Received: 21 March 2024 | Revised: 19 June 2024 | Accepted: 21 June 2024

DOI: 10.1002/evan.22040

RESEARCH ARTICLE

Evolutionary Anthropology ISSUES, NEWS, AND REVIEWS WILEY

Eco-geographic and sexual variation of the ribcage in *Homo sapiens*

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Funding information
Ministerio de Ciencia e Innovación, Grant/Award Numbers: PID2020-115854GB-I00, PRE2021-097584; Universidade de Coimbra, Grant/Award Number: UIDB/04004/2020

Abstract

Up to now, Allen and Bergmann's rules have been studied in modern humans by analyzing differences in limb length, height, or body mass. However, there are no publications studying the effects of latitude in the 3D configuration of the ribcage. To assess this issue, we digitally reconstructed the ribcages of a balanced sample of 109 adult individuals of global distribution. Shape and size of the ribcage was quantified using geometric morphometrics. Our results show that the ribcage belonging to tropical individuals is smaller and slenderer compared to others living in higher latitudes, which is in line with Allen and Bergmann's rules and suggests an allometric relationship between size and shape. Although sexual dimorphism was observed in the whole sample, significant differences were only found in tropical populations. Our proposal is that, apart from potential sexual selection, avoiding heat loss might be the limiting factor for sexual dimorphism in cold-adapted populations.

KEYWORDS

Allen and Bergmann's rule, allometry, geometric morphometrics, latitude, sexual dimorphism, thorax

1 | INTRODUCTION

Global distribution of *Homo sapiens* raises substantial questions about behavioral, cultural, physiological, and morphological adaptations to different environments. If we focus on anatomical traits, these inquiries could be synthesized with Allen's rule.[1] This eco-geographic rule states that body proportions of homeothermic animals, such as *H. sapiens*, are dependent on latitude. This causes, hypothetically, a bigger surface-area-to-volume ratio in individuals living in tropical climates to release heat, and the other way around in those living in colder areas. Previous research tested the effects of Allen's rule in current humans, noticing that individuals from colder regions present lower limb length and, consequently, lower height and greater body mass index (BMI) that those from tropical environments.[2–5] This would be also in line with Bergmann's rule,[6] another eco-geographic rule which states that populations from polar latitudes would be larger in size compared to those from equatorial regions.[7] Even though there are publications about eco-geographic variation in other body parts different from the limbs, like the skull,[8] there are still no studies on a crucial anatomical region to understand the effect of climate in body shape and proportions: the ribcage.

Despite the importance of the ribcage for human biology, its comparative study among different *H. sapiens* populations remains underdeveloped given that its 3D configuration can only be understood by the spatial disposition of its metameric components, which are ribs and vertebrae. This is why most publications on this topic have been carried out either using these isolated elements,[9–12] or through CT scans where the ribcage was already articulated.[13,14] However, accessing to CT scans belonging to worldwide populations is difficult due to technical and ethical constrains, so osteo-archeological collections are the most viable way to conduct research on eco-geographic ribcage variability. This results in several limitations because vertebrae, and particularly ribs, are numerous and fragile, so costo-vertebral series tend to appear incomplete, broken, and/or commingled.[15–17]

Previous research proposed that ribs from cold-adapted populations, such as Inuit, present less torsion and curvature compared to ribs from warmer populations.[10] This would mean that cold-adapted individuals might have relatively larger, wider, and deeper ribcages, suggesting an allometric relationship between size and shape dependent on climate. In fact, stocky ribcages might be linked not only to differences in body proportions, but also to differences in functionality. Ribs with greater torsion from the flatter thorax of equatorial *H. sapiens* might be elevated more effectively by the inspiratory muscles than the more horizontally oriented ribs belonging to cold-adapted populations. This would be compensated by a more intense diaphragmatic action in the latter, which could have an important role on thermoregulation and energetics.[18–21]

In addition, latitudinal differences among populations can be also studied taking sexual dimorphism into account. Some articles have described size and shape differences in the male and female ribcage and have highlighted their effect on breathing kinematics. In particular, since ribcages are stockier in males compared to females, respiration in males is supposed to show a greater diaphragmatic action. Contrary, in the case of females, respiration may rely more on other respiratory muscles such as the scalenes and intercostals. Sexual differences in breathing kinematics could be ultimately explained by the limitations that pregnancy imposes on diaphragmatic contraction.[14,22–25] However, the cited publications sample a limited range of populations, predominantly consisting of individuals of European ancestry, and the dating is constrained as the experiments are conducted in vivo. Thus, incorporating sex as another variable in the study of eco-geographic adaptations would yield new data on the impact of climate in sexual dimorphism.

Considering all this background, the aim of this study is reconstructing the ribcage from individuals belonging to worldwide distributed *H. sapiens* populations and using 3D geometric morphometrics for testing the following hypotheses:

1. According to Allen and Bergmann's rules, the relative shape and size of the modern human ribcage might depend on latitude,[10] suggesting an allometric relationship between both parameters. Hence, we expect that individuals from tropical environments would have smaller and slenderer ribcages compared to those from colder areas.
2. Based on previous publications on European individuals, there is sexual dimorphism in the shape and size of the *H. sapiens* ribcage.[14,22–25] We therefore hypothesize that this is extensive to a worldwide distributed sample.

2 | MATERIALS AND METHODS

The sample chosen for this research belongs to 19 populations distributed along the five inhabited continents and the three main latitudinal zones: polar, temperate, and tropical (Figure 1, Table 1). Except Afro-Americans, sub-Saharans, and Norsemen, all populations had ancestral origins in the region where their remains were collected. The original eco-geographic area where Afro-Americans, sub-Saharans, and Norsemen came from is marked in Figure 1 and based on literature.[26,27] Each population was meant to be balanced in sex and represented by approximately six adult individuals, resulting in a total of 109 subjects of study (50♀, 58♂, 1 indet) whose ribs and vertebrae had no pathological nor taphonomical alterations. Further information about the sample is included in Supporting Information S1: Table S1. 3D virtual models of the thoracic vertebrae and the best-preserved rib form each costal level were obtained using two surface scanners: Artec Space Spider (resolution: 0.1 mm; accuracy: 0.05 points per mm) or Next Engine 3D HD (resolution: 0.38 mm; accuracy: six points per mm). Additionally, we included some CT scans provided by the New Mexico Decedent Image Database (NMDID), who were scanned using the adult OMI protocol for thorax[28] with the following parameters: collimation = 16 × 0.75 mm; pitch = 0.817; voltage = 120 kVp; reference tube current-time = 300 mAs; and rotation time = 1 s. Ribs and vertebrae of these individuals were obtained

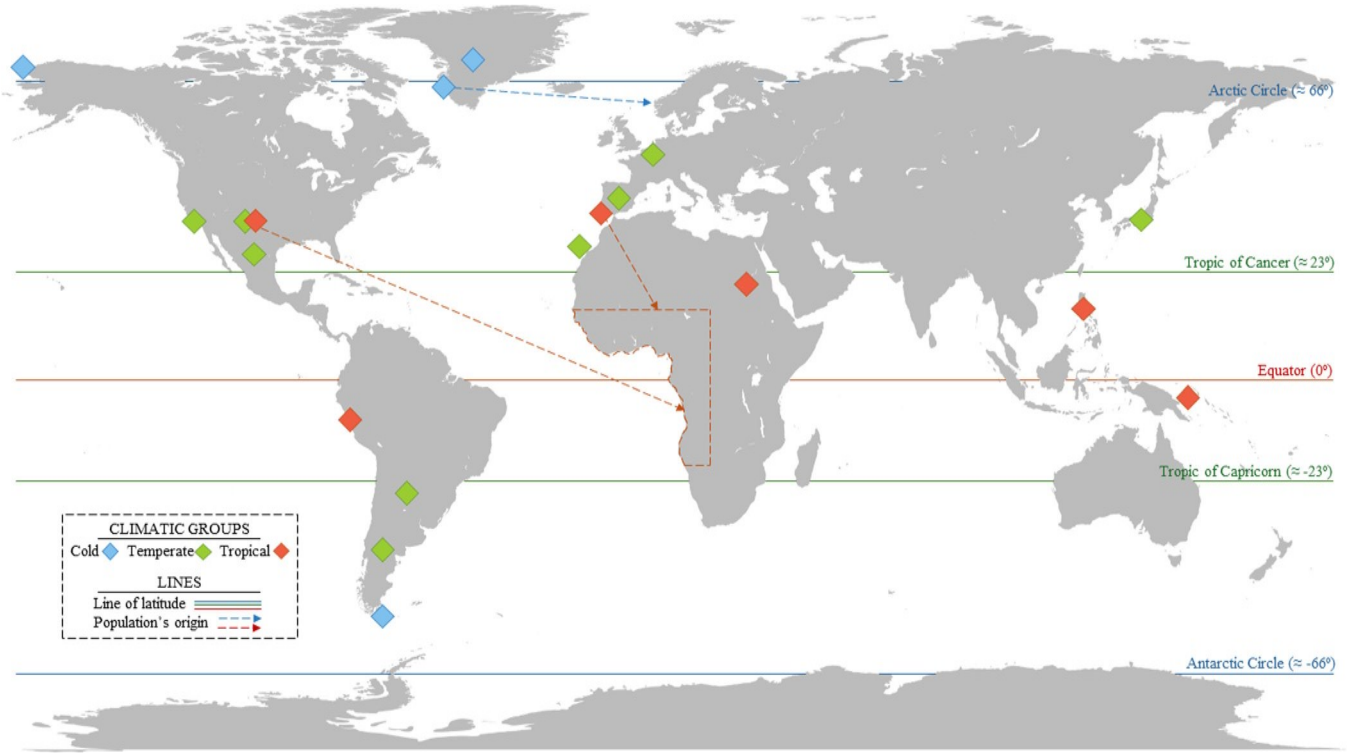

FIGURE 1 Worldwide distribution of the studied populations.

via segmentation by standard methods in Slicer v. 4.10.2[29] using the "Segment Editor" module. All the models were postprocessed by Artec Studio v. 16 (www.artec3d.com) for cleaning, smoothing edges, and filling possible gaps.

Next, we reconstructed the full ribcage of each individual following the protocol developed by López-Rey et al.[30] using the software LhpFusionBox (Université Libre de Bruxelles). Once the reconstructions were completed, we measured the 3D ribcage models in Viewbox v. 4.1 (https://www.dhal.com/viewbox.htm) using a template of 526 (semi)landmarks, which was previously described by Bastir et al.[31] Comparability between meshes obtained both by surface and CT scans when working with 3D geometric morphometrics was previously assessed by several publications.[32,33] Before starting with the statistical analyses, we (1) removed the coordinates from ribs 11 and 12 since these ribs are very variable in form[34] and could introduce noise in the analysis and interpretation of the results; (2) estimated missing data, in case it was needed; and (3) symmetrized each ribcage to avoid the effect of morphological alterations, such as scoliosis, in our analyses.

To study the effects of latitude on the shape and size of the human ribcage, the sample was gathered in three climatic groups: cold (four populations), temperate (nine populations), and tropical (six populations). General differences in shape were statistically tested among the three climatic groups using a pairwise Procrustes analysis of variance (ANOVA) (Table 2). To delve deeper into the study of shape, specific shape differences between groups were studied by a principal components analysis (PCA) over the mean shape of each population's males and females. We checked the normality (Shapiro–Wilk test) and homoscedasticity (Levene's test) of the PC1, PC2, and PC3 scores (together representing a 61.21% of total shape variance) and then compared their distribution among groups by an ANOVA/Kruskal–Wallis test (Table 3). These results were depicted by boxplots in Figure 2. To check whether there are any differences in ribcage size among groups, centroid sizes were compared such as done above with the PC scores (Table 4).

We also studied the effect of sex on the shape and size of the human ribcage taking latitude into consideration. On the one hand, shape differences between sexes were tested by a dummy regression between the Procrustes coordinates of each group and two dummy variables (0—female, 1—male) (Figure 3). On the other hand, size differences between sexes were studied by the analyzing the centroid sizes (Table 5). To check whether there is any allometric relationship between the shape and size of the ribcage, we performed a linear regression between the Procrustes coordinates and the centroid size of the full sample, splitting the data set according to climatic groups and sex (Figure 4). Eventually, we extracted the mean forms of the males and females from each climatic group to visualize size and shape differences beyond the statistics (Figure 5).

All the statistical analyses were done in RStudio v. 2023.12.1-402[35] using the packages "abind" v. 1.4-5,[36] "car" v. 3.1-2,[37] "geomorph" v. 4.04,[38] "ggplot2" v. 3.3.3,[39] "Morpho" v. 2.10, "Rvcg" v. 0.22.1,[40] "RRPP" v. 1.3.1,[41] and "stats" v. 4.2.3.[35] The full R script is included in the Supporting Information S1.

TABLE 1 General information about the sample.

Ancestry	Population	Site	Number of individuals	Datation (centuries)	Latitude (approx.) (°)	Annual average temperature (approx.) (°C)	Climate	Subsistence practices
Native North American	Inuit	Point Hope, Alaska (USA)	3 ♀ | 3 ♂	XIII–XVII	70	≤−2	Cold	Hunther-gatherer
Native North American	Inuit	Greenland (Denmark)	3 ♀ | 3 ♂	XIII–XVIII	68	≤−2		Hunther-gatherer
North European	Norsemen	Nuuk, Greenland (Denmark) - Scandinavian origin	2 ♀ | 2 ♂	XI–XV	64	≤7		Preindustrial
Native South American	South Patagonian—Fuegian	Isla Grande de Tierra del Fuego (Argentina/Chile)	3 ♀ | 3 ♂	XVII–XX	−53	5		Hunther-gatherer
Western European	French	Paris (France)	3 ♀ | 3 ♂	XX	48	11	Temperate	Postindustrial
Southern European	Spanish	Madrid (Spain)	3 ♀ | 3 ♂	XX	40	15		Postindustrial
Native North American	-	New Mexico (USA)	3 ♀ | 3 ♂	XXI	35	16		Postindustrial
Native North American	Niminokotche, Chumash, Alapakassil	California (USA)	3 ♀ | 2 ♂ | 1 indet.	-	34	19		Preindustrial
Yamato	Japanese	Hyōgo Prefecture (Japan)	3 ♀ | 3 ♂	-	34	16		Preindustrial
Native Canarian	Canarian	Gran Canaria, Canary Islands (Spain)	1 ♀ | 5 ♂	-	28	23		Preindustrial
Latinamerican	Mexican	Mexico	3 ♀ | 3 ♂	XXI	25	19		Postindustrial
Native South American	-	Santiago del Estero (Argentina)	2 ♀ | 3 ♂	-	−27	23		Preindustrial
Native South American	North Patagonian	Río Negro and Chubut (Argentina)	1 ♀ | 4 ♂	-	−41	11		Preindustrial
North African	Nubian	Abri, Northern State (Sudan)	3 ♀ | 3 ♂	III–I b.C.	21	≥25	Tropical	Preindustrial
Native Southeastern Asian	Negrito	Luzon (Philippines)	3 ♀ | 3 ♂	-	15	27		Preindustrial
Melanesian	Papuan	New Britain (Papua New Guinea)	2 ♀ | 3 ♂	-	−6	27		Preindustrial
Native South American	-	Ancón (Peru)	3 ♀ | 3 ♂	XVI	−9	21		Preindustrial
Sub-Saharan	-	Lagos (Portugal)—Subsaharan origin	3 ♀ | 3 ♂	XV–XVII	15 to −20	≥25		Preindustrial
Sub-Saharan	Afro-American	New Mexico (USA)—Subsaharan origin	3 ♀ | 3 ♂	XXI	15 to −20	≥25		Postindustrial

3 | RESULTS

General shape analysis based on pairwise Procrustes ANOVA showed that there are statistical differences ($p < 0.05$) between cold-adapted populations and both temperate and tropical individuals (Table 2). Contrary, specific shape analysis based on PCA did not find significant differences among any group ($p > 0.05$) for PC1 (26.82% of total shape variation), PC2 (19.73% of total shape variation) nor PC3 (14.66% of total shape variation) (Table 3). Figure 2 provides more information about the meaning of the PCs and the distribution of the PC scores among groups. Specifically, PC1 shows variations in ribcage width and depth (negative: wide and deep, positive: narrow and flat); PC2 shows different degrees of rib declination (negative: high declination; positive: low declination); and PC3 is about how rib torsion affects ribcage 3D configuration (negative: high torsion, "barrel-shaped," positive: low torsion, "bell-shaped"). If we interpret the distribution of the PC scores per population, it can be noticed that (1) tropical populations tend to have a slender, "barrel-shaped" ribcage with variable rib declination; (2) temperate populations tend to have a "barrel-shaped" ribcage with medium rib declination and variable width and depth; and (3) cold-adapted populations tend to have a "bell-shaped" ribcage with medium rib declination and variable width and depth. Related to size, tropical individuals were significantly smaller ($p < 0.05$) than the temperate and cold-adapted individuals (Table 4). Considering sex, we found significant shape differences ($p < 0.05$) between tropical males and females (Figure 3) and significant size differences between both temperate and tropical males and females (Table 5). The linear regression between the Procrustes coordinates and the centroid sizes of the sample was significant ($p < 0.05$) and showed that there is an allometric relationship between size and shape where stocky ribcages (cold/temperate populations and males) are bigger than slender ribcages (tropical populations and females) (Figure 4). These differences among climatic groups and sexes can be graphically observed in Figure 5.

TABLE 2 Pairwise procrustes analysis of variance results.

	d^a	UCL (95%)	Z	p-Value
Cold versus temperate	0.043	0.037	2.45	**0.006***
Cold versus tropical	0.047	0.038	2.59	**0.007***
Temperate versus tropical	0.031	0.031	1.65	0.052

Note: Significant *p*-values are marked with an asterisk (*) and highlighted in bold.

Abbreviation: UCL, upper confidence limit.

[a]Procrustes distance between the group means.

4 | DISCUSSION

According to Allen and Bergmann's eco-geographic rules,[1,6] the relative shape and size of the modern human ribcage might depend on the average temperature of the environment.[10] Specifically, individuals from tropical areas would have a smaller, narrower, and flatter ribcage compared to temperate and cold-adapted populations, which would potentially determine an allometric relation between ribcage size and shape. Even though some authors suggest that biological adaptations to climate could have been buffered in *H. sapiens* because of cultural adaptations such as fire or clothes,[42–45] results of the last three decades confirm different Bauplan in individuals depending on latitude.[2,4,8,10] To test whether Allen and Bergmann's eco-geographic rules are applicable to the 3D configuration of human ribcage, we studied a balanced sample of 109 adult individuals belonging to 19 populations of global distribution, which were divided in three climatic groups: cold, temperate and tropical (Figure 1, Table 1). First, we tested if there were general shape differences among these groups by a pairwise Procrustes ANOVA. Our results pointed out significant differences ($p < 0.05$, Table 2) between the ribcage of cold-adapted populations and that of both temperate and tropical populations, such as seen for ribs in previous publications.[10] Shape differences among groups were further

TABLE 3 Statistical study of the principal components (PC) scores.

		PC1 (26.82% of total variance)			PC2 (19.73% of total variance)			PC3 (14.66% of total variance)		
Test	Statistics	Cold	Temperate	Tropical	Cold	Temperate	Tropical	Cold	Temperate	Tropical
Shapiro–Wilk	*W*	0.87	0.93	0.88	0.93	0.95	0.96	0.85	0.89	0.88
	p-Value	0.144	0.157	0.077	0.547	0.254	0.722	0.104	**0.043***	0.098
Levene	*F*	0.63			1.54			4.97		
	p-Value	0.539			0.229			**0.013***		
Analysis of variance	*F*	1.28			0.09			-		
	p-Value	0.29			0.914					
Kruskal–Wallis	χ^2	-			-			4.26		
	p-Value							0.119		

Note: Significant *p*-values are marked with an asterisk (*) and highlighted in bold. Each PC measures: PC1—ribcage width and depth; PC2—rib declination; PC3—rib torsion.

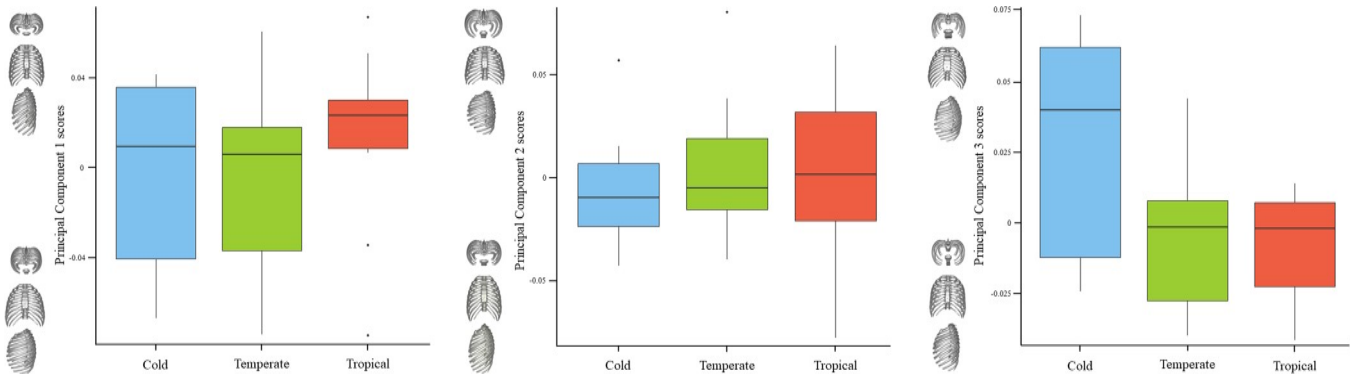

FIGURE 2 Bloxplots showing the distribution of the principal components (PC) 1, PC2, and PC3 scores according to each climatic group. The accompanying visualizations show the shape of the ribcage at the extremes of the axes.

TABLE 4 Statistical study of the centroid sizes per climatic group.

Test	Statistics	Cold	Temperate	Tropical	
Mean + standard deviation	$\bar{x}$	2575.1	2594.4	2392.8	
	σ	191.9	174.1	184.8	
Shapiro–Wilk	*W*	0.96	0.97	0.98	
	p-Value	0.529	0.125	0.841	
Levene	*F*	0.69			
	p-Value	0.502			
Analysis of variance	*F*	13.96			
	p-Value	**<0.001***			
Post hoc (paired *t*-test)	*p*-Value Bonferroni adj.	1	-	-	Temperate
		0.001*	**<0.001***	-	Tropical

Note: Significant *p*-values are marked with an asterisk (*) and highlighted in bold.

explored by a PCA (Figure 2). Although there were no statistical differences in the distribution of the PC1, PC2, and PC3 scores (Table 3), these results bring interesting information that is worth mentioning.

Except two outliers, all tropical populations were exclusively distributed along the positive side of PC1 (slender ribcages). Furthermore, if these outliers are removed from the plot, ANOVA results for PC1 are significant ($p < 0.05$) and tropical populations are statistically different from cold and temperate populations, which are distributed all along the axis. In addition, PC scores from these outliers have a statistically different distribution along PC1 compared to the rest of the tropical populations (Student's *t*-test, $p < 0.05$, $t = 1.32$). Once we checked the identity of the outliers, we noticed that they were the Afro-American males and females. This phenomenon could be explained by the fact that current Afro-Americans might have a European-mixed ancestry that masks their Sub-Saharan roots and has an impact in their phenotype,[46] so their ribcages are wider and deeper. Another potential explanation could be that there is some degree of phenotypic plasticity in the *H. sapiens* Bauplan where phenotype is adapted to the environment through the centuries independently from ancestry.[47] Furthermore, previous research found a great genotypic and phenotypic variability in African populations,[48] which could be in line with our results. This could also explain that rib declination (PC2), that mostly affects the width of the thorax, is also very variable in tropical populations compared to the others. To conclude, the distribution along PC3 shows that the "barrel-shaped" ribcage typically described for *H. sapiens*[49] is present in the three climatic groups. Nevertheless, the cold-adapted individuals present less rib torsion, which confers that their ribcages a more "bell-shaped" configuration. These results agree with previous research that suggest similarities in ribcage shape between fossil *Homo* such as Neanderthals and cold-adapted *H. sapiens* populations.[10,20]

Apart from shape, we also studied size differences between the three climatic groups. Our results showed that tropical individuals were significantly smaller ($p < 0.05$) than their cold and temperate counterparts (Table 4). Together with the aforementioned shape analyses, these results may confirm our first hypothesis: tropical individuals have a smaller and slenderer ribcage than the rest of the sample, which would be favorable for heat loss.[2,4,7,10] Hence,

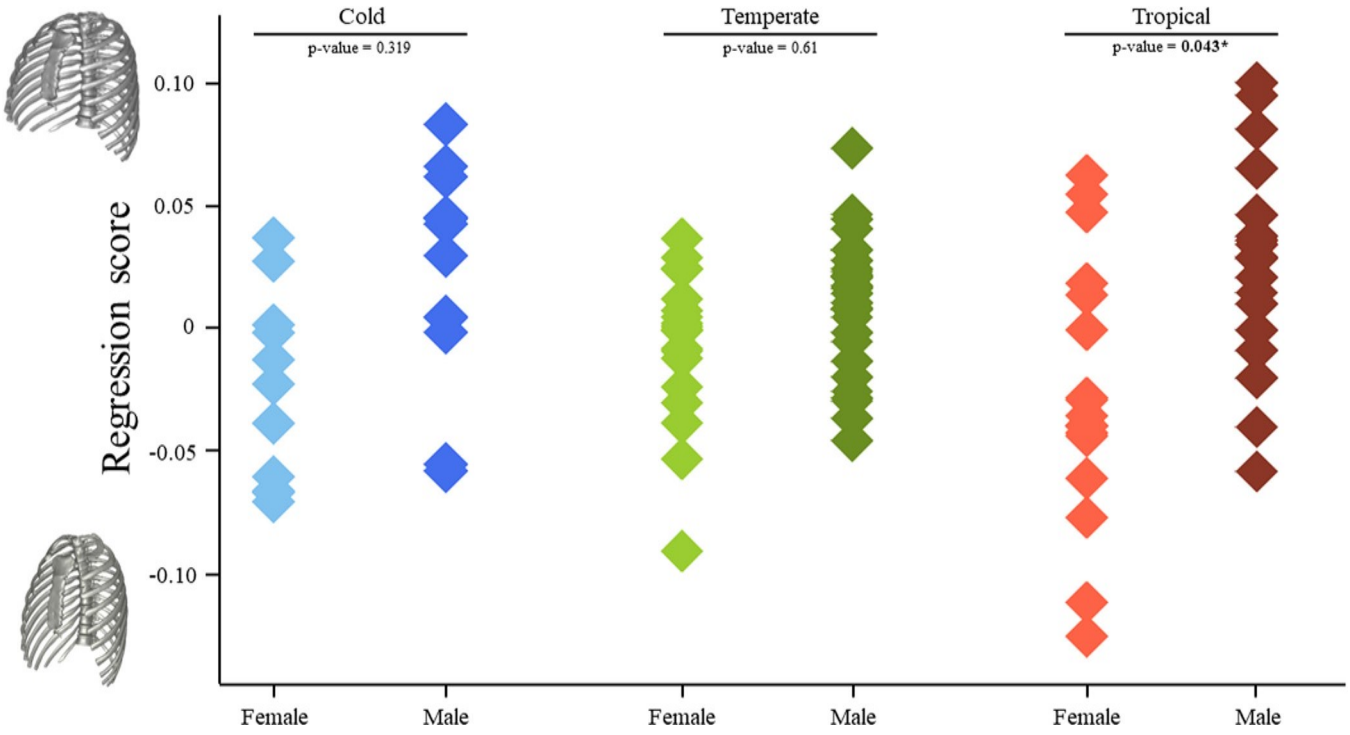

FIGURE 3 Dummy regressions between the male and female ribcages of each eco-geographic zone. Significant *p*-values are marked with an asterisk (*) and highlighted in bold.

TABLE 5 Statistical study of the centroid sizes per climatic group and sex.

Test	Statistics	Cold Female	Male	Temperate Female	Male	Tropical Female	Male
Mean + standard deviation	$\bar{x}$	2518.3	2631.5	2503.9	2660.8	2314.5	2466.7
	σ	182.7	192.1	147.3	163.6	188.2	151.7
Shapiro–Wilk	*W*	0.95	0.93	0.94	0.96	0.97	0.97
	p-Value	0.712	0.445	0.208	0.259	0.825	0.812
Levene	F	0.02		0.01		0.55	
	p-Value	0.88		0.906		0.464	
Student's *t*	*t*	−1.41		−3.56		−2.64	
	p-Value	0.17		**<0.001***		**0.013***	

Note: Significant *p*-values are marked with an asterisk (*) and highlighted in bold.

although Allen and Bergmann's eco-geographic rules seem to be applicable to the *H. sapiens* ribcage, the effect of temperature on thorax proportions is not as pronounced as on the limbs.[3–5] In this context, limbs are independent anatomical regions whereas the ribcage is subjected to the viscera it contains.[50] Our hypothesis is, therefore, that the space occupied by internal organs might be a limiting factor on ribcage latitudinal variations in modern humans. However, our results are tentative given the low sample size of the cold (N_c = 22 individuals) and tropical (N_{tr} = 35 individuals) groups, so further research would be needed to confirm this proposition.

Additionally, there is a bunch of publications describing sexual dimorphism in the morphology and functionality of the human ribcage.[14,22–25] Generally, these articles suggest larger, wider, and deeper ribcages in males compared to females. Ribcage shape differences are mainly achieved by variations in the spatial configuration of the ribs, which are less declined and with lower torsion in males than in females.[14,22–25] Given that these studies have been performed only in individuals from European ancestry, they are not extensive to the worldwide *H. sapiens* population. Therefore, our research is the first attempt to describe sexual dimorphism in the ribcage taking into consideration individuals distributed globally.

Figure 5 and Table 5 show that the ribcage is larger in males than females along the three studied latitudinal zones. Furthermore, as it was previously described, ribs are less declined and with lower

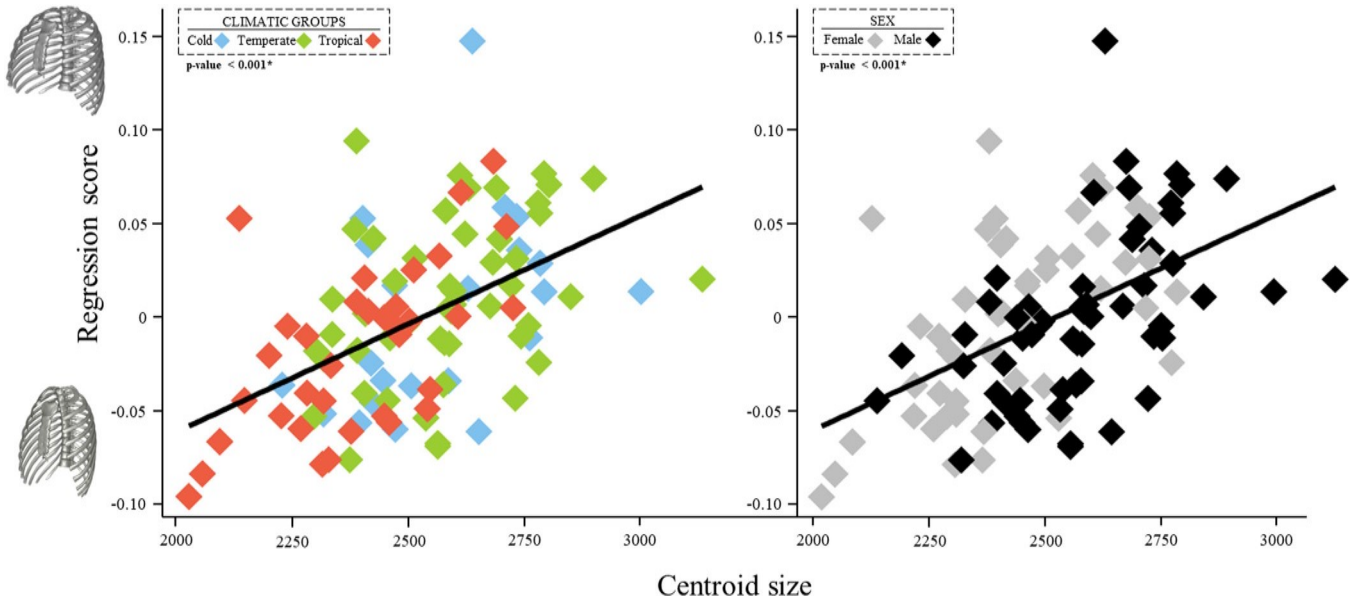

FIGURE 4 Linear regressions between the Procrustes coordinates (shape) and the centroid size (size) of the full sample, grouped by climate and sex.

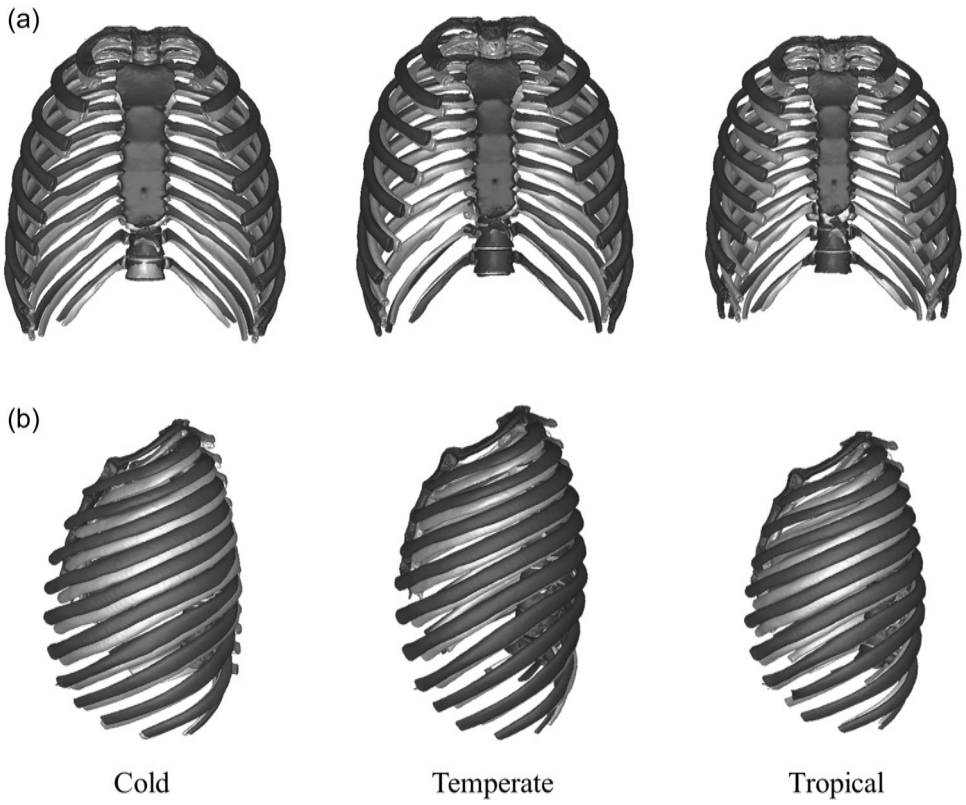

FIGURE 5 Overlapped mean forms (shape + size) of the male (colored in black) and female (colored in gray) ribcages of each eco-geographic zone. (a) Frontal view, (b) lateral view.

torsion in males than in females (Figure 5), which may confirm our second hypothesis. In statistical terms, we have found that there might be a specific Bauplan regarding latitude since sexual dimorphism is statistically significant in shape and size for tropical populations ($p < 0.05$) but it is not for cold-adapted populations ($p > 0.05$). For temperate populations, we found significant differences in size ($p < 0.05$) but not in shape ($p > 0.05$) (Figure 3, Table 5). These results might suggest that the human ribcage configuration is

constrained by the average temperature of the environment. Specifically, it seems that a Bauplan adapted to cold latitudes may be conservative in terms of sexual dimorphism (large and stocky ribcages in both males and females), possibly to avoid heat loss.[2,4,7,10] Contrary, a Bauplan adapted to tropical areas, although slender compared to other eco-geographic regions, could be less constrained in terms of sex since females are notably smaller and slenderer than males. Besides, the possible implications of sexual selection must be taken into consideration, mostly related to size differences between males and females.[51] These results are supported by Figure 4, which is a significant ($p < 0.05$) linear regression between the Procrustes coordinates (shape) and the centroid sizes (size) of the sample. As it can be seen, there might be an allometric relationship between size and shape where stocky ribcages (cold/temperate populations and males) are bigger than slender ribcages (tropical populations and females).

Eventually, the described morphological differences among climatic groups and between sexes could be tentatively explained in terms of thermoregulation and energetics. Specifically, the greater BMI expected for cold/temperate populations and males would require higher basal metabolic rate (BMR) and, therefore, a larger oxygen supply. This would be possible for their stocky ribcages, whose total lung capacity is expected to be greater compared to the slender ribcages described for tropical populations and females.[2,4,5,25,52] Nevertheless, our results suggest that heat retention is a limiting factor in ribcage shape and size. This would be the reason why we cannot find sexual dimorphism in cold-adapted populations such as we do in tropical ones.

5 | CONCLUSIONS

Allen and Bergmann's rules seem to be applicable to the modern human thorax since the ribcage belonging to tropical individuals is smaller and slenderer compared to others living in higher latitudes. This might show an allometric relationship between the shape and size of the ribcage. In addition, although sexual dimorphism was observed in the whole sample, males and females had significant differences in both shape and size only in tropical populations. Apart from potential sexual selection, we hypothesize that avoiding heat loss might be the limiting factor for sexual dimorphism in cold-adapted populations.

ACKNOWLEDGMENTS

We would like to thank Dr. Carlos A. Palancar and Marta Gómez-Recio for their advice related to statistics. We also would like to acknowledge the following researchers and technicians for their help in accessing and scanning the sample: Prof. Ashley Hammond, Dr. Niels Lynnerup, Dr. Chiara Villa, Dr. Martin Friess, Liliana Huet, Véronique Laborde, Prof. Bernardo Perea, Dr. Maria Teresa Ferreira, Dr. Miguel Almeida, Dr. Luis Ríos, Jorge Sanz and Mar Carrascosa. Funded by Grant PRE2021-097584 to José M. López-Rey and grant PID2020-115854GB-I00 to MarkusBastir are funded by MCIN/AEI/10.13039/501100011033 of the Spanish Ministry of Science and Innovation and the European Union. The work of DGM 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) (DOI 10.54499/UIDB/04004/2020).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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How to cite this article: López-Rey JM, D'Angelo del Campo MD, Seldes V, García-Martínez D, Bastir M. (2024). Eco-geographic and sexual variation of the ribcage in *Homo sapiens*. *Evolutionary Anthropology*, 33, e22040. doi:10.1002/evan.22040