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Ribcage Morphology in Native South American Populations From Different Altitudes: Insights From a Global Comparative Framework

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ABSTRACT

Objectives: Altitude shapes human morphology as highland populations must cope with cold and hypoxic environments. Although Andean highlanders have been proposed to exhibit larger and deeper ribcages, this idea is mainly based on research using disarticulated skeletal elements or non-South American controls. The objective of this research is to study 3D ribcage configuration of native South American populations considering altitude and worldwide ribcage variation.

Methods: Ribcages of 37 adult South Americans (17 highlanders, 20 lowlanders) were reconstructed and analyzed using 3D geometric morphometrics. Shape variation was assessed through Procrustes MANOVA and PCA, while centroid size was used to test for size differences. Comparisons were also made with a sample of 92 adult worldwide lowlanders.

Results: South American highlanders and lowlanders show similar ribcage shapes, both exhibiting a deeper thorax than worldwide lowlanders. No significant differences in absolute ribcage size were detected between South American highlanders and lowlanders. However, a marked sexual dimorphism was observed in both groups, with males having wider and significantly larger ribcages than females.

Conclusions: The pronounced ribcage depth in native South Americans could represent a population-specific trait maintained through long-term interactions, potentially advantageous in high-altitude settings but neutral in the lowlands. In addition, we propose that South American highlanders have a larger ribcage relative to their smaller body size compared to lowlanders.

Finally, the larger and stockier male ribcage morphology in South Americans supports the notion of greater respiratory capacity and metabolic demands in males.

1 | Introduction

The cosmopolitan distribution of *Homo sapiens* makes the species face a wide variety of environmental conditions, leading to significant postcranial anatomical diversity. For example, individuals from colder climates tend to have stockier bodies with shorter limbs to retain heat, while those from warmer areas typically exhibit slenderer bodies with longer limbs to facilitate heat dissipation. This variation is generally latitudinal, with morphological differences seen across regions at different distances from the equator (Foster and Collard 2013; García-Martínez et al. 2018; Katzmarzyk and Leonard 1998; López-Rey, D'Angelo del Campo, et al. 2024; Roseman and Auerbach 2015; Tilkens et al. 2007). However, altitude also influences anatomical traits, as populations living at higher elevations must cope with a wide range of difficulties—from rugged terrain, potentially low resource availability and high levels of solar radiation, to cold temperatures and lower oxygen levels (Weinstein 2017).

The latter environmental challenges are a direct consequence of the decreased atmospheric pressure at high altitudes. As air pressure drops with elevation, the air expands and cools. This phenomenon leads to a gradual decrease in temperature known as adiabatic lapse rate (Thomson 1857). At the same time, lower pressure means fewer gas molecules per volume of air, so even though the proportion of oxygen remains constant, the number of oxygen molecules available per breath is reduced (Bert 1878). These chronic hypoxic conditions are a physiological challenge for those populations living in high-altitude environments, since adverse effects appear at 2500 m during rest and at 2000 m during physical activity (Frisancho 1993, 2013). Only a few regions on the planet have permanent human settlements at such extreme elevations, being the Andean, Tibetan, and East African plateaus the main centers of high-altitude occupation (Niermeyer et al. 2001). Humans have inhabited these areas for thousands of years, gradually developing distinctive biological adaptations to withstand the challenges of high-altitude environments.

For example, Andean highlanders tend to show increased lung volumes (Callison et al. 2022; Talaminos-Barroso et al. 2021) and elevated hemoglobin concentrations (Beall 2006), enhancing their oxygen uptake and its transport capacity. In contrast, Ethiopian and Tibetan highlanders have lung volumes and hemoglobin levels closer to those of sea-level populations (Beall 2006; Talaminos-Barroso et al. 2021). While Tibetans show increased ventilation rates (Curran et al. 1997) and greater blood flow (Erzurum et al. 2007) that optimize oxygen delivery, Ethiopian physiological responses to altitude are subtler—possibly due to their earlier emergence—and remain under investigation (Beall 2006; Talaminos-Barroso et al. 2021). At the skeletal level, nasal adaptations to high altitude have been reported in Tibetans, but not in other populations like Andeans (Butaric and Klocke 2018). Curiously, Andeans are the only high-altitude group suggested to exhibit postcranial skeletal adaptations, as they have a relatively larger and deeper ribcage to accommodate their larger lungs (Callison et al. 2022; Talaminos-Barroso et al. 2021).

Although the characteristic thoracic proportions of living Andean individuals have been extensively studied since the 20th century (Beall 1982; Brutsaert et al. 1999; Callison et al. 2022; Frisancho 1993; Greksa 1986; Greksa and Beall 1989; Niermeyer et al. 2001; Stinson 1980), Weinstein (2007) was the first to investigate the potential ribcage adaptations to high altitude in precontact Andean populations. Her research suggests a relatively wider and deeper thorax in these groups, which was indicated by larger sternal and clavicular dimensions, greater rib cross-sectional areas, and reduced rib curvature compared to precontact lowlanders. She also reported a pronounced sexual dimorphism in the studied highland populations, with females exhibiting ribcage morphologies more similar to those of lowland individuals. Interestingly, this study stands out for addressing thoracic adaptations in Andean populations through comparisons with other native South American groups, rather than with subjects of European ancestry (Brutsaert et al. 1999; Callison et al. 2022; Greksa 1986; Stinson 1980) or other high-altitude individuals from different continents (Beall 1982). Weinstein (2007, 2017) also points to the potential influence of gene flow between highland and lowland precontact South American populations in shaping ribcage morphology, a factor also suggested regarding nasal morphology (Butaric and Klocke 2018) that may be particularly relevant when interpreting postcranial skeletal adaptations to high altitude in Andeans.

Despite the relevance of these results, Weinstein's studies were based on disarticulated thoracic elements and relied on traditional measurements. To understand thoracic morphology as an integrated and functional structure, it is essential to consider the spatial relationships among its metameric components. Recent advances in digital imaging now allow for the 3D reconstruction of costovertebral elements, enabling precise and holistic quantification of full ribcage size and shape through methodologies such as geometric morphometrics (Bastir et al. 2020; García-Martínez, Bastir, Gómez-Olivencia, et al. 2020; Gómez-Olivencia et al. 2018; López-Rey, D'Angelo del Campo, et al. 2024; López-Rey, García-Martínez, and Bastir 2024, 2025; López-Rey, Crevecoeur, et al. 2025). Thus, the aim of this manuscript is to study the 3D ribcage configuration of native South American populations considering altitude (lowlands vs. highlands) and worldwide ribcage variation in order to test the following hypotheses:

1. South American highlanders have wider and deeper ribcages compared to lowlanders.
2. South American highlanders have larger ribcages compared to lowlanders.
3. South American highlanders have more sexual dimorphism at their ribcages compared to lowlanders.

2 | Materials and Methods

The costovertebral sample chosen for this research belongs to 37 adult skeletons recovered from various archaeological

sites in South America (19♀, 18♂, Table 1). These individuals are assumed to have native South American ancestry due to several reasons. First, most remains are dated to periods preceding or coinciding with the onset of Spanish colonial presence in South America, which became prominent from 1536 CE onwards (Hancock 2022). Second, except for Arroyito 137/09 C3, those skeletons that lack dating are housed at the Musée de l'Homme (Paris, France) and come from expeditions to South America conducted by French archaeologists and ethnographers. These individuals are regarded as precontact and are included in the following osteo-archaeological collections: Cessac et Savatier (Ancón), Jehan Albert Vellard (B_124_19383), Reichlen (B_310_26816), Rivet (Ecuador), and Wagner (Icaño).

Selected ribs and vertebrae belonging to this native South American sample had no pathological nor taphonomical alterations that could significantly alter ribcage 3D configuration. Three-dimensional virtual models of the thoracic vertebrae and the best-preserved rib from each costal level were obtained using three different surface scanners, which might not have affected their comparability (D'Angelo del Campo et al. 2023). Devices used for scanning were Artec Spider (resolution: 0.1 mm; accuracy: 0.05 points per mm), Next Engine 3D HD (resolution: 0.38 mm; accuracy: 6 points per mm), and Creality CR-Scan Lizard 3D (resolution: 0.2 mm; accuracy: 5 points per mm). All the resulting 3D volumes were post-processed by Artec Studio v. 16 (www.artec3d.com) for cleaning, smoothing edges, and filling possible gaps.

The full ribcage of each individual was reconstructed following the protocol developed by López-Rey, García-Martínez, and Bastir (2024) using the software LhpFusionBox (Université Libre de Bruxelles). To sum up, the thoracic spine was reconstructed through the corrected "zygapophyseal facet method" (Bastir et al. 2019; Been et al. 2019), which aligns the zygapophyseal facets to maximize their contact while accounting for vertebral body wedging. Then ribs are positioned according to their expected orientation at functional residual capacity (FRC; Wanger et al. 2005). Once all ribcages were reconstructed, we quantified their form in Viewbox v. 4.1 (https://www.dhal.com/viewbox.htm) using a template of 526 (semi)landmarks (Figure S1), which was previously described by Bastir et al. (2017). Before starting with the statistical analyses, we (1) removed the coordinates from ribs 11 and 12 since these ribs are very variable in form (Gómez-Olivencia et al. 2009) and could bias the analysis and interpretation of the results; (2) estimated missing data by thin plate spline (TPS; Mitteroecker and Gunz 2009), in case it was needed; and (3) symmetrized each ribcage to avoid the effect of slight morphological alterations, such as scoliosis, in our analyses. The final 450 (semi)landmarks were subsequently subjected to generalized Procrustes analysis (GPA; Mitteroecker and Gunz 2009) to remove the effects of size, position and rotation on the 3D Cartesian coordinates.

To study the effects of altitude on the shape and size of the human ribcage, the South American sample was distributed in two groups depending on the altitude of their settlements above sea level (highlands > 2500 m.a.s.l.; lowlands < 750 m.a.s.l.). General shape differences were tested by a Procustes MANOVA taking into consideration two levels of grouping (altitude and sex; Table S1A), while specific shape differences among groups were explored through a principal component analysis (PCA; Mitteroecker and Gunz 2009) in shape space (Figure 1). Eventually, size differences among groups were studied using the centroid size. Distribution of the centroid size (Table 2), PC1, and PC2 scores (Table S2)—grouped by altitude, sex, and the interaction between both—was analyzed through the appropriate tests (e.g., *t*-test, Wilcoxon rank sum test, ANOVA + Tukey) after testing the normality (Shapiro–Wilk test) and homoscedasticity (Levene's test) of the groups. This statistical workflow was conducted in RStudio v. 2023.12.1-402 (R Core Team 2023) using the packages "car" v. 3.1-3 (Fox and Weisberg 2019), "dplyr" v. 1.1.4 (Wickham et al. 2023), "geomorph" v. 4.04 (Adams et al. 2022), "ggplot2" v. 3.3.3 (Wickham 2016), "Morpho" v. 2.10, "Rvcg" v. 0.22.1 (Schlager 2017), and "stats" v. 4.2.3 (R Core Team 2023). The full R script is included in Supporting Information.

Finally, we repeated all the analyses including an additional comparative dataset to assess whether our results were influenced by the geographic origin of the sample. Hence, we performed a new GPA, Procrustes MANOVA (two levels of grouping: location and sex; Table S1B), PCA (Figure 2, Figure S2, Table S3), and study of the centroid size (Table S4) to compare the ribcage form of the 37 South American individuals to other 92 lowlanders (44♀, 48♂) of worldwide distribution. These subjects, previously studied by López-Rey, D'Angelo del Campo, et al. (2024), belong to 16 different populations distributed along the five inhabited continents and the three main latitudinal zones: polar, temperate, and intertropical. Each population was meant to be balanced in sex and represented by approximately six adult subjects. Additional information regarding their ancestry, dating, and location of their archaeological site is provided in Table S5.

3 | Results

According to Procrustes MANOVA, general shape differences among South American individuals were not significant ($p > 0.05$; Table S1A) when comparing sex (males vs. females), altitude (highlands vs. lowlands) or the interaction between sex and altitude. Subsequently, specific shape variation was studied through PCA. While PC1 (23.37% of total shape variation) shows differences in thoracic width (positive: narrow thorax, narrow sternal region, high rib curvature, high rib torsion; negative: wide thorax, wide sternal region, low rib curvature, low rib torsion), PC2 (14.31% of total shape variation) shows differences in thoracic depth (positive: deep thorax, low rib torsion; negative: shallow thorax, high rib torsion). Together, PC1 and PC2 indicate that the 3D configuration of the ribcage is strongly affected by rib curvature and torsion: the less curvature and torsion ribs have, the stockier ribcages are. Figure 1A–C show the distribution of PC scores considering altitude, sex, and the interaction between both variables, respectively; and Figure 1D depicts the morphological variation along the principal components. Even though there is an evident overlap, highlanders (Figure 1A), males (Figure 1B) and highlander males (Figure 1C) are stockier compared to lowlanders, females and lowlander females. Nevertheless, among all possible combinations, we did not find significant shape differences ($p > 0.05$; Table S2). Although shape differences between males and females are not statistically significant, they are evident in Figure 1B: male ribcages show

TABLE 1 | General information about the native South American sample.

Group	ID	Location	Sex	~AMSL[a]	~Dating[b]	Host institution	Scanner	References (if any)
Highlands	B_299_23992	Ingapirca (Cañar, Ecuador)	Female	3150	—	1	Artec Spider	—
	B_299bis_23993		Female					
	B_365_23978	Timburay (Carchi, Ecuador)	Female	3000	—	1	Artec Spider	—
	749 (C15)	Los Amarillos (Jujuy, Argentina)	Female	3000	1250–1430	2	Next Engine	Nielsen (2001)
	B_310_26816	Pongomal (Amazonas, Perú)	Female	2800	—	1	Artec Spider	—
	Huichairas 1	Huichairas (Jujuy, Argentina)	Female	2700	1250–1430	2	Next Engine	Mercolli et al. (2014)
	10448–17851	Pucará de Tilcara (Jujuy, Argentina)	Female	2500	1201–1600	3	Next Engine	—
	10402–17852		Female					
	10304–17949		Female					
	10452–17954		Female					
	17823		Female					
	17844		Male					
	10475–17952		Male					
	17846		Male					
	Rasgo 1	Til 43 (Jujuy, Argentina)	Male	2500	1460–1639	4	Next Engine	Arrieta et al. (2018); Boasso et al. (2024)
	Rasgo 13		Male					
	Rasgo 17		Male					

(Continues)

TABLE 1 | (Continued)

Group	ID	Location	Sex	~AMSL[a]	~Dating[b]	Host institution	Scanner	References (if any)
Lowlands	Guasmara 2	Villa de las Rosas (Córdoba, Argentina)	Male	740	1030 ± 20	6	Creality Lizard	Fabra et al. (2009), Fabra and González (2015), Laguens et al. (2009)
	Nunsacat 2	Copacabana (Córdoba, Argentina)	Male	730	1563 ± 41	6	Creality Lizard	Fabra (2014)
	Potrero de Garay E9	Los Molinos (Córdoba, Argentina)	Male	710	1530 ± 41	6	Creality Lizard	Fabra (2014)
	Country "El Golf" VCP 386–18	Villa Carlos Paz (Córdoba, Argentina)	Female	660	1574 ± 21	5	Creality Lizard	—
	Loteo 5 I1	Santa Rosa de Calamuchita (Córdoba, Argentina)	Female	580	1417 ± 42	5	Creality Lizard	Salega and Fabra (2018)
	Loteo 5 I2		Female					
	B_333_25458	Icaño (Catamarca, Argentina)	Female	330	—	1	Artec Spider	—
	B_322_25472		Male					
	B_353_25478		Male					
	B_278_25463		Male					
	Arroyito 137/09 C3	Arroyito (Córdoba, Argentina)	Male	150	—	5	Creality Lizard	—
	El Diquecito 08 B1	Laguna de Mar Chiquita (Córdoba, Argentina)	Male	530	1200 ± 85	6	Creality Lizard	Fabra et al. (2008, 2009, 2014)
	El Diquecito 08 E1		Male		758 ± 40			
	El Diquecito 08 M1		Female		1413 ± 57			
	B_124_19383	Laguna El Espinillo (Entre Ríos, Argentina)	Female	25	—	1	Artec Spider	—
	B_117_19849	Ancón (Lima, Perú)	Female	0	1501–1600	1	Artec Spider	—
	B_301_19850		Female					
	B_117_23943		Male					
	B_121_19855		Male					
	B_328bis_19852		Male					

Note: (1) Musée de l'Homme (Paris, France), (2) Instituto Interdisicplinario Tilcara, Facultad de Filosofía y Letras, Universidad de Buenos Aires (Argentina), (3) Museo Etnográfico "Juan B. Ambrosetti" (Buenos Aires, Argentina), (4) Universidad Nacional del Río Cuarto (Argentina), (5) Dirección de Patrimonio Cultural, Agencia Córdoba Cultura, Gobierno de Córdoba (Argentina), (6) Museo de Antropologías, Universidad Nacional de Córdoba (Argentina).

[a]Approximate altitude above mean sea level (in meters).

[b]Approximate dating in years of the common era (CE).

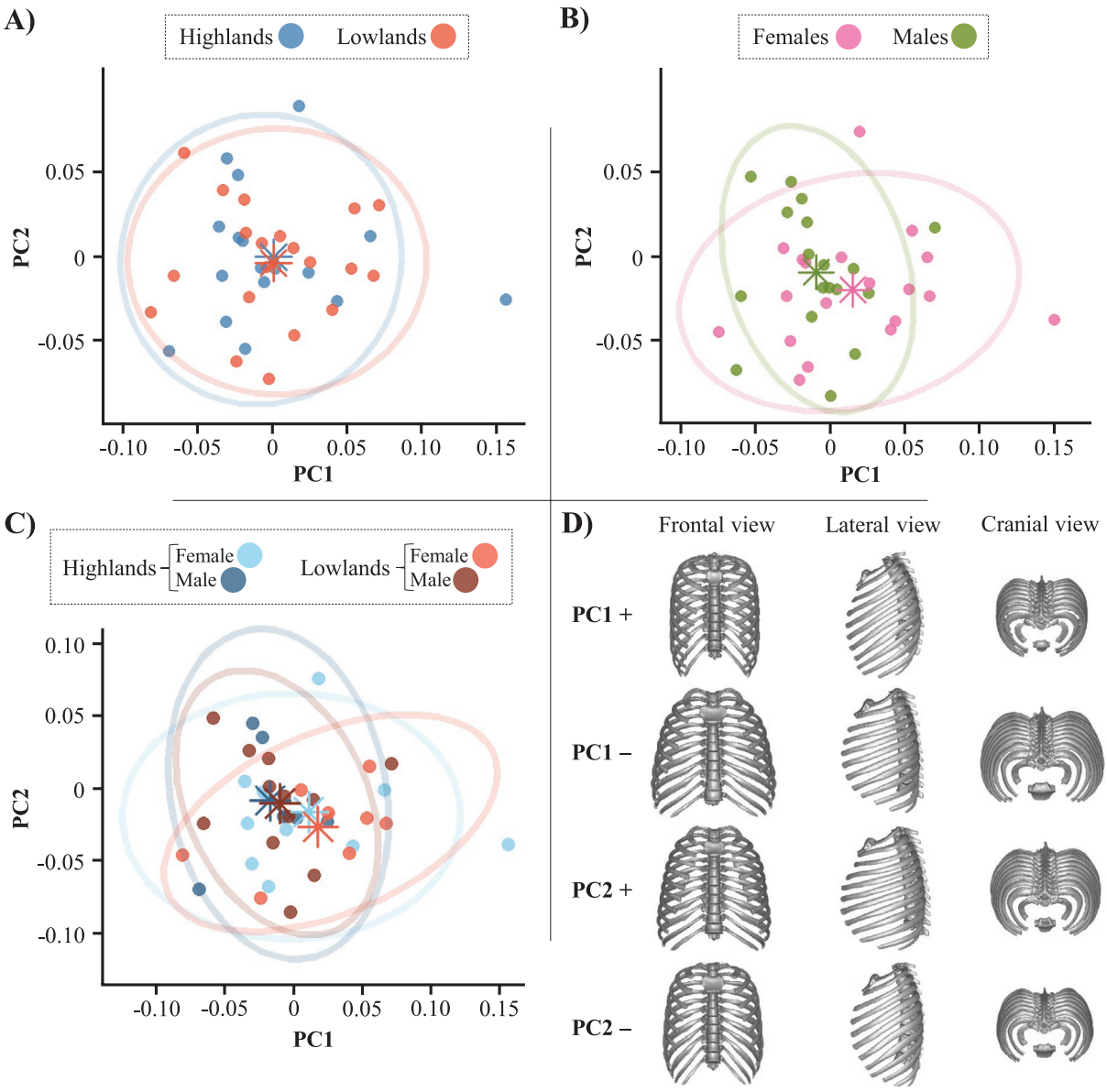

FIGURE 1 | Scatterplots showing the distribution of the principal component (PC) 1 and PC2 scores extracted from PCA on the native South American sample. Coordinates are grouped considering (A) altitude, (B) sex, and (C) both, accompanied by (D) visualizations of ribcage shape at the extremes of the axes. Mean values are indicated in each plot using asterisks (*) and the distribution of groups is outlined by ellipses indicating the 95% confidence interval.

greater variability in depth—ranging from shallow to deep—, while female ribcages are more variable in width—ranging from narrow to wide. The study of size expanded the results obtained regarding shape. An analysis of the centroid size suggested that South American highlanders were smaller than South American lowlanders ($p > 0.05$, Table 2A), and females were significantly smaller than males ($p < 0.05$, Table 2B). Considering both, altitude and sex, highlanders and lowlanders of the same sex have similar ribcage size, with highlander males being significantly larger compared to all females ($p < 0.05$), and lowlander males compared to highlander females ($p < 0.05$, Table 2C).

Next, we repeated these analyses including a new dataset of individuals from worldwide distribution. Procrustes MANOVA found significant differences ($p < 0.05$; Table S1B) considering location (South America vs. worldwide), but not sex (males vs. females), or the interaction between sex and location. Ribcage shape variation was further explored by PCA, which showed significant differences ($p < 0.05$; Table S3A) between South Americans and the worldwide sample at PC2 (18.15% of total shape variation), but not at PC1 (20.84% of total shape variation). This can be graphically seen in Figure 2, where South Americans are distributed along the entire range of PC1 but mostly restricted to the negative values of PC2. In contrast, the global comparative sample is spread all along PC1 and PC2. Considering that PC1 reflects variations in thoracic width (positive: narrow thorax; negative: wide thorax) and PC2 variations in thoracic depth (positive: deep thorax; negative: shallow thorax), the South American sample has deeper ribcages compared to the worldwide sample. Although there were no significant differences between males and females ($p > 0.05$; Figure S2A), when groups were made by the combination of location and sex,

TABLE 2 | Study of the centroid size on the native South American sample.

(A) Altitude			
Tests	**Statistics**	**Highlands**	**Lowlands**
—	Mean ± SD	2516 ± 202	2560 ± 160
Shapiro–Wilk	*W*	0.93	0.96
	p	0.26	0.63
Levene	*F*	0.96	
	p	0.33	
Student's *t*	*t*	−0.75	
	p	0.46	

(B) Sex			
Tests	**Statistics**	**Females**	**Males**
—	Mean ± SD	2435 ± 165	2650 ± 119
Shapiro–Wilk	*W*	0.94	0.97
	p	0.31	0.69
Levene	*F*	1.44	
	p	0.24	
Student's *t*	*t*	−4.52	
	p	**< 0.001***	

(C) Altitude + sex					
Statistics		**Highlander females**	**Highlander males**	**Lowlander females**	**Lowlander males**
—	Mean ± SD	2416 ± 171	2698 ± 107	2461 ± 166	2626 ± 122
Shapiro–Wilk	*W*	0.95	0.85	0.31	0.92
	p	0.57	0.15	0.9	0.28
Levene	*F*		0.85		
	p		0.48		
ANOVA	*F*		7.15		
	p		**< 0.001***		
Tukey (*p*)	Highlander Males	**0.003***	—	—	—
	Lowlander Females	0.91	**0.024***	—	—
	Lowlander Males	**0.008***	0.76	0.081	—

*Significant *p* values (< 0.05) are highlighted in bold.

South American males were significantly different from worldwide females at PC2 ($p < 0.05$; Figure S2B). Finally, differences on the centroid size were only significant ($p < 0.05$) considering males and females (Table S4).

4 | Discussion

Our results comparing native South American highlanders and lowlanders did not find significant differences between the size and shape of their ribcages (Figure 1A, Table S2A, Table 2A). These findings, apparently striking considering previous literature (Beall 1982; Brutsaert et al. 1999; Callison et al. 2022; Frisancho 1993; Greksa 1986; Greksa and Beall 1989; Niermeyer et al. 2001; Stinson 1980), can be better understood if they are interpreted in the light of Weinstein's (2005, 2007, 2017) research. Particularly, Weinstein compared limb and thoracic proportions in precontact South American individuals from two highland (San Pedro de Atacama, Chile; Machu Picchu and Cuzco, Perú) and two lowland locations (Ancón, Perú; Arica, Perú). Although the majority of Weinstein's samples do not geographically coincide with those analyzed in the present study, her publications are the only research examining rib variability in relation to altitude in precontact South American populations. Hence, they

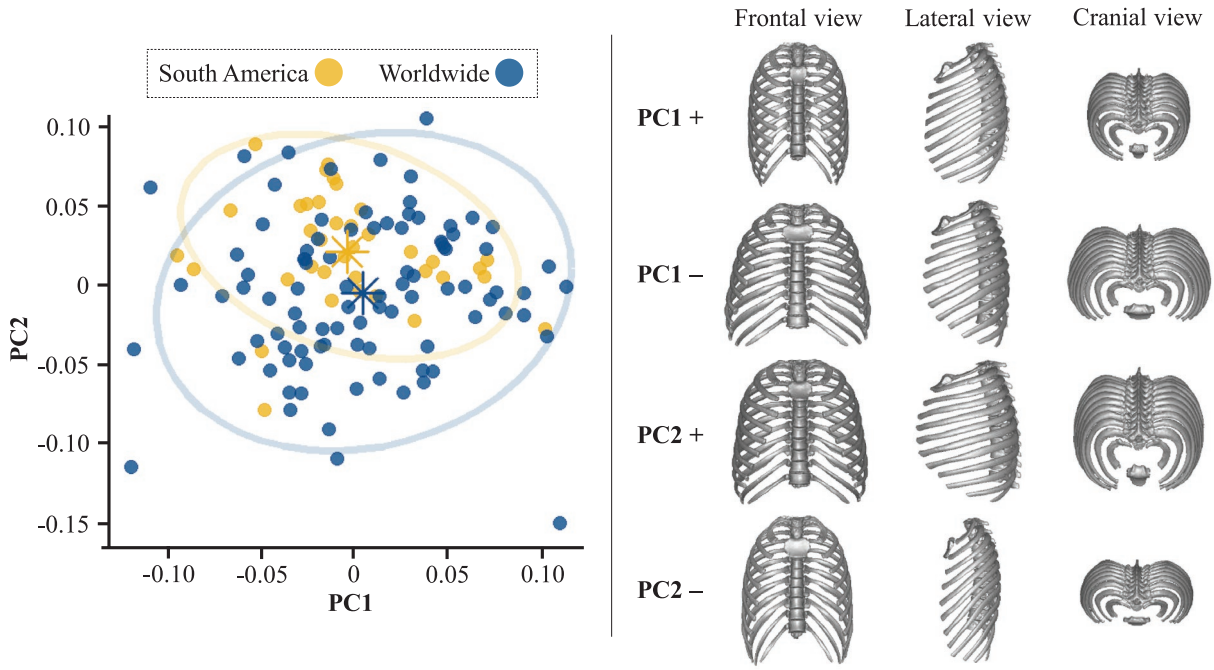

FIGURE 2 | Scatterplot showing the distribution of the principal component (PC) 1 and PC2 scores extracted from PCA comparing native South Americans to a worldwide control sample. Visualizations of ribcage shape at the extremes of the axes are also included. Mean values are indicated in each plot using asterisks (*) and the distribution of groups is outlined by ellipses indicating the 95% confidence interval.

provide the closest available reference for interpreting ribcage variation in this manuscript.

In terms of ribcage shape, Weinstein (2007) showed mixed results. Highlanders from San Pedro de Atacama and lowlanders from Ancón exhibited thoracic proportions consistent with eco-geographic expectations, that is, stockier ribcages for highlanders and more gracile ribcages for lowlanders. However, lowlanders from Arica displayed a rib curvature similar to that of highlanders from San Pedro de Atacama, while highlanders from Machu Picchu and Cuzco had thoracic proportions that encompassed the full range of variability observed in the sample. Therefore, the overlapping ribcage shape we found between native South American highlanders and lowlanders (Figure 1A) does not contradict the patterns observed by Weinstein (2007).

In terms of ribcage size, our results suggest a similar centroid size between lowlanders and highlanders (Table 2A), although the latter are slightly smaller. This is in line with Weinstein (2005) given that she predicted that highlanders have a smaller body size compared to lowlanders. Curiously, since Weinstein (2007) observed larger ribcages relative to body size in highlanders from San Pedro del Atacama, we hypothesize that ribcages included in our study might also be relatively larger in highlanders compared to lowlanders. This could indicate that, in Andeans, ribcage adaptations to altitude manifest in relative rather than absolute proportions when compared to their lowlander counterparts. Unfortunately, we lack data to confirm this assumption, which should be explored in future research.

In addition, our findings align with Weinstein's (2017) and indicate that sexual dimorphism in ribcage size is significant, with males exhibiting larger ribcages than females (Table 2B) in both highland and lowland groups (Table 2C). Previous research reported that the larger thorax in males allows for a greater total lung capacity (Bellemare et al. 2003), which in turn may enable higher oxygen uptake (García-Martínez et al. 2016) to meet the demands of their greater basal metabolic rate (BMR; Henry 2005). Although shape differences were not statistically significant (Table 2A), the distribution of the coordinates along PC1 is mostly constricted to the negative values in males, indicating a consistently wider thorax compared to females (Figure 1B). Functionally, larger thoracic width has been proposed to indicate a greater diaphragmatic contribution to breathing kinematics (García-Martínez et al. 2016).

Whether considering or not sexual dimorphism, ribcage size and shape in native South Americans is not especially different regarding altitude. Our results therefore suggest that changes in ribcage morphology cannot be attributed to this variable alone, but might result from the combined effects of other ontogenetic, physiological, and cultural factors. To begin with, several studies have reported that ribcage shape changes during late ontogeny, typically becoming stockier with aging (e.g., García-Martínez, Bastir, Villa, et al. 2020; Holcombe et al. 2017; Joshua et al. 2014; Weaver et al. 2014). Although we do not have precise age data beyond the general classification of adults, the presence of older individuals in our sample, combined with a random low inter-individual variability, could contribute to homogenizing our results and partially explain the lack of detectable differences between highlanders and lowlanders.

In addition, poorer food diversity in highland areas (Moseley 2001; Núñez 1991) would lead to smaller body

sizes (Bogin 1999), while chronic hypoxia would make the body allocate more energy to growth on the heart and lungs (Frisancho 1993, 2013). Consequently, this would explain that, although ribcage absolute size is similar between highlanders and lowlanders, it is larger in the former relative to their smaller body size (Weinstein 2007, 2017). Furthermore, similarities between both groups might have been driven by potential long-term interactions between populations.

First, these interactions likely involved genetic exchange, making it more probable to find overlapping morphological traits in individuals inhabiting different ecosystems (Fehren-Schmitz et al. 2017; Nakatsuka et al. 2020; Russo et al. 2018; Weinstein 2007, 2017). Second, interactions between native South Americans might have also allowed highland populations to obtain lowland resources—such as aliments, livestock, or cultivable plants—either by direct or indirect contact through trading networks (Capriles et al. 2024; Cuéllar 2013; Silverman and Isbell 2008). The aforementioned interactions between populations would not be exclusively explained by distance, but also by temporal, socio-cultural and political factors. General trends suggest that mobility and gene flow were lower between more distant regions in earlier times. In other words, older populations had lower genetic variability and fewer trading networks and were possibly more distinct from each other than those from later periods, such as the Inca Empire (1438–1533 CE; Covey 2008; Russo et al. 2018).

Regarding our sample (Table 1), remains of all highlanders were recovered from regions that were—or would later become—part of the Inca Empire (Covey 2008; Silverman and Isbell 2008), which also included our lowland sample from Ancón (Perú). In contrast, our remaining lowland specimens do not come from Pacific coastal regions but from inland areas of present-day Argentina, located on the periphery of the Inca Empire. Nevertheless, recent research suggests that these populations also had some degree of genetic exchange with Andean highlanders (García et al. 2021), supporting the idea of widespread population interactions in precontact South America that could have affected the relationship between environment and postcranial phenotype.

Our results on South Americans are, however, disconnected from the broader spectrum of human variability, as they do not include individuals from other geographical regions beyond western South America. To address this issue, we repeated our analyses including a worldwide comparative sample of lowlanders, and we found that both highland and lowland South Americans have a significantly deeper ribcage (Figure 2, Table S3). Although this trait has been proposed to be beneficial at high altitudes (e.g., Callison et al. 2022; Talaminos-Barroso et al. 2021; Weinstein 2007, 2017), its presence in lowlanders suggests that (1) it might be specific to native South Americans regardless of altitude; and that (2) it might be selectively neutral among lowlanders, since it apparently does not compromise their survival.

In order to summarize the discussion of our findings, let's see to what extent they support, refine, or contradict the hypotheses we proposed. Our Hypothesis 1 suggested that South American highlanders have a wider and deeper ribcage compared to lowlanders. This must be rejected since we found no shape differences between South American highlanders and lowlanders (Figure 1A, Table S2A), the ribcage of both groups being deeper than that of the worldwide lowland sample (Figure 2, Table S3A) possibly due to South American population dynamics (Capriles et al. 2024; Cuéllar 2013; Fehren-Schmitz et al. 2017; Nakatsuka et al. 2020; Russo et al. 2018; Silverman and Isbell 2008; Weinstein 2007, 2017). Hypothesis 2 proposed larger ribcages in highlanders compared to lowlanders. Although this hypothesis must also be rejected given that no absolute size differences were found among South American highlanders, lowlanders, and worldwide lowlanders (Tables 2A and S4A), previous literature suggests that ribcages of Andeans are larger in relation to their body size (Weinstein 2007, 2017). Consequently, highlanders would have relatively—rather than absolutely—larger ribcages than lowlanders. In addition, our Hypothesis 3 stated that South American highlanders have a more marked ribcage sexual dimorphism compared to lowlanders. This hypothesis must be rejected since (1) sexual dimorphism was not significant in shape (Figure 1B, Table S2B); and (2) sexual dimorphism in size, although significant, occurred equally in lowland and highland populations (Table 2C, Table 4C).

While these results enrich the knowledge of thoracic adaptations to high altitude through a 3D perspective, it is important to acknowledge certain limitations of our study. First, the overall sample size ($N = 129$) remains relatively small to study human ribcage variability. More specifically, apart from Tilcara—from where we included 11 individuals (Table 1)—it was extremely difficult to assemble robust samples for each site due to the fragmentary nature of osteoarchaeological remains, particularly the costovertebral material required for these kinds of analyses (Abdel-Maksoud et al. 2022; Manifold 2012; Schotsmans et al. 2017). Additionally, interesting information such as stature, BMI, or subsistence activities are mostly unavailable for the 129 subjects of study, which limits the interpretation of our results. Moreover, highlanders included in this research were recovered from settlements below 3200 m.a.s.l., so anatomical variations in populations living at higher elevations are not addressed in the present manuscript. Finally, sex estimation in high-altitude samples presents a further challenge, as these assemblages are often biased toward female individuals (Seldes 2007), which affects the robustness of our findings regarding sexual dimorphism.

5 | Conclusions

In conclusion, our results show no significant differences in ribcage shape between highland and lowland South Americans, with their ribcages being deeper compared to a worldwide lowland sample. This feature could respond to long-term population interactions across precontact South America and might be advantageous in high altitude but neutral in the lowlands. Regarding ribcage size, although no differences were found between highlanders and lowlanders in absolute terms, we rely on previous literature and propose that highlanders have a larger ribcage relative to their body size. Finally, we found sexual dimorphism in both South American highlanders and lowlanders, with males having wider and significantly larger ribcages than

females. These features would allow males to have greater oxygen uptake through intense diaphragmatic action to maintain their higher metabolism.

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Ethics Statement

This research studied human osteoarchaeological remains from documented collections housed in accredited institutions, with appropriate permissions from curators. All analyses were noninvasive and conducted in accordance with ethical guidelines and institutional standards. We recognize the cultural and historical significance of these remains and we are committed to treating them with respect and scientific integrity.

Conflicts of Interest

The authors declare no conflicts 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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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Template of landmarks (red) and semilandmarks (green) used to capture the size and shape of the studied ribcages. The 3D distribution of the Cartesian coordinates is shown in (A) frontal, (B) dorsal, (C) lateral, and (D) cranial view. **Figure S2:** Scatterplot showing the distribution of the principal component (PC) 1 and PC2 scores extracted from PCA comparing native South Americans to a worldwide control sample. Coordinates are grouped considering (A) sex, and (B) the interaction between location and sex; accompanied by (C) visualizations of ribcage shape at the extremes of the axes. Mean values are indicated in each plot using asterisks (*) and the distribution of groups is outlined by ellipses indicating the 95% confidence interval. **Table S1:** Procrustes MANOVA analyses (A) on the native South Americans considering altitude, and also (B) comparing South Americans to a globally distributed sample. Significant p values (<0.05) are highlighted in bold and with an asterisk (*). **Table S2:** Statistics on the PC scores on the native South American individuals. Significant p values ($p<0.05$) are highlighted in bold and with an asterisk (*). **Table S3:** Statistics on the PC scores on the native South American individuals compared to the worldwide lowland sample. Significant p values ($p<0.05$) are highlighted in bold and with an asterisk (*). **Table S4:** Study of the centroid size on the native South American individuals compared to a globally-distributed sample. Significant p values (<0.05) are highlighted in bold and marked with an asterisk (*). **Table S5:** Detailed information about the worldwide comparative sample.