White Rose Research Online

eprints@whiterose.ac.uk
https://eprints.whiterose.ac.uk
Universities of Leeds, Sheffield and York

Deposited via The University of York.

White Rose Research Online URL for this paper:
https://eprints.whiterose.ac.uk/id/eprint/144881/

Version: Accepted Version

Article:
García-Martínez, Daniel, Bastir, Markus, Torres-Tamayo, Nicole et al. (2019) Three-dimensional analysis of sexual dimorphism in ribcage kinematics of modern humans. American journal of physical anthropology. ISSN: 1096-8644

https://doi.org/10.1002/ajpa.23829

Reuse
Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown
If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.

UNIVERSITY OF LEEDS
University of Sheffield
UNIVERSITY of York

American Journal of Physical Anthropology **(Brief Communication)**

Title: 3D analysis of sexual dimorphism in ribcage kinematics of modern humans

Daniel García-Martínez*[1,2,3], Markus Bastir[2], Nicole Torres-Tamayo[2], Paul O´Higgins[4], Isabel Torres-Sánchez[5], Francisco García-Río[5,6], Yann Heuzé[7]

[1]University of Bordeaux, CNRS, MCC, PACEA, UMR5199 (Pessac, France)

[2]Departamento de Paleobiología, Museo Nacional de Ciencias Naturales (CSIC), José Gutiérrez Abascal 2, 28006 (Madrid, Spain)

[3]Centro de Estudios del Campo de Montiel (CECM), Ciudad Real (Castilla-La Mancha, Spain)

[4]Department of Archaeology and Hull York Medical School, the University of York (York, United Kingdom)

[5]Hospital La Paz Institute for Health Research (IdiPAZ). Paseo de la Castellana 261, 28046 (Madrid, Spain)

[6]Centro de Investigación Biomédica en Red en Enfermedades Respiratorias (CIBERES), Av. de Monforte de Lemos 5, 28029 (Madrid, Spain)

[7]CNRS, University of Bordeaux, MCC, PACEA, UMR5199 (Pessac, France)

Number of text pages: 11. **Number of text pages plus bibliography:** 17

Number of figures: 3

Number of tables: -

Abbreviated title: 3D sexual dimorphism of thorax kinematics

Keywords: ribcage; kinematics; geometric morphometrics; sexual dimorphism

***Corresponding author:** Dr. Daniel García-Martínez (Ph.D.).

UMR5199 PACEA, Univ. Bordeaux, Allée Geoffroy Saint Hilaire Bat. B8, CS 50023, 33615 Pessac Cedex, France; +34.620.745.821; daniel.garcia-martinez@u-bordeaux.fr

Grant sponsorship: This work was funded by the IdEx University of Bordeaux Investments for the Future program (ANR-10-IDEX-03-02), projects CGL2012-37279 and CGL2015-63648P (Ministry of Science and Competitivity, Spain) and PI10/02089 (Fondo de Investigación Sanitaria, Ministry of Health, Social Services and Equality, Spain).

Abstract

Sexual dimorphism is an important biological factor underlying morphological variation in the human skeleton. Previous research found sex-related differences in the static ribcage, with males having more horizontally oriented ribs and a wider lower ribcage than females. Furthermore, a recent study found sex-related differences in the kinematics of the human lungs, with cranio-caudal movements of the caudal part of the lungs accounting for most of the differences between sexes. However, these movements cannot be quantified in the skeletal ribcage, so we do not know if the differences observed in the lungs are also reflected in sex differences in the motion of the skeletal thorax.

To address this issue, we quantified the morphological variation of 42 contemporary human ribcages (sex-balanced) in both maximal inspiration and expiration using 526 landmarks and semilandmarks. Thoracic centroid size differences between sexes were assessed using a t-test, and shape differences were assessed using Procrustes shape coordinates, through mean comparisons and dummy regressions of shape on kinematic status. A principal components analysis (PCA) was used to explore the full range of morphological variation.

Our results show significant size differences between males and females both in inspiration and expiration ($p<0.01$) as well as significant shape differences, with males deforming more than females during inspiration, especially in the mediolateral dimension of the lower ribcage. Finally, dummy regressions of shape on kinematic status showed a small but statistically significant difference in vectors of breathing kinematics between males and females (14.78^{o}; $p<0.01$).

We support the hypothesis that sex-related differences in skeletal ribcage kinematics are discernable, even when soft tissues are not analyzed. We hypothesize that this differential breathing pattern is primarily a result of more pronounced diaphragmatic breathing in males, which might relate to differences in body composition, metabolism, and ultimately greater

oxygen demand in males compared to females. Future research should further explore the links between ribcage morphological variation and basal metabolic rate (BMR).

Introduction

Sexual dimorphism is a well-documented source of morphological variation in recent and fossil hominins, and is observed in the entire human skeleton (Frayer & Wolpoff, 1985; Franciscus, 2009; Krishtalka, Stucky & Beard, 1990; Lam, Pearson & Smith, 1996; Lockwood, 1999; Lockwood, Menter, Moggi-Cecchi & Keyser, 2007; McHenry, 2005; Plavcan, 1994, 2000, 2001, 2005; Ponce de León et al., 2008; Rehg & Leigh, 1999; Reno, Meindl, McCollum & Lovejoy, 2003; Reno, McCollum, Meindl & Lovejoy, 2010; Richmond & Jungers, 1995; Wood, 1976). In modern humans, sexual dimorphism has been intensively studied in the skull (e.g. Bastir, Godoy & Rosas, 2011; Hall, 2005; Holton, Yokley, Froehle & Southard, 2014; Rosas & Bastir, 2002, 2004; Rosas, Bastir, Martínez-Maza & de Castro, 2002), and in the postcranium (e.g. Bastir, Higuero, Ríos & Garcia-Martinez, 2014; Carlson, Grine & Pearson, 2007; Fischer & Mitteroecker, 2015, 2017; Iscan & Shishai, 1995; Kranioti, Bastir, Sánchez-Meseguer & Rosas, 2009; García-Martínez et al., 2016; Mitteroecker & Fischer, 2016; Rascón Pérez, 2017; Rosas et al., 2016, 2017; Weinstein, 2017). Skeletal morphological differences between sexes are usually accompanied by differences in size, so static allometry (Klingenberg, 1992) is a factor to take into account when studying sex-related differences in the human skeleton (Cheverud, 1982; Fischer & Mitteroecker, 2017; Freidline, Gunz & Hublin, 2015; García-Martínez et al., 2016; Humphrey, 1998; Rosas & Bastir, 2002, 2004; Viðarsdóttir, O'Higgins & Stringer, 2002).

In the respiratory system, three-dimensional studies of cranial airways (Bastir et al., 2011; Holton et al., 2014; Rosas & Bastir, 2002) showed that sexual dimorphism in the human skull influences the morphology of the upper airways, since males tend to have larger nasal cavities and a relatively longer, narrower, and higher nasal floor than females relative to body size (but see Heuzé, 2018). These modifications in the cranial respiratory tract have also been

related to differences in the thoracic post-cranial respiratory tract. Previous research found that male ribcages are around 10-12% larger than female ribcages, and that males have a relatively shorter ribcage and mediolaterally larger lower thorax compared to females, coupled with more horizontally orientated ribs (Bellemare, Jeanneret & Couture, 2003; García-Martínez et al., 2016; Shi et al., 2014; Weaver, Schoell & Stitzel, 2014). Finally, García-Martínez et al. (2016) also found that these morphological differences, except for the relative length of the ribcage, were not related to allometry.

Bellemare et al. (2003) hypothesized that declination of ribs in females should allow for a greater contribution of intercostal muscles to breathing at rest than in males (Contreras et al., 1991; Gilroy, Mangura & Lavietes, 1988). García-Martínez et al. (2016) added that, since males move a greater tidal volume (i.e., normal air volume displaced between normal/non-forced inspiration and expiration; Hopkins & Harms, 2004), the hypothesized lesser contribution of intercostal muscles in males should be compensated for by the diaphragm´s greater contribution to inspiration, probably via a larger diaphragmatic excursion (García-Martínez et al., 2016). This is consistent with the larger mediolateral diameter of the thorax, and thus the diaphragmatic area, of male ribcages compared to those of females (Bellemare at al., 2003; García-Martínez et al., 2016; Shi et al., 2014; Weaver at al., 2014). The greater tidal volume produced by a greater thoracic expansion in males relative to females during breathing (Harms et al., 1998; Jammes et al., 1979; Valenza Demet et al., 2011) suggests a greater oxygen demand in males. This fact may be linked to sex-specific differences in the musculoskeletal system, body composition, and basal metabolic rate (BMR) (Bastir et al., 2011; Bitar, Fellmann, Vernet, Coudert & Vermorel, 1999; Hall, 2005; García-Martínez et al., 2018; Wells, 2007).

However, if we assume that the sexes differ in ventilatory advantage (in terms of a greater tidal volume) and diaphragmatic contributions to breathing kinematics, we should also expect different kinematic breathing patterns. In this regard, recent research (Torres-Tamayo

et al., 2018) found sex-related morphological differences in the breathing kinematics of human lungs, which is also supported by physiological data (Guenette, Witt, McKenzie, Road & Sheel, 2007; Hopkins & Harms, 2004). However, it is important to note that many of the sex-related kinematic differences in lungs are due to differences in cranio-caudal movements of the inferior portions of the lungs directly related to the diaphragm. Since it is not possible to quantify cranio-caudal diaphragmatic movements in the skeletal ribcage, sex-related kinematic differences in the lungs might not be reflected in the thoracic skeleton. Therefore, the aim of this paper is to test the null hypothesis **H0** that humans do not show sexual dimorphism in breathing kinematics when measuring only the skeletal thorax.

Material and methods

We used computed tomography images (CT-scans) of the rib cages of 42 healthy adult individuals (18 males and 24 females; mean age = 50.9±1.2). Each individual was CT-scanned in both maximal inspiration and maximal expiration, and therefore a total of 84 thoracic CT-scans were included in the study. The individuals were previously recruited as a healthy control group for a different research project at the Hospital Universitario La Paz (Madrid, Spain). Consent was given to use these CT images for research purposes and all CT images were anonymized to comply with the Helsinki declaration (Goodyear, Krleza-Jeric & Lemmens, 2007).

Ribcages were segmented through a semi-automatic protocol for DICOM images using Mimics 8.0 software program (http://biomedical.materialise.com/mimics) and subsequently reconstructed as 3D models. These 3D models were imported into Viewbox 4.0 software (www.dhal.com) for (semi-) landmarking using the protocol from Bastir et al. (2017) for ribs 1-11. The protocol was updated to include the 12th thoracic level. Thoracic morphology was quantified through 20 homologous 3D landmarks and sliding curve semilandmarks (seven fixed landmarks and 13 semilandmarks) on each rib 1-10, and 18 3D landmarks and sliding curve

semilandmarks (five fixed landmarks and 13 semilandmarks) on each rib 11 and 12. In addition, four landmarks were placed on each thoracic vertebra and two additional landmarks were placed on the sternum (526 landmarks and sliding semilandmarks on each thorax; Fig. 1). Semilandmarks were slid along their corresponding curves with respect to the fixed landmarks in order to minimize bending energy (BE) as is common in semilandmark based analyses (Gunz, Mitteroecker & Bookstein, 2005; Gunz & Mitteroecker, 2013).

Centroid size (CS), defined by the square root of the sum of squared distances of a set of landmarks from their centroid (Dryden & Mardia, 1998), was used as a proxy for thorax size. Size differences between sexes in each kinematic status (males in maximal inspiration, MI; males in maximal expiration, ME; females in maximal inspiration, FI; females in maximal expiration, FE) were assessed through a t-test (significance level 0.01), after testing for normality of each subsample through a Kolmogorov-Smirnov analysis (significance level 0.01). Shape data were obtained by generalized Procrustes analysis (GPA) of the entire configurations (Gower, 1975; Zelditch, Swiderski & Sheets, 2012), and shape differences between sexes were assessed by computing mean comparisons in MorphoJ software (Klingenberg, 2011), which test for differences in Procrustes distances (Pd) between groups via a permutation test (N=1,000). Differences in kinematic patterns were explored in a form space principal component analysis (form space PCA) (Mitteroecker, Gunz, Windhager & Schaefer, 2013) and thorax shape differences associated with variations along the PC1-2 axes were visualized using EVAN Toolkit (version 1.71; http://www.evan-society.org/). Kinematic differences were statistically tested by computing a dummy regression of shape on the kinematic state for each sex and calculating the angle between those regressions (Torres-Tamayo et al., 2018), the significance being assessed via a permutation test (N=1,000).

Results

The distributions of centroid sizes for each of the four groups (ME, MI, FE, FI)were found to be normal (p=0.57, 0.25, 0.46 and 0.48, respectively). T-tests yielded statistically significant centroid size (CS) differences between males and females both in maximal expiration (ME_{MEAN}=3275.0 and FE_{MEAN}=2927.1; t=-9.58, p<0.01) and maximal inspiration (MI_{MEAN}=3332.6 and FI_{MEAN}=2972.1; t=-10.67, p<0.01). The results of the mean shape comparisons yielded statistically significant differences between males and females both in maximal expiration (Pd=0.04, p<0.01) and maximal inspiration (Pd=0.04, p<0.01). These morphological differences are reflected in the more horizontal orientation of the ribs and the mediolateral expansion of the ribcage of males (Fig. 2). In addition, the mean comparisons showed that the morphological differences between maximal expiration and inspiration were larger in males (Pd=0.06, p<0.01) than in females (Pd=0.04, p<0.01). In regard to sex-related variation, PC1 from the PCA of shape accounts for 43.65% of the total variance in shape and is clearly related to sexual dimorphism (Fig. 3), with males distributed towards the positive extreme of PC1 and females towards the negative. Positive PC1 scores (where males tend to lie) are linked to ribcage morphologies that are relatively short in the cranio-caudal axis with a relatively wider caudal part and more horizontally oriented ribs. On the other hand, negative PC1 scores (where females tend to lie) are associated with relatively elongated ribcages in the cranio-caudal direction and a relatively narrow caudal part with less horizontally oriented ribs. Fig. 3 shows that PC2 (16.98% of total shape variance) is more related to kinematics, with individuals of both sexes in maximal expiration having negative PC2 negative values, and individuals in maximal inspiration having positive values. Morphological variation along this PC includes elevation of the sternum and the ribs at every level, with rib displacements being more in the cranio-caudal direction in the upper ribs and more in the mediolateral direction in the lower thorax (Fig. 3). To test whether PC1 and PC2 were related to sex and kinematics respectively, we carried out dummy regressions of PC1 scores on sex and PC2 scores on respiratory kinematic status, finding a statistically significant correlation in both cases (r^2=0.63

and 0.17, respectively for PC1 and PC2; $p<0.01$ in both cases). Finally, it is important to note that the difference between mean inspiration and mean expiration is slightly larger in males than in females, and the vectors of shape change between expiration and inspiration are almost parallel (Fig. 3). This observation was supported by the dummy regression of full shape on respiratory kinematic status where male ($r^2=0.30$) and female regressions ($r^2=0.32$) show a statistically significant but small angle between them (14.78^o, $p<0.01$). These results reject the null hypothesis **H0.**

Discussion and conclusions

Sexual dimorphism is an important factor underlying morphological variation in the entire human body, including the respiratory system (Frayer & Wolpoff, 1985; Franciscus, 2009; Krishtalka, Stucky & Beard, 1990; Lam, Pearson & Smith, 1996; Lockwood, 1999; Lockwood, Menter, Moggi-Cecchi & Keyser, 2007; McHenry, 2005; Plavcan, 1994, 2000, 2001, 2005; Ponce de León et al., 2008; Rehg & Leigh, 1999; Reno, Meindl, McCollum & Lovejoy, 2003; Reno, McCollum, Meindl & Lovejoy, 2010; Richmond & Jungers, 1995; Wood, 1976; Bastir, Godoy & Rosas, 2011; Hall, 2005; Holton, Yokley, Froehle & Southard, 2014; Rosas & Bastir, 2002, 2004; Rosas, Bastir, Martínez-Maza & de Castro, 2002; Bastir, Higuero, Ríos & Garcia-Martinez, 2014; Carlson, Grine & Pearson, 2007; Fischer & Mitteroecker, 2015, 2017; Iscan & Shishai, 1995; Kranioti, Bastir, Sánchez-Meseguer & Rosas, 2009; García-Martínez et al., 2016; Mitteroecker & Fischer, 2016; Rascón Pérez, 2017; Rosas et al., 2016, 2017; Weinstein, 2017). García-Martínez et al. (2016) quantified static thoracic morphology and found that males have more horizontally oriented ribs than females, as well as relatively shorter and wider ribcages, particularly in the caudal part. The relatively longer female thorax has been hypothesized to be an adaptation for housing the internal organs of the reproductive system, and to ultimately accommodate volumetric expansion of the fetus during pregnancy (Bellemare et al., 2003).

In addition, it was reported that males have a 33% greater size increase in total lung capacity (TLC) during inspiration than females, which is not only consistent with a greater capacity for intake of air (and thus oxygen) in their larger upper airways (Rosas & Bastir, 2002), but also with the fact that males have significantly larger total lung capacities (TLC) than females (García-Martínez et al., 2018).

From a biomechanical point of view, it has been demonstrated that differences in the morphological configuration of the thoracic and abdominal walls strongly influence the function of the respiratory muscles (De Troyer, Kirkwood & Wilson, 2005; Goldman, Grassino, Mead & Sears, 1978; Grassino, Goldman, Mead & Sears, 1978; Pinet, 1998). Since abdominal breathing with diaphragmatic action is more predominant in males (Kaneko & Horie, 2012; Ragnarsdóttir & Kristinsdóttir, 2006; Verschakelen & Demedts, 1995), we can infer that the larger thoracic size increase of males and their large TLC are caused by differences in the ways that intercostal muscles and the diaphragm act to increase thoracic volume (the so-called breathing pattern) between males and females. In this regard, recent research on human lungs (Torres-Tamayo et al., 2018) observed that the base of the lungs, which largely tracks the diaphragmatic domes, undergoes a larger expansion in males than in females, also pointing to a larger diaphragmatic contribution to breathing kinematics in males than in females. However, it is important to note that differences in the kinematics of the diaphragmatic domes are not directly quantified by our measures of rib cage form and kinematics.

Our results show that not only are there sex-related centroid size and shape differences at the extremes of inspiration and expiration but also that the kinematics differ, with the shape differences (Procrustes distances) between maximal expiration and maximal inspiration being larger in males than in females (Fig. 3). In addition, males show a larger mediolateral expansion of the lower thorax during breathing than females. It is important to note that the lower ribcage of males is also wider in expiration, which is probably caused by

differences in the orientation of the transverse processes of the lower thoracic vertebrae (Bastir et al., 2014), which orient the lower ribs more laterally than in females. This ribcage morphology therefore suggests that males tend to undergo greater mediolateral movements (bucket-handle motion; Drake, Vogl & Mitchell, 2005) than females. This could also be reflected in the slight but significantly different morphological kinematic vector that we found (14.78o). These results reject the null hypothesis **H0** that humans are not sexually dimorphic in thorax morphology.

We hypothesize that the greater oxygen demand in in males is linked to sex-specific differences in the musculoskeletal system, body composition and BMR, and is associated with greater energy expenditure compared to females (Bastir et al., 2011; Bitar et al., 1999; García-Martínez et al., 2018; Hall, 2005; Wells, 2007). This is because, on average, adult males have greater total lean mass and less fat mass than females (Wells, 2007). To test this association, future studies should address the correlation between ribcage morphology, respiratory function, and body composition (e.g. BMR or lean body mass). Finally, while sex differences in breathing patterns contribute to differences in oxygen consumption (probably in a discrete way, since VO2 also depends on the cardiovascular and metabolic response), they may also impact sex differences in the development of dyspnea, the perception of breathing discomfort during intense exercise. The fact that women are more prone than males to report experiencing dyspnea (Cory et al., 2015) could be related to their greater reliance on thoracic rather than abdominal breathing.

Finally, it is important to note that differences in ribcage kinematics between males and females may contribute to a better understanding of energetics and lifestyle in fossil hominins. Further work incorporating the several well-preserved ribcages of Neanderthals in which sex is reliably estimated (e.g., the females from Tabun C1 and Sima de las Palomas, or

the males from Shanidar 3 and Kebara 2) will allow researchers to gain insights about sexual differences in energetic demands in hominins.

Acknowledgments

This work was partially funded by the IdEx University of Bordeaux Investments for the Future program (ANR-10-IDEX-03-02), the projects CGL2012-37279 and CGL2015-63648P (Ministry of Economy, Industry and Competitiveness, Spain) and PI10/02089 (Fondo de Investigación Sanitaria, Ministry of Health, Social Services and Equality Spain). We acknowledge the two reviewers for their positive input in previous versions of the manuscript as well as Dr. Kate McGrath for copy editing of the manuscript.

Author contributions

Conception and design of the experiments: DGM, MB, FGR. Acquisition of data: DGM, ITS, FGR. Data analysis/interpretation: DGM, MB, NTT. Drafting of the manuscript: DGM. Critical revision of the article: DGM, ITS, FGR, NTT, MB, YH, PO.

Data sharing statement

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

Bibliography

Bastir, M., Godoy, P., & Rosas, A. (2011). Common features of sexual dimorphism in the cranial airways of different human populations. American Journal of Physical Anthropology, 146(3), 414-422.

Bastir, M., Higuero, A., Ríos, L., & Garcia Martinez, D. (2014). Three-dimensional analysis of sexual dimorphism in human thoracic vertebrae: implications for the respiratory system and spine morphology. American Journal of Physical Anthropology, 155(4), 513-521.

Bastir, M., García-Martínez, D., Williams, S. A., Recheis, W., Torres-Sánchez, I., Río, F. G., ... & Ogihara, N. (2017). 3D geometric morphometrics of thorax variation and allometry in Hominoidea. Journal of Human Evolution, 113, 10-23.

Bellemare, F., Jeanneret, A., & Couture, J. (2003). Sex differences in thoracic dimensions and configuration. American Journal of Respiratory and Critical Care Medicine, 168(3), 305-312.

Bitar, A., Fellmann, N., Vernet, J., Coudert, J., & Vermorel, M. (1999). Variations and determinants of energy expenditure as measured by whole-body indirect calorimetry during puberty and adolescence. The American Journal of Clinical Nutrition, 69(6), 1209-1216.

Carlson, K. J., Grine, F. E., & Pearson, O. M. (2007). Robusticity and sexual dimorphism in the postcranium of modern hunter-gatherers from Australia. American Journal of Physical Anthropology, 134(1), 9-23.

Cheverud, J. M. (1982). Relationships among ontogenetic, static, and evolutionary allometry. American Journal of Physical Anthropology, 59(2), 139-149.

Contreras, G., Gutiérrez, M., Beroíza, T., Fantín, A., Oddó, H., Villarroel, L., ... & Lisboa, C. (1991). Ventilatory drive and respiratory muscle function in pregnancy. American Review of Respiratory Disease, 144(4), 837-841.

Cory, J. M., Schaeffer, M. R., Wilkie, S. S., Ramsook, A. H., Puyat, J. H., Arbour, B., ... & Jensen, D. (2015). Sex differences in the intensity and qualitative dimensions of exertional dyspnea in physically active young adults. Journal of Applied Physiology, 119(9), 998-1006.

De Troyer, A., Kirkwood, P. A., & Wilson, T. A. (2005). Respiratory action of the intercostal muscles. Physiological Reviews, 85(2), 717-756.

Valenza Demet, G., Villaverde Gutierrez, C., Valenza, M. C., Moreno Lorenzo, C., Botella López, M., Ocaña Peinado, F. M., ... & de la Salud, F. D. C. (2011). Movilidad torácica y abdominal en adultos jóvenes de ambos sexos sin patología conocida. Scientia, 16(2), 85-94.

Dominelli, P. B., Ripoll, J. G., Cross, T. J., Baker, S. E., Wiggins, C. C., Welch, B. T., & Joyner, M. J. (2018). Sex-differences in large conducting airway anatomy. Journal of Applied Physiology, 215, 960–965.

Drake, R., Vogl, A.W., & Mitchell, A.W., 2005. Gray's anatomy for students. Philadelphia, PA: Elsevier.

Dryden, I. L., & Mardia, K. V. (1998). Statistical shape analysis. Wiley, London.

Fischer, B., & Mitteroecker, P. (2017). Allometry and sexual dimorphism in the human pelvis. The Anatomical Record, 300(4), 698-705.

Fischer, B., & Mitteroecker, P. (2015). Covariation between human pelvis shape, stature, and head size alleviates the obstetric dilemma. Proceedings of the National Academy of Sciences, 201420325.

Franciscus, R. G. (2009). When did the modern human pattern of childbirth arise? New insights from an old Neandertal pelvis. Proceedings of the National Academy of Sciences, 106(23), 9125-9126.

Frayer, D. W., & Wolpoff, M. H. (1985). Sexual dimorphism. Annual Review of Anthropology, 14(1), 429-473.

Freidline, S. E., Gunz, P., & Hublin, J. J. (2015). Ontogenetic and static allometry in the human face: Contrasting Khoisan and Inuit. American Journal of Physical Anthropology, 158(1), 116-131.

García-Martínez, D., Torres-Tamayo, N., Torres-Sánchez, I., García-Río, F., & Bastir, M. (2016). Morphological and functional implications of sexual dimorphism in the human skeletal thorax. American Journal of Physical Anthropology, 161(3), 467-477.

García-Martínez, D., Torres-Tamayo, N., Torres-Sánchez, I., García-Río, F., Rosas, A., & Bastir, M. (2018). Ribcage measurements indicate greater lung capacity in Neanderthals and Lower Pleistocene hominins compared to modern humans. Communications Biology, 1(1), 117.

Gilroy, R. J., Mangura, B. T., & Lavietes, M. H. (1988). Rib cage and abdominal volume displacements during breathing in pregnancy1–3. The American Review of Respiratory Disease, 137, 668-672.

Goldman, M. D., Grassino, A., Mead, J., & Sears, T. A. (1978). Mechanics of the human diaphragm during voluntary contraction: dynamics. Journal of Applied Physiology, 44(6), 840-848.

Goodyear, M. D., Krleza-Jeric, K., & Lemmens, T. (2007). The declaration of Helsinki. BMJ: British Medical Journal, 335(7621), 624.

Gower, J. C. (1975). Generalized Procrustes analysis. Psychometrika, 40(1), 33-51.

Grassino, A., Goldman, M. D., Mead, J., & Sears, T. A. (1978). Mechanics of the human diaphragm during voluntary contraction: statics. Journal of Applied Physiology, 44(6), 829-839.

Guenette, J. A., Witt, J. D., McKenzie, D. C., Road, J. D., & Sheel, A. W. (2007). Respiratory mechanics during exercise in endurance-trained men and women. The Journal of Physiology, 581(3), 1309-1322.

Gunz, P., Mitteroecker, P., & Bookstein, F. L. (2005). Semilandmarks in three dimensions. In Modern morphometrics in physical anthropology (pp. 73-98). Springer, Boston, MA.

Gunz, P., & Mitteroecker, P. (2013). Semilandmarks: a method for quantifying curves and surfaces. Hystrix, the Italian Journal of Mammalogy, 24(1), 103-109.

Hall, R. L. (2005). Energetics of nose and mouth breathing, body size, body composition, and nose volume in young adult males and females. American Journal of Human Biology: The Official Journal of the Human Biology Association, 17(3), 321-330.

Harms, C. A., McClaran, S. R., Nickele, G. A., Pegelow, D. F., Nelson, W. B., & Dempsey, J. A. (1998). Exercise-induced arterial hypoxemia in healthy young women. The Journal of Physiology, 507(2), 619-628.

Heuzé, Y. (2018). What Does Nasal Cavity Size tell us about Functional Nasal Airways? Bulletins et Mémoires de la Société d'Anthropologie de Paris.

Holton, N. E., Yokley, T. R., Froehle, A. W., & Southard, T. E. (2014). Ontogenetic scaling of the human nose in a longitudinal sample: implications for genus *Homo* facial evolution. American Journal of Physical Anthropology, 153(1), 52-60.

Hopkins, S. R., & Harms, C. A. (2004). Gender and pulmonary gas exchange during exercise. Exercise and Sport Sciences Reviews, 32(2), 50-56.

Humphrey, L. T. (1998). Growth patterns in the modern human skeleton. American Journal of Physical Anthropology, 105(1), 57-72.

İşcan, M. Y., & Shihai, D. (1995). Sexual dimorphism in the Chinese femur. Forensic Science International, 74(1-2), 79-87.

Jammes, Y., Auran, Y., Gouvernet, J., Delpierre, S., & Grimaud, C. (1979). The ventilatory pattern of conscious man according to age and morphology. Bulletin Europeen de Physiopathologie Respiratoire-Clinical Respiratory Physiology, 15(3), 527-540.

Kaneko, H., & Horie, J. (2012). Breathing movements of the chest and abdominal wall in healthy subjects. Respiratory Care, 57(9), 1442-1451.

Klingenberg, C. P., & Zimmermann, M. (1992). Static, ontogenetic, and evolutionary allometry: a multivariate comparison in nine species of water striders. The American Naturalist, 140(4), 601-620.

Klingenberg, C. P. (2011). MorphoJ: an integrated software package for geometric morphometrics. Molecular Ecology Resources, 11(2), 353-357.

Kranioti, E. F., Bastir, M., Sánchez-Meseguer, A., & Rosas, A. (2009). A geometric morphometric study of the Cretan humerus for sex identification. Forensic Science International, 189(1-3), 111-e1.

Krishtalka, L., Stucky, R. K., & Beard, K. C. (1990). The earliest fossil evidence for sexual dimorphism in primates. Proceedings of the National Academy of Sciences, 87(13), 5223-5226.

Lam, Y. M., Pearson, O. M., & Smith, C. M. (1996). Chin morphology and sexual dimorphism in the fossil hominid mandible sample from Klasies River Mouth. American Journal of Physical Anthropology, 100(4), 545-557.

Lockwood, C. A. (1999). Sexual dimorphism in the face of *Australopithecus africanus*. American Journal of Physical Anthropology, *108*(1), 97-127.

Lockwood, C. A., Menter, C. G., Moggi-Cecchi, J., & Keyser, A. W. (2007). Extended male growth in a fossil hominin species. Science, 318(5855), 1443-1446.

LoMauro, A., & Aliverti, A. (2018). Sex differences in respiratory function. Breathe, 14(2), 131.

McHenry, H. M. (2005). Sexual dimorphism in fossil hominids and its socioecological implications. In: The archaeology of human ancestry (pp. 97-114). Routledge.

Mitteroecker, P., Gunz, P., Windhager, S., & Schaefer, K. (2013). A brief review of shape, form, and allometry in geometric morphometrics, with applications to human facial morphology. Hystrix, the Italian Journal of Mammalogy, 24(1), 59-66.

Mitteroecker, P., & Fischer, B. (2016). Adult pelvic shape change is an evolutionary side effect. Proceedings of the National Academy of Sciences, 113(26), E3596-E3596.

Molgat-Seon, Y., Peters, C. M., & Sheel, A. W. (2018). Sex-differences in the human respiratory system and their impact on resting pulmonary function and the integrative response to exercise. Current Opinion in Physiology.

Pinet C. 2004. Propriétés mécaniques et fonctionnelles de la cage thoracique. Revue des Maladies Respiratoires 21(3, Part 1), 652-655.

Plavcan, J. M. (1994). Comparison of four simple methods for estimating sexual dimorphism in fossils. American Journal of Physical Anthropology, 94(4), 465-476.

Plavcan, J. M. (2000). Inferring social behavior from sexual dimorphism in the fossil record. *Journal of Human Evolution*, *39*(3), 327-344.

Plavcan, J. M. (2001). Sexual dimorphism in primate evolution. American Journal of Physical Anthropology, 116(S33), 25-53.

Ponce de León, M. S., Golovanova, L., Doronichev, V., Romanova, G., Akazawa, T., Kondo, O., ... & Zollikofer, C. P. (2008). Neanderthal brain size at birth provides insights into the evolution of human life history. Proceedings of the National Academy of Sciences, 105(37), 13764-13768.

Ragnarsdóttir, M., & Kristinsdóttir, E. K. (2006). Breathing movements and breathing patterns among healthy men and women 20–69 years of age. Respiration, 73(1), 48-54.

Rascón Pérez, J. (2017). Análisis de las diferencias sexuales en la morfología del esqueleto y de la distribución de caracteres de interés relacionados con el sexo. Estudio de dos

series medievales de la Península Ibérica. PhD dissertation. Universidad Autónoma de Madrid (Madrid, Spain).

Rehg, J. A., & Leigh, S. R. (1999). Estimating sexual dimorphism and size differences in the fossil record: a test of methods. American Journal of Physical Anthropology, *110*(1), 95-104.

Reno, P. L., Meindl, R. S., McCollum, M. A., & Lovejoy, C. O. (2003). Sexual dimorphism in Australopithecus afarensis was similar to that of modern humans. Proceedings of the National Academy of Sciences, 100(16), 9404-9409.

Reno, P. L., McCollum, M. A., Meindl, R. S., & Lovejoy, C. O. (2010). An enlarged postcranial sample confirms Australopithecus afarensis dimorphism was similar to modern humans. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 365(1556), 3355-3363.

Richmond, B. G., & Jungers, W. L. (1995). Size variation and sexual dimorphism in Australopithecus afarensis and living hominoids. Journal of Human Evolution, 29(3), 229-245.

Rosas, A., & Bastir, M. (2002). Thin-plate spline analysis of allometry and sexual dimorphism in the human craniofacial complex. American Journal of Physical Anthropology, 117(3), 236-245.

Rosas, A., & Bastir, M. (2004). Geometric morphometric analysis of allometric variation in the mandibular morphology of the hominids of Atapuerca, Sima de Los Huesos site. The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology: An Official Publication of the American Association of Anatomists, 278(2), 551-560.

Rosas, A., Bastir, M., Martínez-Maza, C., & de Castro, J. M. B. (2002). Sexual dimorphism in the Atapuerca-SH hominids: the evidence from the mandibles. Journal of Human Evolution, 42(4), 451-474.

Rosas, A., Rodriguez-Perez, F. J., Bastir, M., Estalrrich, A., Huguet, R., García-Tabernero, A., ... & de la Rasilla, M. (2016). Adult Neandertal clavicles from the El Sidrón site (Asturias, Spain) in the context of Homo pectoral girdle evolution. Journal of Human Evolution, 95, 55-67.

Rosas, A., Ferrando, A., Bastir, M., García-Tabernero, A., Estalrrich, A., Huguet, R., ... & de la Rasilla, M. (2017). Neandertal talus bones from El Sidrón site (Asturias, Spain): A 3D geometric morphometrics analysis. American Journal of Physical Anthropology, 164(2), 394-415.

Shi, X., Cao, L., Reed, M. P., Rupp, J. D., Hoff, C. N., & Hu, J. (2014). A statistical human rib cage geometry model accounting for variations by age, sex, stature, and body mass index. Journal of Biomechanics, 47(10), 2277-2285.

Torres-Tamayo, N., García-Martínez, D., Lois Zlolniski, S., Torres-Sánchez, I., García-Río, F., & Bastir, M. (2018). 3D analysis of sexual dimorphism in size, shape and breathing kinematics of human lungs. Journal of Anatomy, 232(2), 227-237.

Verschakelen, J. A., & Demedts, M. G. (1995). Normal thoracoabdominal motions. Influence of sex, age, posture, and breathe size. American Journal of Respiratory and Critical Care Medicine, 151(2), 399-405.

Viðarsdóttir, U. S., O'Higgins, P., & Stringer, C. (2002). A geometric morphometric study of regional differences in the ontogeny of the modern human facial skeleton. Journal of Anatomy, 201(3), 211-229.

Walker, P. L. (2005). Greater sciatic notch morphology: sex, age, and population differences. American Journal of Physical Anthropology, 127(4), 385-391.

Walker, P. L. (2008). Sexing skulls using discriminant function analysis of visually assessed traits. American Journal of Physical Anthropology, 136(1), 39-50.

Weaver, A. A., Schoell, S. L., & Stitzel, J. D. (2014). Morphometric analysis of variation in the ribs with age and sex. Journal of Anatomy, 225(2), 246-261.

Weinstein, K. J. (2017). Morphological signatures of high-altitude adaptations in the Andean archaeological record: Distinguishing developmental plasticity and natural selection. Quaternary International, 461, 14-24.

Wells, J. C. (2007). Sexual dimorphism of body composition. Best Practice & Research Clinical Endocrinology & Metabolism, 21(3), 415-430.

Wood, B. A. (1976). The nature and basis of sexual dimorphism in the primate skeleton. Journal of Zoology, 180(1), 15-34.

Zelditch, M. L., Swiderski, D. L., & Sheets, H. D. (2012). Geometric morphometrics for biologists: a primer. Academic Press.

Figures

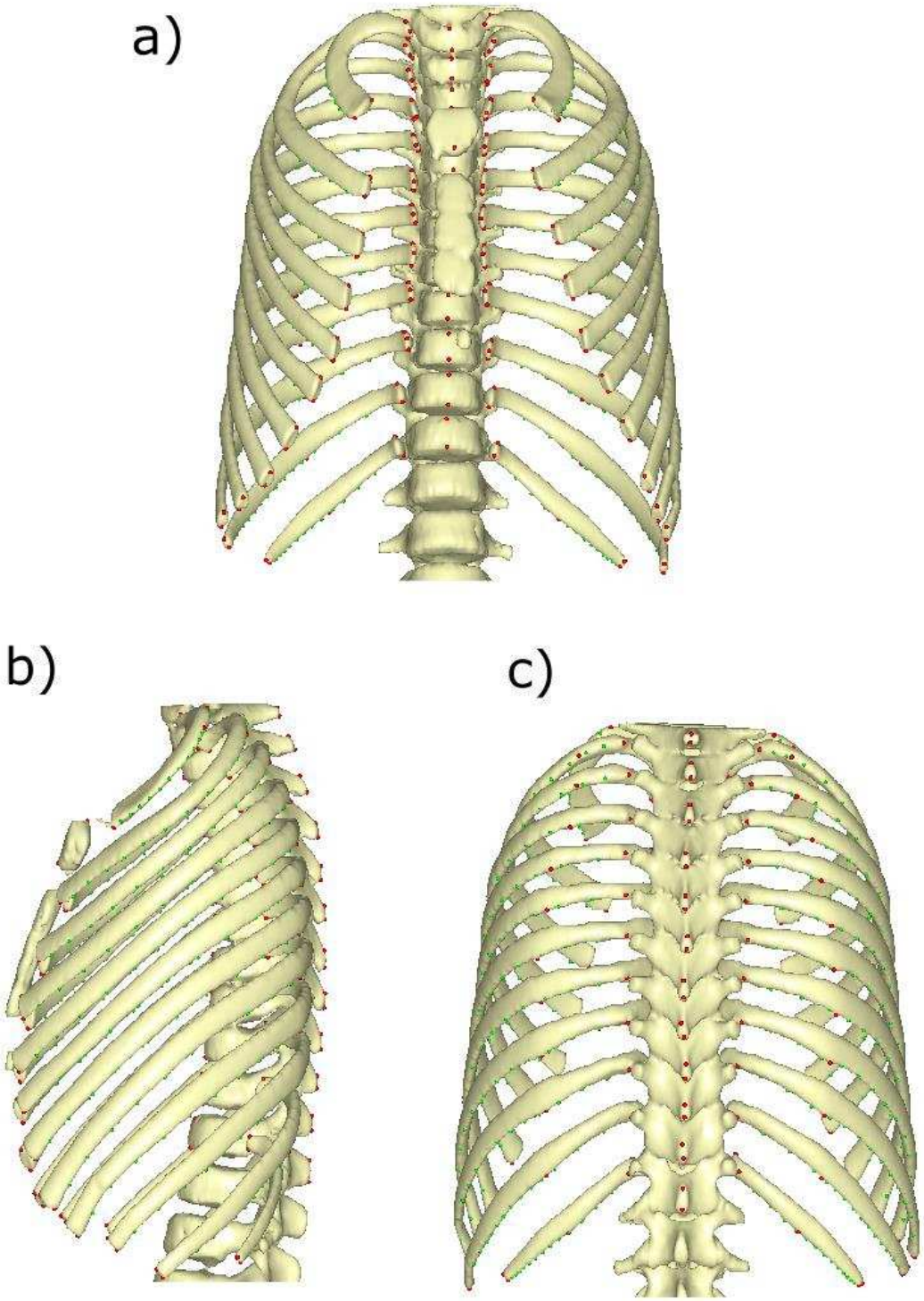

Figure 1: Landmark protocol employed in this study for thoracic levels 1-12, including both ribs and vertebrae. The template is shown in a) ventral view, b) lateral view and c) dorsal view.

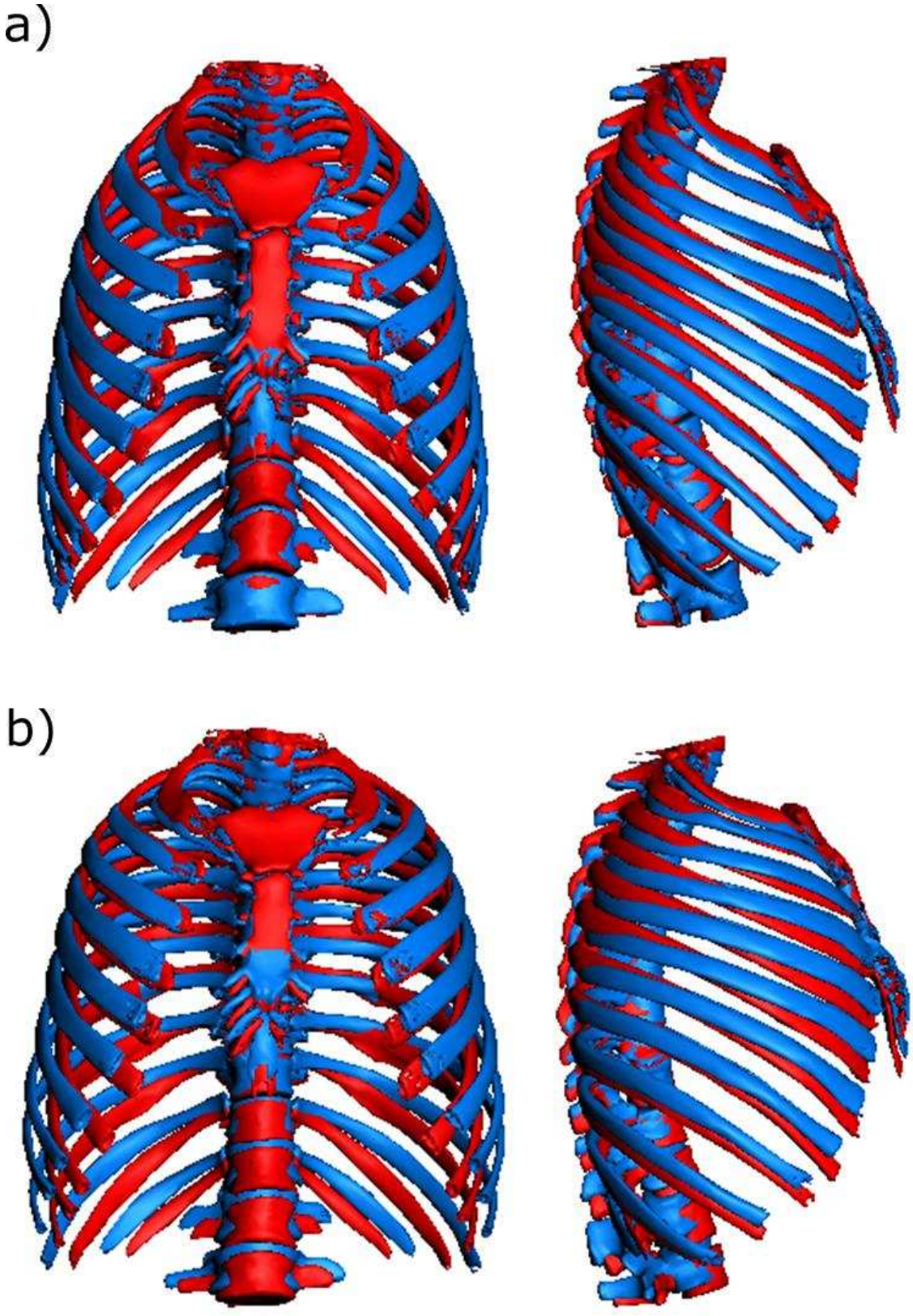

Figure 2: 3D warps between the means of males (blue) and females (red). The top figure (a) represents differences in maximal expiration whereas the bottom figure (b) represents differences in maximal inspiration.

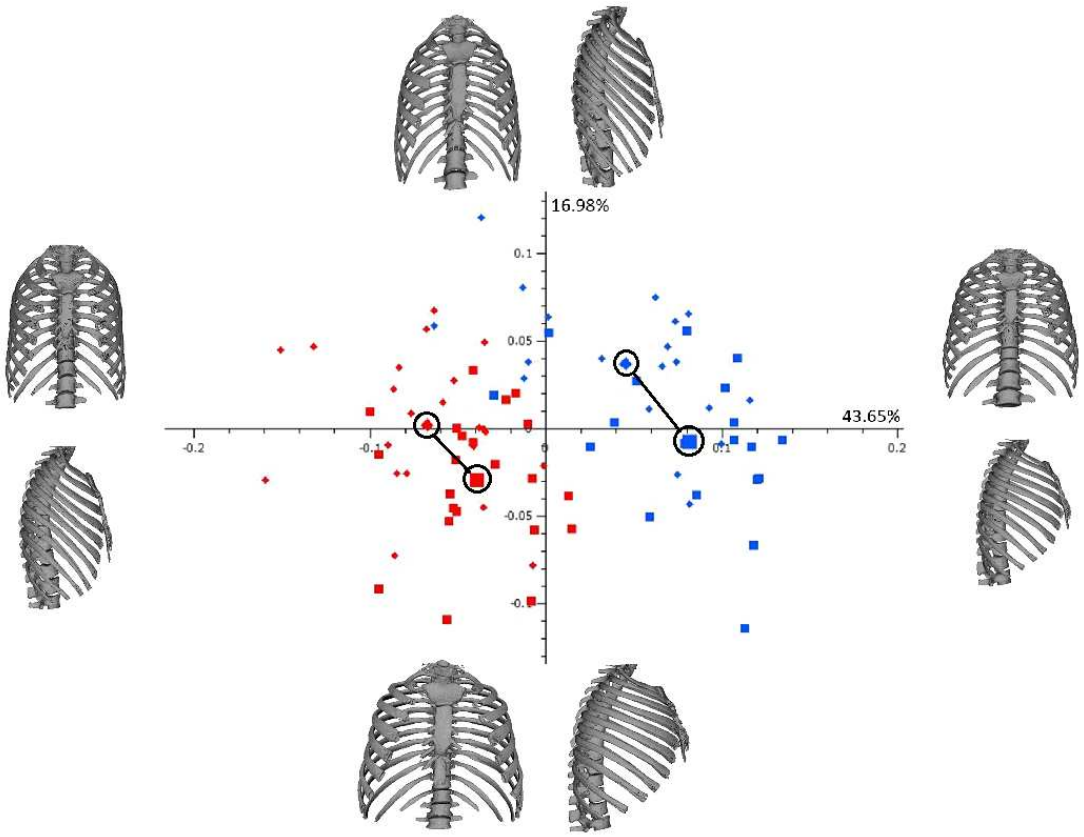

Figure 3: PC1 vs. PC2 plot from PCA of 3D coordinates of ribcages after GPA. Males (blue) lie more towards the positive extreme of PC1 than females (red), and ribcages in maximal expiration (diamonds) are located more towards the positive extreme of PC2 than ribcages in maximal inspiration (squares). Double-sized symbols represent the average of each group.