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Title: Morphological and functional implications of sexual dimorphism in the human skeletal thorax.

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ABSTRACT

Objectives: The human respiratory apparatus is characterized by sexual dimorphism, the cranial airways of males being larger (both absolutely and relatively) than those of females. These differences have been linked to sex-specific differences in body composition, bioenergetics and respiratory function. However, whether morpho-functional variation in the thorax is also related to these features is less clear. We apply 3D geometric morphometrics to study these issues and their implications for respiratory function.

Material and methods: 402 landmarks and semilandmarks were measured in CT-reconstructions of rib cages from adult healthy subjects ($N_{\text{male}}=18$; $N_{\text{female}}=24$) in maximal inspiration (MI) and maximal expiration (ME). After Procrustes registration, size and shape data were analyzed by mean comparisons and regression analysis. Respiratory function was quantified through functional size, which is defined as the difference of rib cage size between MI and ME.

Results: Males showed significantly larger thorax size ($p<0.01$) and functional size ($p<0.05$) than females. In addition, the 3D-shape differed significantly between sexes ($p<0.01$). Male rib cages were wider (particularly caudally) and shorter, with more horizontally oriented ribs when compared to females. While thorax widening and rib orientation were unrelated to allometry, thorax shortening showed a slight allometric signal.

Conclusions: Our findings are in line with previous research on sexual dimorphism of the respiratory system. However, we add that thorax shortening observed previously in males is the only feature caused by allometry. The more horizontally oriented ribs and the wider thorax of males may indicate a greater diaphragmatic contribution to rib cage kinematics than in females, and differences in functional size fit with the need for greater oxygen intake in males.

INTRODUCTION

Sexual dimorphism has been observed as an important source of intraspecific variation in living and fossil hominins (Fruyer and Wolpoff, 1985). In current day human populations, it has been addressed both at cranio-facial (Wood and Willoughby, 1991; Lam et al., 1996; Loth and Hennenberg, 1996; Steyn and İşcan, 1998; Rosas and Bastir, 2002; Hall, 2005; Bulygina et al., 2006; Bastir et al., 2011) and postcranial levels (Ruff, 1987; Arsuaga and Carretero, 1994; Gama et al., 2015; İşcan and Shihai, 1995; Richmond and Jungers, 1995; Reno et al., 2003; Carlson et al., 2007; Kranioti et al., 2009; Bastir et al., 2014; Rodriguez-Perez, 2014; Navega et al., 2015; Rosas et al., 2015; Rosas et al., in press) with size and shape differences between males and females. It is important to note that some of these shape changes could be explained by allometry (shape differences explained by differences in size), since males are generally larger than females.

Sexual dimorphism in the respiratory apparatus

With reference to the respiratory apparatus, geometric morphometric studies of cranial airways (Rosas and Bastir, 2002; Bastir et al., 2011; Holton et al., 2014) showed that sexual dimorphism in the human skull influences the morphology of the upper airways. This is because males present consistently larger nasal cavities and relatively longer, narrower and higher nasal floors than females of the same body size. These differences have been linked to sex-specific differences of the musculo-skeletal system, body composition and basal metabolic rate (BMR) associated with greater energy expenditure and oxygen consumption in males than in females (Bittar et al., 1999; Hall, 2005; Wells, 2007; Froehle and Churchill, 2009; Bastir et al., 2011). This higher oxygen intake is necessary because adult males have larger total lean mass and smaller fat mass than females (Wells, 2007).

Sexual dimorphism of the rib cage has been studied less than that of cranial airways. It was not until the beginning of 21st century that the first detailed two-dimensional approaches began to

emerge in order to study sexual dimorphism of the rib cage in anatomical connection (Bellemare et al., 2003). Bellemare et al. (2003) quantified radiographic pulmonary images through the use of traditional measurements such as lengths and diameters. The authors suggested that adult female thoraces are around 10-12% smaller than those of males. These size differences can be expected since Stahl (1967) proposed that total lung capacity (and thus lungs) scales isometrically with overall body size in static allometry across taxa. So, since males present a larger body size than females (Ruff, 2002), a larger lung size is also expected for them. Regarding shape, Bellemare et al. (2003) observed that female thoraces were characterized by a smaller medio-lateral dimension in relation to height (so a shorter diaphragm length), a greater declination of ribs and a higher position of the sternum compared to males.

Recently, methodological advances in morphometric quantification of rib curvature through the use of semilandmark methods (Bastir et al., 2013; García-Martínez et al., 2014; Shi et al., 2014; Weaver et al., 2014; Bastir et al., 2015; García-Martínez et al., 2016) have allowed for a more accurate quantification of the 3D structure of the rib cage. Specifically, Shi et al. (2014) and Weaver et al. (2014) developed thoracic models that could be used to study thoracic injury patterns due to motor vehicle crashes or falls. These authors addressed thorax shape variation related to several factors from a 3D point of view, including sexual dimorphism (body mass index, stature, etc.). Shi et al. (2014) measured the left side of rib cages of individuals of both sexes through the use of semilandmark methods, quantifying rib orientation relative to the axial and sagittal planes. These authors concluded that male ribs were more horizontally oriented than those of females and that the rib cages of males were deeper than those of females of the same stature, which they linked to a greater rib cage volume in males. Weaver et al. (2014) quantified age and sex-related changes of the 3D rib cage morphology through a semilandmark approach, pointing out the higher degree of rib declination that females of different ages showed compared to males. Importantly, these studies did not specify in which kinematic state (inspiration or expiration) the thorax anatomy was quantified; therefore, controlling for respiratory movements might be required in order to attain a clearer idea

of sexual dimorphism in a neutral kinematic state. This problem could potentially be solved by averaging inspiratory and expiratory thorax form. In addition, it is unclear to what degree overall size and static allometry contribute to the shape differences observed by previous studies.

Functional anatomy related to sexual dimorphism

Bellemare et al. (2003) hypothesized that declination of ribs in females should allow for greater inspiratory muscle contribution during resting breathing than in males. This is mainly caused by intercostal muscle action (Spalteholz, 1970; De Troyer et al., 2005). On the other hand, because of a higher oxygen intake in males than in females via the cranial airways (Rosas and Bastir, 2002; Bastir et al., 2011), a greater inspiratory volume is expected in the male thorax. This greater volume in males is supported by James et al. (1979), Harms (1998) and Valenza-Demet et al. (2011) who suggested ventilatory advantages and a greater thoracic expansion in males relative to females during breathing. Following this evidence, if more efficient intercostal muscle action has been observed in females (Bellemare et al., 2003) but a greater thoracic expansion during inspiration has been observed in males (James et al., 1979; Harms, 1998; Valenza-Demet et al., 2011) it is possible that the lower efficiency of intercostal muscles in males is compensated by their greater diaphragmatic efficiency (producing thus a greater thoracic expansion).

This is because differences in thoraco-abdominal configuration have been demonstrated to impact the function of the respiratory muscles (Grassino et al., 1978; Goldman et al., 1978; Pinet, 1998; De Troyer et al., 2005). Regarding sexual dimorphism, dimorphic features have been found between thoracic and abdominal breathing (by intercostal muscles and diaphragm, respectively): the breathing mode for males and females was proposed as abdominal during quiet breathing but the abdominal movements were significantly stronger in males than in females during deep breathing or vital capacity manoeuvres (Verschakelen and Demedts, 1995; Ragnarsdóttir and Kristinsdóttir, 2006; Kaneko and Horie, 2012). Because abdominal breathing is related to diaphragmatic action, a greater diaphragmatic contribution could be expected in males, at least in specific situations.

This possibility is reinforced by recent studies of 3D thoracic vertebrae morphology (Bastir et al., 2014), where authors found statistical differences in transverse process orientation between sexes. They showed that the transverse processes of thoracic vertebrae are more posteriorly oriented at the lower thorax in males, which could allow for greater medio-lateral expansion at the caudal part of the rib cage and thus a stronger diaphragmatic contribution.

Aims of this study

Sexual dimorphism of the thoracic respiratory system has received little attention compared to the cranio-facial respiratory system. Previous studies have showed sex-related differences in size and shape, but the potential association between these factors and their link to functional anatomy are still unclear. In order to clarify these issues, the present study aims to detail size and shape differences through a 3D approach and test the following hypotheses:

According to Bellemare et al. (2003), males have greater thoracic volume than females, but this has been never quantified through 3D approaches. As a result, we expect the same size differences observed previously in 2D. Therefore, we test Hypothesis 1, which predicts that males have larger thoraces than females (H1).

Since previous studies found shape differences between females and males (Bellemare et al., 2003; Shi et al., 2014; Weaver et al., 2014) we test Hypothesis 2, which predicts that shape differences are presented between both groups (H2). In addition, we provide a detailed explanation of 3D differences.

Moreover, since possible differences observed in shape are perhaps caused by size differences (allometry) and this issue remains unresolved, we aim to test Hypothesis 3, which predicts that sex-related shape differences are caused by allometric factors (H3).

Finally, since higher oxygen intake at the cranial airways has been proposed in males, we also expect them to show a greater size increase during inspiration in order to process this oxygen.

Therefore, we test Hypothesis 4, which predicts that males have a greater increase in thorax size during inspiration than do females (H4).

MATERIAL AND METHODS

Materials

In order to test the hypotheses, we have used computed tomography (CT) reconstructions of the rib cages of 42 adult individuals (18 males and 24 females). The age range studied was from 40 to 67 years old (with an average of 50.9). Each individual was CT-scanned both in maximum inspiration and maximum expiration, so 84 scans of rib cages were ultimately studied. The data were obtained from hospital subjects who had been previously scanned as a healthy control group and compared with pathological individuals belonging to a different research project at the Hospital Universitario La Paz (Madrid, Spain). In none of the cases could any pathologies affecting skeletal thorax form be detected. The ID and sex composition are detailed in Table 1 of Supplementary Information. Consent was given to use these CT-data for research purposes and prior to analysis all CT-data were anonymized to comply with the Helsinki declaration (Goodyear et al., 2007).

Methods

Each thorax was segmented through a semi-automatic segmentation protocol of DICOM images using the Mimics 8.0 (<http://biomedical.materialise.com/mimics>) software program. The post-processing of the 3D surface models of skeletal elements (cleaning, smoothing and mesh hole-filling) was carried out with Artec Studio software (www.Artec3D.com) and the final 3D thorax models were imported into Viewbox4 software (www.dhal.com). Then, landmarks and semilandmarks for sliding (Gunz et al., 2005) were located on thorax models following the protocol of Bastir et al. (2013). The thorax morphology is described thus by 20 homologous 3D landmarks and sliding semilandmarks on each rib (1-10) and two additional landmarks at the sternum (402 landmarks and sliding semilandmarks in each thorax). The breathing ribcage is a mobile structure

with different possible morphologies. In order to best focus on static overall shape differences of the thorax, we calculated the mean shape of each individual between inspiration and expiration. In this way we finally studied 42 individuals (18 males and 24 females) in a neutral kinematic state (average).

Because of uncertainty of their location along the ribs, semilandmarks were slid along their corresponding curves with respect to the fixed landmarks in order to minimize bending energy (BE) following standardized procedures for semilandmark analyses (Gunz et al., 2005; Mitteroecker and Gunz, 2013). First, semilandmarks were slid so as to minimize BE between each specimen of the sample and the template specimen (the first thorax digitized). Then, once the average shape of the total sample was calculated, the semilandmarks were slid so as to minimize BE between each specimen of the sample and the template specimen

First, semilandmarks were slid so as to minimize BE between each specimen of the sample and the template specimen (the first thorax digitized), and a second time, once the average shape of the total sample was calculated, between each specimen and the sample average form.

Size and shape data were obtained by Generalized Procrustes Analysis (GPA) of this landmark data set (Zelditch et al., 2004). Thorax size was quantified as centroid size, which is defined by the square root of the sum of squared distances of a set of landmarks from their centroid (O'Higgins, 2000; Mitteroecker and Gunz, 2009). First, we studied centroid size distribution between groups in a neutral kinematic state (average between inspiration and expiration of each individual) in order to test H1. Then, we studied the difference in centroid size between inspiration and expiration (functional size onwards) of each individual as a proxy to test H4. Patterns of shape variation along the distribution were studied throughout Principal Component Analysis (PCA) in Procrustes shape space (Zelditch et al., 2004) of the thorax in a neutral kinematic state in order to explore changes in thoracic shape possibly attributed to sexual dimorphism (H2). Ordinations were calculated and shape differences of the surface associated with variations along the PC axes were

visualized using EVAN Toolkit (version 1.71; <http://www.evan-society.org/>). In addition, in order to confirm differences in shape between males and females (also H2), a mean shape analysis was carried out in MorphoJ software (Klingenberg et al., 2011). Differences were assessed through Procrustes distance between means and a permutation test for testing equal group means. Group means were also warped and showed using EVAN Toolkit. Finally, in order to test H3 and explore the degree to which allometry causes morphological differences, we first carried out a regression of shape (Procrustes coordinates) on size (centroid size) and analyzed the residuals of this regression model for potential sex specific differences, similar to a MANCOVA approach (Rosas and Bastir, 2002, Bastir et al., 2011).

RESULTS

Analyses revealed significant evidence for sexual dimorphism between male and female thorax in size (both in neutral kinematic state and in functional size) and shape, including the PC scores of the first component of shape space PCA, the mean shapes comparison based on Procrustes coordinates, as well as the mean shape comparison based on regression residuals.

Size differences

Table 1 shows 95% confidence intervals which reveal statistical size differences between females and males in centroid size (CS) of the thorax in neutral kinematic status as well as in their functional size. Males are larger in neutral kinematic state than females (Mean Fem. CS = 2521.40; Mean Male CS = 2864.10; $t = -12.22$; $p < 0.01$) and they also present a larger functional size (Mean Fem. = 31.26; Mean Male = 41.67; $t = -2.09$; $p < 0.05$). These results allow us to accept H1 and H4.

[Insert Table 1 here]

Shape differences

The first three main components of the PCA explain 65.3% of the variance (see Table 2 from Supplementary Information for more details). Figure 1 shows variation along PC1-PC2-PC3, and

polarization between groups occurs mainly along PC1. PC1 shows statistical differences between distributions of both groups (Table 2), since males are more polarized towards negative values than are females. Morphological variation along PC1 (35.4% of the variance) is related to height and width of the rib cage as well as to rib orientation relative to sagittal plane (rib torsion and rib declination) and sternum position (Figure 2). Morphological variation in PC2 (20.8% of the variance) is associated with thorax depth and the sagittal orientation of the distal end of the ribs of the cranial third, which is related to a volumetric expansion of this part of the rib cage (Figure 1 of Supplementary Information). Finally, morphological variation related to PC3 (9.1% of the variance) is associated with sagittal orientation of the midshaft of the ribs, which is also related to volumetric expansion of the cranial third of the rib cage (Figure 2 of Supplementary Information).

[Insert Table 2 here]

[Insert Figure 1 here]

Morphological differences associated with PC1 are the ones linked to sexual dimorphism, whereas the ones associated with PC2 and PC3 reflect other factors of intra-specific variation. Anatomical details explained by PC1 are shown in Figure 2 and anatomical details explained by PC2 and PC3 are shown in Figures 1 and 2 of Supplementary Information, respectively.

[Insert Figure 2 here]

Mean shape comparison of Procrustes coordinates ($d=0.04$; $p<0.01$) showed statistical differences between sexes of thoraces in neutral kinematic status. Surface warps associated with mean shapes based on Procrustes coordinates (Figure 3 of the main text and Figure 3 of Supplementary Information; differences magnified two times in order to observe them clearly) show that thoraces in males are wider (more evident at the lower thorax) and present the ribs in a more horizontal position than females. Moreover, male thoraces are shorter craniocaudally and present

the sternum in a lower position than females. Therefore, these results allow us to accept H2, providing a detailed explanation of differences in three-dimensional configurations.

[Insert Figure 3 here]

Size and shape covariation

Although the regression of shape on size presented statistically significant results, it is important to note that only a low percentage of total variance was predicted ($r^2=0.07$; $p=0.03$). Moreover, as we can see in Figure 4, it is interesting to note the lack of overlap between the distributions of the sexes; this could indicate different ontogenetic trajectories for each sex. When we remove the allometric component and carry out mean comparison of regression residuals between groups, we still observe statistical shape differences between them (Proc. Dist. = 0.009; $p<0.01$). We observe in the associated warps (Figure 5 of the main text and Figure 4 from Supplementary Information; differences magnified ten times in order to observe them clearly) that the relative shortening of the thorax in males disappears when removing the allometric component. However, other features are retained, for example, the more horizontal disposition of ribs, the lower position of the sternum, and the wider thorax which is more pronounced at the lower part in males. Finally, an emergent feature is observed when removing the allometric component, since then we can observe a very different curvature of the distal part of ribs belonging to the upper thorax, which shift caudally in males and cranially in females.

[Insert Figure 4 here]

[Insert Figure 5 here]

DISCUSSION

Sexual dimorphism in the thoracic respiratory system has received less attention than that of the cranio-facial respiratory system. A few studies were carried out on this topic through 2D and 3D approaches (Bellemare et al., 2003; Bellemare et al., 2006; Shi et al., 2014; Weaver et al., 2014).

These studies expanded the knowledge of sex-related differences in the human rib cage, revealing differences in both size and shape. However, detailed knowledge on the full 3D configuration (in frontal, lateral and axial views), the possible allometric component of these differences as well as the functional implications of sexual dimorphism are not well known. Additionally, some studies have looked at sexual dimorphism of the respiratory system from a functional point of view (Verschakelen and Demedts, 1995; Ragnarsdóttir and Kristinsdóttir, 2006; Kaneko and Horie, 2012), but detailed knowledge of these differences in full 3D configuration is also still missing. This study addresses sexual dimorphism of the 3D configuration of the rib cage by testing hypotheses about size and shape differences as well as sex-specific differences not related to allometry.

Larger size in males relative to females has been found in many parts of both the cranial and postcranial skeleton (Fruyer and Wolpoff, 1985, Wood and Willoughby, 1991; Lam et al., 1996; Loth and Hennenberg, 1996; Steyn and İşcan, 1998; Rosas and Bastir, 2002; Hall, 2005; Bulygina et al., 2006; Bastir et al., 2011; Ruff, 1987; Arsuaga and Carretero, 1994; Gama et al., 2015; İşcan and Shihai, 1995; Richmond and Jungers, 1995; Reno et al., 2003; Carlson et al., 2007; Kranjoti et al., 2009; Bastir et al., 2014; Rodriguez-Perez, 2014; Navega et al., 2015; Rosas et al., 2015; Rosas et al., in press). Regarding the respiratory apparatus, absolutely and relatively larger cranial airways have been attributed to males both in the soft and hard tissues (Rosas and Bastir, 2002; Hall, 2005; Bulygina et al., 2006; Bastir et al., 2011; Holton, 2014); this has been linked to body composition and bio-energetics (Bittar et al., 1999; Hall, 2005; Wells, 2007; Froehle and Churchill, 2009) since males have a greater demand for oxygen than do females due to males' larger lean mass and lower fat mass percentage.

Because of the functional link between the cranio-facial (nasal cavity) and post-cranial (thorax) respiratory systems (Bastir, 2008), greater oxygen intake through the nasal cavities should also be reflected in the thoracic skeleton. Moreover, since human males generally present a larger

body size than females, and since lung size scales isometrically with body size in static allometry, differences in thorax size could also be expected in humans.

Size differences

We evaluated differences in thorax size through a centroid size (CS) approach. Our results show statistical differences between males and females. Males show 12.4% larger thoraces than females in a neutral kinematic state (Table 1). This supports previous findings made by Bellemare et al. (2003) in lung size and as well as our H1 (which predicts that males have larger thoraces than females). Regarding thoracic expansion during inspiration, we studied this variation in thorax size through the approach of functional size, observing that males present a statistically larger size increase during inspiration than females (33.3% larger; taking female functional size mean as the 100% reference; see Table 1). This is consistent with the larger cranial airways in males proposed by previous authors both in the skeleton (Rosas and Bastir, 2002; Bastir et al., 2011) and in the soft tissue (Hall, 2005; Holton, 2014) and allows us to accept our H3 (which predicts that sex-related shape differences are caused by allometric factors).

It is interesting to note that the 12.4% absolute size difference does not correspond to the 33% difference in functional size. We believe that this is due to geometric features that influence the capacity of thoracic expansion. Barrel-shaped inferior expansions appear to produce less volumetric difference than pyramidal-shaped expansion, at least at the pulmonary level (Torres-Tamayo et al., 2016). The larger volumetric expansion of the male thorax compared to the female thorax could allow for the greater oxygen intake needed to sustain males' higher basal metabolic rate (BMR), which has been observed across different populations (Froehle and Churchill, 2009).

Shape differences

Mean shape comparisons and PC1 scores based on 3D Procrustes shape coordinates showed statistical differences between both sexes. In accordance with previous findings (Bellemare et al.,

2003, Weaver et al., 2014; Shi et al., 2014), we confirm that male thoraces are relatively broader and shorter than those of females. In addition, our findings demonstrate that this feature is more evident at the lower thorax (Figure 3), which was not specified in Bellemare et al. (2003). The relatively larger craniocaudal length of females compared to that of males (as observed in Figure 3) could be related to the scaling process during the Procrustes superimposition with wider male rib cages. However, female thoraces have been hypothesized to be adapted to accommodate volumetric expansion during pregnancy (Bellemare et al., 2003). Similarly, the relatively larger craniocaudal length observed in females (Figure 3) could be involved in housing the internal reproductive organs as well as the accommodation of a potential fetus during pregnancy. This does not exclude that other factors, such as the muscles arising from the upper limbs or pelvis, could also be involved in the differences observed in the upper and lower thorax. We confirm that female ribs are more declined than those of males and that the sternum is located in a higher position in females (Figure 3). However, our results do not allow us to support the hypothesis that males have a deeper thorax in males than females (as proposed by Shi et al., 2014), since differences in thorax depth between sexes are not observed in the surface warps associated with mean comparison nor in the ones associated with PC1 scores (Figure 2 and 3). However, although PC2 clearly reflects variation in thorax depth, our results show that this is unrelated to sexual dimorphism and could reflect intra-specific variation.

Allometric implications

Regression analysis of shape on size showed a statistically significant correlation between both factors ($p=0.03$). However, the percentage of total variation explained was low ($r^2=0.0722$). More interestingly, because of the lack of overlap between the distributions of the sexes (Figure 4), we hypothesize different ontogenetic trajectories for each sex. Furthermore, when we carried out mean comparisons of regression residuals, we still observed statistical shape differences between males and females ($d=0.009$; $p<0.01$). This supports the view that the male thorax is not an

allometrically scaled version of a female thorax and that shape differences may be caused by different ontogenetic trajectories.

Different trajectories during postnatal ontogeny in the respiratory system between sexes have been observed in human lung volumes or alveolar surface areas (Thurlbeck, 1982; Becklake and Kauffman, 1999). Specifically, Thurlbeck (1982) showed that boys have larger lungs than girls at the same age and body size, a difference that becomes significant at the age of two or at a height of 110 cm. Ontogenetic differences between sexes have also been observed in the cranio-facial respiratory system, for example, in the human face (Bulygina et al., 2006) or nose (Holton et al., 2014).

As for shape, when removing the allometric component the shorter thorax in males is not detected, but other features, such as males' broader thorax (more evident at the lower part), or a higher sternum in females, are observed in the same way as before removing the allometric component. However, other features, such as the declination of the ribs, seem to be combined with an emergent phenomenon not fully observed previously: rib torsion. Males and females seem to differ in the torsion pattern of the distal part of the rib at the upper thorax (Figure 4): in males they shift cranially, while in females they shift caudally. It is important to note that while this feature is observed while looking at the thorax in anatomical connection, a recent study (García-Martínez et al., 2015) showed that rib torsion is a morphological pattern more easily observed when looking at individual ribs.

Regarding sexual dimorphism of individual ribs, some studies have addressed this question from a forensic point of view. Specifically, the width and height of the sternal end of the human fourth rib were proposed as dimorphic in the mid-80s (Işcan, 1985), a fact that was later confirmed in different populations (Wiredu et al., 1999 – Ghana population; Koçak et al., 2003 – Turkish population; Macaluso et al., 2012 – Spanish population; Meena et al., 2015 – Indian population). Meanwhile, Bellemare et al. (2006) quantified the rib length of the third, sixth and ninth ribs of a Canadian population and found no statistical differences in this measurement between both sexes.

Later, Cirillo et al. (2012) quantified sexual dimorphism in human ribs through seven traditional measurements both at the proximal and distal end, concluding that although males were larger in some dimensions, a low level of sexual dimorphism was detected in the population they studied.

Although these studies expanded our knowledge of dimorphic features observed in human ribs, rib architecture is defined by complex 3D curves and two-dimensional measurements that are difficult to quantify for the entire rib form, thus complicating the study of sexual dimorphism in ribs. Future studies should address sexual dimorphism of individual ribs from a 3D point of view in order to confirm previous findings.

Functional implications

Biomechanical action of intercostal muscles elevates ribs from a declined state to a horizontal state; this process produces thoracic inspiration (De Troyer et al., 2005). When ribs are more declined (as found in females), the intercostal muscles could raise ribs efficiently producing thoracic breathing. However, when ribs are less declined (as found in males) the intercostal muscles cannot raise the ribs effectively and abdominal breathing has to compensate the lack of intercostal muscle efficiency throughout the diaphragmatic action.

Following this principle, Bellemare et al. (2003) proposed a mechanical advantage of the inspiratory muscles in females over those of males due to the greater declination of females' ribs. Despite the hypothetical lower efficiency of inspiratory muscles in males, we observed that they present a 33% larger functional size than females, which is consistent with the higher oxygen intake proposed in the upper airways (Rosas and Bastir, 2002). To explain this, differences in the thoraco-abdominal configuration have been observed to impact the function of the respiratory muscles (Grassino et al., 1978; Goldman et al., 1978; Pinet, 1998; De Troyer et al., 2005). Since abdominal breathing (related to diaphragmatic action) has been observed to be stronger in males, at least in some situations (Verschakelen and Demedts, 1995; Ragnarsdóttir and Kristinsdóttir, 2006; Kaneko

and Horie, 2012), we can deduce that the aforementioned male thorax morphology (wider at the caudal part) leads their functional size to be greater than that of females. This difference is probably linked to the stronger diaphragmatic action found in males. It is important to note that if this hypothesis is accepted and a different diaphragmatic contribution is accepted for males, we should expect different breathing patterns between groups, which should be tested in future studies.

Additionally, it is important to note that a stronger diaphragmatic action supported by the horizontal orientation of male ribs and medio-lateral expansion of the lower thorax mentioned above could imply an advantage for physical activity of high intensity or endurance. This is because the diaphragm has traditionally been observed to be more resistant to fatigue than the intercostal muscles during breathing (Derenne et al., 1978; Gallagher et al., 1985; Roussos, 1985). It could also be essential for understanding the evolution of the thorax in different hominin species. For example, Neanderthals have been shown to present a medio-lateral expansion of the lower thorax compared to modern humans (Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009; García-Martínez et al., 2014; Bastir et al., 2015) and also a greater energetic expenditure than modern humans related to the greater oxygen demand associated with high levels of activity (Churchill, 2006).

Limitations of the study

This study addressed sexual dimorphism of the rib cage in anatomical connection by collecting information of ribs 1-10. Ribs 11 and 12 could not be digitized because no CT-data from this area were available. Therefore, future studies must address this issue. This study is based on a Spanish population, so the results presented here should also be tested in other populations. Finally, here we addressed the size differences between inspiration and expiration through a centroid size approach, but future studies should combine these measurements with physiological or volumetric values in order to confirm our results.

Conclusions of the study

For the first time, this study tests for sex-related differences both in size and shape of the rib cage in a European population through the use of a 3D approach that accounts for allometric and non-allometric factors with functional implications. Our findings allow us to confirm results observed in 2D by previous authors of a larger thorax size in males than in females. However, we add that males also showed a larger functional size than females due to males' greater inspiratory size increase. We confirm sex-related differences in shape pointed out by previous authors, but we also provide a detailed explanation of these differences in frontal, superior and lateral views: we observed that male rib cages are wider than females ones, a fact that is more evident at the caudal part, and that the sternum is in a higher position in females. We also observed that male ribs are more horizontally oriented than those of females and we did not find differences in thorax depth between sexes. Additionally, we conclude that features like the thorax shortening observed in males are only caused by size differences (allometric factors), whereas other differences, such as the thorax widening observed in males or a higher position of the sternum in females, are not caused by allometric factors. We also hypothesize that differences observed in shape between groups are not caused by allometric scaling; rather, they may be caused by different ontogenetic trajectories for each sex.

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Author contribution

Conceived and designed the experiments: DGM, MB. Performed the experiments: DGM MB.
Analyzed the data: DGM MB. Contributed discussion/materials/analysis tools: DGM MB NTT FGR ITS.
Wrote the manuscript: DGM.

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