BRIEF COMMUNICATION

Covariation between the shape and mineralized tissues of the rib cross section in *Homo sapiens*, *Pan troglodytes* and Sts 14

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Abstract

Objectives: Studying rib torsion is crucial for understanding the evolution of the hominid ribcage. Interestingly, there are variables of the rib cross section that could be associated with rib torsion and, consequently, with the morphology of the thorax. The aim of this research is to conduct a comparative study of the shape and mineralized tissues of the rib cross section in different hominids to test for significant differences and, if possible, associate them to different thoracic morphotypes.

Materials and Methods: The sample consists of the rib cross sections at the midshaft taken from 10 *Homo sapiens* and 10 *Pan troglodytes* adult individuals, as well as from *A. africanus* Sts 14. The shape of these rib cross sections was quantified using geometric morphometrics, while the mineralized tissues were evaluated using the compartmentalization index. Subsequently, covariation between both parameters was tested by a Spearman's ρ test, a permutation test and a linear regression.

Results: Generally, *P. troglodytes* individuals exhibit rib cross sections that are rounder and more mineralized compared to those of *H. sapiens*. However, the covariation between both parameters was only observed in typical ribs (levels 3–10).

Although covariation was not found in the rib cross sections of Sts 14, their parameters are closer to *P. troglodytes*.

Discussion: On the one hand, the differences observed in the rib cross sections between *H. sapiens* and *P. troglodytes* might be related to different degrees of rib torsion and, consequently, to different thoracic 3D configurations. These findings can be functionally explained by considering their distinct modes of breathing and locomotion. On the other hand, although the rib cross sections belonging to Sts 14 are more similar to those of *P. troglodytes*, previous publications determined that their overall morphology is closer to modern humans. This discrepancy could reflect a diversity of post-cranial adaptations in *Australopithecus*.

KEYWORDS

compartmentalization index, geometric morphometrics, mineralized tissues, rib cross section, thorax

Research Highlights

- The rib cross sections of *Pan troglodytes* tend to be rounder than that of *Homo sapiens*.
- In typical ribs, rounder cross sections have a larger mineralized area in *P. troglodytes* and *H. sapiens*.
- Rib cross sections from Sts 14 are more similar to *P. troglodytes* than to *H. sapiens*.

1 | INTRODUCTION

Primates exhibit an important intertaxic locomotor diversity, which is reflected not only in the variable anatomy of their limbs but also in some particularities in the rest of their skeleton (Almécija et al., 2021; Fleagle, 2013; Williams et al., 2023). Given that the ribcage and the lumbar spine are the nexus between the shoulder and pelvic girdles, their configuration is highly related to the mode of locomotion in this group (Fleagle & Lieberman, 2021). Focusing on the ribcage of current hominid species, two different thoracic morphotypes have been traditionally defined according to locomotion as well as breathing kinematics (Bastir et al., 2017; Gea, 2008; Jellema et al., 1993; Latimer et al., 2016). On the one hand, the "funnel-shaped" thorax of *Pan*, *Gorilla*, and *Pongo* species, which is relatively narrower in its cranial part and wider in its caudal part, is associated with non-bipedal posture and predominant diaphragmatic breathing with a residual collaboration of other respiratory muscles. On the other hand, the so-called "barrel-shaped" thorax of *Homo sapiens*, which is relatively expanded in its cranial part and narrower in its caudal part, indicates bipedal posture and breathing kinematics that actively combine the action of the diaphragm and the intercostal muscles (among others such as the scalenes or abdominals) (Callison et al., 2019).

Following these distinctions, traditional studies have taken the ribcage morphology of *Pan troglodytes* as a potential reference for modeling the ribcage of early hominins from the genus *Australopithecus* (Schmid, 1983, 1991). On the contrary, recent research suggests that the ribcage of some well-preserved *Australopithecus* specimens was characterized by a configuration closer to that of *H. sapiens* (Bastir et al., 2016; García-Martínez et al., 2021; Haile-Selassie et al., 2010; Latimer et al., 2016; Schmid et al., 2013; Williams et al., 2018). This is

mostly according to rib torsion and declination, which are respectively defined as (1) the three-dimensional spiraling of the rib shaft and (2) the degree of rib lowering dependent on the position of the costo-vertebral joint (García-Martínez et al., 2016). Even though some efforts have been made in comparing the costal anatomy of these species, there are other less studied features from both the internal and external costal anatomy that still need to be addressed.

For example, analyzing the torsion of the rib shaft has been considered fundamental to understanding the evolution of the hominid ribcage given its contribution to determining the 3D configuration of the thorax, mostly via the effects on its depth and flatness (Bastir et al., 2020; García-Martínez et al., 2016; García-Martínez et al., 2018, 2020, 2021; Latimer et al., 2016; Schmid, 1983, 1991). Interestingly, rib torsion in hominids has been linked to other costal variables such as rib cross-sectional anatomy since ribs with rounder cross sections apparently present less torsion than those with flattened cross sections (Franciscus & Churchill, 2002; García-Martínez et al., 2018; Gómez-Olivencia et al., 2009; Latimer et al., 2016; Schmid, 1983, 1991). Complementing these analyses, the morphology of the entire rib has been linked to covariation between the shape and the percentage of mineralized area (% Min. Ar.) of the rib cross section at the midshaft such that the shape of the rib cross sections would be rounder in those with larger % Min. Ar. However, up to now, it has only been tested in the first rib (García-Martínez et al., 2017).

In this regard, recent research by López-Rey et al. (2022) observed that the % Min. Ar. of the rib cross sections at the midshaft is higher in adult *P. troglodytes* than in adult *H. sapiens*, such as expected given the systemic gracility of the modern human skeleton (Chirchir et al., 2015). This would be in line with previous observations that the rib cross

sections at the midshaft may be expected to be rounder in adult *P. troglodytes* compared to adult *H. sapiens* (Latimer et al., 2016; Schmid, 1983, 1991). Nevertheless, there are no studies that statistically test for differences in the shape of the rib cross sections at the midshaft as well as its covariation with the % Min. Ar. between *H. sapiens* and *P. troglodytes*. If found, this potential covariation could represent a biomechanical compromise between ribs and muscle attachments given that bone modeling and remodeling are closely dependent on bone exposure to mechanical stresses (Allen & Burr, 2014; Barak, 2019). As mechanical stimuli change during ontogeny under physiological constraints related to growth and development, the shape might covary with the mineralization of the rib cross sections at the midshaft until adulthood (Beresheim et al., 2019; Carter, 1987; Kivell, 2016). Additionally, López-Rey et al. (2022) also observed that the % Min. Ar. of *Australopithecus africanus* Sts 14 cross sections from ribs 7–9 (Sts 14w, Ward et al., 2020) is closer to *H. sapiens* than to *P. troglodytes*, potentially indicating similar lower thorax breathing kinematics between this fossil specimen and modern humans. However, because mineralization is also affected by ontogeny, biomechanical explanations could be biased since this specimen did not reach full maturity (Bonmatí et al., 2008).

Thus, this study aims to test for significant differences in the shape of the rib cross sections at the midshaft belonging to *H. sapiens* and *P. troglodytes* adult individuals and those of *A. africanus* specimen Sts 14 as well. In addition, we also test whether shape covaries with the percentage of mineralized area (% Min. Ar.) described by López-Rey et al. (2022). In order to achieve these goals, we have formulated the following hypotheses:

1. Rib cross sections at the midshaft are rounder in *P. troglodytes* than in *H. sapiens* adult individuals because of the lower rib torsion of *P. troglodytes* ribs.
2. Rounder rib cross sections at the midshaft tend to have a higher % Min. Ar. than mid-laterally flattened ones in response to their greater exposure to mechanical stimuli.
3. The shape and covariation pattern of the rib cross sections at the midshaft belonging to specimen Sts 14 are closer to *P. troglodytes* adult individuals due to its incomplete skeletal growth.

2 | MATERIALS AND METHODS

The proposed hypotheses were tested using the sample described by López-Rey et al. (2022), which consists of 255 rib cross sections at the midshaft selected from the complete set of ribs (levels 1–12) of 10 *H. sapiens* ($N = 120$ ribs) and 10 *P. troglodytes* ($N = 130$ ribs) adult individuals, as well as from five fossil ribs of *A. africanus* Sts 14 catalogued as Sts 14x, Sts 14y, and Sts 14w (Ward et al., 2020). These fossil ribs were sorted in the costal series of specimen Sts 14 by López-Rey et al. (2022) according to their tubercle-iliocostal line distance (Franciscus & Churchill, 2002) and were tentatively identified as costal levels 6, 5, and 7–9, respectively. Further information on the taxonomy, sex and origin of the whole sample is provided in Table S1.

Firstly, the shape of each rib cross section was quantified by 2D geometric morphometrics. The whole sample was measured in accordance to standard workflows in geometric morphometrics (Bastir et al., 2019) by Viewbox 4.0 software (dHAL software, Kifissia, Greece) using a reference model (template) of 16 points: four landmarks and 12 semilandmarks distributed in four curves (Figure 1). As a result of their uncertain location, we applied a "sliding" process to the semilandmarks along the tangent vectors of their corresponding curves in order to minimize shape variation derived from their arbitrary position. This process also minimized the bending energy required for shape deformation of each sample in comparison into the template (Gunz et al., 2005; Gunz & Mitteroecker, 2013).

Later, the whole sample was subjected to a generalized Procrustes analysis (GPA) to apply translation, rotation, and scaling for removing any variation not related to the shape. Then the shape of the rib cross sections at the midshaft was explored by a principal component analysis (PCA) in shape space (Mitteroecker & Gunz, 2009). The variation in shape was visualized along the principal component 1 (PC1) and PC2 as these two components combined account for more than 80% of the total variability in the sample. The scatterplot shown in Figure 2 was carried out using MorphoJ software (University of Manchester, United Kingdom; Klingenberg, 2011). To compare the inter and intraspecific distribution of the PC1 and PC2 scores, we performed the following statistical tests using Past 4.03 software (University of Oslo, Norway; Hammer et al., 2001). To begin with, we tested the normality of these scores by a Kolmogorov–Smirnov test (Lilliefors correction) and, setting 0.05 as our limit for significance, we found that there is statistical evidence to reject the normal distribution of the scores at PC2 ($p = 0.001$), but not at PC1 ($p = 0.2$). The inter and intraspecific distribution of the rib cross sections along PC1 and PC2 was subsequently tested by splitting the costal series of species *H. sapiens* and *P. troglodytes* into two groups: typical (costal levels 3–10) and atypical ribs (costal levels 1, 2, 11, and 12, also 13 in *P. troglodytes*). This traditional division is supported by differences in costal position, external morphology, muscular attachments and contributions to breathing kinematics (Graeber & Nazim, 2007; Gray, 1918). Once these groups were settled, we ran a Kruskal-Wallis test that confirmed the different distribution of their scores along PC1 ($p < 0.001$) and PC2 ($p < 0.001$). Next, a Dunn-Bonferroni post hoc analysis was executed in order to determine the groups whose PC1 and PC2 scores have a different distribution (Table 1).

We also tested whether there is a covariation between the general shape of the rib cross sections at the midshaft (quantified using the PC1 scores) and their corresponding percentage of mineralized area (% Min. Ar.), which was described for this sample by López-Rey et al. (2022) using the compartmentalization index (Comp. Index).

$$\text{Compartmentalization index} = \frac{x}{100 - x}$$

Based on the histomorphological bone analyses of Cambra-Moo et al. (2014), the Comp. Index is a parameter calculated as the ratio between the percentage of mineralized (% Min. Ar., x) and
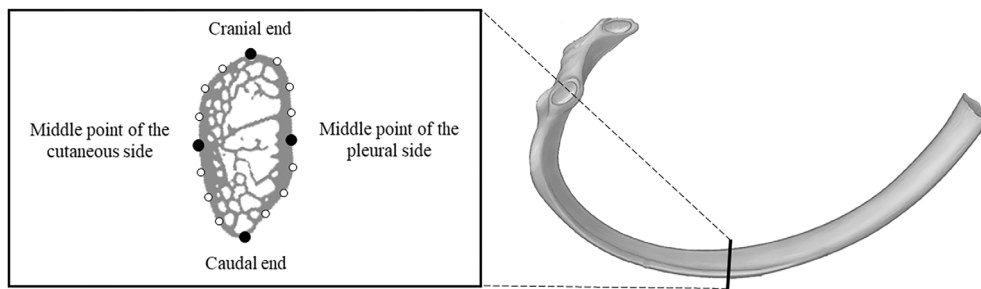
FIGURE 1 Template of digitalization with the landmarks (named and colored in black) and sliding curve semilandmarks (colored in white) used to describe the rib cross sections of the whole sample. The rib imaged in this figure was previously published by Graeber and Nazim (2007).
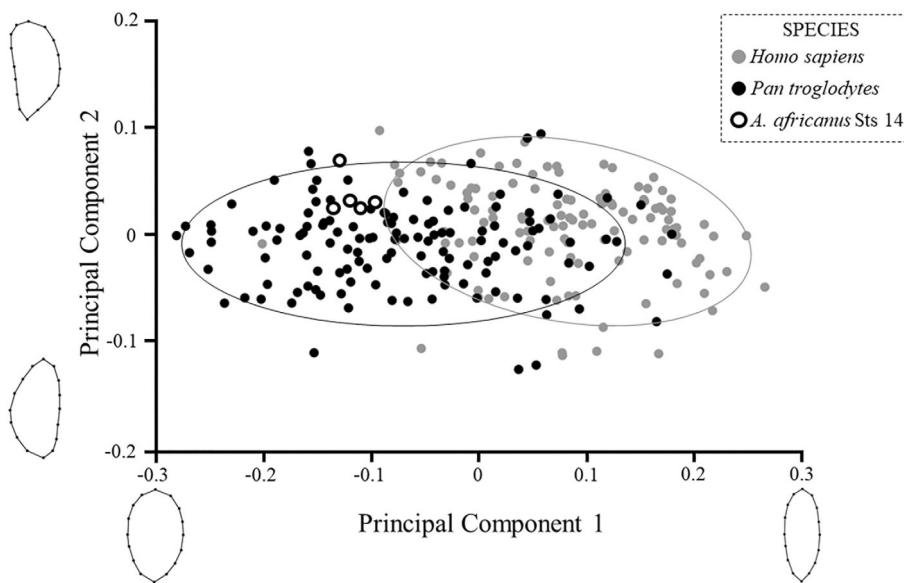

FIGURE 2 Scatterplot showing the relationship of the studied rib cross sections at the principal component 1 (PC1)–PC2 in shape space. Eighty-five percent confidence ellipses for the scores of species *Homo sapiens* and *Pan troglodytes* are also included. The accompanying visualizations show the shape of the rib cross sections at the extremes of both axes.

TABLE 1 Dunn-Bonferroni post hoc analysis.

|	Costal group	Typical *Homo sapiens*	Atypical *H. sapiens*	Typical *Pan troglodytes*	Atypical *P. troglodytes*	Sts 14
PC1	Typical *H. sapiens*	–	1.000	**0.000**	**0.002**	**0.003**
	Atypical *H. sapiens*	–	–	**0.000**	**0.001**	**0.001**
	Typical *P. troglodytes*	–	–	–	**0.000**	1.000
	Atypical *P. troglodytes*	–	–	–	–	0.358
	Sts 14	–	–	–	–	–
PC2	Typical *H. sapiens*	–	**0.000**	**0.000**	**0.000**	1.000
	Atypical *H. sapiens*	–	–	0.588	**0.012**	**0.002**
	Typical *P. troglodytes*	–	–	–	0.766	**0.021**
	Atypical *P. troglodytes*	–	–	–	–	0.189
	Sts 14	–	–	–	–	–

Note: p values are adjusted for multiple comparisons. Those who are significant, remarked in bold, indicate statistical differences between groups.

non-mineralized areas (% nMin. Ar, 100-x) of a bone section. Graphically, the Comp. Index exhibits a non-linear behavior with two asymptotes ($y = 0$, $x = 100$) and enables a clear visualization of the mineralization differences for % Min. Ar. values from 50% onwards.

Next, the normality of the PC1 scores and the Comp. Index was studied by the Kolmogorov–Smirnov test (Lilliefors correction), which determined that there is statistical evidence to reject a normal distribution of the Comp. Index ($p = 0.001$), but not of the PC1 scores ($p = 0.2$). After that, covariation between the PC1 scores and the Comp. Index was tested in accordance to the costal groups (typical and atypical ribs) of each species (*H. sapiens*, *P. troglodytes* and *A. africanus*) by a Spearman's rho (ρ) test and a permutation test (number of randomization rounds = 10,000). Significant covariations were finally interpreted by a linear regression between the PC1 scores and the Comp. Index (Figure 3). All these analyses were also performed using MorphoJ and Past 4.03 software.

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FIGURE 3 Linear regression between the principal component 1 (PC1) scores and the compartmentalization index (Comp. Index) of the studied typical rib cross sections. Regression line, its equation and 85% confidence ellipses for the scores of species *Homo sapiens* and *Pan troglodytes* are also included. The accompanying visualizations show the shape of these rib cross sections at the extremes of the vertical axis.
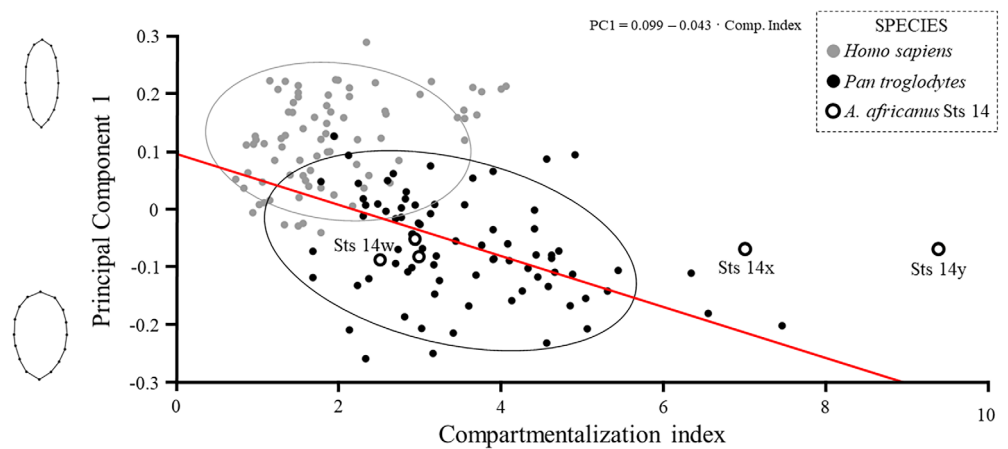
3 | RESULTS

On the one hand, PC1 reflects variations related to the overall configuration of the rib cross sections across serial levels and explains 72.18% of the total shape variation of the sample. Negative PC1 scores are related to rounder rib cross sections and positive PC1 scores to mid-laterally flattened rib cross sections. Despite a large overlap, Dunn-Bonferroni post hoc test found significant interspecific differences in the distribution of the PC1 scores belonging to *H. sapiens* and *P. troglodytes* along PC1. Generally, *P. troglodytes* individuals show rounder rib cross sections than *H. sapiens*. Significant intraspecific differences between the typical and atypical rib cross sections were only found in *P. troglodytes*. This indicates that the morphological variability of their rib cross sections is greater as they have a wide range of exclusive negative PC1 scores, mainly from typical rib cross sections, that do not overlap with those belonging to modern humans. This is valid except for the outlier rib cross section of costal level 12 form individual ID 87, PC1 score = −0.207. The PC1 scores for the five Sts 14 rib cross sections are negative, close to each other and only statistically different from that of *H. sapiens* (Figure 2, Table 1).

On the other hand, PC2 represents variations linked to the pleural and cutaneous outlines of the rib cross sections and explains 8.53% of the total shape variation. While negative PC2 scores are related to rib cross sections with greater curvature on its cutaneous side than on its pleural side, positive values mean the opposite. Although variation in PC2 could indicate the presence or absence of the costal groove, it was not further explored as the explanation of the total shape variation is much lower in PC2 than in PC1 (Figure 2, Table 1).

The *p* value obtained for the Spearman's rho (ρ) and permutation tests was below 0.05 for the typical rib cross sections of *H. sapiens* ($\rho = -0.372$ / permutation score = −0.369) and *P. troglodytes* ($\rho = -0.368$ / permutation score = −0.327), so there is statistical support for accepting the covariation between the PC1 scores and the Comp. Index only in these groups of ribs. The covariation between the PC1 scores and the Comp. Index belonging to the typical rib cross sections of modern humans and chimpanzees can be graphically observed in Figure 3. This linear regression (*p* < 0.001) suggests that rounder rib cross sections such as seen in *P. troglodytes* have a higher

Comp. Index and, consequently, a higher % Min. Ar. Scores belonging to Sts 14 were also included to highlight that covariation was not significant in the rib cross sections of this specimen because of the higher mineralization of ribs Sts 14x and Sts 14y.

4 | DISCUSSION

As proposed in previous publications (Latimer et al., 2016; Schmid, 1983, 1991), we found that rib cross sections at the midshaft are generally rounder in adult *P. troglodytes* than in adult *H. sapiens* individuals, which confirms our first hypothesis. However, the morphological variability found in *P. troglodytes* seems to be greater than that of *H. sapiens* since chimpanzees present both rounder and mid-laterally flattened rib cross sections in their typical and atypical ribs, respectively. In contrast, both types of ribs have mid-laterally flattened cross sections in adult modern humans (Figure 2, Table 1). The increased precision of our findings can be attributed to the implementation of 2D geometric morphometrics to the study of the rib cross sections, something that was tentatively done by García-Martínez et al. (2017) and that improves on the traditional measurements performed by previous research (Franciscus & Churchill, 2002).

To test whether there is a relationship between the outlines and mineralization of the rib cross sections exists, which is our second hypothesis, we compared covariation between the shape and the percentage of mineralized area (% Min. Ar.) of the sample. Our results show that, in the typical ribs of adult *H. sapiens* and adult *P. troglodytes* individuals, rounder rib cross sections tend to have a higher % Min. Ar. than do mid-laterally flattened ones (Figure 3). No covariation was found in the atypical ribs of the two species, which may indicate different geometric requirements because of the specific morphology, position and function of these bones in the ribcage (Graeber & Nazim, 2007; Gray, 1918). These results support the traditional division between typical and atypical ribs from a new perspective that includes inter and intraspecific analyses of the rib cross sections at the midshaft.

Although there is a systemic gracility in the modern human skeleton compared to *P. troglodytes*, other hominins and even Upper

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Paleolithic *H. sapiens* (Chirchir et al., 2015), Ryan and Shaw (2015) noted that mineralization in modern human weight-bearing bones with higher physical activity can be similar to that of primates such as *P. troglodytes*. However, Tommerup et al. (1993) concluded that direct loading on weight-bearing bones such as the femur has no effect on ribs. Thus, differences in shape and % Min. Ar. between the typical rib cross sections of *H. sapiens* and *P. troglodytes* might respond to their local loading environment, which might be related to the particular modes of breathing and locomotion they are adapted to. Indeed, firstly, the breathing of adult *H. sapiens* actively combines the diaphragmatic action with that of other respiratory muscles compared to *P. troglodytes*, where breathing is predominantly diaphragmatic (Callison et al., 2019; Gea, 2008). Secondly, the bipedal locomotion of *H. sapiens* entails that the weight of the head, neck, and arms pass through the spinal column, so it has no effect on chest wall biomechanics. On the contrary, the knuckle-walking locomotion of *P. troglodytes* entails that the weight of the head, neck, and upper thorax pass through the upper ribs to the forelimbs (Callison et al., 2019; Casha et al., 2015). This would imply that both the lower and upper ribs of *P. troglodytes* are potentially more exposed to local mechanical stresses than are the ribs of *H. sapiens*, which may explain the differences between their rib cross sections (Beresheim et al., 2019; Carter, 1987; Kivell, 2016; Ruff et al., 2006) and, consequently, the overall 3D shape of their thoraces (Bastir et al., 2017; Gea, 2008; Jellema et al., 1993; Latimer et al., 2016).

Regarding the *A. africanus* specimen Sts 14, the shape and the covariation pattern of its rib cross sections at the midshaft are closer to *P. troglodytes* than to *H. sapiens*, as we proposed in the third hypothesis. Even though the five rib cross sections of this specimen have a similar, rounded shape (Figure 2), the position of their corresponding PC1 scores in Figure 3 is heterogeneous because of the higher mineralization of ribs Sts 14x (costal level 6) and Sts 14y (costal level 5) compared to Sts 14w (costal levels 7–9). To interpret these results, the incomplete skeletal growth of specimen Sts 14 (Bonmatí et al., 2008) should be taken into consideration given that the shape and % Min. Ar of the rib cross sections at the midshaft change with ontogeny. Specifically, early stages of growth and development are linked to rounder and more mineralized rib cross-sections (Beresheim et al., 2019; García-Martínez et al., 2016, 2017, 2023). Hence, although our results might indicate that the rib morphology of Sts 14 is similar to that of *P. troglodytes* based on their rib cross sections (Franciscus & Churchill, 2002; García-Martínez et al., 2018; Gómez-Olivencia et al., 2009; Schmid, 1983, 1991), previous publications determined that the rib torsion and declination is closer to modern humans not only in Sts 14 (Ward et al., 2020) but also in other *Australopithecus* specimens with different states of maturity like KSD-VP-1/1 (*A. afarensis*) (Haile-Selassie et al., 2010; Latimer et al., 2016), MH1 and MH2 (*A. sediba*) (Schmid et al., 2013; Williams et al., 2018). Alternatively, as stated for other post-cranial elements (Prabhat et al., 2021), *Australopithecus* species could demonstrate a wide range of costal features such as a chimpanzee-like rib cross-sectional anatomy and a modern human-like rib torsion and declination. This would indicate potentially opposed selective pressures acting over locomotion and breathing, such as seen in other post-cranial elements like the (meta)tarsus and pedal phalanges (Ward, 2013). Future research should study the

shape and % Min. Ar of the rib cross sections at the midshaft belonging to *Australopithecus* specimens with different states of maturity in order to confirm this hypothesis.

5 | CONCLUSIONS

The shape of the rib cross sections at the midshaft tend to be rounder in adult *Pan troglodytes* than in adult *Homo sapiens* individuals. Moreover, there is a covariation between the shape and percentage of mineralized area (% Min. Ar.) of the cross section from typical ribs in both species, such that rounder typical rib cross sections are associated with a larger % Min. Ar. than mid-laterally flattened ones. It is also important to state that, although the shape and covariation pattern of the five studied rib cross sections (costal levels 5–9) of *Australopithecus africanus* Sts 14 are similar to *P. troglodytes*, previous publications determined that the overall morphology of Sts 14 ribs is closer to modern humans. This discrepancy could reflect a diversity of adaptations in the post-cranial skeleton of *Australopithecus*.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available upon reasonable request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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