

# Eco-geographic adaptations in the human ribcage throughout a 3D geometric morphometric approach

Daniel García-Martínez<sup>1</sup>  | Shahed Nalla<sup>2,3</sup> | Maria Teresa Ferreira<sup>4</sup> |  
Ricardo A. Guichón<sup>5</sup> | Manuel D. D'Angelo del Campo<sup>5,6</sup> | Markus Bastir<sup>1</sup>

<sup>1</sup>Paleoanthropology Group, Museo Nacional de Ciencias Naturales, Madrid, Spain

<sup>2</sup>Department of Human Anatomy and Physiology, Faculty of Health Sciences, University of Johannesburg, Johannesburg, South Africa

<sup>3</sup>Evolutionary Studies Institute (ESI) and Center of Excellence in Palaeosciences, University of the Witwatersrand, Johannesburg, South Africa

<sup>4</sup>Laboratory of Forensic Anthropology, Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, Coimbra, Portugal

<sup>5</sup>Núcleo de Estudios Interdisciplinarios de Poblaciones Humanas de Patagonia Austral, Laboratorio de Ecología Evolutiva Humana, Facultad de Ciencias Sociales, Universidad del Centro de la Provincia de Buenos Aires, Argentina (CONICET)

<sup>6</sup>Laboratorio de Poblaciones de Pasado, Departamento de Biología, Facultad de Ciencias, Universidad Autónoma de Madrid, Madrid, España

## Correspondence

Daniel García-Martínez, Paleoanthropology Group, Museo Nacional de Ciencias Naturales, Madrid, Spain.  
Email: dan.garcia@mncn.csic.es

## Funding information

MINECO, Grant Number: CGL2015-63648-P; the Leakey Foundation; the Synthesys Project, Grant Numbers: DK-TAF-3494, DK-TAF-6405; CONICET, Grant Number: PICT0575; Gerda Henkel Foundation

## Abstract

**Objectives:** According to eco-geographic rules, humans from high latitude areas present larger and wider trunks than their low-latitude areas counterparts. This issue has been traditionally addressed on the pelvis but information on the thorax is largely lacking. We test whether ribcages are larger in individuals inhabiting high latitudes than in those from low latitudes and explored the correlation of rib size with latitude. We also test whether a common morphological pattern is exhibited in the thorax of different cold-adapted populations, contributing to their hypothetical widening of the trunk.

**Materials and methods:** We used 3D geometric morphometrics to quantify rib morphology of three hypothetically cold-adapted populations, viz. Greenland (11 individuals), Alaskan Inuit (8 individuals) and people from Tierra del Fuego (8 individuals), in a comparative framework with European (Spain, Portugal and Austria; 24 individuals) and African populations (South African and sub-Saharan African; 20 individuals).

**Results:** Populations inhabiting high latitudes present longer ribs than individuals inhabiting areas closer to the equator, but a correlation ( $p < 0.05$ ) between costal size and latitude is only found in ribs 7–11. Regarding shape, the only cold adapted population that was different from the non-cold-adapted populations were the Greenland Inuit, who presented ribs with less curvature and torsion.

**Conclusions:** Size results from the lower ribcage are consistent with the hypothesis of larger trunks in cold-adapted populations. The fact that only Greenland Inuit present a differential morphological pattern, linked to a widening of their ribcage, could be caused by differences in latitude. However, other factors such as genetic drift or specific cultural adaptations cannot be excluded and should be tested in future studies.

## KEYWORDS

Allen's rule, Bergmann's rule, cold-adaptation, geometric morphometrics, Inuit, thorax, Tierra del Fuego

## 1 | INTRODUCTION

Despite the major importance of the ribcage for human biology, its 3D morphological variability associated with geographical variation is still not well known (Gómez-Olivencia et al., 2009). This is in great part due

to methodological limitations of the accurate quantification of the complex 3D curvature and torsion of the ribs (García-Martínez, Recheis, & Bastir, 2016a). This is also due to the fact that 3D rib cage morphology can only be understood as the result of the sum of its metameric components: ribs and vertebrae (Bastir et al., 2017a; García-Martínez,

2017; García-Martínez et al., 2017a). Moreover, besides these technical limitations, researchers have paid more attention to the quantification of the thorax variability in fossil hominin species than in the study of modern human thoracic variability (Bastir et al., 2015, 2017a; Chapman et al., 2017; Franciscus and Churchill, 2002; Gómez-Olivencia, 2015; Gómez-Olivencia et al., 2009; García-Martínez et al., 2014, 2017a; Latimer, Lovejoy, Spurlock, & Haile-Selassie, 2016; Schmid, 1991; Schmid et al., 2013; Williams et al., 2017). Although one study included a cold-adapted population, it was used as a comparative sample for addressing the possible cold-adaptation in the Neanderthal Kebara 2 thorax (Gómez-Olivencia et al., 2009).

The Neanderthal Kebara 2 study (Gómez-Olivencia et al., 2009) produced interesting results regarding cold adaptations, such as the presence of longer ribs relative to humeral length in Inuits compared to Euromericans. However, some improvements can be applied to this groundwork. Firstly, they only included one cold-adapted population in their study (Alaskan Inuit), so whether the morphological pattern they found actually represented an overall cold-adapted morphotype is still unknown. In addition, they collected the tubercle-ventral arch of the rib (called TVA2 in their study) in order to quantify rib morphology. Although the tubercle-ventral arch, along with the tubercle-ventral cord, is useful for quantifying differences in rib curvature in the cranial view (Gómez-Olivencia et al., 2009), several attempts using angles have been used to try to quantify other important features, such as rib torsion (Jellema, Latimer, & Walker, 1993), but this feature is not well quantified using traditional measurements. This is because rib torsion modifies the curvature not only in the transverse plane but also in the sagittal and the coronal planes (García-Martínez et al., 2016a), therefore necessitating for the use of 3D geometric morphometrics in order to quantify the 3D rib morphological variability (Bastir et al., 2013, 2015, 2017a, 2017b, 2017c; Chapman et al., 2017; García-Martínez et al., 2014, 2016a, 2017a, 2017b; García-Martínez, Torres-Tamayo, Torres-Sanchez, García-Río, & Bastir, 2016b; Shi et al., 2014; Weaver, Schoell, & Stitzel, 2014). Finally, Gómez-Olivencia et al. (2009) did not account for latitude, which has been related to temperature. This variable has been previously used by other authors in order to address eco-geographical variation in the human body shape (Foster and Collard, 2013; Ruff, 1991, 2002; Ruff, Niskanen, Junno, & Jamison, 2005), so it is potentially interesting to study when addressing variability of the human ribcage.

This compendium of facts has made it difficult to answer some questions that are important for biological anthropology and human ecology as well as for human evolution. For instance, it was hypothesized by Jellema et al. (1993) that the modern body shape and ribcage morphology (i.e., narrow in the caudal part and expanded in the cranial part) has remained invariable since its appearance with *Homo ergaster*. However, several studies dealing with the ribcage of other extinct hominin species, such as the Neanderthals, which are geologically younger than *H. ergaster*, found statistical differences in both size and shape between this species' ribcages and those of modern humans (Bastir et al., 2015, 2017a; Franciscus and Churchill, 2002; García-Martínez et al., 2014, 2017a; Gómez-Olivencia, 2015; Gómez-Olivencia et al., 2009; Weinstein, 2008). This morphology, which was likely caused by an adaptation to high energetic requirements instead

of by an adaptation to cold-environments (Churchill, 2006, 2014; Froehle and Churchill, 2009), would support the evidence of recent variation in the rib cage morphology.

In addition, it is well known that the body proportions of humans from cold-adapted populations are different from the proportions of humans from populations inhabiting mild or hot climates (Foster and Collard, 2013; Holliday, 1997, 1999; Holliday and Hilton, 2010; Holliday and Ruff, 2001; Katzmarzyk and Leonard, 1998; Pearson et al., 2000; Roberts, 1973, 1978; Ruff, 1991, 1994; Ruff and Walker, 1993; Schreider, 1964; Trinkaus, 1981). Specifically, individuals from cold-adapted populations are expected to present longer and wider trunks along with shorter extremities than individuals inhabiting mild or hot climates. These longer and wider trunks would include, among other features, a wide and large pelvis and rib cage, which would also support the recently observed variation in thorax morphology.

This is because theoretically, the evolution of endothermic mammals' body shape under extreme cold or hot conditions could be driven by natural selection and adaptation according to several generic ecological rules. On the one hand, Bergmann's (1847) eco-geographical rule states that an animal inhabiting cold climate (usually at high latitudes) are characterized by a body shape that tends to present a low surface area to volume ratio, contributing to heat retention. The opposite pattern is observed in hot-adapted animals (usually living at low latitudes), that tend to present a high surface-to-volume ratio, facilitating heat loss and helping to cool the body. This would possibly explain why polar animals, e.g. bears or foxes, are much larger than their counterparts of mild climates. On the other hand, Allen's (1877) eco-geographical rule states that endothermic mammals from cold climates are characterized by shorter limbs than their counterparts of warmer climates in order to retain body heat.

With regard to the eco-geographic hypothesis, several studies showed that as the Allen's and Bergmann's rules apply to endothermic nonhuman mammals (Aldrich and James, 1991; Ashton, 2002; Graves, 1991; Hamilton, 1961; Klein, 1986; Paterson, 1996), they also apply to humans adapted to extreme climatic conditions (Foster and Collard, 2013; Holliday, 1997, 1999; Holliday and Hilton, 2010; Holliday and Ruff, 2001; Katzmarzyk and Leonard, 1998; Pearson et al., 2000; Roseman and Auerbach, 2015; Ruff, 1991, 1994, 2002; Ruff et al., 2005; Ruff and Walker, 1993; Symchych, 2016; Trinkaus, 1981).

For instance, it is recognized that circumpolar populations, such as Inuit or Aleuts, have more foreshortened limb segments and broader trunks on average than populations inhabiting mid-latitudes and thus a lower surface area-to-body mass ratio is proposed for them (Holliday, 1997; Holliday and Hilton, 2010; Ruff, 1994; Trinkaus, 1981). Regarding the pelvis, bi-iliac breadth has been demonstrated as the most important reflection of cold adaptation in archaeological populations (Holliday and Hilton, 2010; Ruff, 1991). However, regarding the thorax, its potential impact has not been addressed in any of these studies and it is somehow inferred from the bi-iliac breadth and the hypothetical morphological link between the upper pelvis and the lower thorax (Bastir et al., 2014; Jellema et al., 1993; Torres-Tamayo et al., 2017).

Other examples of adaptation in the rib cage according to extreme climatic conditions can be found in recent studies that addressed rib cage variation in high altitude-adapted populations from the Andes

(Weinstein, 2005, 2007, 2017), which found statistical differences in size and shape of the trunk, including a rib cage that was larger in high altitude-adapted archaeological populations compared with populations inhabiting similar geographical regions but living on the coast. This would also support the possibility that extreme climatic conditions, such as hypoxia, in this case, would contribute to adaptations in thorax morphology.

Even though all the aforementioned evidence supports the application of those eco-geographical rules to modern humans, other authors argue that technological adaptations to climate, e.g. clothing, shelters, etc., could have been successful enough in order to buffer the biological adaptations to extreme climate conditions (Irving, 1957; Scholander, 1955, 1956; Wilber, 1957).

Here we address the 3D morphological variability of the rib cage in several populations from Europe, Africa, and both North and South America, including three hypothetically cold-adapted populations: Greenland Inuit, Alaskan Inuit and people from Tierra del Fuego (Southern Patagonia, Argentina). With all the aforementioned evidence in hand, we will test two null hypotheses, **H1** and **H2**, respectively:

1. Individuals from populations inhabiting high latitudes are larger (Bergmann, 1847) and present relatively larger trunks than those inhabiting close to the equator (Holliday, 1997, 1999; Holliday and Hilton, 2010; Holliday and Ruff, 2001; Roberts, 1973, 1978; Ruff, 1991, 1994; Trinkaus, 1981). Therefore, we should also expect them to present larger rib cages, but this has never been tested until now. We will test H1 which predicts that rib cages are larger in individuals inhabiting high latitudes than in those inhabiting low latitudes. In addition, we will explore how correlated rib size is with latitude at a statistical level. This issue will be addressed throughout rib size at levels 1–11 using centroid size as a proxy.
2. Aside from the size hypothesis, little is known about thorax morphology in cold-adapted populations (Gómez-Olivencia et al., 2009). However, according to Allen's and Bergmann's rule and previous research on trunk shape, we should expect individuals inhabiting high latitudes to have wider thoraces than individuals inhabiting areas closer to the equator. Therefore, we will test H2 which predicts that there are common morphological traits in high-latitude populations belonging to different regions contributing to the hypothetical widening of their ribcages. This issue will be addressed throughout rib shape at levels 1–11.

The test of these hypotheses will not only contribute to our understanding of human biology and ecology but also would lay the foundation for understanding possible adaptations to the climate in the ribcage of past human species such as the Neanderthals.

## 2 | MATERIALS AND METHODS

### 2.1 | Materials

To test the thorax adaptation in cold-adapted populations, we studied three hypothetically cold-adapted archaeological populations from both

the Northern and Southern hemispheres: the Greenland Inuit (GI;  $N = 11$  individuals, 106 ribs), whose remains are housed at the Panum Institute (Faculty of Health Sciences, University of Copenhagen, Denmark); the Alaskan Inuit (AI;  $N = 8$  individuals, 88 ribs), whose remains are housed at the American Museum of Natural History (NY); and the Tierra del Fuego people (TF;  $N = 8$  individuals, 88 ribs), of which six individuals are housed at Laboratorio de Ecología Evolutiva Humana (Universidad del Centro de la Provincia de Buenos Aires, Argentina) and two individuals are housed at the Musée de l'Homme (Paris, France). In addition, we studied archaeological individuals belonging to a Greenland population but with European ancestry (Viking or Norsemen people - VP;  $N = 4$  individuals, 44 ribs), whose remains are also housed at the Panum Institute (Copenhagen, Denmark). These Viking specimens were included as a control group of Greenland individuals that are hypothetically not cold-adapted, because of the short period of time that they lived there compared to the Inuit populations. For this study, we only chose individuals whose thoracic material was in a good degree of preservation, the sex ratio was balanced in every population and only adult individuals (according to teeth and fusion of epiphyses; Scheuer and Black, 2000) were studied. We chose the best-preserved ribs of each side of the rib cage for scanning (no lateral asymmetry has been observed in the ribs to date) and when a rib was too damaged, it was not studied in order to avoid excessive missing data estimation. The number of ribs, as well as information about the populations they belong to, their geographical origin, chronology and latitude, can be found in Table 1 (see also Table 1 in Supporting Information for more details).

To contrast the rib morphology of these cold-adapted populations, we used thoracic material from individuals belonging to European and Sub-Saharan African populations. Europeans included contemporary individuals from a Mediterranean climate (Spain and Portugal) and from a more continental climate (Austria). Only adult individuals were studied and sex was balanced, as in the cold-adapted populations. The European Portuguese (EP;  $N = 10$  individuals, 110 ribs) costal material belongs to the 21st century Identified Skeletal Collection, housed at the Laboratory of Forensic Anthropology of the University of Coimbra (Portugal; Ferreira et al., 2014). The European Spanish (ES;  $N = 10$  individuals, 110 ribs) and Austrian (EA;  $N = 4$  individuals, 44 ribs) material were obtained throughout CT-scan of hospital subjects at the Hospital Universitario La Paz (Madrid, Spain) and the Medizinischen Universität (Innsbruck, Austria). The first Sub-Saharan African population was a contemporary South African population (SA;  $N = 10$  individuals, 110 ribs) whose ribs were obtained throughout CT-scan of hospital subjects at Charlotte Maxeke Hospital (Johannesburg, South Africa). The second African sample is an archaeological Sub-Saharan African population (SSA;  $N = 10$  individuals, 110 ribs) excavated in Valle da Gafaria site (Lagos, Portugal) and housed at Dryas Octopetala (Coimbra, Portugal) (Martiniano et al., 2014; Wasterlain, Neves, & Ferreira, 2016).

To get measurable 3D models of individual ribs, costal elements from ES, EA and SA populations were segmented from CT scans of healthy subjects by semiautomatic methods in Mimics software (www.materialise.com). This semiautomatic method allows the researcher to select a density threshold (density of bone, in this case), select voxels

TABLE 1 Basic information of the populations under study

Abbreviation	General origin	Specific origin	Average latitude	Chronology	Individuals (N)	Ribs (N)
SA	Africa	South Africa (Johannesburg)	−26°	Contemporary	10	110
SSA	Africa	Sub-Saharan African	From −35° to 9°	15th–17th century	10	110
ES	Europe	Spain (Madrid)	40°	Contemporary	10	110
EP	Europe	Portugal (Santarém)	39°	Contemporary	10	110
EA	Europe	Austria (Innsbruck)	47°	Contemporary	4	44
GI	Greenland	Greenland (several localities)	70°	13th–18th century	11	106
AI	Alaska	Alaska (Point Hope)	68°	Tigara Period (13th–17th century)	8	88
TF	Tierra del Fuego	Tierra del Fuego (several localities)	−53°	20th century	8	88
VP	Greenland	Greenland (Ameralla, Nuuk)	64°	11th–15th century (Viking period)	4	44

according to the selected density and create 3D models of the parts fitting that threshold. The data were obtained from hospital subjects that were scanned previously as a healthy control group in order to compare with pathological individuals belonging to a different research project at the Hospital Universitario La Paz (Madrid, Spain), Medizinische Universität Innsbruck (Innsbruck, Austria) and Charlotte Maxeke Hospital, respectively. The subjects were scanned in the supine position for medical reasons not related to respiratory affections and not showing pathologies that could affect the thorax shape. Legal permits were acquired to use this kind of data, all CT-data were anonymized during and prior to analysis in order to comply with the Helsinki declaration (Goodyear et al., 2007). Ribs from TF were segmented from medical CT scans (Brilliance 64 detectors, Philips; Slice 0.9 mm). Finally, ribs from GI, AI, VP, and SSA were scanned utilizing a Next Engine 3D HD laser scanner to create 3D models of the ribs 1–11 of each individual. The scanning process was done in “wide mode,” which resolution is: 0.38-mm accuracy and around 6 points per mm.

From each individual, the rib 12 was avoided because these are very variable in size (Gómez-Olivencia et al., 2009) and could introduce unwanted data (considered noise) in the analysis and interpretation of the results.

## 2.2 | Methods

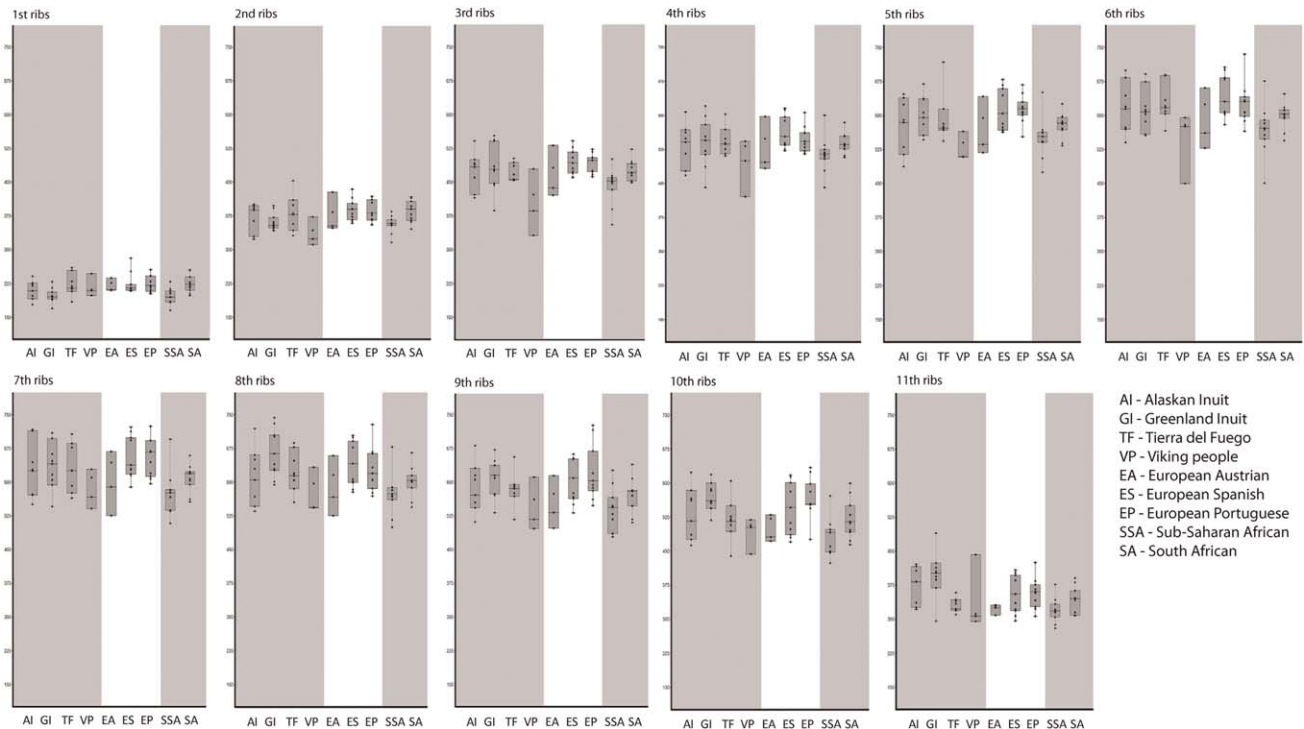
The 3D geometric morphometric methods were applied in order to collect the morphological information of ribs 1–11 of each individual. Levels 1 and 11 lack anatomical structures, such as the costal angle and articular tubercle (Gray, 1918; Spalteholz, 1970), respectively, were landmarks are digitized in ribs 2–10. Therefore, the same landmark protocol could not be used for ribs 1 and 11 and we used three different digitation protocols, which have been successfully tested and published previously (García-Martínez et al., 2017a).

In the 1st rib sample (total  $N = 74$ ) we measured 55 3D landmarks and semi-landmarks per rib (Supporting Information Figure S5) in Viewbox4 software (www.dhal.com), whereas we measured 61 3D landmarks and semilandmarks per rib (Supporting Information Figure S6) in the 2nd to 10th ribs sample (total  $N = 663$ ) and 44 3D landmarks and semilandmarks per rib (Supporting Information Figure S7) in the 11th

rib sample (total  $N = 73$ ). In this way, we quantified rib head morphology, 3D rib curvature, the shaft height and shaft thickness for geometric morphometric analyses. We followed digitation protocol of García-Martínez et al. (2017a). Missing data estimation was also carried out in Viewbox 4 software (www.dhal.com) through Thin Plate Spline and following bending energy approach (Gunz, 2005; Gunz, Mitteroecker, & Bookstein, 2005; Gunz, Mitteroecker, Neubauer, Weber, & Bookstein, 2009). When missing data needed to be estimated at the proximal or distal ends the mean coordinates of their respective sample and level was used as a reference for estimating missing landmarks. Because of uncertainty in terms of landmark location along a rib, semilandmarks were slid along their corresponding curves relative to the fixed landmarks to minimize bending energy. First, this was done between each specimen and the template (first specimen) and after that, semilandmarks were slid a second time along their curves so as to minimize bending energy between each specimen and the sample average (Mitteroecker and Gunz, 2009). This sliding procedure adjusts their relative locations along the curve. Once the whole rib sample was measured, the three sets of 3D coordinates (ribs 1, ribs 2–10 and ribs 11, respectively) were subjected to 3D geometric morphometrics (3DGM) analyses.

The size was quantified as centroid size (CS), defined as the square root of the summed squared distances of each landmark to the centroid. The centroid of a configuration is calculated as the average coordinate ( $x, y, z$ ) of the whole set of coordinates (Zelditch, Swiderski, Sheets, & Fink, 2012). Size relations by level between populations were explored throughout a box plot analysis and analyzed with an ANOVA test by level followed by a Bonferroni posthoc analysis between the populations under study. Means and standard deviations by population and level were also calculated.

Shape data was obtained by partial generalized procrustes analysis (GPA) of landmarks and subjected to principal components analysis (PCA) in order to reduce the dimensionality of data, visualize the main axes of variation (O'Higgins, 2000; Zelditch et al., 2012) and explore the morphological affinities between hypothetically cold-adapted populations. Ordinations were computed in the software package MorphoJ 1.05f (Klingenberg, 2011) and shape differences of the surface



**FIGURE 1** Box-plot distributions of centroid size (CS) in the different populations studied and in ribs 1–11. AI—Alaskan Inuit; GI—Greenland Inuit; TF—Tierra del Fuego; VP—Viking people; EA—European Austrian; ES—European Spanish; EP—European Portuguese; SSA—Sub-Saharan African; SA—South African

associated with variations along the axes were warped and visualized using the EVAN Toolkit version 1.63 (<http://www.evan-society.org/>). One PCA was carried out for each subsample (1, 2–10, and 11 levels, respectively). In addition, since the group 2–10 clustered a large range of the costal sequence, we also split this group in triplets (2–4, 5–7, and 8–10) for the PCA in order to reduce the effect of a sequential change in the morphological variation observed and focus more easily on eco-geographic variability.

Finally, in order to explore the correlation of rib size with latitude, we performed a regression analysis between CS on latitude (absolute values) by each rib level. Therefore, eleven regression analyses were carried out. Latitude of geographical locations was online obtained from <http://www.bufo.es/google-maps-latitud-longitud/>.

### 3 | RESULTS

The results of CS on the boxplot show that rib size exhibits variability at the inter-population and also at the intrapopulation level, which is observed at every rib position (Figure 1). Even though CS distribution is dispersed for every population and level, some common patterns can be observed in the mean values for population and level (Figure 1 from SOM): (1) Cold-adapted populations, both from northern (GI and AI) and southern hemispheres (TF) present larger ribs than the Greenland population with European ancestry (VP); (2) the CS distribution of the Austrian population (EA) is smaller than in the other two European populations (EP and ES), which presented a very similar distribution of CS to each other; (3) the African populations (SSA and SA) present smaller CS than the rest populations, but the SSA population presented even

smaller values than the SA population; (4) Greenland Inuit are larger than the rest of the sample at ribs 8th and 11th. Mean values, as well as standard deviations for each population and level, are observed in Table 2.

ANOVA showed statistical differences by geographical region ( $p < 0.01$ ) at levels 3 and 7–11. Specifically, Bonferroni analysis ( $p < 0.01$ ) showed that at level 3, differences were found between VP (mean = 404.83) and GI (mean = 482.68), ES (mean = 492.77), and EP (mean = 489.95), respectively. At level 7, differences were found between SSA (mean = 575.46) and ES (mean = 654.38), and EP (mean = 655.60), respectively. At level 8, differences were found between SSA (mean = 572.34) and GI (mean = 663.33). At level 9 and 10, differences were found between SSA (mean = 537.55 and 478.92, respectively) and EP (mean = 620.52 and 567.06). At level 11, statistical differences were found between GI (mean = 397.72) and TF (mean = 330.84) and SSA (mean = 319.49).

Principal component analysis (PCA) was carried out separately for every subsample (ribs 1, ribs 2–10 and ribs 11; see methods). For 1st ribs subsample (Figure 2), PCA in PC1 vs. PC2 projection (56.17% of the variability of the sample) shows that the only population that is polarized from the rest is the Greenland Inuit population, which is located more towards the positive values of PC1 and the negative values of PC2 than the rest of the samples. As can be observed in the associated warps, this part of the morphospace is linked to first ribs presenting less curvature in the cranial view. The other hypothetically cold-adapted populations (AI and TF) are in the centre of the distribution and close to the Europeans and Africans, as well as to the Greenland population of European origin (VP).

TABLE 2 Mean and standard deviation (in parentheses) of centroid size (CS) of each costal level and population studied

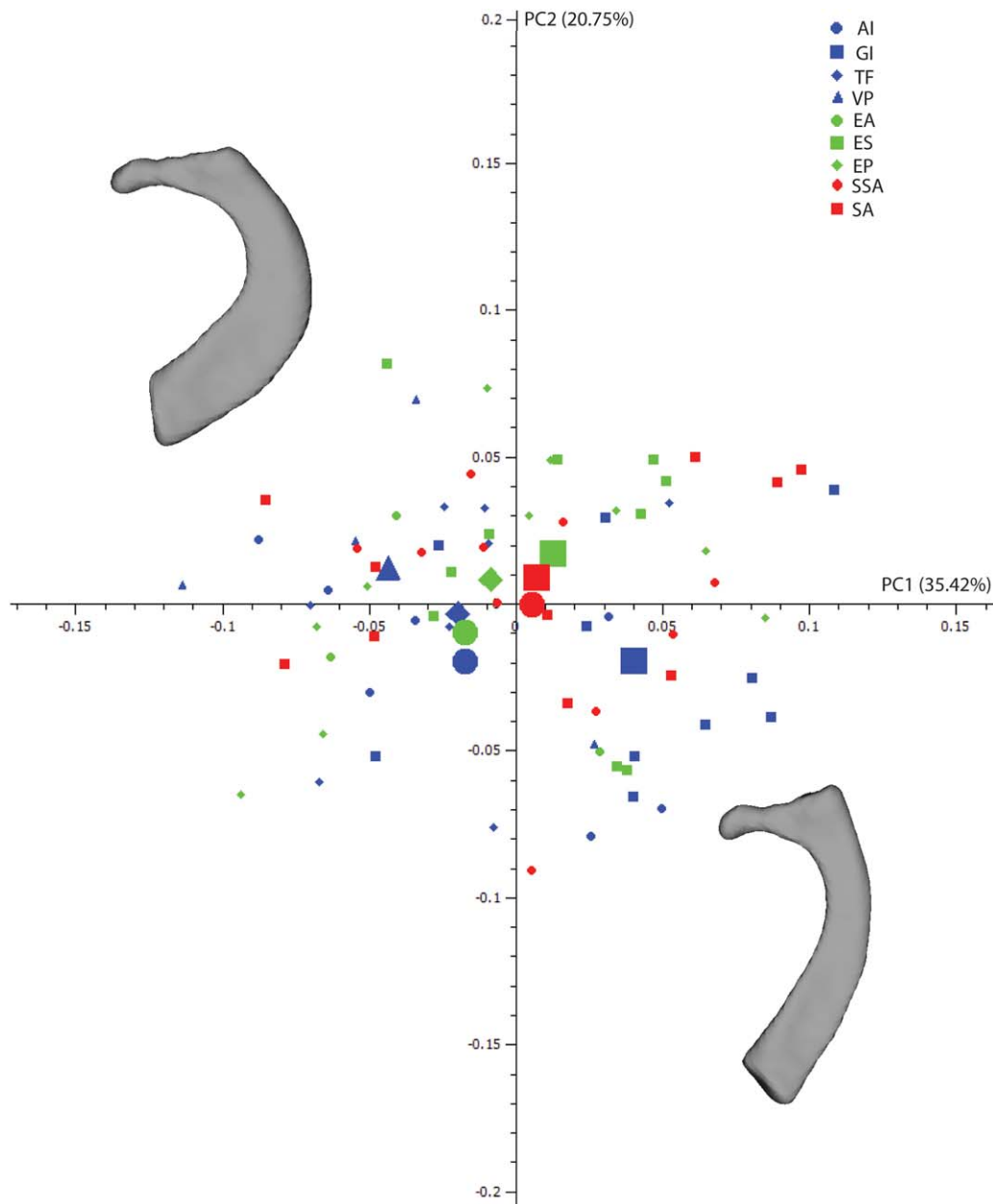
	GI	AI	TF	VP	EA	ES	EP	SSA	SA
1st	197.14 (16.23)	210.53 (20.82)	222.75 (24.83)	216.5 (21.24)	221.02 (12.98)	224.56 (23.68)	223.18 (18.24)	195.91(18.25)	224.51 (19.85)
2nd	360.97 (18.75)	373.94 (31.63)	381.46 (39.50)	337.78 (26.93)	377.94 (36.68)	387.51 (24.33)	385.45 (25.14)	355.82 (19.31)	384.56 (24.40)
3rd	482.68 (49.29)	475.37 (41.84)	471.11 (20.16)	404.83 (62.11)	467.89 (49.61)	492.77 (28.73)	489.85 (22.15)	441.17 (40.85)	475.1 (23.35)
4th	538.27 (53.41)	536.18 (47.24)	543.39 (30.38)	498.89 (55.35)	531.51 (52.33)	562.28 (36.78)	546.64 (29.28)	513.8 (40.42)	536.89 (22.79)
5th	603.07 (42.46)	576.86 (60.21)	592.44 (54.13)	530.53 (27.17)	572.41 (56.53)	610.34 (46.89)	613.46 (31.67)	550.34 (45.58)	577.99 (27.54)
6th	612.1 (46.15)	617.84 (55.95)	628.38 (42.07)	549.69 (67.31)	593.5 (60.05)	640.13 (47.08)	625.63 (46.73)	567.93 (57.04)	598.72 (29.05)
7th	635.22 (51.63)	627.84 (63.23)	631.6 (53.42)	586.6 (39.98)	606.45 (63.24)	654.38 (47.35)	655.6 (47.32)	575.46 (50.54)	607.92 (31.32)
8th	663.33 (53.55)	614.13 (63.06)	623.73 (45.01)	579.13 (44.02)	591.62 (58.10)	637.98 (50.38)	625.17 (49.28)	572.34 (47.76)	601.79 (34.86)
9th	610.26 (41.71)	589.08 (54.69)	584.78 (38.17)	546.56 (50.88)	554.53 (50.68)	601.43 (49.71)	620.52 (62.45)	537.55 (49.34)	568.02 (39.43)
10th	569.25 (30.74)	534.58 (57.78)	519.78 (47.16)	493.03 (33.86)	501.22 (28.86)	540.61 (58.48)	567.06 (45.51)	478.92 (42.79)	521.04 (44.27)
11th	397.72 (50.95)	374.18 (40.96)	330.84 (16.01)	339.04 (69.39)	323.39 (10.10)	352.91 (42.42)	356.76 (34.38)	319.49 (27.47)	340.18 (30.84)

GI = Greenland Inuit; AI = Alaskan Inuit; TF = Tierra del Fuego; VP = viking population; EA = European Austrian; ES = European Spanish; EP = European Portuguese; SSA = Sub-Saharan African; SA = South African.

PCA analysis of ribs 2–10 in PC1 vs. PC2 projection, which accounts for 81.16% of the variability of the sample, shows that most of the variability of the sample is caused by a variation in rib position. This is because we observe in this projection a gradual morphological change from 2nd ribs, polarized to the negative values of PC1 and PC2, to 10th ribs, which are polarized to the positive values of PC1 and negative values of PC2 (Figure 3). Along the morphological trajectory, surface warps associated to the PC scores confirm that the left part of the trajectory coincides with the typical morphology of a second rib (very curved in the cranial view and a short relative tubercle-angle distance) and the right part of the trajectory coincides with the morphology of 10th ribs (low curvature in the cranial view and a long relative tubercle-angle distance). In this projection, inter-population differences are difficult to observe. However, PC2 vs. PC3 projection (17.29% of the variability; Figure 4) yields interpopulation differences very like the ones observed for 1st ribs. In Figure 4, we observe that the GI population is polarized towards the positive values of PC2 and the negative values of PC3, whereas the rest of the hypothetically cold-adapted populations (AI and TF) along with the VP, are in the centre of the distribution, close to Europeans and Africans. The part of the morphospace where the GI ribs are, as observed in the surface warps associated (Figure 4), is linked to ribs that present a low degree of curvature in the cranial view, caused by a more closed angle of curvature at the *angulus costae*, as well as a low degree of rib torsion.

When we split this group in groups-of-three (viz. ribs 2–4, ribs 5–7, and ribs 8–10) we observe on each group a similar pattern as in the PC2 vs. PC3 projection of the entire group, since GI is the only group that is differentially polarized (Supporting Information Figures S2–S4). They are also linked with rib morphologies which present a low degree of rib torsion and less curvature in the cranial view (Supporting Information Figures S2–S4). It is important to mention here that, when splitting the group, the eco-geographic differences are better observed, since they are already present in PC1 vs. PC2 projections. This is because the information about the sequential change, observed in PC1 of Figure 4 and partially hiding the eco-geographic differences, is reduced when splitting into sub-groups. There are also two facts are also important to mention. First, an eco-geographical grouping of GI is clearer in central and lower ribs (Supporting Information Figures S3–S4), supporting what was observed in Figure 4. Second, PC1 vs. PC2 projections of lower ribs explained a larger percentage of the variability than that projection for upper ribs. This could be caused because upper rib morphology associated with sequential change is larger than the sequential change for lower ribs.

PCA of 11th ribs subsample in PC1 vs. PC2 projection (82.92% of variability explained; Figure 5) shows a very similar result to the one observed for the rest of the ribs. This is because the only population that was polarized from the rest was the Greenland Inuit one, which is located more toward the positive values of PC1 and the negative values of PC2 (Figure 5). In the associated warps, we observe that this part of the morphospace is linked to 11th ribs that present less curvature in the cranial view. The other hypothetically cold-adapted populations (AI and TF) are close to the Europeans and Africans, as the Greenland population of European origin (VP) is.



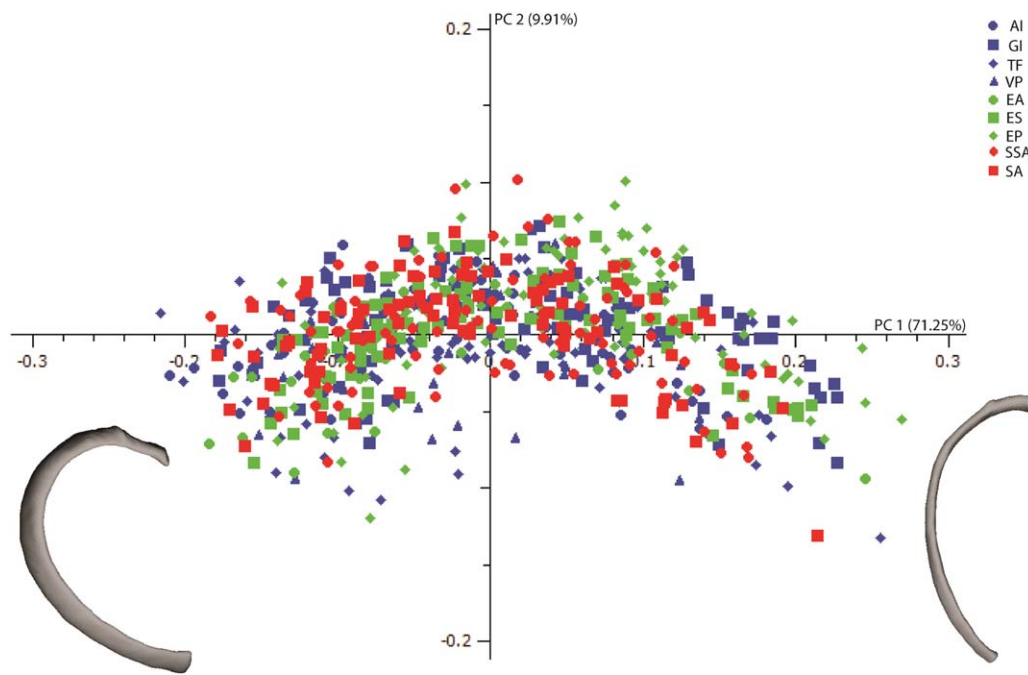
**FIGURE 2** PC1 vs. PC2 plot in shape space of 1st ribs, as well as the surface warps showing morphological variation associated with different parts of the morphospace. Larger symbols represent means by population

Finally, regarding the correlation of rib size with latitude (in absolute values), we observe in Table 3 that rib size is statistically correlated ( $p < 0.05$ ) with absolute values of latitude only for ribs belonging to the lower thorax (from 7th to 11th), whereas upper ribs are not correlated with latitude (Table 3).

#### 4 | DISCUSSION

Bergmann (1847) stated the eco-geographical rule that animals inhabiting high latitudes are larger than their corresponding relatives inhabiting equatorial latitudes, caused by differences in the body surface-to-area ratio to keep or release corporal heat. Although some authors

proposed that this rule was somehow buffered for modern humans since we present cultural adaptations that could mitigate possible biological adaptations (Irving, 1957; Scholander, 1955, 1956; Wilber, 1957), results of the last 30 years showed that differences in body shape are found among populations inhabiting cold-, mild-, and hot-environments (Foster and Collard, 2013; Holliday, 1997, 1999; Holliday and Hilton, 2010; Holliday and Ruff, 2001; Katzmarzyk and Leonard, 1998; Pearson et al., 2000; Roseman and Auerbach, 2015; Ruff, 1991, 1994, 2002; Ruff and Walker, 1993; Ruff et al., 2005; Symchych, 2016; Trinkaus, 1981). Specifically, it has been proposed that individuals inhabiting cold climates present short limbs and larger trunks than their counterparts inhabiting noncold environments as an adaptation in their body. These larger trunks would hypothetically account for a wide



**FIGURE 3** PC1 vs. PC2 plot in shape space of ribs 2–10, as well as the surface warps showing morphological variation associated with different parts of the morphospace. Surface warps associated show that left part of the plot corresponds to 2nd ribs while the right part to 10th ribs, making evident that this projection mainly explains rib position

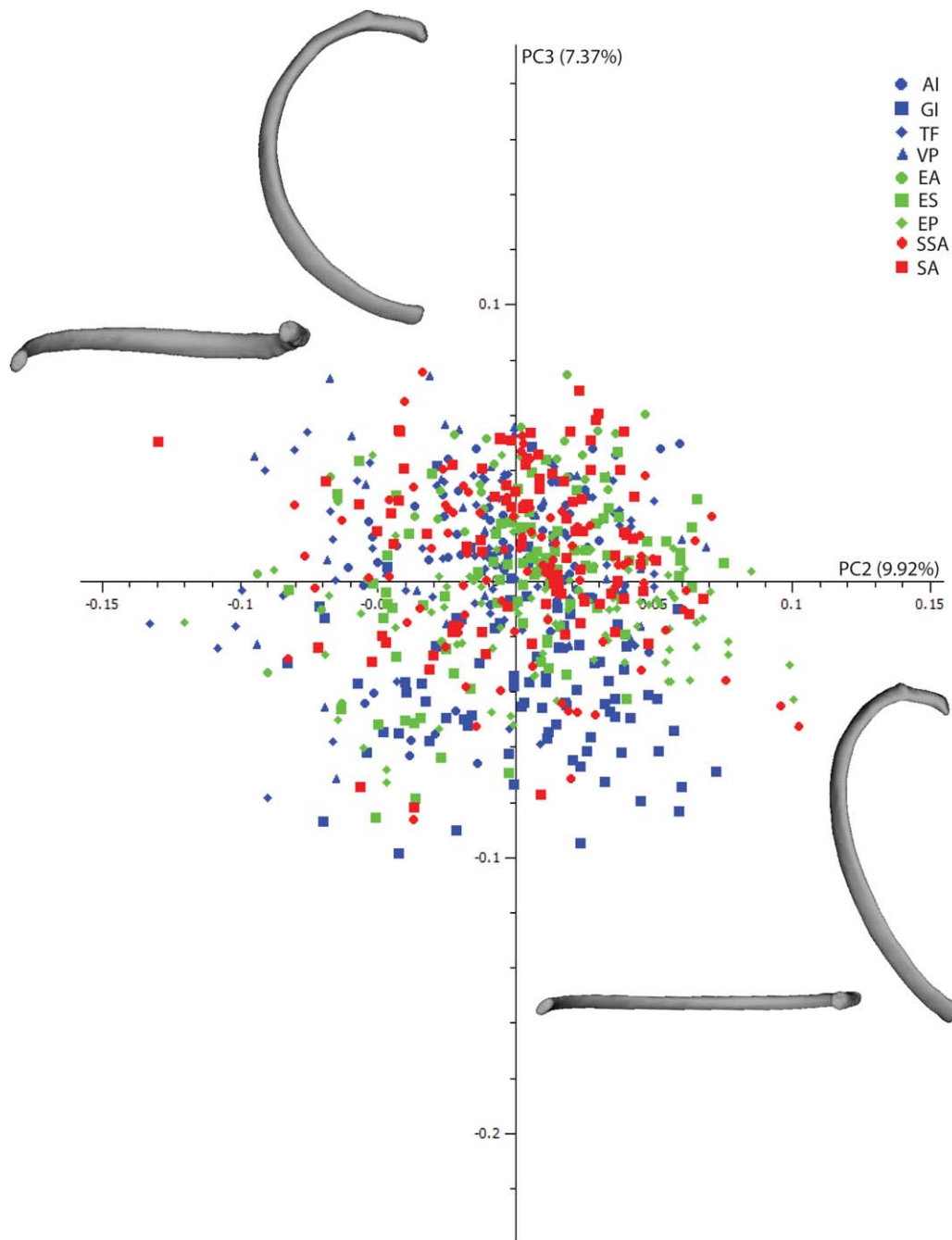
pelvis and a wide rib cage. Even though differences in bi-iliac breadth has been thoroughly studied by other researchers (Holliday and Hilton, 2010; Ruff, 1991, 1993, 1994), differences in the rib cage have been only inferred from data of the pelvis and a hypothetical morphological link between the lower thorax and the pelvis. The only work that studied Alaskan Inuit ribs (Gómez-Olivencia et al., 2009), used traditional measurements such as tubercle-ventral arch and chord, finding that Alaskan Inuit ribs were longer relative to humeral length compared to Euro-Americans, which would be consistent with our results of CS. Even though these measurements have been demonstrated as very useful to quantify rib curvature in the cranial view (Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009), other features such as the rib torsion, which alters rib morphology in the three dimensions, are not well quantified (García-Martínez et al., 2016a). However, in order to expand the knowledge on this issue, we here include different hypothetically cold-adapted populations belonging to both hemispheres as well as populations from Europe and Africa in order to find some common cold-adapted morphological patterns in the rib cage. In addition, we also include information about the latitude of the populations in order to study if rib size is correlated with latitude. This value is a good proxy for the climatic conditions and has been used in previous studies for similar aims (Maddux, Butaric, Yokley, & Franciscus, 2017).

#### 4.1 | Reflections of cold-adaptation in rib size

Even though CS results show that rib size is variable between level but also between populations, we observe general patterns such as the small size of African ribs compared to the rest of the samples as well as the large costal size in the lower thorax of Greenland Inuit, which are the

ones inhabiting highest latitudes. The fact that the VP population presents much smaller values than their Inuit counterparts inhabiting the same regions, is consistent with biological and historical reasons because the Viking people who inhabited Greenland had a European origin and lived there for a relatively short period (Arneborg et al., 1999), insufficient for biological adaptations at that environment. Among the cold-adapted populations (AI, GI, and TF), the Greenland Inuit are the ones that present larger ribs, even larger than their Alaskan and Tierra del Fuego counterparts (Figure 1). This could be caused by the slight differences in latitude (absolute values) observed between them and would be also consistent with Bergmann's rule (1847). Among the populations that are not cold-adapted, the Africans present smaller values of CS, being even more marked in the SSA population than in the SA. The larger values of the Europeans compared to the African ones, could be also caused by absolute latitude values since it is higher for Europeans than for the Africans, supporting Bergmann's rule (1847). Whether the differences observed between the two African populations could be caused by latitude is actually uncertain, since genetic works on SSA population could not specify further than an origin from countries such as current Mauritania, Guinea, Senegal, Sierra Leone, Gambia, Angola, or Mozambique. Although genetics do not exclude Angola or Mozambique, the Carbon-14 results and the historical documents suggest that this sample originated from central-western sub-Saharan Africa, never to the south of the present Equatorial-Guinea (Wasterlain et al., 2016). Regarding our analyses, since the SSA sample present the smaller values of CS and, considering that rib size is correlated with latitude per our study, we hypothesize that this population should have had a more equatorial African origin. This hypothesis should be tested in future studies on that population using genetic techniques.



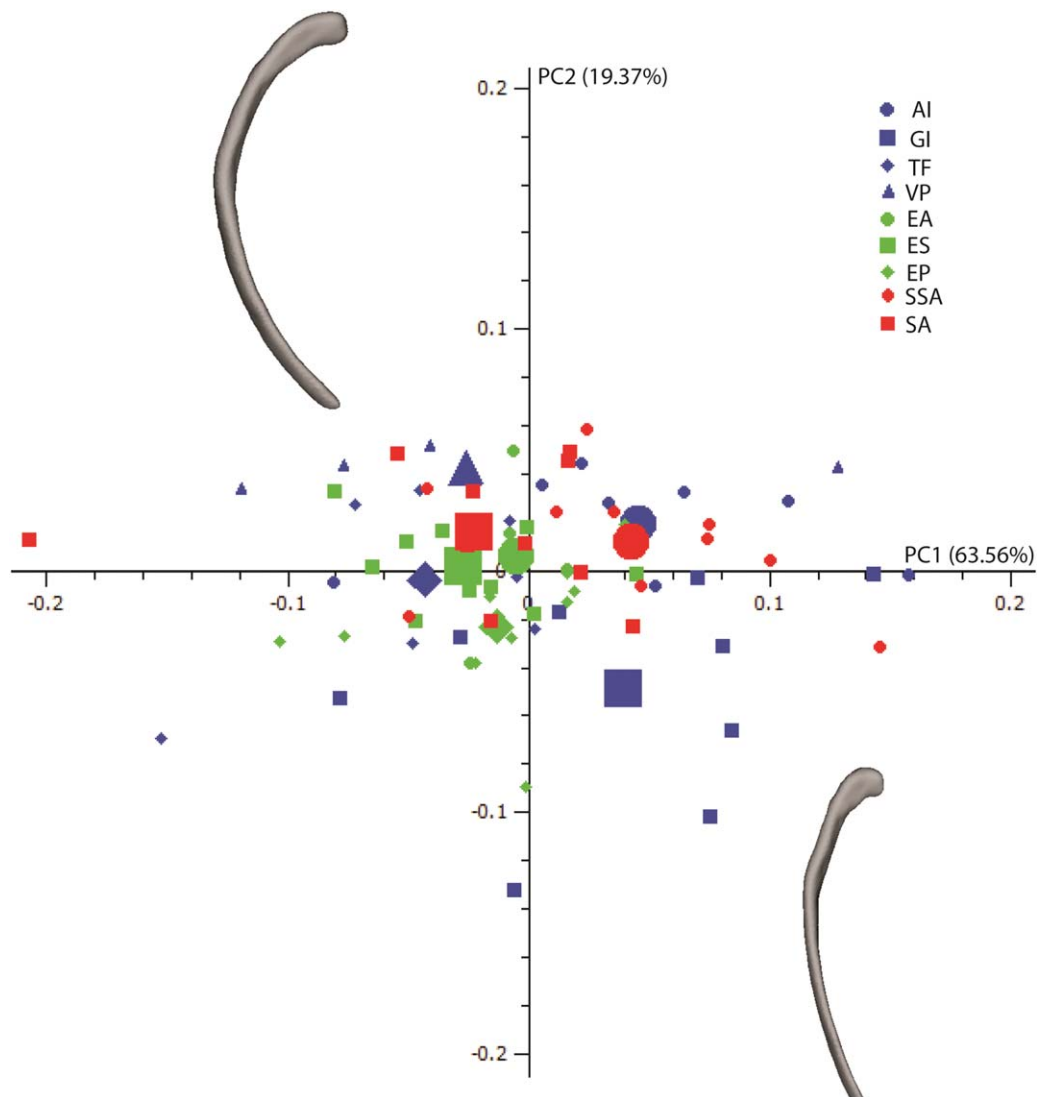


**FIGURE 4** PC2 vs. PC3 plot in shape space of ribs 2–10, as well as the surface warps showing morphological variation associated with different parts of the morphospace

All this evidence, along with the fact that ribs belonging to the lower rib cage statistically correlate with absolute values of latitude (Table 3), allow us to partially accept **H1** which predicts that rib cages of individuals inhabiting cold environments are larger than the ones of individuals belonging to mild and hot climates. We propose for the first time that this hypothesis is only accepted for the lower rib cage. This is important because previous authors found that bi-iliac breadth is also very much correlated with latitude (Holliday and Hilton, 2010; Ruff, 1991, 1993, 1994) and it has been classically accepted that both structures (the lower rib cage and pelvis) co-vary with each other morphology (Bastir et al., 2014; Jellema et al., 1993; Torres-Tamayo et al.,

2017). It is also important to note that different patterns in the upper and lower rib cage are not rare, since previous authors have shown that the upper and lower rib cage have not only differential developments (Bastir et al., 2013; García-Martínez et al., 2016a), but also they could evolve separately (Bastir et al., 2015; Schmid et al., 2013). Differential postnatal development in the lower rib cage could be linked to growth changes in breathing patterns, but it could be also encompassed with the development of the pelvis (Bastir et al., 2013).

Lastly, our results of the thoracic respiratory system are also consistent with recent results of the craniofacial respiratory system, because it has been found that the internal nasal fossa exhibits a strong



**FIGURE 5** PC1 vs. PC2 plot in shape space of 11th ribs, as well as the surface warps showing morphological variation associated with different parts of the morphospace. Larger symbols represent means by population

correlation with climate (Maddux et al., 2017), suggesting that ecogeographic variation could reflect demands for heat and moisture exchange through the air passageway dimensions.

#### 4.2 | Variation in rib morphology and its importance for body shape

Our results show that the only population that is different from the rest is the Greenland Inuit population, in which the differences are observed in the entire rib sequence studied here (ribs 1–11). This will

allow us to reject **H2**, which predicts that there are some common morphological traits in high-latitude populations belonging to different regions. Specifically, Greenland Inuit ribs present less rib torsion and curvature in the cranial view than their counterparts in the rest of the populations, including the other hypothetically cold-adapted populations. Previous work on comparative and evolutionary anatomy (Schmid, 1991) hypothesized that ribs with a low degree of rib torsion, such as the ones of chimpanzees, are linked to ribcages that are wider in the caudal part. Extending this argument to modern human variability, Greenland Inuit (who are characterized by ribs with a low degree of

**TABLE 3** TABLE 3 Results of regression analyses of size on absolute latitude by level, showing the percentage of variance explained by every regression as well as its significance

	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th
% variance	0.11	0.62	1.34	0.41	1.51	2.56	4.99	10.7	6.41	8.46	17.04
<i>p</i> value	0.71	0.48	0.29	0.5	0.27	0.22	0.03*	<0.01*	0.04*	0.01*	<0.01*

Values showing \* are statistically significant at level  $p < 0.05$ .

torsion) would be also characterized by a wide lower rib cage. Even though this is just an extrapolation from Schmid's (1991) hypothesis, it would be consistent with results on the bi-iliac breadth of other authors (Holliday and Hilton, 2010), who found that Greenland Inuit are the ones that present larger values of this measurement, linked to a wide body shape which would include a large trunk. However, it has been recently observed that to fully account for the 3D thorax morphology, not only the ribs but also the thoracic vertebrae should be considered (Bastir et al., 2014, 2017a; García-Martínez, 2017; García-Martínez et al., 2017a). This is because the orientation of the transverse processes of the thoracic vertebrae could play an important role regarding the orientation of the ribs and the mediolateral amplitude of the thorax. Future studies should also study thoracic vertebrae variability to confirm if differences observed in the ribs could be also observed in the thoracic spine, which could have implications for trunk and body shape.

The reason why Greenland Inuit ribs are more different from Africans and Europeans than the Alaskan Inuit or the people from Tierra del Fuego could be due to several factors, viz. (1) absolute latitude of Greenland individuals (70°) is slightly larger than Alaskan Inuit latitude (68°) and much larger than in the people from Tierra del Fuego latitude (53°), which, according to our results on size, could also account for the observed shape differences in the Greenland Inuit. It is important to note in this regard that Foster and Collard (2013) found that human populations should span more than 50° latitude in order to conform Bergmann's rule, and Tierra del Fuego people would be closer to that threshold than Inuit populations; (2) genetic drift causing that Greenland population, which likely originated from the Alaskan population (Saillard, Forster, Lynnerup, Bandelt, & Nørby, 2000; Raghavan et al., 2014), present some specific and unique features caused by genetic isolation and perhaps founder effect; (3) specific cultural adaptations that differentiate Alaskan and Greenland Inuit, as well as people from Tierra del Fuego, could buffer in a different way the possible biological adaptations. It is important to note that several of these factors could act together to explain the observed rib morphology. However, it is important to note that only the factor of latitude is accounted for in our study. The other factors viz. cultural adaptations and genetic drift are not considered here and should be addressed in future research.

With reference to the differences between the two cold-adapted populations of the northern hemisphere, our results are consistent with other authors who also found Alaskan Inuit populations not as cold-adapted as expected (Holliday and Hilton, 2010), with Tigara period population (1200–1600 AD) showing even fewer cold-adaptations than the Ipiutak period population (100 BC to AD 500). The fact that the people of Viking origin from Greenland do not present any similarities neither in size nor in shape with the Greenland Inuit is totally consistent with biological and historical reasons, since the short period of time that they lived there was not enough for allowing biological adaptations (Arneborg et al., 1999). In addition, it is possible that temperature range in Greenland was different from the one from Alaska because of geographical reasons such as the complete exposure of eastern Greenland to the North Sea and the lack of connections with the land. However, the lack of historical records of specific

temperatures for different regions, along with the fact that cold-adapted populations studied here are archaeological, make it difficult to delve into this possibility.

### 4.3 | Evolutionary aspects

Jellema et al. (1993) stated that the modern human thorax shape arose around 1.6 Mya with the emergence of *Homo erectus*, based on the Nariokotome fossils, and it remained invariable until today. Previous researchers have shown that our relatives and partial ancestors, the Neanderthals, probably presented a different thorax shape (Bastir et al., 2015, 2017a; Franciscus and Churchill, 2002; García-Martínez et al., 2014, 2017a; Gómez-Olivencia, 2015; Gómez-Olivencia et al., 2009; Weinstein, 2008; ) adapted to the high energetic requirements they had (Churchill, 2006; Froehle and Churchill, 2009). Therefore, some variation in rib cage morphology is expected in species later than *Homo erectus*.

Apart from this evidence, our results also show that some morphological variability in the rib cage is expected for individuals adapted to some specific environments, such as the Greenland Inuit, who are adapted to polar environments. Differences in thorax morphology have been also observed for Andean populations (Weinstein, 2005, 2007, 2017) because they are adapted to hypoxic environments. Therefore, all this evidence points to the rejection of Jellema's (1993) hypothesis which predicts that modern rib cage morphology remained invariable since its emergence with *Homo erectus*. In addition, recent evidence on pelvic morphology, which is linked to lower thorax shape (Bastir et al., 2014; Jellema et al., 1993; Torres-Tamayo et al., 2017), suggest that the Nariokotome pelvis was probably mediolaterally wider than originally assumed (Fornai and Haeusler, 2017). This wide body shape has been also observed in other individuals of *Homo erectus* such as Gona pelvis (Simpson et al., 2008), or in the Sima de los Huesos (Burgos, Spain) specimens (Arsuaga et al., 1999). Therefore, the modern and narrow body shape could be only specific to *Homo sapiens*; but including some variation in extreme environments as observed in this work. Also, recent studies on torso morphology have shown sex-related differences underlying body shape, showing that sex is an important factor to consider when discussing body shape in hominins (Torres-Tamayo et al., 2017). Even though some recent studies have looked at sexual dimorphism in individual ribs and finding differences in both size and shape (Bellemare, Fuamba, & Bourgeault, 2006; Chapman et al., 2017), none of them has considered this issue in cold-adapted populations and it should be addressed in future studies.

### 4.4 | Limitations

Even though this study considerably impacts our understanding of thorax adaptation to cold-environments, some limitations must be noticed: (1) Asian individuals are not represented in our sample and future studies should cover also this large geographical region in order to confirm the hypotheses presented here; (2) Analyzing rib morphology is difficult in terms of amassing statistically significant sample sizes as every individual is made up of 12 ribs, especially when the number

of individuals with complete ribs available for analysis are limited. While we analyze a fair amount of data, more effort must be paid in the future in order to expand sample sizes; (3) we only included fairly complete individuals in our sample in order to avoid uncertain caused because of missing data estimation but future studies could increase the sample using less complete individuals using different protocols for missing data estimation; (4) here we address thorax morphology based on the rib evidence but the thorax is actually an anatomical composite in which the thoracic vertebrae should be also considered in order to describe 3D detailed thorax morphology, which should be addressed in future studies (Bastir et al., 2017a,b,c; García-Martínez, 2017; García-Martínez et al., 2017a).

## 5 | CONCLUSION

In this study of the costal remains of three different hypothetically cold-adapted populations: Greenland and Alaskan Inuit and people from Tierra del Fuego, we address the manner in which climatic conditions could impact thoracic morphology. We found that populations inhabiting high latitudes (and thus cold climates) present larger rib cages than individuals from mild or hot climates, but the correlation between size and latitude is only found in the lower thorax. Different patterns in upper and lower thorax are not strange to expect since both regions could develop in different ratios according to different factors such as breathing patterns or the development of other anatomical regions (Bastir et al., 2013; García-Martínez et al., 2016a). Size results are consistent with the hypothesis of larger trunks in cold-adapted populations proposed by previous researchers (Holliday, 1997, 1999; Holliday and Hilton, 2010; Holliday and Ruff, 2001; Roberts, 1973, 1978; Ruff, 1991, 1994; Trinkaus, 1981). However, only cold-adapted populations that differ in rib shape from the not cold-adapted ones, are the Greenland Inuit, which would probably be linked with wider rib cages. The lack of differences between the Greenland Inuit and the rest of the cold-adapted populations could be caused by factors such as differences in latitude, genetic drift or specific cultural adaptations, but this two last points should be addressed in future studies. Future studies should include a sample from Asian regions and account for sexual dimorphism or ontogeny in order to have a more precise understanding of this biological problem in humans.

## ACKNOWLEDGMENTS

We acknowledge the Paleoanthropology group of MNCN-CSIC for support. This study was funded by the Leakey Foundation and the Ministerio de Economía y Competitividad of Spain (CGL2015-63648-P). The authors acknowledge Dr Niels Lynnerup and Dr Chiara Villa (University of Copenhagen) for access to the Greenland Inuit collection and also for support during data collection. The authors acknowledge Instituto Radiológico de Mar del Plata and Mr Sebastian Constantino for carrying out CT-scans of individuals from Tierra del Fuego. The European Commission's Research Infrastructure Action funded DGM via the Synthesys Project (DK-TAF-3494 and DK-TAF-6405) and MTF was funded by Gerda Henkel Foundation.

## AUTHOR CONTRIBUTIONS

DGM designed the project, performed the analyses and analyzed the results. DGM, SN, MTF, RAG, MDDAC and MB contributed discussion/materials/analyses. DGM wrote the paper.

## ORCID

Daniel García-Martínez  <http://orcid.org/0000-0001-7518-3866>

## REFERENCES

- Aldrich, J. W., & James, F. C. (1991). Ecogeographic variation in the American Robin (*Turdus migratorius*). *The Auk*, 108, 230–249.
- Allen, J. A. (1877). The influence of physical conditions in the genesis of species. *Radical Review*, 1, 108–140.
- Arneborg, J., Heinemeier, J., Lynnerup, N., Nielsen, H. L., Rud, N., & Sveinbjörnsdóttir, Á. E. (1999). Change of diet of the Greenland Vikings determined from stable carbon isotope analysis and <sup>14</sup>C dating of their bones. *Radiocarbon*, 41, 157–168.
- Arsuaga, J. L., Lorenzo, C., Carretero, J. M., Gracia, A., Martínez, I., García, N., ... Carbonell, E. (1999). A complete human pelvis from the middle Pleistocene of Spain. *Nature*, 399, 255–258. <https://doi.org/10.1038/20430>
- Ashton, K. G. (2002). Do amphibians follow Bergmann's rule?. *Canadian Journal of Zoology*, 80, 708–716.
- Bastir, M., García-Martínez, D., Barash, A., Been, E., Torres, I., & García Río, F. (2014). Thorax kinematics and the reconstruction of body models in hominin evolution. Paper presented at the European Society for the Study of Human Evolution, Florence.
- Bastir, M., García-Martínez, D., Estalrich, A., García-Taberner, A., Huguet, R., Rios, L., ... Rosas, A. (2015). The relevance of the first ribs of the El Sidron site (Asturias, Spain) for the understanding of the Neandertal thorax. *Journal of Human Evolution*, 80, 64–73. <https://doi.org/10.1016/j.jhevol.2014.10.008>
- Bastir, M., García Martínez, D., Recheis, W., Barash, A., Coquerelle, M., Rios, L., ... O'higgins, P. (2013). Differential growth and development of the upper and lower human thorax. *PLoS ONE*, 8, e75128. <https://doi.org/10.1371/journal.pone.0075128>
- Bastir, M., Martínez, D. G., Rios, L., Higuero, A., Barash, A., Martelli, S., ... de la Rasilla, M. (2017a). Three-dimensional morphometrics of thoracic vertebrae in Neandertals and the fossil evidence from El Sidrón (Asturias, Northern Spain). *Journal of Human Evolution*, 108, 47–61.
- Bastir, M., García-Martínez, D., Torres-Tamayo, N., Sanchis-Gimeno, J. A., O'Higgins, P., Utrilla, C., ... García Río, F. (2017b). In vivo 3D analysis of thoracic kinematics: Changes in size and shape during breathing and their implications for respiratory function in recent humans and fossil hominins. *The Anatomical Record*, 300, 255–264. <https://doi.org/10.1002/ar.23503>
- Bastir, M., García-Martínez, D., Williams, S. A., Recheis, W., Torres-Sánchez, I., García Río, F., ... Ogihara, N. (2017c). 3D geometric morphometrics of thorax variation and allometry in Hominioidea. *Journal of Human Evolution*, 113, 10–23. doi: <https://doi.org/10.1016/j.jhevol.2017.08.002>
- Bellemare, F., Fuamba, T., & Bourgeault, A. (2006). Sexual dimorphism of human ribs. *Respiratory Physiology and Neurobiology*, 150, 233–239.
- Bergmann, C. (1847). Über die Verhältnisse der Warmeökonomie der Thiere zu ihrer Grosse. *Gottinger Studien*, 3, 595–708.
- Chapman, T., Beyer, B., Sholukha, V., Semal, P., Feipel, V., Louryan, S., & Jan, S. V. S. (2017). How different are the Kebara 2 ribs to modern humans? *Journal of Anthropological Sciences*, 95, 1–20.

- Churchill, S. E. (2006). Bioenergetic perspectives on Neanderthal thermoregulatory and activity budgets. In K. Harvati & T. Harrison (Eds.), *Neanderthals revisited* (pp. 113–156). New York City: Springer Verlag.
- Churchill, S. E. (2014). *Thin on the ground: Neanderthal biology, archeology and ecology*: Hoboken, New Jersey: Wiley Blackwell.
- Ferreira, M. T., Vicente, R., Navega, D., Gonçalves, D., Curate, F., & Cunha, E. (2014). A new forensic collection housed at the University of Coimbra, Portugal: The 21st century identified skeletal collection. *Forensic Science International*, 245, 201–202.
- Fornai, C., & Haeusler, M. (2017). Virtual reconstruction of the pelvic remains of KNM-WT 15000 *Homo erectus* from Nariokotome, Kenya. *American Journal of Physical Anthropology*, 162, 183.
- Foster, F., & Collard, M. (2013). A reassessment of Bergmann's rule in modern humans. *PLoS One*, 8, e72269.
- Franciscus, R. G., & Churchill, S. E. (2002). The costal skeleton of Shanidar 3 and a reappraisal of Neanderthal thoracic morphology. *Journal of Human Evolution*, 42, 303–356.
- Froehle, A., & Churchill, S. E. (2009). Energetic competition between Neanderthals and anatomically modern humans. *Paleoanthropology*, 2009, 96–116.
- García-Martínez, D. (2017). Contributions to the study of the morphological, functional and evolutionary variability of the human rib cage. PhD dissertation, Universidad Autónoma de Madrid.
- García-Martínez, D., Barash, A., Recheis, W., Utrilla, C., Torres Sánchez, I., García Río, F., & Bastir, M. (2014). On the chest size of Kebara 2. *Journal of Human Evolution*, 70, 69–72.
- García-Martínez, D., Bastir, M., Huguet, R., Estalrich, A., García-Taberner, A., Ríos, L., & Rosas, A. (2017a). The costal remains of the El Sidrón Neanderthal site (Asturias, northern Spain) and their importance for understanding Neanderthal thorax morphology. *Journal of Human Evolution*, 111, 85–101. doi: <https://doi.org/10.1016/j.jhevol.2017.06.003>
- García-Martínez, D., Gil, O. G., Cambra-Moo, O., Canillas, M., Rodríguez, M. A., Bastir, M., & Martín, A. G. (2017b). External and internal ontogenetic changes in the first rib. *American Journal of Physical Anthropology*, 164, 750–762. <https://doi.org/10.1002/ajpa.23313>
- García-Martínez, D., Recheis, W., & Bastir, M. (2016a). Ontogeny of 3D rib curvature and its importance for the understanding of human thorax development. *American Journal of Physical Anthropology*, 159, 423–431. <https://doi.org/10.1002/ajpa.22893>
- García-Martínez, D., Torres-Tamayo, N., Torres-Sanchez, I., García-Río, F., & Bastir, M. (2016b). Morphological and functional implications of sexual dimorphism in the human skeletal thorax. *American Journal of Physical Anthropology*, 161, 467–477. <https://doi.org/10.1002/ajpa.23051>
- Gómez-Olivencia, A. (2015). The costal skeleton of the Neanderthal individual of La Chapelle-aux-Saints 1. *Annales De Paléontologie*, 101, 127–141. doi: <https://doi.org/10.1016/j.annpal.2015.04.005>
- Gómez-Olivencia, A., Eaves-Johnson, K. L., Franciscus, R. G., Carretero, J. M., & Arsuaga, J. L. (2009). Kebara 2: New insights regarding the most complete Neanderthal thorax. *Journal of Human Evolution*, 57, 75–90.
- Goodyear, M. D. E., Krleza-Jeric, K., & Lemmens, T. (2007). The Declaration of Helsinki. *BMJ*, 335(7621), 624–625. doi: <https://doi.org/10.1136/bmj.39339.610000.BE>
- Graves, G. R. (1991). Bergmann's rule near the equator: Latitudinal clines in body size of an Andean passerine bird. *Proceedings of the National Academy of Sciences of the United States of America*, 88, 2322–2325.
- Gray, H. (1918). *Anatomy of the human body*. Philadelphia: Lea & Febiger.
- Gunz, P. (2005). Statistical and geometric reconstruction of hominid crania: Reconstructing australopithecine ontogeny. PhD thesis, University of Vienna, Vienna.
- Gunz, P., Mitteroecker, P., & Bookstein, F. L. (2005). Semilandmarks in three dimensions. In D. Slice (Ed.), *Modern morphometrics in physical anthropology* (pp. 73–98). New York: Kluwer Academic/Plenum.
- Gunz, P., Mitteroecker, P., Neubauer, S., Weber, G. W., & Bookstein, F. L. (2009). Principles for the virtual reconstruction of hominid crania. *Journal of Human Evolution*, 57, 48–62.
- Hamilton, T. (1961). The adaptive significances of intraspecific trends of variation in wing length and body size among bird species. *Evolution*, 15, 180–195.
- Holliday, T. W. (1997). Postcranial evidence of cold adaptation in European Neanderthals. *American Journal of Physical Anthropology*, 104, 245–258.
- Holliday, T. W. (1999). Brachial and crural indices of European late upper paleolithic and mesolithic humans. *Journal of Human Evolution*, 36, 549–566.
- Holliday, T. W., & Hilton, C. E. (2010). Body proportions of circumpolar peoples as evidenced from skeletal data: Ipiutak and Tigara (Point Hope) versus Kodiak Island Inuit. *American Journal of Physical Anthropology*, 142, 287–302.
- Holliday, T. W., & Ruff, C. B. (2001). Relative variation in human proximal and distal limb segment lengths. *American Journal of Physical Anthropology*, 116, 26–33.
- Irving, L. (1957). The usefulness of Scholander's views on adaptive insulation of animals. *Evolution*, 11, 257–259.
- Jellema, L. M., Latimer, B., & Walker, A. (1993). The rib cage. In R. E. Leaky & A. Walker (Eds.), *The nariokotome Homo erectus skeleton* (pp. 294–325). Cambridge: Harvard University Press.
- Katzmarzyk, P. T., & Leonard, W. R. (1998). Climatic influences on human body size and proportions: Ecological adaptations and secular trends. *American Journal of Physical Anthropology*, 106, 483–503.
- Klein, R. G. (1986). Carnivore size and quaternary climatic change in southern Africa. *Quaternary Research*, 26, 153–170.
- Klingenberg, C. P. (2011). MorphoJ: An integrated software package for geometric morphometrics. *Molecular Ecology Resources*, 11, 353–357.
- Latimer, B. M., Lovejoy, C. O., Spurluck, L., & Haile-Selassie, Y. (2016). The thoracic cage of KSD-VP-1/1 The Postcranial Anatomy of *Australopithecus afarensis* (pp. 143–153). Springer.
- Maddux, S. D., Butaric, L. N., Yokley, T. R., & Franciscus, R. G. (2017). Ecogeographic variation across morphofunctional units of the human nose. *American Journal of Physical Anthropology*, 162, 103–119.
- Martiniano, R., Coelho, C., Ferreira, M. T., Neves, M. J., Pinhasi, R., & Bradley, D. G. (2014). Genetic evidence of African slavery at the beginning of the trans-Atlantic slave trade. *Scientific Reports*, 4, 5994.
- Mitteroecker, P., & Gunz, P. (2009). Advances in geometric morphometrics evolutionary biology. *Evolutionary Biology*, 36(2), 235–247.
- O'Higgins, P. (2000). The study of morphological variation in the hominid fossil record: Biology, landmarks and geometry. *Journal of Anatomy*, 197, 103–120.
- Paterson, J. D. (1996). Coming to America: Acclimation in macaque body structures and Bergmann's rule. *International Journal of Primatology*, 17, 585–611.
- Pearson, O. M., Borgognini Tarli, S. M., Marini, E., Formicola, V., Holliday, T. W., Hublin, J., ... Petersen, H. C. (2000). Activity, climate, and postcranial robusticity: Implications for modern human origins and scenarios of adaptive change. *Current Anthropology*, 41, 569–607.
- Raghavan, M., DeGiorgio, M., Albrechtsen, A., Moltke, I., Skoglund, P., Korneliusson, T. S., ... Friesen, T. M. (2014). The genetic prehistory of the New World Arctic. *Science*, 345, 1255832.
- Roberts, D. (1973). *Climate and human variability. An Addison-Wesley module in anthropology*, No. 34. Reading, MA: Addison-Wesley.

- Roberts, D. F. (1978). *Climate and human variability*, 2nd edn. Menlo Park: Cummings.
- Roseman, C. C., & Auerbach, B. M. (2015). Ecogeography, genetics, and the evolution of human body form. *Journal of Human Evolution*, 78, 80–90.
- Ruff, C. B. (1991). Climate and body shape in hominid evolution. *Journal of Human Evolution*, 21, 81–105. doi: [https://doi.org/10.1016/0047-2484\(91\)90001-C](https://doi.org/10.1016/0047-2484(91)90001-C)
- Ruff, C. B. (1994). Morphological adaptation to climate in modern and fossil hominids. *American Journal of Physical Anthropology*, 37, 65–107.
- Ruff, C. (2002). Variation in human body size and shape. *Annual Review of Anthropology*, 31, 211–232.
- Ruff, C., Niskanen, M., Junno, J.-A., & Jamison, P. (2005). Body mass prediction from stature and bi-iliac breadth in two high latitude populations, with application to earlier higher latitude humans. *Journal of Human Evolution*, 48, 381–392.
- Ruff, C., & Walker, A. (1993). Body size and body shape. In A. Walker & R. Leakey (Eds.), *The nariokotome Homo erectus skeleton* (pp. 234–265). Cambridge: Harvard University Press.
- Saillard, J., Forster, P., Lynnerup, N., Bandelt, H.-J., & Nørby, S. (2000). mtDNA variation among Greenland Eskimos: The edge of the Beringian expansion. *The American Journal of Human Genetics*, 67, 718–726.
- Scheuer, L., & Black, S. (2000). *Developmental juvenile osteology*. San Diego: Academic Press.
- Schmid, P. (Ed.). (1991). *The trunk of the australopithecines*. Anatole, France: Éditions du Centre National de la Recherche Scientifique.
- Schmid, P., Churchill, S. E., Nalla, S., Weissen, E., Carlson, K. J., de Ruiter, D. J., & Berger, L. R. (2013). Mosaic morphology in the thorax of *Australopithecus sediba*. *Science*, 340, 1234598. <https://doi.org/10.1126/science.1234598>
- Scholander, P. F. (1955). Evolution of climatic adaptation in homeotherms. *Evolution*, 9, 15–26.
- Scholander, P. F. (1956). Climatic rules. *Evolution*, 10, 339–340.
- Schreider, E. (1964). Ecological rules, body-heat regulation, and human evolution. *Evolution*, 18, 1–9.
- Shi, X., Cao, L., Reed, M. P., Rupp, J. D., Hoff, C. N., & Hu, J. (2014). A statistical human rib cage geometry model accounting for variations by age, sex, stature and body mass index. *Journal of Biomechanics*, 47, 2277–2285. doi: <https://doi.org/10.1016/j.jbiomech.2014.04.045>
- Simpson, S. W., Quade, J., Levin, N. E., Butler, R., Dupont-Nivet, G., Everett, M., & Semaw, S. (2008). A female *Homo erectus* pelvis from Gona, Ethiopia. *Science*, 322, 1089–1092.
- Spalteholz, W. (1970). *Atlas de anatomía humana*, 5th ed. Barcelona: Labor S.A.
- Symchych, N. (2016). An ecogeographic study of body proportion development in the Sadlermiut Inuit of Southampton Island, Nunavut. PhD dissertation. The University of Toronto.
- Torres-Tamayo, N., García-Martínez, D., Nalla, S., Barash, A., Blanco, E., Mata Escolano, F., ... Bastir, M. (2017). The human torso: Variation in relation to sexual dimorphism, ancestry and allometry. Proceedings of the VI Iberian Primatological Conference (Burgos, Spain).
- Trinkaus, E. (1981). Neanderthal limb proportions and cold adaptation. In C. B. Stringer (Ed.), *Aspects of human evolution*. London, UK: Taylor & Francis.
- Wasterlain, S., Neves, M., & Ferreira, M. (2016). Dental modifications in a skeletal sample of enslaved Africans found at Lagos (Portugal). *International Journal of Osteoarchaeology*, 26, 621–632.
- Weaver, A. A., Schoell, S. L., & Stitzel, J. D. (2014). Morphometric analysis of variation in the ribs with age and sex. *Journal of Anatomy*, 225, 246–261. <https://doi.org/10.1111/joa.12203>
- Weinstein, K. J. (2005). Body proportions in ancient Andeans from high and low altitudes. *American Journal of Physical Anthropology*, 128, 569–585.
- Weinstein, K. J. (2007). Thoracic skeletal morphology and high-altitude hypoxia in Andean prehistory. *American Journal of Physical Anthropology*, 134, 36–49.
- Weinstein, K. J. (2008). Thoracic morphology in Near Eastern Neandertals and early modern humans compared with recent modern humans from high and low altitudes. *Journal of Human Evolution*, 54, 287–295.
- Weinstein, K. J. (2017). Morphological signatures of high-altitude adaptations in the Andean archaeological record: Distinguishing developmental plasticity and natural selection. *Quaternary International*.
- Wilber, C. G. (1957). Physiological regulations and the origin of human types. *Human Biology*, 29, 329.
- Williams, S. A., García-Martínez, D., Bastir, M., Meyer, M. R., Nalla, S., Hawks, J., ... Berger, L. R. (2017). The vertebrae and ribs of *Homo naledi*. *Journal of Human Evolution*, 104, 136–154. doi: <https://doi.org/10.1016/j.jhevol.2016.11.003>
- Zelditch, M. L., Swiderski, D. L., Sheets, H. D., & Fink, W. L. (2012). *Geometric morphometrics for biologists: A primer* (2nd ed.). San Diego: Elsevier Academic Press.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**How to cite this article:** García-Martínez D, Nalla S, Ferreira MT, Guichón RA, D'Angelo del Campo MD, Bastir M. Eco-geographic adaptations in the human ribcage throughout a 3D geometric morphometric approach. *Am J Phys Anthropol*. 2018;00:1–14. <https://doi.org/10.1002/ajpa.23433>