of the cervical vertebrae. Regarding the curvature of the cervical spine and its differences between sexes, the present study supports the works of Meyer (Meyer 2016; Meyer and Williams 2019), suggesting that the intervertebral discs wedging explain the lordosis better than the vertebral body shape or the orientation of the articular facets, the cervical wedging being kyphotic (except C2, Meyer and Williams 2019).

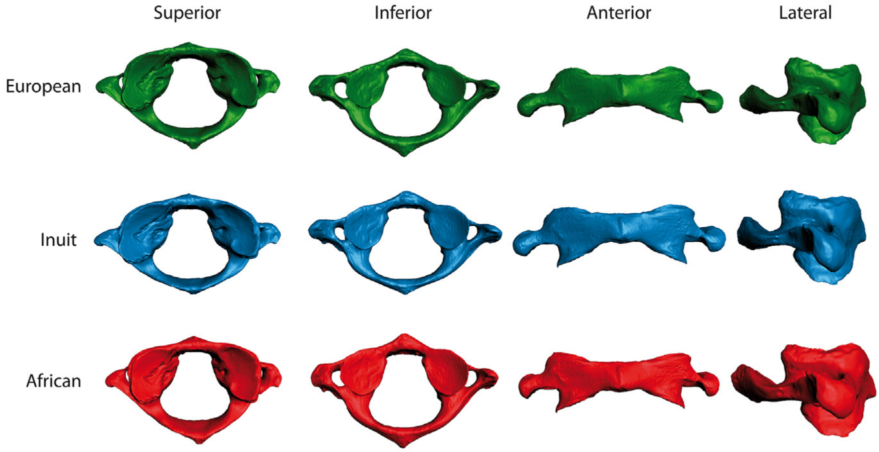

***Fig. 4** - Mean shapes of the atlas vertebrae by populations. Differences are focused on both anterior and posterior tubercles, superior articular facets, and neural canal. The posterior tubercle is much developed in Africans and slightly visible in Inuit. The anterior tubercle is caudally oriented in Africans. Europeans have the most concave superior articular facets and the Africans the flattest ones.*

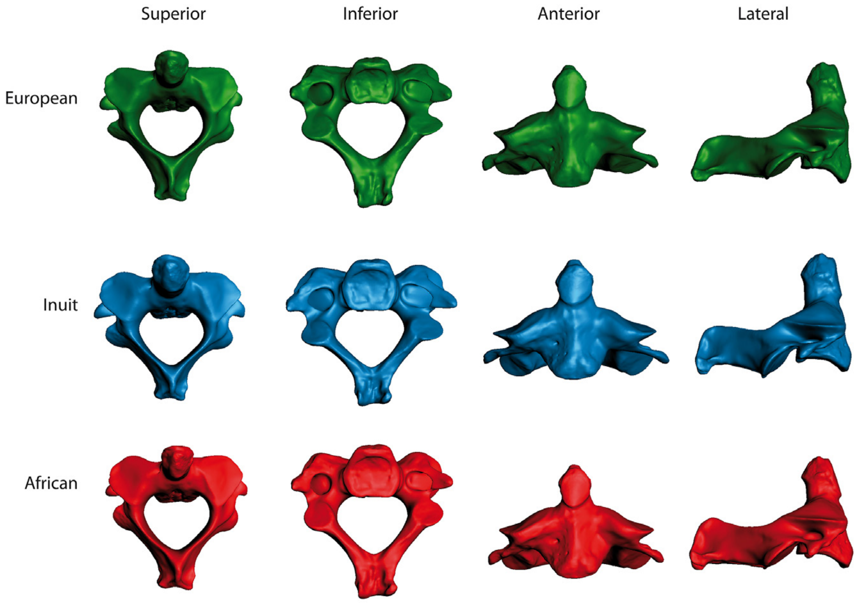

***Fig. 5** - Mean shapes of the axis vertebrae by populations. The spinous process of Europeans is the longest, while the Inuit have the shortest spinous process. The orientation of the dens of the axis is also different between populations, vertically oriented in Europeans and Inuit and more inclined in Africans. The vertebral body is more concave in Europeans and flatter in Inuit.*

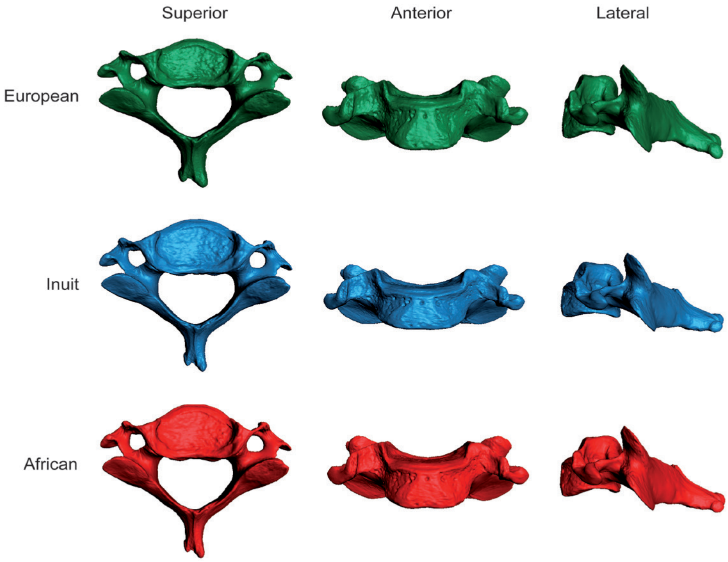

***Fig. 6** - Mean shapes of the subaxial cervical vertebrae by populations. Differences are focused on the vertebral body height and width and the spinous process length and orientation.*

Variation in relation to population

The second hypothesis is supported, as the geographic and genetic origin is a factor of shape variability of the cervical vertebrae. As expected, the three populations present notable differences between each other. A gradient can be established, indeed, between the three populations in several features of subaxial vertebrae, i.e., the Inuit population has the lowest relative vertebral body height and the most horizontally oriented spinous processes, while Europeans show the tallest vertebral bodies and the least horizontally oriented spinous processes (Fig. 6). The fact that the different shape of Inuit points to a relatively shorter and wider morphology of the cervical spine, could suggest that this structure is eco-geographically adapted in this population. This could be related to the different morphology of the thorax, which is also shorter and wider in high latitude populations like the Inuit (García-Martínez et al. 2018). The close relationship between the lowest cervical vertebrae with the thorax and the morphological (Hox) integration of the entire spine may lead to a different pattern of variability also in the neck. This way, the possible relation between the cervical spine morphology, the upper airways, and the breathing skills is reinforced.

This can seem contradicted with the result of the centroid size analysis (Fig. 7), where no differences in the size of the vertebrae were detected between populations (Tab. 5). Following the results of García-Martínez et al. (2018), where they also obtained differences in the size of the ribs depending on the latitude of the population, the cervical spine would show different sizes if it was eco-geographically adapted. Even so, centroid size in geometric morphometrics is a size estimator that allows for similar values in structures with different surface/volume ratios. It is not the size but this ratio, which is important for the understanding of Allen and Bergmann`s rules. Inuit's cervical vertebrae can present the same centroid size as Africans and Europeans but their surface/volume is different as they have a shorter and wider morphology.

Regarding the population variation presented in the atlas and axis vertebrae, the patterns are not so clear. In this case, the different morphology of the cranium (Galland and Friess 2016; Kuroe et al. 2004) may lead to differences in the center of

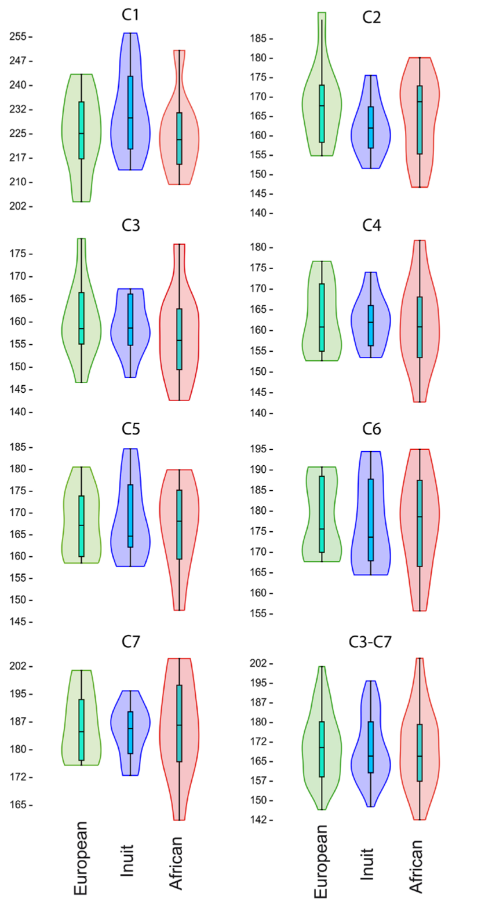

***Fig. 7** - Box and violin plots of the Centroid size by populations. Y-axis corresponds to the CS values (in mm.). As shown, none of the levels present differences in the means. Within the vertebrae, the atlas and axis are the most variables in size while within populations, it is the African one the most variable.*

gravity of the skull and thus, implying differences in the internal architecture of the structure bearing it. It has been suggested that in Neandertals the cervical morphology and lordosis could be different to compensate for the loading of the antero-posteriorly elongated cranial base in this species (Been et al. 2019; Gómez-Olivencia et al. 2013; Palancar et al. 2020b). Same way, in modern humans, the basicranium shape changes between populations (Kuroe et al. 2004) and could be influencing the upper cervical vertebrae morphological variation. In fact, the superior articular facets morphology and orientation of atlas vertebrae vary between the three populations (Fig. 3) as well as the orientation of the dens of the axis (Fig. 5). These variations could be related to the different static circumstances and needs between populations.

In regards to the differences between Europeans and Africans, the vertebral body height (C3-C7) and the total vertebral height (C1-C7) are greater in Europeans than in Africans. This is probably related to the fact that the architecture of the entire torso and body shape in Africans is different: some studies have shown Africans have longer legs but shorter and deeper torsos than Europeans (Holliday and Hilton 2010; Ruff 1991; Torres-Tamayo et al. 2018b). The cervical spine seems to share this pattern of shortening of the spine and torso in Africans.

Whether these shape differences between populations are observable during earlier stages of the ontogeny or they appear in the adults is an interesting focus for future works under both evolutionary and functional perspectives.

Conclusions

This study reveals the lack of sexual dimorphism of 3D shape in cervical vertebrae, contrary to the findings in other regions of the axial skeleton. The fact that functional differences between sexes, such as in the mobility or lordosis, have been found in the cervical segment but no shape differences are shown, point to a weak relationship of the bony structure of the cervical spine with its functionality. It seems probable that the soft tissues (ligaments and intervertebral discs) affect mobility and curvature of the cervical spine more than the hard tissue. Regarding the population variation, it seems that the cervical vertebrae morphological variations are related to differences in the cranium or the thorax. Besides, possible eco-geographic adaptation has been identified in the Inuit population, as this population presents shorter and wider subaxial cervical vertebrae, similar to the morphology observed in the thorax in previous studies.

Acknowledgements

This research was supported by a grant from the Ministerio de Economía y Competitividad of Spain (CGL2015-63648-P). The European Commission's Research Infrastructure Action funded DGM via the SYNTHESYS PLUS Project (DK-TAF-6405 and DK-TAF-3494). DGM was funded by the American Museum of Natural History (collection study grant; Alaskan Inuit collection) and by the Juan de la Cierva Formación program (FJCI-2017-32157), from the Spanish Ministry of Science, Innovation, and Universities. The author MT Ferreira work is carried out at the R&D Unit Center for Functional Ecology - Science for People and the Planet (CFE), with reference UIDB/04004/2020, financed by FCT/MCTES through national funds (PIDDAC). MB was funded by the European Union (PID2020-115854GB-I00 by MCIN/AEI and 10.13039/501100011033). We acknowledge Niels Lynnerup (University of Copenhagen), Chiara Villa (University of Copenhagen), Ana Luisa Santos (Universidade de Coimbra) and Miguel Almeida (Dryas Octopetala) for providing access to the comparative sample and support during data collection. We also thank Benoît Beyer and Juan Alberto Sanchis-Gimeno for several discussions related to this manuscript.

References

Allen JA (1877) The influence of physical conditions in the genesis of species. Radic Hist Rev 1:108-140.

Arlegi M, Gómez-Olivencia A, Albessard L, et al (2017) The role of allometry and posture in the evolution of the hominin subaxial cervical spine. J Hum Evol 104:80-99. https://doi.org/10.1016/j.jhevol.2017.01.002

Arsuaga JL, Carretero, JM (1994) Multivariate analysis of the sexual dimorphism of the hip bone in a modern human population and early hominids. Am J Phys Anthropol 93:241–257. https://doi.org/10.1002/ajpa.1330930208

Asvat R (2012) The configuration of cervical spinous processes in black and white South African skeletal samples. J Forensic Sci 57:176-181. https://doi.org/10.1111/j.1556-4029.2011.01942.x

Bastir M, García-Martínez D, Torres-Tamayo N, et al (2019) Workflows in a Virtual Morphology Lab: 3D scanning, measuring, and printing. J Anthropol Sci 96:107-134 https://doi.org/10.4436/jass.97003

Bastir M, Godoy P, Rosas A (2011) Common features of sexual dimorphism in the cranial airways of different human populations. Am J Phys Anthropol 146:414–422. https://doi.org/10.1002/ajpa.21596

Bastir M, Higuero A, Rios L, et al (2014) Three-dimensional analysis of sexual dimorphism in human thoracic vertebrae: Implications for the respiratory system and spine morphology. Am J Phys Anthropol 155:513-521. https://doi.org/10.1002/ajpa.22604

Bastir M, Rosas A, Kuroe K. (2004) Petrosal orientation and mandibular ramus breadth: Evidence for an integrated petroso-mandibular developmental unit. Am J Phys Anthropol 123:340-350. https://doi.org/10.1002/ajpa.10313

Beaudet A, Clarke RJ, Heaton JL, et al (2020) The atlas of StW 573 and the late emergence of human-like head mobility and brain metabolism. Sci Rep 10:1-13. https://doi.org/10.1038/s41598-020-60837-2

Been E, Shefi S, Soudack M (2017) Cervical lordosis: the effect of age and gender. Spine J 17:880-888. https://doi.org/10.1016/j.spinee.2017.02.007

Bergmann C (1847) Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Göttinger Studien 3:595-708.

Bigoni L, Velemínská J, Brůžek J (2010) Three-dimensional geometric morphometric analysis of cranio-facial sexual dimorphism in a Central European sample of known sex. HOMO 61:16-32. https://doi.org/10.1016/j.jchb.2009.09.004

Bogduk N, Mercer S (2000) Biomechanics of the cervical spine. I: Normal kinematics. Clin Biomech 15:633-648. https://doi.org/10.1016/S0268-0033(00)00034-6

Bookstein FL (1991) Morphometric tools for landmark data: geometry and biology, Cambridge University Press, Cambridge.

Bruner E, Ripani M (2008) A quantitative and descriptive approach to morphological variation of the endocranial base in modern humans.

Am J Phys Anthropol 137:30-40. https://doi.org/10.1002/ajpa.20837

Bulygina E, Mitteroecker P, Aiello L (2006) Ontogeny of facial dimorphism and patterns of individual development within one human population. Am J Phys Anthropol 131:432–443. https://doi.org/10.1002/ajpa.20317

Carlson KJ, Grine FE, Pearson OM (2007) Robusticity and sexual dimorphism in the postcranium of modern hunter-gatherers from Australia. Am J Phys Anthropol 134:9–23. https://doi.org/10.1002/ajpa.20617

Carpenter EM (2002) Hox Genes and Spinal Cord Development. Dev Neurosci 24:24–34. https://doi.org/10.1159/000064943

Cunningham C, Scheuer L, Black S (2016) Developmental juvenile osteology, Academic Press, London.

Del Río MPA, Sánchez SJA, Prieto CJL (2000) Determinación del sexo mediante el análisis de imagen en el atlas. Cuad Med Forense 6:45-52.

Del Río MPA, Sánchez SJA (1997) Discriminación sexual en la séptima vértebra cervical mediante el análisis de imagen. Rev Espanola de Medicina Leg 6:49-54.

Duray SM, Morter HB, Smith FJ (1999) Morphological variation in cervical spinous processes: potential applications in the forensic identification of race from the skeleton. J Forensic Sci 44:937-944. https://doi.org/10.1520/JFS12020J

Evteev A, Cardini AL, Morozova I, et al (2014) Extreme climate, rather than population history, explains the mid-facial morphology of Northern Asians. Am J Phys Anthropol 153:449-462. https://doi.org/10.1002/ajpa.22444

Ferreira MT, Coelho C, Wasterlain SN (2019) Discarded in the trash: burial of African slaves in Valle da Gafaria, Lagos, Portugal (15th-17th centuries). Int J Osteoarchaeol 29:670-680. https://doi.org/10.1002/oa.2747)

Fischer B, Mitteroecker P (2017) Allometry and sexual dimorphism in the human pelvis. Anat Rec 300:698-705. https://doi.org/10.1002/ar.23549

Foster F, Collard M (2013) A reassessment of Bergmann's rule in modern humans. PLoS One, 8:e72269. https://doi.org/10.1371/journal.pone.0072269

Galland M, Friess M (2016) A three-dimensional geometric morphometrics view of the cranial shape variation and population history in the New World. Am J Hum Biol 28:646-661. https://doi.org/10.1002/ajhb.22845

Gama I, Navega D, Cunha E (2015) Sex estimation using the second cervical vertebra: A morphometric analysis in a documented Portuguese skeletal sample. Int J Legal Med 129:365–372. https://doi.org/10.1007/s00414-014-1083-0

García-Martínez D, Bastir M, Torres-Tamayo N, et al (2019) Three-dimensional analysis of sexual dimorphism in ribcage kinematics of modern humans. Am J Phys Anthropol 169:348-355. https://doi.org/10.1002/ajpa.23829

García-Martínez D, Nalla S, Ferreira MT, et al (2018) Eco-geographic adaptations in the human ribcage throughout a 3D geometric morphometric approach. Am J Phys Anthropol 166:323-336. https://doi.org/10.1002/ajpa.23433

García-Martínez D, Torres-Tamayo N, Torres-Sanchez I, et al (2016) Morphological and functional implications of sexual dimorphism in the human skeletal thorax. Am J Phys Anthropol 161:467-477. https://doi.org/10.1002/ajpa.23051

Garvin HM (2020) Adult sex estimation from cranial morphological traits. In: Klales A (ed) Sex Estimation of the human skeleton, Academic Press, London, p. 95-112.

Gómez-Olivencia A, Been E, Arsuaga JL, et al (2013) The Neandertal vertebral column 1: The cervical spine. J Hum Evol 64:608-630. https://doi.org/10.1016/j.jhevol.2013.02.008

Gower JC (1975) Generalized Procrustes analysis. Psychometrika 40:33-51. https://doi.org/10.1007/BF02291478

Grider-Potter N, Nalley TK, Thompson NE, et al (2020) Influences of passive intervertebral range of motion on the cervical vertebral form Am J Phys Anthropol 172:300-313. https://doi.org/10.1002/ajpa.24044

Gunz P, Mitteroecker P (2013) Semilandmarks: a method for quantifying curves and

surfaces. Hystrix 24:103-109. https://doi.org/10.4404/hystrix-24.1-6292
Gunz P, Mitteroecker P, Bookstein FL (2005) Semilandmarks in three dimensions. In: Gunz P, Mitteroecker P, Bookstein FL, et al (eds) Modern morphometrics in physical anthropology, Springer, Boston, p. 73-98
Gunz P, Mitteroecker P, Neubauer S, et al (2009) Principles for the virtual reconstruction of hominin crania. J Hum Evol 57:48-62. https://doi.org/10.1016/j.jhevol.2009.04.004
Hall RL (2005) Energetics of nose and mouth breathing, body size, body composition, and nose volume in young adult males and females. Am J Hum Biol 17:321–330. https://doi.org/10.1002/ajhb.20122
Hammer Ø, Harper DA, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. Palaeontol Electron 4:9.
Hardy MA (1993) Regression with dummy variables, Sage Publications, London.
Harvati K, Weaver TD (2006) Human cranial anatomy and the differential preservation of population history and climate signatures. Anat Rec A 288A:1225-1233. https://doi.org/10.1002/ar.a.20395
Holliday TW (1997) Postcranial evidence of cold adaptation in European Neandertals. Am J Phys Anthropol 104:245–258.
Holliday TW (1999) Brachial and crural indices of European late upper paleolithic and mesolithic humans. J Hum Evol 36:549–566. https://doi.org/10.1006/jhev.1998.0289
Holliday TW, Hilton CE (2010) Body proportions of circumpolar peoples as evidenced from skeletal data: Ipiutak and Tigara (Point Hope) versus Kodiak Island Inuit. Am J Phys Anthropol 142:287–302. https://doi.org/10.1002/ajpa.21226
Holliday TW, Ruff CB (2001) Relative variation in human proximal and distal limb segment lengths. Am J Phys Anthropol 116:26–33. https://doi.org/10.1002/ajpa.1098
Kapandji I (1974) The trunk and the vertebral column, Churchill Livingstone, Edinburgh.
Katzmarzyk PT, Leonard WR (1998) Climatic influences on human body size and proportions: Ecological adaptations and secular trends. Am J Phys Anthropol 106:483–503. https://doi.org/10.1002/(SICI)1096-8644(199808)106:4<483::AID-AJPA4>3.0.CO;2-K
Klingenberg CP (2011) MorphoJ: an integrated software package for geometric morphometrics. Mol Ecol Resour 11:353-357. https://doi.org/10.1111/j.1755-0998.2010.02924.x
Klingenberg CP Monteiro LR (2005) Distances and directions in multidimensional shape spaces: implications for morphometric applications. Syst Biol 54:678–688. https://doi.org/10.1080/10635150590947258
Kranioti EF, Michalodimitrakis M (2009) Sexual dimorphism of the humerus in contemporary Cretans - A population-specific study and a review of the literature. J Forensic Sci 54:996–1000. https://doi.org/10.1111/j.1556-4029.2009.01103.x
Kuroe K, Rosas A, Molleson T (2004) Variation in the cranial base orientation and facial skeleton in dry skulls sampled from three major populations. Eur J Orthod 26:201-207. https://doi.org/10.1093/ejo/26.2.201
Lind B, Sihlbum H, Nordwall A, et al (1989) Normal range of motion of the cervical spine. Arch Phys Med Rehabil 70:692-695. https://doi.org/10.5555/uri:pii:0003999389901688
Lois-Zlolniski S, Torres-Tamayo N, García-Martínez D, et al (2019) 3D geometric morphometric analysis of variation in the human lumbar spine. Am J Phys Anthropol 170:361-372. https://doi.org/10.1002/ajpa.23918
Marino EA (1995) Sex estimation using the first cervical vertebra. Am J Phys Anthropol 97:127-133. https://doi.org/10.1002/ajpa.1330970205
Marino EA (1997) A pilot study using the first cervical vertebra as an indicator of race. J Forensic Sci 42:1114-1118. https://doi.org/10.1520/JFS14271J
Martiniano R, Coelho C, Ferreira MT, et al (2014) Genetic evidence of African slavery at the beginning of the trans-Atlantic slave trade. Sci Rep 4:5994. https://doi.org/10.1038/srep05994
Medina CS, Polo LC, Botella MC (2011) Dimorfismo sexual en primera vértebra cervical

en una muestra de población colombiana. Rev Espanola Med Legal 37:140-145. https://doi.org/10.1016/S0377-4732(11)70080-3
Mercer SR, Bogduk N (2001) Joints of the cervical vertebral column. J Orthop Sports Phys Ther 31:174-182. https://www.doi.org/10.2519/jospt.2001.31.4.174
Meyer MR (2016) The cervical vertebrae of KSD-VP-1/1. In: Haile-Selassie Y Su DF (eds) The Postcranial Anatomy of Australopithecus afarensis, Springer, Dordrecht, p. 63-111.
Meyer MR, Williams SA, Schmid P, et al (2017) The cervical spine of Australopithecus sediba. J Hum Evol 104:32-49. https://doi.org/10.1016/j.jhevol.2017.01.001
Meyer MR, Williams SA (2019) Earliest axial fossils from the genus Australopithecus. J Hum Evol 132:189-214. https://doi.org/10.1016/j.jhevol.2019.05.004
Meyer MR, Woodward C, Tims A, et al (2018) Neck function in early hominins and suspensory primates: insights from the uncinate process. Am J Phys Anthropol 166:613-637. https://doi.org/10.1002/ajpa.23448
Mitteroecker P, Gunz P (2009) Advances in geometric morphometrics. Evol Biol 36:235-247. https://doi.org/10.1007/s11692-009-9055-x
Muto T, Takeda S, Kanazawa M, et al (2002) The effect of head posture on the pharyngeal airway space (PAS). Int J Oral Maxillofac Surg 31:579-583. https://doi.org/10.1054/ijom.2002.0279
Nalley TK, Grider-Potter N (2015) Functional morphology of the primate head and neck. Am J Phys Anthropol 156:531-542. https://doi.org/10.1002/ajpa.22729
Nalley TK, Grider-Potter N (2017). Functional analyses of the primate upper cervical vertebral column. J Hum Evol 107:19-35. https://doi.org/10.1016/j.jhevol.2017.03.010
Navega D, Vicente R, Vieira DN, et al (2015) Sex estimation from the tarsal bones in a Portuguese sample: A machine learning approach. Int J Legal Med 129:651–659. https://doi.org/10.1007/s00414-014-1070-5
Netter FH (2008) Atlas de anatomía humana, Elsevier, Río de Janeiro.
O'Higgins P (2000) The study of morphological variation in the hominid fossil record: biology, landmarks, and geometry. J Anat 197:103-120. https://doi.org/10.1046/j.1469-7580.2000.19710103.x
Palancar CA, García-Martínez D, Radovčić D, et al (2020a) Krapina atlases suggest a high prevalence of anatomic variations in the first cervical vertebra of Neandertals. J Anat 237:579-586. https://doi.org/10.1111/joa.13215
Palancar CA, Torres-Tamayo N, García-Martínez D, et al (2019) Comparative anatomy of the seventh cervical vertebra of KNM-WT 15000 through 3D geometric morphometrics. Paper presented at the biannual meeting of the East African Association for Paleoanthropology and Paleontology (EAAPP), Nairobi, Kenya.
Palancar CA, Torres-Tamayo N, García-Martínez D, et al (2020b) Comparative anatomy and 3D geometric morphometrics of the El Sidrón atlases (C1). J Hum Evol 149:102897. https://doi.org/10.1016/j.jhevol.2020.102897
Pan F, Arshad R, Zander T, et al (2018) The effect of age and sex on the cervical range of motion–A systematic review and meta-analysis. J Biomech 75:13-27. https://doi.org/10.1016/j.jbiomech.2018.04.047
Pearson OM (2000) Activity, climate, and postcranial robusticity: Implications for modern human origins and scenarios of adaptive change. Curr Anthropol 41:569–607. https://doi.org/10.1086/317382
Reno PL, Meindl RS, McCollum MA, et al (2003) Sexual dimorphism in Australopithecus afarensis was similar to that of modern humans. Proc Natl Acad Sci USA 100:9404–9409. https://doi.org/10.1073/pnas.1133180100
Reverte-Coma JM (1999) Antropología Forense, Ministerio de Justicia, Madrid.
Rosas A, Bastir M (2002) Thin-plate spline analysis of allometry and sexual dimorphism in the human craniofacial complex. Am J Phys Anthropol 117:236–245. https://doi.org/10.1002/ajpa.10023
Rosas A, Bastir M, Martínez-Maza C, et al (2002) Sexual dimorphism in the Atapuerca-SH hominids: The evidence from the mandibles. J Hum Evol 42:451–474. https://doi.org/10.1006/jhev.2001.0536
Rosas A, Perez-Criado L, Bastir M, et al (2015) A geometric morphometrics comparative analysis

of Neandertal humeri (epiphyses-fused) from the El Sidron cave site (Asturias, Spain). J Hum Evol 82:51–66. https://doi.org/10.1016/j.jhevol.2015.02.018
Roseman CC, Auerbach BM (2015) Ecogeography, genetics, and the evolution of the human body form. J Hum Evol 78:80–90. https://doi.org/10.1016/j.jhevol.2014.07.006
Ruff CB (1987) Sexual dimorphism in human lower limb bone structure: Relationship to subsistence strategy and the sexual division of labor. J Hum Evol 16:391–416. https://doi.org/10.1016/0047-2484(87)90069-8
Ruff CB (1991) Climate and body shape in hominid evolution. J Hum Evol 21:81–105. https://doi.org/10.1016/0047-2484(91)90001-C
Ruff CB (1994) Morphological adaptation to climate in modern and fossil hominids. Am J Phys Anthropol 37:65–107. https://doi.org/10.1002/ajpa.1330370605
Ruff CB (2002) Variation in human body size and shape. Annu Rev Anthropol 31:211–232. https://doi.org/10.1146/annurev.anthro.31.040402.085407
Ruff CB, Walker A (1993) Body size and body shape. In: Walker A, Leakey R (eds) The nariokotome Homo erectus skeleton, Harvard University Press, Cambridge, p. 234– 265.
Ruff CB, Niskanen M, Junno JA, et al (2005) Body mass prediction from stature and biiliac breadth in two high latitude populations, with application to earlier higher latitude humans. J Hum Evol 48:381–392. https://doi.org/10.1016/j.jhevol.2004.11.009
Scholtz Y, Steyn M, Pretorius E (2010) A geometric morphometric study into the sexual dimorphism of the human scapula. HOMO 61:253-270. https://doi.org/10.1016/j.jchb.2010.01.048
Solow B, Tallgren A (1971) Natural head position in standing subjects. Acta Odontol Scand 29:591-607. https://doi.org/10.3109/00016357109026337
Solow B, Tallgren A (1976) Head posture and craniofacial morphology. Am J Phys Anthropol 44:417-435. https://doi.org/10.1002/ajpa.1330440306
Solow B, Siersbæk-Nielsen S, Greve E (1984) Airway adequacy, head posture, and craniofacial morphology. Am J Orthod 86:214-223. https://doi.org/10.1016/0002-9416(84)90373-7
Stock MK (2020) Analyses of the postcranial skeleton for Sex estimation. In: Klales A (ed) Sex Estimation of the human skeleton, Academic Press, London, p. 113-130.
Strait DS, Ross CF (1999) Kinematic data on primate head and neck posture: implications for the evolution of basicranial flexion and an evaluation of registration planes used in paleoanthropology. Am J Phys Anthropol 108:205-222. https://doi.org/10.1002/(SICI)1096-8644(199902)108:2<205::AID-AJPA6>3.0.CO;2-F
Swenson VM (2013) Ancestral and sex estimation using EA Marino's analysis of the first cervical vertebra applied to three modern groups (PhD dissertation), The University of Montana, Montana
Tallgren A, Solow B (1987) Hyoid bone position, facial morphology, and head posture in adults. Eur J Orthod 9:1-8. https://doi.org/10.1093/ejo/9.1.1
Torres-Tamayo N, García-Martínez D, Lois-Zlolniski S, et al (2018a) 3D analysis of sexual dimorphism in size, shape and breathing kinematics of human lungs. J Anat 232:227-237. https://doi.org/10.1111/joa.12743
Torres-Tamayo N, García-Martínez D, Nalla S, et al (2018b) The torso integration hypothesis revisited in Homo sapiens: Contributions to the understanding of hominin body shape evolution. Am J Phys Anthropol 167:777-790. https://doi.org/10.1002/ajpa.23705
Trinkaus E (1981) Neanderthal limb proportions and cold adaptation. In: Stringer CB (ed) Aspects of human evolution, Taylor & Francis, London.
Wasterlain SN, Neves MJ, Ferreira MT (2016) Dental modifications in a skeletal sample of enslaved Africans found at Lagos (Portugal). Int. J. Osteoarchaeol 26:621–632. https://doi.org/10.1002/oa.2453
Wescott JM (2000) Sex variation in the second cervical vertebra. J Forensic Sci 45:462-466. https://doi.org/10.1520/JFS14707J
White A, Panjabi M (1990) Clinical biomechanics of the spine, Lippincott, Philadelphia.

Williams MF (2002) Primate encephalization and intelligence. Med Hypotheses 58:284-290. https://doi.org/10.1054/mehy.2001.1516

Zdilla MJ, Russell ML, Bliss KN, et al (2017) The size and shape of the foramen magnum in man. J Craniovertebr Junction Spine 8:205-221. https://doi.org/10.4103/jcvjs.JCVJS_62_17

Associate Editor, Fabio Di Vincenzo