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Assessing thoraco-pelvic covariation in *Homo sapiens* and *Pan troglodytes*: A 3D geometric morphometric approach

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ABSTRACT

Objectives. Understanding thoraco-pelvic integration in *Homo sapiens* and their closest living relatives (genus *Pan*) is of huge importance within the context of human body shape evolution. However, studies assessing thoraco-pelvic covariation across Hominoidea species are scarce, although recent research would suggest shared covariation patterns in humans and chimpanzees but also species-specific features, with sexual dimorphism and allometry influencing thoraco-pelvic covariation in these taxa differently.

Material and Methods. *N*=30 adult *H. sapiens* and *N*=10 adult *Pan troglodytes* torso 3D models were analyzed using 3D geometric morphometrics and linear measurements. Effects of sexual dimorphism and allometry on thoraco-pelvic covariation were assessed via regression analysis, and patterns of thoraco-pelvic covariation in humans and chimpanzees were computed via Two-Block Partial Least Squares analysis.

Results. Results confirm the existence of common aspects of thoraco-pelvic covariation in humans and chimpanzees, and also species-specific covariation in *H. sapiens* that was strongly influenced by sexual dimorphism and allometry. Species-specific covariation patterns in chimpanzees could not be confirmed because of the small sample size, but metrics pointed to a correspondence between the most caudal ribs and iliac crest morphology that would be irrespective of sex.

Conclusions. This study suggests that humans and chimpanzees share common aspects of thoraco-pelvic covariation but might differ in others. In humans, torso integration is strongly affected by sexual dimorphism and allometry, whilst in chimpanzees it may not be. This study also highlights the importance not only of torso widths but also of torso depths when describing patterns of thoraco-pelvic covariation in primates. Larger samples are necessary to support these interpretations.

1. INTRODUCTION

Torso morphology in extant primates has been of interest since Ancient Greece, when Galen (129-200 AD) carried out the first documented anatomical description of the primate *Macaca sylvanus* that served as an approximation to human anatomy for at least 1500 years (Diogo, 2018). After some sporadic works on this matter (e.g. Casserius, 1600-1601; Vesalius, 1543), it was not until 1699 when the British anatomist Edward Tyson (1651-1708) published the first detailed anatomical description of a primate. Edward Tyson carried out the first comprehensive work comparing the anatomy of a young chimpanzee with that of monkeys and humans (Tyson, 1699; Wood, 2020). Since Tyson's work, extensive research on the primate torso configuration has shown complex interactions between thorax, vertebral column, pelvis and soft tissue connecting these structures (e.g. Lovejoy, 2005; Middleton, 2013, 2015, 2017; Schultz, 1924, 1926, 1930, 1950, 1953; 1961; Torres-Tamayo et al. 2018; Ward, 1993; Ward, Maddux, & Middleton, 2018; Wilson-Rawls, Hurt, Parsons, & Rawls, 1999).

1.1. 20th Century primate torso morphology studies

Among the first comparative works assessing torso morphology in primates are those by Adolph H. Schultz describing thorax shape variation in primates. Schultz (1924, 1926) described patterns of chest growth at different primate ontogenetic stages and concluded that in apes the shape of the chest becomes wider with advanced growth, while the opposite occurs in monkeys. These differences in chest shape between apes and monkeys were explained as a consequence of posture under the effect of gravity on the organs: in pronograde monkeys the weight of the organs on the sternum results in an increased dorsoventral chest diameter, while in orthograde apes the weight of the organs on the diaphragm would lead to an increased transverse diameter.

Schultz & Straus (1945) quantified variations in the vertebral number in primates. These authors reported that catarrhine monkeys possess six or seven lumbar vertebrae (long lumbar spines), humans and lesser apes such as gibbons and siamangs possess five lumbar vertebrae and all great apes show up to four lumbar vertebrae (short lumbar spines) (see Williams, Middleton, Villamil, & Shattuck, 2016 for an updated report of primate vertebral formulae). The study by Schultz & Straus (1945) revealed the importance of the lumbar spine length in the torso morphology of primates, since it connects the thorax and the pelvis within the torso. Based on these findings, Schultz (1950) depicted for the first time the relationship between thorax, length of the lumbar spine and pelvis in *M. mulatta*, *Hylobates lar*, *Homo sapiens* and *Pan troglodytes,* and noticed that the lowest ribs of chimpanzees, gorillas and orangutans (shorter lumbar spines) are placed closer to the ilia than those of humans and gibbons (longer lumbar spines). Later, Schultz (1961) clearly stated: "*The last few ribs are more curved in man than in the great apes to conform with the direction and curvature of the ilia which have become bent and rotated in man in contrast to their dorsal position in apes*" (p. 53). To our knowledge, this is the first documented reference to state that (lower) thoracic widths and curvatures track (upper) pelvic widths and curvatures in apes (hereafter Schultz's hypothesis).

Subsequently, Benton (1967) further analyzed morphological aspects of the epaxial (lower back) region of primates. This work contributed to the understanding of anatomical adaptations to posture and locomotion in primates not only by investigating osteological features of the lumbar vertebrae and sacrum, but also by dissecting different primate specimens and describing their epaxial muscles. Benton (1974) concluded that lumbar spine length and sacrum morphology are crucial to characterize the lower back morphology of different primate superfamilies – including Lemuroidea, Ceboidea, Cercopithecoidea and Hominoidea-, as they ultimately determine the mass and orientation of the epaxial muscles. Together, these studies helped lay the ground for understanding morpho-functional relationships in the primate torso.

In the late 20th century, Ward (1993) refined Schultz's hypothesis and described two main patterns of torso morphology among catarrhines that have been explained in light of anatomical adaptations to different posture and locomotor modes. Cercopithecoids show a "monkey-like" torso morphology characterized by craniocaudally long, mediolaterally narrow and dorsoventrally deep torsos with a long flexible (lumbar) spine and short ilia. This torso morphology favors pronograde posture and quadrupedal locomotion by allowing a greater flexion-extension of forelimbs, hind limbs and spine in the parasagittal plane. Conversely, non-human hominoids show an "ape-like" torso morphology characterized by craniocaudally shorter, mediolaterally wider and dorsoventrally flatter torsos, with a shorter, stiffer and entrapped lumbar spine and lengthened iliac bones (Schultz, 1930, 1950, 1953, 1961). This ape-like torso morphology favors orthograde posture and locomotor patterns on which the forelimb abduction-adduction plays a crucial role, as is the case of arboreal climbing in apes.

1.2 Torso morphology in *H. sapiens* and *Pan*: locomotor adaptations

Differences in torso morphology between *H. sapiens* and *Pan* have been classically described in light of biomechanical adaptations to posture and locomotion. The axial skeleton, forelimbs and hind limbs of African apes show predominantly adaptations to arboreal climbing although they also spend time on the ground, especially when seeking food. These modifications, such as the shortening of the forearm extensor tendons, require great apes to adopt knuckle-walking (African great apes) and fist-walking (Asian great apes), which in turn lead to secondary specializations in the hands and wrists for quadruped knuckle walking (Isler, 2002, 2005). In chimpanzees, the torso has been described as immobile and rigid during bipedal gait due to the existence of a short and entrapped lumbar spine and the resulting close relationship between the lowest ribs and the ilia (Schmid & Piaget, 1994; Schultz, 1950, 1961; Ward, 1993; but see Thompson, Demes, O'Neill, Holowka, & Larson, 2015). This torso morphology has been hypothesized as stabilizing the lower back by counteracting the propulsive forces of the hind limbs during climbing (Jungers, 1984; Tuttle & Basmajiam, 1974). In turn, knuckle walking requires that limbs and abdominal muscles support the weight of the specimen, so in chimpanzees the center of gravity falls in the middle of the area bounded by arms and legs (Fagan, 2016). Consequently, chimpanzees use forelimbs to counterbalance the body during locomotion as it lacks spinal curvatures to play this role (Legaye, 2011; Le Huec, Saddiki, Franke, Rigal, & Aunoble, 2011).

Conversely, the elongated narrow waist of *H. sapiens* leads to a separation between the thorax and the pelvis that allows rotatory motions of these anatomical systems. This configuration contributes to stabilize and counter-rotate the torso during walking (Bramble & Lieberman, 2004; LaFiandra, Wagenaar, Holt, & Obusek, 2003; Lovejoy, 2005; Schmid & Piaget, 1994; Ward, 1993). Furthermore, in *H. sapiens* the thorax is positioned above the pelvis (Lovejoy, 2005), so that the line of gravity passes through the femoral head, with the center of gravity lying close to the acetabulum (Legaye, 2011; LeHuec et al. 2011). This, together with pelvic morphology, spinal curvatures and strong ligamentous apparatus, allows support of the torso weight in an upright posture during bipedal locomotion with minimal effort from the musculature.

These adaptations to different locomotor modes are the basis for explaining differences in the magnitude of integration found among apes. For example, some studies propose that humans and chimpanzees show integration in the subaxial cervical spine (C3-C7) but it is not clear whether the magnitude of this integration is greater in one group compared to the other (Arlegi, Gómez-Robles, & Gómez-Olivencia, 2018; Villamil, 2018). Arlegi, Veschambre-Couture, & Gómez-Olivencia (2019) investigated the integration of the vertebral column in *H. sapiens* and they detected that the thoracic region is more integrated than the cervical and lumbar regions. These authors related this greater magnitude of integration with specific functional requirements of the thoracic region (i.e. respiratory function) that would be independent from the cervical and lumbar regions. In turn, Grabowski, Polk, & Roseman (2011) compared patterns of integration within the os coxa of African apes and modern humans and found that *H. sapiens* has a weaker integrated os coxa than African apes. They linked these findings to a greater evolvability (i.e the ability to respond to selective pressures) of the os coxa in our species compared to African apes as an adaptation to habitual bipedalism. However, when tested in a wider comparative framework composed also of quadruped primates, evolvability in *Homo* might not be significantly different from that of any other hominoid (Lewton, 2012). Lastly, Middleton (2015) went one step further in analyzing patterns of integration and covariation not only in elements within the pelvis, but also within the whole torso (i.e. costal skeleton, vertebral column and pelvis). Analyses of linear measurements and 3D data in *H. sapiens* and *Pan* showed that these two taxa might have similar patterns of torso integration but different magnitude, with *H. sapiens* showing overall lower levels of integration within the torso than *Pan*. Middleton (2015) explained these findings mainly in the light of locomotor adaptations as well, suggesting that "*bipedality may require less functional correspondence among trunk elements than knuckle-walking and arboreal climbing*" (p. 341-342).

1.3 Torso morphology in *H. sapiens* and *Pan*: sexual dimorphism

Apart from clear locomotor differences, *H. sapiens* and *P. troglodytes* may differ in the role that sexual dimorphism plays in the torso skeletal elements. Several studies support the existence of sexual dimorphism in the morphology of the human ribcage, with females showing mediolaterally narrower thoraces than males (Bellemare, Jeanneret, & Couture, 2003; García-Martínez et al. 2016, 2019). These sex-related differences have been associated to different bioenergetic demands in females and males (Bitar, Fellmann, Vernet, Coudert, & Vermorel, 1999). But also, sexual dimorphism is even more evident in the human pelvis, as *H. sapiens* is unique among extant hominoid species not only because of its adaptation to habitual bipedalism but also to parturition (Dunsworth, Warrener, Deacon, Ellison, & Pontzer, 2012; Dunsworth, 2015, 2016; Grunstra et al. 2019; Lovejoy, 1988, 2005; Pavličev, Romero, & Mitteroecker, 2020; Rosenberg, 1992; Rosenberg & Trevathan, 1995; Tague, 1992). According to the "obstetric dilemma" (Washburn, 1960) humans evolved pelvic morphologies to deal both with adaptations to bipedalism (Gruss & Schmitt, 2015; Lovejoy, 1988) and to give birth to offspring with large brains (Gruss & Schmitt, 2015; Huseynov et al., 2016; Leigh, 1992; Leutenegger, 1987; Rightmire, 2004; Rosenberg, 1992; Rosenberg & Trevathan, 1995; Tague & Lovejoy, 1986).

Unlike *H. sapiens*, sexual dimorphism in the morphology of torso skeletal elements is not very clear in *P. troglodytes.* The few respiratory experiments carried out on chimpanzees refer to oxygen consumption in relation to locomotor costs, but samples are so small that no sexual dimorphism in oxygen consumption could be established (e.g. see Pontzer et al., 2014). Furthermore, sexual dimorphism in ribcage morphology is largely unknown in chimpanzees as well. Conversely, sexual dimorphism in the chimpanzee pelvis morphology has been widely studied, but no consensus has been reached regarding this matter. Some authors defend that chimpanzees show no sexually dimorphic pelves because of the lack of obstetric pressures (Huseynov, Ponce de León, & Zollikofer, 2017; Schultz, 1949), while others report that chimpanzees do show sex-related differences in pelvis morphology (Grunstra, Zaffarini, Fischer, & Mitteroecker, 2019). Considering everything, there is no evidence suggesting that shape variation in chimpanzees responds to bioenergetic demands as human thorax shape does, and obstetric pressures do not affect pelvis morphology in chimpanzees as it does in humans. Furthermore, like modern humans, chimpanzees are only moderately sexually size dimorphic (e.g. Pusey et al., 2005). Within this scenario, predictions about relationships between sexual dimorphism in the torso morphology of chimpanzees are difficult to make.

The body of work introduced provides a framework to further investigate the complex relationships within and between the skeletal torso elements in hominoids. However, 3D assessment of torso morphology would show more varied and subtle patterns of overall torso shape than disarticulated bones (Ward, Peacock, Winkler, Hammond, & Maddux, 2015). Therefore, Ward, Maddux, & Middleton (2018) proposed capturing the 3D relationships between the torso elements in anatomical connection for an appropriate assessment of the correspondence between thorax and pelvis morphology within the torso. In this line, Torres-Tamayo et al. (2018) investigated the effect of sexual dimorphism on thoraco-pelvic covariation in *H. sapiens*. They used 3D geometric morphometrics (GMM) of sliding semilandmarks for analyzing 50 torso 3D models segmented from thoraco-abdominopelvic computed tomography (CT) scans of two different adult populations, and found that modern human females showed mediolaterally narrower (lower) thoraces than their wide (upper) pelves and modern human males showed the opposite trend in both populations. These authors reported that sexual dimorphism would be the main factor driving thoraco-pelvic covariation in adult *H. sapiens*, and their results are consistent with those of previous studies analyzing sex-related variation in the thorax and pelvis separately (Bellemare, Jeanneret & Couture, 2003; Fischer & Mitteroecker, 2015, 2017; García-Martínez et al. 2016, 2019; Lo-Mauro & Aliverti, 2018; Molgat-Seon, Peters, & Sheel, 2018). Thus, Torres-Tamayo et al. (2018) proposed a new and more complex torso integration model in *H. sapiens* (torso integration hypothesis) that called into question the correspondence between a narrow thorax and a narrow pelvis classically reported for this species (Lovejoy, 2005; Middleton, 2013, 2015, 2017; Schultz, 1950, 1961; Ward, 1993).

1.4 Research objectives

The present study is a continuation of Torres-Tamayo et al. (2018) work on the human torso. In the mentioned research, high-density geometric morphometrics were applied on torso 3D models segmented from CT scans to investigate thoraco-pelvic covariation in *H. sapiens*. In the current study we now aim at expanding what is known about hominoid thoraco-pelvic covariation by including *P. troglodytes* in this investigation. Therefore, the objectives of this study are:

Objective 1. Carrying out a preliminary exploration of the potential common patterns of torso integration in *H. sapiens* and *P. troglodytes* previously proposed by Middleton (2015).

Objective 2. Testing the hypothesis that *H. sapiens* and *P. troglodytes* will also show species-specific aspects of thoraco-pelvic covariation because sexual dimorphism would influence this covariation differently in these taxa. Specifically, we predict that *H. sapiens* will show thoraco-pelvic covariation highly influenced by sexual dimorphism and characterized by wider (lower) thoraces than (upper) pelves in males and the opposite trend in females (Torres-Tamayo et al. 2018). In turn, *P. troglodytes* will show a pattern of correspondence between the most caudal ribs and iliac crest morphology irrespective of sex, in line with observations about overall great ape trunk shape as defined by Schultz (1961) (Schultz's hypothesis) and to correspond with demands on trunk stability as further refined by Ward (1993). As potential effects of allometry on sex-related human thoraco-pelvic covariation were overlooked in Torres-Tamayo et al. (2018), in the current work we paid special attention to this factor when testing the hypothesis.

2. MATERIAL AND METHODS

2.1 Sample composition and CT segmentation

We examined thoraco-abdominopelvic CT scans of living adult *H. sapiens* (*N*=30, 15 females and 15 males) that were collected for clinical purposes in ASCIRES ERESA (Exploraciones Radiológicas Especiales Sociedad Anónima, Valencia, Spain) (Table 1) and a cadaveric sample of adult *P. troglodytes* (*N*=10, three females and seven males) obtained in collaboration with different institutions (Table 2). The use of the human sample for research purposes was approved in the context of the mutual scientific collaboration agreement between ASCIRES ERESA and the Universidad de Valencia (Valencia, Spain). The subjects were anonymized and the study was carried out in accordance with the Declaration of Helsinki (Goodyear, Krleza-Jeric, & Lemmens, 2007). Threshold-based segmentation of CT scans was carried out using the open source software 3D Slicer v. 4.8 (http://www.3Dslicer.org) that applied the marching cubes algorithm to render 3D triangular meshes (Lorensen & Cline, 1987). Thus, we obtained *N*=40 torso 3D models that were post-processed (hole filling, surface smoothing, mesh simplification) in Artec Studio v. 13 (www.Artec3D.com) to obtain optimal 3D models for virtual measurements.

2.2 Landmark and semilandmark digitization

Three dimensional models were measured in the free-license version of Viewbox v. 4.0 software (www.dhal.com, see Bastir et al. 2019 for guidelines) by the same researcher (N.T.T) to avoid inter-observer measurement error. 1,080 landmarks and semilandmarks were semi-automatically located on the torso 3D models following the protocol of digitization previously published in Torres-Tamayo et al. (2018) but adding some modifications for the current study (Figure 1a, b). Since this work includes the species *P. troglodytes,* the twelfth pair of ribs was added to the landmark configuration used in Torres-Tamayo et al. (2018) to obtain the maximum amount of information possible of the chimpanzee torso morphology. Note that although chimpanzees usually have 13 pairs of ribs (Williams, Middleton, Villamil, & Shattuck, 2016), in this study we needed to exclude the 13th pair from the chimpanzee sample in order to homologize the number of pairs of ribs between *P. troglodytes* and *H. sapiens* (twelve pairs). Also, *H. sapiens* presents five lumbar vertebrae and five sacral vertebrae, while *P. troglodytes* has three or four lumbar vertebrae and five or six sacral vertebrae (Williams, Middleton, Villamil, & Shattuck, 2016). Consequently, we removed five semilandmarks located on L1-L5 vertebral bodies, one true landmark located on the sacral promontory and four true landmarks at the site of fusion of sacral vertebrae that were present in the protocol of digitization used by Torres-Tamayo et al. (2018). These modifications allowed homologization of landmark configurations between the two species, a necessary requirement to carry out GMM comparisons.

In order to assess intra-observer measurement error (the repeatability or precision of the measurements) for landmark configurations, the same (random) specimen was measured three times on three different days by the same researcher (N.T.T). Then, the Euclidean distance between sets of Procrustes shape coordinates (i.e. Procrustes distance, the squared root of summed squared inter-landmark distances between corresponding landmarks following Mitteroecker & Gunz, 2009) was calculated between ten random specimens and the three repetitions. For an acceptable intra-observer measurement error, the highest Procrustes distance between two repetitions is expected to be lower than the lowest Procrustes distance between two random specimens (Supporting Information Table S1) (Morecroft, Fieller, Dryden & Evison, 2010).

The subsequent GMM procedures were performed in the open source software R v. 3.6.2 (R Development Core Team, 2017) and R Studio v. 1.2, mostly using the R-packages Morpho v. 2.7 (Schlager, 2017) and geomorph v. 3.2.1 (Adams, Collyer, Kaliontzopoulou, & Sherrat, 2017) for 3D GMM analyses and rgl v. 0.100.30 for 3D visualizations (Adler et al. 2019). All of the analyzed data, R code and guidelines are freely available in Open Science Framework platform (https://osf.io/zrgbf/?view_only=ffd87b50e6744ca780d43a758403d05a). Since we used a random specimen as a template to digitize our sample, any feature inherent to this individual could be transferred to the rest of the specimens. Therefore, raw coordinates were firstly reflected and relabeled according to a previous definition of paired landmarks and then rotated onto the original configurations. The resulting symmetrized coordinates were then re-slid against a previously calculated torso mean configuration to minimize the bending energy of each specimen with respect to this mean (Gunz, Mitteroecker, & Bookstein, 2005). This procedure reduced the uncertainty of the semilandmarks location as these are not anatomically homologous points (Gunz & Mitteroecker, 2013).

2.3 Preliminary exploration of the effects of sexual dimorphism and allometry in the torso morphology of *H. sapiens* and *P. troglodytes*

As potential effects of allometry on sex-related human thoraco-pelvic covariation were overlooked in Torres-Tamayo et al. (2018), here we paid special attention to this factor. For this reason, we preliminarily assessed sexual dimorphism and allometry in the torso morphology of *H. sapiens* and *P. troglodytes* in an exploratory manner prior to addressing objectives 1 and 2.

Firstly, the landmarks configurations were translated, rotated and scaled (to Unit Centroid Size, CS, the square root of the sum of squared distances of each landmark to the center following Zelditch, Swiderski, & Sheets, 2012 same size) to remove any variation not related to shape in a process called generalized Procrustes analysis (GPA) (Gower, 1975; Rohlf & Slice, 1990). GPA yielded Procrustes shape coordinates that were further analyzed using GMM.

For a preliminary visual exploration of sexual dimorphism in the torso morphology of *H. sapiens* and *P. troglodytes*, mean shapes comparison between females and males within each species was assessed. Morphological differences between females and males within each species were visualized via thin plate spline (TPS) interpolation (Bookstein, 1991) of a reference configuration onto a target configuration (male and female mean shapes of each species). Regarding the choice of the reference configuration, a mesh of a 73-year-old human male not included in the comparative sample (the same specimen used by Torres-Tamayo et al. 2018) and a mesh of a 27-year-old chimpanzee male were used for these and subsequent TPS interpolations in *H. sapiens* and *P. troglodytes* respectively.

Since the existence of torso size differences between females and males is necessary to demonstrate if an allometric factor accounts for torso shape differences between sexes, mean CS of females and males was calculated within each species. After testing for normal distribution via Shapiro-Wilk tests (Shapiro & Wilk, 1965) (Supporting Information Table S2), these means were compared between females and males within each species using Mann-Whitney U tests under the null-hypothesis of true difference in means is equal to zero (10,000 permutations) (Mann & Whitney, 1947).

Once CS differences between females and males within each species were assessed, an allometric regression was performed within each species separately in order to assess the influence of torso size (CS, independent variable) on torso shape variation (Procrustes shape coordinates, dependent variable) (10,000 permutations) (Klingenberg, 2016). Shape changes corresponding to these regression vectors (torso shape at minimum CS and torso shape at maximum CS) were visualized using TPS interpolation.

Lastly, to explore whether possible sex-differences in torso morphology are a consequence of potential size differences between females and males (sexual size dimorphism), we controlled for the effects of allometry by regressing the resulting allometric regression residuals (dependent variable) on sex (independent variable) in a binary form (females=-1, males=1) within each species (10,000 permutations). Thereby, we assessed the "non-allometric" component of sexual dimorphism that was lastly visualized by means of TPS interpolation.

2.4 Thoraco-pelvic covariation in *H. sapiens* and *P. troglodytes*

Two-block Partial Least Squares (2B-PLS) analysis has been revealed as a useful method to statistically assess the covariation between two different sets of original variables, for example, between two sets of shape data (2D or 3D) (Adams & Collyer, 2016; Arlegi, Gómez-Robles, & Gómez-Olivencia, 2018; Bastir, Rosas, & Sheets, 2005; Bookstein et al. 2003; Klingenberg & Marugán-Lobón, 2013; Mitteroecker & Bookstein, 2007; Mitteroecker, Gunz, Neubauer, &

Müller, 2012; Neaux et al. 2018; Rohlf & Corti, 2000; Scott, Strauss, Hublin, Gunz, & Neubauer, 2018; Torres-Tamayo et al. 2018).

Here we provide a brief explanation of how this analysis works with 3D shape coordinates. One can have *n* specimens on which *p* landmarks are measured to obtain two 3D sets of variables: block 1 (*x, y, z*) and block 2 (*x',y',z'*). After performing a GPA to remove any variation related to position, orientation and size of the specimens (Gower, 1975; Rohlf & Slice, 1990), PLS computes the variance-covariance matrix that comprises the within-block variance-covariance matrices of block 1 and block 2, and the covariance matrix between the two blocks (Zelditch, Swiderski, & Sheets, 2012). Then, PLS performs the singular value decomposition of the covariance matrix to extract two unit vectors (called 'singular vectors', one for block 1 and one for block 2) that are linearly combined to generate new pairs of variables (each pair called latent variable, LV or singular warps, SW) showing decreasing covariance between the two blocks in *n* different dimensions (LV1, LV2, LV3, LV*n*, etc.), i.e. from the LV explaining the maximum covariance between blocks (LV1) to the LV explaining the minimum covariance (LV*n)*. Permutation tests allow exploration of covariance in each PLS dimension with p-values against the null hypothesis that covariance explained by the singular values does not exceed what one might obtain by chance. Also, correlation between singular vectors on each dimension of the PLS (pairs of PLS axis) can be quantified via permutation tests with p-values against the null-hypothesis of complete independence between the PLS scores associated to each block.

Lastly, since these blocks are shape coordinates, each vector can be visualized using TPS interpolation. However, morphological visualizations of PLS loading vectors should be interpreted with caution, as according to Mitteroecker & Bookstein (2007): "*When they are visualized or interpreted as one joint shape deformation—when they serve as singular warps—they have to be rescaled appropriately because the amount of shape change depicted by one (unit-length) PLS loading vector does not necessarily correspond to the associated amount of shape change depicted by the other (unit-length) loading vector*" (p.824). Thus, ideally one should compute these shape changes between two blocks along the common axis of deformation for proper anatomical interpretations.

In this study, 2B-PLS analyses of Procrustes shape coordinates were applied to assess the patterns of covariation between the thorax and pelvis in *H. sapiens* and *P. troglodytes*. For this purpose, after performing a GPA of the entire landmark configurations, the torso dataset was subdivided into two *a priori* assumed modules: thorax (block 1) and pelvis (block 2). As 2B-PLS results depend on the covariance matrix on which the analysis is based (Mitteroecker & Bookstein, 2008), 2B-PLS analyses were performed based on two approaches in line with objective 1 and objective 2 respectively, and following Scott, Strauss, Hublin, Gunz, & Neubauer (2018).

Objective 1. Common patterns of evolutionary integration between *H. sapiens* and *P. troglodytes* can be missed by doing separate 2B-PLS analyses on each species. This is because 2B-PLS method is based on eigendecomposition and the directions of separate-species singular warps could differ, even if those species share a common pattern of integration, simply because the species' variances differ in those common directions. Therefore, we analyzed *H. sapiens* and *P. troglodytes* within the same 2B-PLS analysis based on a common variance-covariance matrix in line with the objective 1 of this study. To ensure that this analysis reflects common patterns of covariation rather than confounding species-specific effects driven by sexual dimorphism, allometry and/or species itself, this 2B-PLS analysis was performed on the covariance matrix of regression residuals of Procrustes shape coordinates on species, sex and CS. Resulting PLS scores correlation slopes were statistically compared between *H. sapiens* and *P. troglogytes* in the first three LV.

Objective 2. Species-specific aspects of the thoraco-pelvic covariation might be lost to some extent in the common 2B-PLS analysis. For this reason, a 2B-PLS analysis based on the covariance matrix of each species was calculated separately to investigate species-specific covariation patterns in *H. sapiens* and *P. troglodytes* in line with the objective 2 (hypothesis testing) of this study. In order to evaluate whether these species-specific covariation patterns are influenced by allometry, an additional 2B-PLS analysis was performed on the covariance matrix of the allometric regression residuals previously calculated for each species separately (see section 2.3).

Lastly, shape changes associated to these PLS analyses were computed along the common axis of deformations associated to each explored LV (Mitteroecker & Bookstein, 2007) and visualized via TPS interpolation for anatomical interpretations.

2.5 Quantification of thorax and pelvis relationships in *H. sapiens* and *P. troglodytes*

In order to complement the results of the 2B-PLS analysis with supportive metrics in the hypothesis testing, relationship between thorax and pelvis dimensions was quantified in *H. sapiens* and *P. troglodytes* by means of linear measurements collected using Artec Studio v. 13 (Figure 1c, d). In *H. sapiens,* thoracic widths (mm) were measured at seventh and eighth rib levels because they represent the maximum breadth of the ribcage in humans (Middleton, 2015); but also, the most adjacent caudal levels (ninth and tenth) were measured to have a more complete quantification of the relationships between the lower thorax and the ilia. In *P. troglodytes*, thoracic widths were measured as the maximum transverse diameter (mm) at eleventh, twelfth and thirteenth rib levels as these most caudal rib levels represent the broadest level of the chimpanzee thorax (Middleton, 2015). Pelvic width was measured as the maximum transverse distance (mm) between the outer edges of the two iliac blades in *H. sapiens* and *P. troglodytes*.

Thoracic and pelvic linear measurements were measured three times on three different days by the same researcher (N.T.T) (Supporting Information Table S3, S4), and the mean values of these three repetitions were calculated to perform comparative analyses. After testing for normal distribution via Shapiro-Wilk tests (Supporting Information Table S3, S4), thoracic and pelvic widths were compared within females and males in *H. sapiens* and *P. troglodytes* through Mann-Whitney U tests.

Intra-observer measurement error was assessed via Intraclass Correlation Coefficients (ICC) and their 95% confident intervals (CI) were calculated based on a 2-way mixed-effects model (Koo & Li, 2016). ICC among linear measurements repetitions was calculated (Supporting

Information Table S5). ICC values lower than 0.5 are considered to be indicative of poor reliability, values between 0.5 and 0.75 indicate moderate reliability, values between 0.75 and 0.9 indicate good reliability, and values greater than 0.90 indicate excellent reliability (Koo and Li, 2016).

3. RESULTS

3.1 Sexual dimorphism and allometry in the torso morphology of *H. sapiens* and *P. troglodytes*

Visual mean shape comparisons showed that female *H. sapiens* have relatively narrow (lower) thoraces compared to their (upper) pelves (Figure 2a), while male *H. sapiens* have relatively wide (lower) thoraces compared to their (upper) pelves (Figure 2b). By contrast, chimpanzee females (Figure 2c) and males (Figure 2d) showed morphological correspondence in thoracic and pelvic widths between lower (thorax) and (upper) pelvis and no apparent sex-related differences were visually detected. These 3D morphological trends were quantitatively confirmed by Mann-Whitney U tests analyses on linear measurements (Table 3). In female *H. sapiens*, mean thoracic width was significantly smaller than mean pelvic width at three of the four lower rib levels analyzed (seventh, eight and tenth) while in male *H. sapiens*, mean thoracic width was significantly larger than mean pelvic width at the three most caudal levels analyzed (eight, ninth and tenth). In *P. troglodytes*, both females and males showed no statistically significant differences between mean thoracic and mean pelvic widths (Table 4), with the caveat that only three females are included in our sample.

Female *H. sapiens* have statistically significantly smaller torsos ($CS_{females}$=6451.71) than males (CS_{males}=6880.71) ($U = 20$, p-value <0.05). These size differences between males and females were consistent with significant allometric effects found in *H. sapiens* (12.77% explained; $p<0.05$), as shorter torsos mostly belonged to females and larger torsos mostly belonged to males (Figure 3a). When allometry was controlled for, the non-allometric component of sexual dimorphism showed a statistically non-significant sexually dimorphic signal in *H. sapiens* torso morphology (6% explained; p=0.06) (Figure 3b).

Female *P. troglodytes* showed smaller torsos ($CS_{females}$=5636.03) than males (CS_{males}=6110.76) although this difference was not statistically significant (U=2; p=0.06) probably because of the small sample size. Statistically non-significant allometric effects were found in *P. troglodytes* (14% explained; p=0.22) (Figure 4). Although points distribution on the plot seems to indicate that large torsos might belong to males, suggesting a potential sex-related allometric trend, it is not possible to support this statement with only three chimpanzee females and non-significant allometric signal in the data. As non-significant allometric effects were found in our chimpanzee sample, regression of allometric regression residuals on sex was no longer calculated.

3.2 Common patterns of thoraco-pelvic covariation in *H. sapiens* and *P. troglodytes*

Results of the 2B-PLS analysis combining the two taxa are shown in Table 5. Almost 90% of the covariance was explained by the first three LV of the 2B-PLS analysis and covariance explained by the singular values in each of these three LV significantly exceeded what we might obtain by chance. Figure 5 shows PLS scores for the thorax plotted against those for the pelvis in the first three LV. Statistical comparisons of slopes between species (Supporting Information Table S6) show similar point distributions (i.e overall common patterns of thoraco-pelvic covariation) for *P. troglodytes* and *H. sapiens* in the first two LV and significantly different slopes (i.e. somewhat different thoraco-pelvic covariation pattern) in the third LV. The morphological aspects of thoraco-pelvic covariation associated with the singular vectors of the first three LV are described as follows (Figure 5).

The first LV shows the main pattern of thoraco-pelvic covariation shared by *H. sapiens* and *P. troglodytes* in our sample (Figure 5a). Towards negative PLS scores, we found that hominoids (both humans and chimpanzees) that have mediolaterally narrow upper ribcage compared to the lower ribcage ('funnel-shaped' thorax) also show a relatively tall iliac body, a coronally oriented and tall iliac blade and a sagittal oval pelvic inlet. In these hominoids, the iliocostal space is relatively small, the ribs are declined and have only a small degree of curvature, and the spine overall appears 'C-shaped'. Towards positive PLS scores we found that hominoids with a mediolaterally more expanded upper and lower ribcage ('barrel-shaped' thorax) also show a short iliac body, a sagittaly oriented and short iliac blade and a transverse oval pelvic inlet. These hominoids also have an iliocostal space that is relatively greater than that towards negative PLS scores and the spine shows a significant degree of curvature ('S-shape').

The second LV shows covariation mainly driven by the spinal curvature and the relative width of the torso (Figure 5b). Thus, hominoids with narrower torsos and 'S-shaped' spines also show sagittaly oriented iliac blades towards negative PLS scores, while hominoids with relatively wider torsos and 'C-shaped' spines also show coronally oriented iliac blades towards positive PLS scores.

The third LV shows thoraco-pelvic covariation mainly linked to torso width, dorso-ventral diameter of the thorax, relative pelvic height and iliocostal space: negative PLS scores show narrow torsos with flattened thoraces, relatively taller pelves, a more kyphotic thoracic spine and a relatively smaller iliocostal space, while positive PLS scores show wider torsos with deeper thoraces, relatively shorter pelves, a less kyphotic thoracic spine and a relatively greater iliocostal space (Figure 5c). The third LV is interesting as it also revealed a somewhat different aspect of the thoraco-pelvic covariation pattern between *H. sapiens* and *P. troglodytes* according to their different slopes (Supporting Information Table S6). Thus, *P. troglodytes* specimens with more "barrel-shaped" and dorsoventrally flattened ribcages have an even narrower pelvis than *H. sapiens* with a similar ribcage shape. Vice versa, *P. troglodytes* specimens with "funnel-shaped" and dorsoventrally deeper thoraces have an even broader and more flaring pelvis than *H. sapiens* with a similar ribcage morphology.

3.3 Species-specific thoraco-pelvic covariation in *H. sapiens* and *Pan*

In *H. sapiens*, covariance explained by singular values of the first three LV significantly exceeded what we might obtain by chance (Table 6). Shape changes associated to the PLS axes in the first LV (Figure 6a) showed a human-specific covariation pattern that is shared by females (positive PLS scores) and males (negative PLS scores), with a clear mean difference between them: for a given thorax shape there is a specific pelvis shape, irrespective of being female or male, but there are thoracic and pelvic shapes more likely to be found only in males or in females. As result, humans with relatively wider thoraces and more horizontal ribs show relatively narrower pelves with sagittaly oval pelvic inlets and this trend is more common in males. Likewise, humans with relatively narrower thoraces and more declined ribs show relatively wider pelves with less sagittaly oval pelvic inlets, this trend being more common in females. Looking at the dorso-ventrally depth and ribs orientation in both sexes, potential effects of breathing on thorax morphology (see section 4.4) are not discarded in the first LV (Figure 6a). In the second LV (Figure 6b), sexual dimorphism also drives thoraco-pelvic covariation in a similar manner to what is shown in the first LV, but dorso-ventral depth and rib declination differences between males (negative PLS scores) and females (positive PLS scores) are more subtle than in the first LV. This human-specific 2B-PLS analysis shows that the influence of sexual dimorphism in human thoraco-pelvic covariation is so strong that emerges in the first and second LV (~80% of the total covariance, Table 6).

In order to investigate whether these sex-related human covariation patterns are consequence of sexual size dimorphism, allometry was controlled for and a 2B-PLS analysis was calculated on the covariance matrix of the regression residuals of Procrustes shape coordinates on CS (see section 2.3). Covariance explained by the singular values of the first three LV of this 2B-PLS analysis significantly exceeded what we might obtain by chance (Table 6). The first LV (Figure 7a) shows relatively wide thoraces with declined ribs, wide pelves and a relatively small iliocostal space towards negative PLS scores, whereas positive PLS scores show relatively narrow thoraces, more horizontal ribs, relatively narrow pelvis and a slightly greater iliocostal space. Interestingly, the second LV (Figure 7b) of this 2B-PLS analysis shows a sexually dimorphic signal in the thoraco-pelvic covariation, although with clear overlapping between males (negative PLS scores) and females (positive PLS scores): in negative values the ribs are slightly more horizontal, the ribcage is slightly deeper and the pelvic inlet is sagittaly more oval than in positive values. According to these results, a new pattern of thoraco-pelvic covariation not driven by sexual dimorphism arises in the first LV when allometric effects are removed (~45% of the total covariance, Table 6, Figure 7a), and remaining sexually dimorphic signal now emerges only in the second LV (~27% of the total covariance, Table 6, Figure 7b). Therefore, sexual dimorphism in *H. sapiens* thoraco-pelvic covariation exists even in absence of allometric effects but becomes considerably weaker when the effect of size is removed from the data.

In *P. troglodytes*, covariance explained by the singular values in the first three LV did not exceed that expected by chance (Table 7) likely because of the small sample size. For this reason, it was not possible to describe and interpret the morphological visualizations in biological terms as they were not different from what was expected by chance. However, PLS scores for the thorax and pelvis showed significant correlation in the first three LV (Table 7) and no apparent sexually dimorphic signal was detected in the PLS scores plots of the first and second LV (Figure 8), although only three female *P. troglodytes* did not suffice to support such a statement. Lastly, as non-significant allometric effects were found in our chimpanzee sample, 2B-PLS analysis on allometric regression residuals was no longer calculated.

4. DISCUSSION

The purpose of this study was contributing to the knowledge of torso integration in modern Hominoidea (Lovejoy, 2005; Middleton, 2013, 2015, 2017; Schultz, 1950, 1961; Torres-Tamayo et al. 2018; Ward, 1993; Ward, Maddux, & Middleton, 2018) by assessing and comparing patterns of thoraco-pelvic covariation in *H. sapiens* and *P. troglodytes.* This study combined 3D GMM and linear measurements, with results suggesting that *H. sapiens* and *P. troglodytes* share some aspects of the thoraco-pelvic covariation, while other features might be species-specific. However, the small chimpanzee sample size did not suffice to test the hypothesis in an appropriate manner. In the following section we briefly debate the conservative nature of these covariation patterns in line with objective 1. The role that sexual dimorphism and allometry play on species-specific covariation (objective 2) is discussed in a purely exploratory manner because of the small chimpanzee sample size.

4.1 Common thoraco-pelvic covariation in *H. sapiens* and *P. troglodytes*

The vast majority of the research on patterns of integration and covariation in hominoids are focused on the skull (e.g. Ackermann, 2002; Bastir, 2008; Bastir, Rosas, & Sheets, 2005; Bookstein et al. 2003; Bruner, Pereira-Pedro, & Bastir, 2017; Mitteroecker & Bookstein, 2008; Neaux et al. 2018; Profico et al. 2017; Püschel, Friess, & Manríquez, 2020; Scott, Strauss, Hublin, Gunz, & Neubauer, 2018; Singh, Harvati, Hublin, & Klingenberg, 2012; Stelzer, Gunz, Neubauer, & Spoor, 2018), but studies investigating integration and covariation within and between elements of the torso are scarce (Arlegi, Veschambre-Couture, & Gómez-Olivencia, 2019; Huseynov, Ponce de León, & Zollikofer, 2017; Grabowski, Polk, & Roseman, 2011; Lewton, 2012; Middleton, 2015; Ward, Peacock, Winkler, & Maddux, 2015; Torres-Tamayo et al. 2018). Among those, Middleton (2015) quantified and compared for the first time trunk relationships between *H. sapiens* and *Pan* collecting linear metrics and 3D coordinates on disarticulated trunk skeletal elements. Middleton (2015) found that these two taxa show the same pattern of integration within the torso but different magnitude. As Middleton (2015), the majority of the above mentioned authors mainly focused their research on the magnitude of integration and interpreted their findings in light of implications for evolvability. The current study complements this body of work by assessing the 3D patterns of thoraco-pelvic covariation in humans and chimpanzees.

In line with Objective 1, patterns of thoraco-pelvic covariation shared by *H. sapiens* and *Pan* are tested here for the first time in 3D anatomically connected torsos. Our results suggest that some aspects of thorax and pelvis morphology might have evolved as part of a maintained (i.e. shared) thoraco-pelvic covariation in *H. sapiens* and *P. troglodytes* (Figure 5). This shared thoraco-pelvic covariation in humans and chimpanzees is unrelated to allometry, sexual dimorphism or species itself and might have been maintained since the last common ancestor of *Homo* and *Pan*. By extension, members of the human lineage might have presented any of these thoraco-pelvic covariation aspects shared by humans and chimpanzees, i.e. hominins that had relatively craniocaudally longer 'funnel-shaped' ribcages and a more 'C-shaped' spine likely had taller iliac bodies, taller and more coronally oriented iliac blades and a short iliocostal distance, and hominins that had more "barrel-shaped" ribcages and a 'S-shaped' spine likely showed shorter iliac bodies, short and more sagittaly oriented iliac blades and a great iliocostal distance (Figure 5).

However, for broader evolutionary interpretations of these shared patterns of covariation it is convenient to study *H. sapiens* and *P. troglodytes* within the entire Hominoidea superfamily and even within a comparative framework composed of non-hominoid primates. Only then can it be confirmed whether these patterns of covariation are shared by hominoids and thus different from other taxa. In summary, shared patterns of integration in *H. sapiens* and *P. troglodytes* are not unexpected, not only because they were found is previous research (Middleton, 2015), but also because these taxa possess aspects in their hominoid body plans that differ from those of other non-hominoid primates. The novel aspect of this work is the different role that sexual dimorphism and allometry might play on thoraco-pelvic covariation in humans and chimpanzees, as discussed below.

4.2. Species-specific patterns of thoraco-pelvic covariation in *H. sapiens*

In line with Objective 2, we analyzed thoraco-pelvic covariation in N=30 *H. sapiens* and N=10 *P. troglodytes* and its relationship to sexual dimorphism and allometry. Our results show that torso morphology and thoraco-pelvic covariation in adult *H. sapiens* are mainly driven by sexual dimorphism, with relatively wider (lower) thoraces than (upper) pelves in males and the opposite trend in females (Figure 2, 3a, 6a, Table 3). These results replicate the findings of Torres-Tamayo et al. (2018) and are consistent with previous works showing that sexual dimorphism plays an important role in the thorax and pelvis shape variation in *H. sapiens* (Bellemare, Jeanneret, & Couture, 2003; Fischer & Mitteroecker, 2017; García-Martínez et al. 2016, 2019; Gruss & Schmitt, 2015; Rosenberg & Trevathan, 1995).

At respiratory skeletal level, male *H. sapiens* have larger ribcages than females of the same stature and certainly wider lower thoraces (Bellemare, Jeanneret, & Couture, 2003; García-Martínez et al. 2016). Also, sex-related kinematic differences have been linked to a greater activity of the diaphragm as well as to greater bioenergetic demands and high metabolic rates in males than in females (García-Martínez et al. 2019; Torres-Tamayo et al. 2018). With regards to pelvic sexual shape dimorphism, human female pelvis morphology evolved to give birth to large-brained offspring over the last 2 M.a with the increase of cranial capacity in the genus *Homo* (Gruss & Schmitt, 2015; Leigh, 1992; Leutenegger, 1987; Rightmire, 2004; Rosenberg, 1992; Rosenberg & Trevathan, 1995; Tague & Lovejoy, 1986). This adaptation is unique to our species among extant hominoids, as *H. sapiens* shows larger cephalopelvic proportions compared to other hominoids (except gibbons, which also give birth to comparatively large newborns) (Schultz, 1949). Yet, recent work by Laudicina (2019) calls into question these largely assumed obstetric constraints in *H. sapiens* compared to other non-human primates, suggesting that childbirth is no more difficult in humans than in other primates.

However, several previous studies also proposed that these sex-related differences can be explained by differences in body size between males and females (sexual size dimorphism) (Fischer & Mitteroecker, 2017; Tague, 2000, 2005). Therefore, it is reasonable to think that sex-related torso morphology and thoraco-pelvic covariation found in our study might be a consequence of body size differences between males and females too. When we investigated the non-allometric component of sexual dimorphism in torso morphology, we found that sex-related differences were non-significant (Figure 3b) unlike when allometric effects were accounting for them (Figure 3a). However, this non-allometric component of sexual dimorphism was at the edge of significance (6% explained; p=0.06), suggesting that this result was a consequence of the human sample size. Likewise, covariation analysis on allometric regression residuals showed no signal of sexual dimorphism in the first LV of the 2B-PLS analysis (Figure 7a), with relatively wide torsos and a relatively shorter iliocostal distance towards negative PLS scores, and relatively narrow torsos and a relatively greater iliocostal distance towards positive PLS scores. However, we found a subtle signal of sexual dimorphism in the second LV of this 2B-PLS analysis: males tend to plot towards negative PLS scores and show slightly more horizontal rib orientation, smaller subpubic angles and more sagittaly oval pelvic inlets than females towards positive PLS scores. According to these results, we suggest that sex-related trends in thoraco-pelvic covariation are mainly explained by allometry, although a sexually dimorphic signal still remains in absence of allometric effects as previously proposed (Fischer & Mitteroecker, 2017; García-Martínez et al. 2016).

García-Martínez et al. (2016) analyzed differences in ribcage morphology between females and males and demonstrated that males show mediolaterally wider and craniocaudally relatively shorter ribcages than females with size accounting for sex-related differences. When they explored the non-allometric component of sexual dimorphism, the wider thorax in males was retained but the relative shortening of the thorax disappeared. Conversely, there is no consensus about the extent to which sexual dimorphism in *H. sapiens* pelvis morphology is influenced by differences in body size (Fischer & Mitteroecker, 2017; Kurki, 2007, 2010; Lewton, 2015; Tague, 2005). Tague (2000) found a positive correlation between clavicular length and femoral head diameter with pelvic size, suggesting that large individuals have a large pelvis, irrespective of being female or male. However, Tague (2000) also found that other obstetric-relevant dimensions were independent of body size in females and would respond to obstetric selection, so that small females would not necessarily have small obstetric dimensions. This would suggest a possible adaptation of these obstetric dimensions in small-bodied females. Along these lines, Kurki (2007) tested Tague's (2000) hypothesis specifically in small-bodied human populations and found that smaller females show certain obstetric dimensions of the pelvis that were larger relative to their body size. This would support that "*the obstetric canal is protected in small-bodied adults through adaptive allometric modeling*" (Kurki, 2007; p. 1163). Moreover, Tague (2005) proposed a response of pelvic growth to differences in testosterone levels, which would be greater in sexually dimorphic species. Kurki (2013) whether human populations with high degrees of size dimorphism showed high pelvic shape dimorphism and found no correlation between body size dimorphism and pelvic shape dimorphism in the sample analyzed, suggesting that populations with larger degrees of body size sexual dimorphism do not necessarily show higher pelvic sexual shape dimorphism. More recently, Fischer & Mitteroecker (2017) investigated allometric and non-allometric components of sexual dimorphism affecting pelvic morphology. They found that tall individuals (both males and females) have relatively taller and narrower pelves than short ones (allometric component), but they also found that females (tall and short) showed relatively flatter and wider pelves and shorter iliac blades compared to males regardless of size (non-allometric component).

In sum, although thorax and pelvis separately show sex-related variation regardless of size (Bellemare, Jeanneret, & Couture, 2003; Fischer & Mitteroecker, 2017; García-Martínez et al. 2016; Kurki, 2012), the current study proposes that allometry plays a key role in the extent that sexual dimorphism affects torso morphology and thoraco-pelvic covariation in *H. sapiens*. These results complement our previous work (Torres-Tamayo et al., 2018) where we overlooked allometry as a potential factor influencing sex-related human thoraco-pelvic covariation.

4.3. Species-specific patterns of thoraco-pelvic covariation in *P. troglodytes*

Contrary to the findings in humans, mean shape comparisons (Figure 2c, d) did not reveal sexually dimorphic features in the chimpanzee torso morphology, with size differences being statistically non-significant between sexes. Also, because covariance explained by the singular values in the first three LV of the 2B-PLS analysis was not statistically significant, it was not possible to describe and interpret the morphological visualizations in biological terms, as they were not different from what we expected by chance (Table 7, Figure 8). Supportive metrics (Table 4) suggested that both females and males show no statistically significant differences between mean thoracic and mean pelvic widths, thus pointing to a pattern of correspondence between the most caudal ribs and iliac crest morphology (Schultz's hypothesis) that would be irrespective of sex. Once again one must keep in mind the caveat that only three females were included in our sample.

Previous studies show weak sexual dimorphism in the chimpanzee post-cranial skeleton (e.g. Huseynov, Ponce de León, & Zollikofer, 2017; Schultz, 1949; Wood & Chamberlain, 1986). As sex-related differences in the human thorax have been linked to different metabolic rates and bioenergetics demands in females and males (Bitar, Fellmann, Vernet, Coudert, & Vermorel, 1999), it is reasonable to explore if the same might apply to chimpanzees. Unfortunately, experiments on thorax morphology and respiratory function in non-human primates are not possible to carry out. However, Bruhn & Benedict (1936) did not find conclusive evidence to support metabolic differences between males and females in chimpanzees, contrary to what was found in humans. Although not focusing on sexual dimorphism in their metabolic data related to costs of locomotion, Pontzer et al., (2014) reported similar rates of oxygen consumption in male and female chimpanzees for the same locomotor tasks. More recently, Zihlman & Bolter (2015) investigated differences in body composition between *H. sapiens* and *P. paniscus* and found that for a given fat-free mass, humans show higher metabolic rates than other hominoids including chimpanzees (Pontzer et al. 2016). Despite Nakakuki (1992) conclusions of overall similarities in the bronchial tree, lobular division and overall lung structure between chimpanzees and humans, the aforementioned evidence suggests that metabolic rates are not comparable between humans and chimpanzees. By extension, thoracic shape variation in chimpanzees is not necessarily expected to respond to bioenergetic demands the way as human thorax shape does (i.e. with males showing wider lower part of the thorax than the upper part and females showing the opposite trend), albeit that comparative studies of human and chimpanzee locomotion indicate similar metabolic costs for it (e.g. Halsey & White, 2012).

Contrary to studies of the ribcage, chimpanzee pelvic sexual dimorphism has been widely assessed in light of (or lack thereof) obstetric pressures (Grunstra, Zaffarini, Fischer, & Mitteroecker, 2019; Huseynov, Ponce de León, & Zollikofer, 2017; Schultz, 1949). In order to explore potential effects of obstetric pressure in primate pelvis morphology, Schultz (1949) measured the ischium-pubis index, the relative pelvic inlet breadth and the newborn head and shoulder dimensions on a large sample composed of nine species of catarrhine monkeys and apes. This study revealed that gibbons and chimpanzees have the least sexually dimorphic pelves among primates. In line with this, Huseynov, Ponce de León, & Zollikofer (2017) applied 3D GMM techniques to investigate the variation of the chimpanzee os coxa morphology. Although they found relatively larger transverse pelvic diameter, anteroposterior inlet dimensions and a more everted ischial region in females than in males, no significant differences in pelvis size and pelvis shape were found between males and females. Conversely, Grunstra, Zaffarini, Fischer, & Mitteroecker (2019) recently investigated pelvic sexual dimorphism in chimpanzees and found that males have larger and more laterally flared ilia, a smaller sub-pubic angle and a superiorly narrower sacrum than females. They proposed that pelvic sexual dimorphism may exist in the absence of obstetric selection as a pattern that might have been shared among hominids or even mammals.

Unfortunately, the small chimpanzee sample size did not suffice to test the hypothesis in an appropriate manner. As a consequence, we could not properly evaluate whether sexual dimorphism and allometry affect thoraco-pelvic covariation in *P. troglodytes* to the extent it does in *H. sapiens*. Although supportive metrics (Table 4) pointed to a correspondence between the most caudal ribs and iliac crest morphology in chimpanzees that would be irrespective of sex, these results cannot be interpreted as conclusive findings as the *P. troglodytes* sample size included in this study is small and unfortunately the number of females and males is not balanced. More research on larger sample sizes is necessary to confirm the validity of our interpretations.

4.4 Limitations of the study

In this study, respiratory kinematics has not been controlled for and the thorax could show variation due to the different respiratory status of living *H. sapiens*, along with the fact that cadavers composing the *P. troglodytes* sample have no respiratory status. To deal with this constraint, apart from including only CT scans collected in the same institution (ASCIRES ERESA, Valencia, Spain) and thus performed under the same protocol, Torres-Tamayo et al. (2018) suggested to standardize the torso shape for the effect of respiratory kinematic status by calculating the mean shape between forced inspiration or expiration as a proxy for 'neutral kinematic status'. However, it is unlikely that the thoraco-abdominopelvic CT scan data has been acquired in forced expiration and forced inspiration, since those respiratory protocols are usually indicated to explore pulmonary pathologies, which only require the acquisition of thoracic CT scans (from the apex of the lungs to the level of the diaphragm). Being aware of this limitation, we consider that 2B-PLS analysis is the best statistical approach to deal with this constraint, since this analysis generates linear combinations that maximize the covariance between the thorax and the pelvis instead of focusing on the variation within each block. Therefore, 2B-PLS analysis should not show any thoracic variation due to respiratory kinematics, but covariation of this structure with the pelvis, which is a structure completely independent of breathing.

Furthermore, the authors are aware that the samples used in this study are small, especially that of *P. troglodytes*. Since CT scans are not usually performed for clinical purposes on these specimens, they are much less available than those for living *H. sapiens*. This is one of the reasons why the number of chimpanzees used in this work is limited. Ideally, the common covariance matrix to find shared patterns of covariation should be based on equal sample sizes for both species. Otherwise, the dominant species (*H. sapiens*) could mask the effect of the smaller one (*P. troglodytes*). Also, the existence of a species-specific covariation pattern in chimpanzees could not be confirmed because of the small chimpanzee sample size, but metrics preliminarily pointed to correspondence between the most caudal ribs and iliac crest morphology that would be irrespective of sex. Future research on larger and sex-balanced samples will redo these analyses to confirm the validity of our interpretations.

5. CONCLUSIONS

This study supports the existence of shared patterns of thoraco-pelvic covariation between adult *H. sapiens* and *Pan* that might have been maintained since the last common ancestor. Results also confirm the existence of clear species-specific covariation patterns for *H. sapiens* that are strongly affected by sexual dimorphism and allometry. However, the existence of species-specific covariation patterns in chimpanzees could not be established because of the small chimpanzee sample size. Thus, larger samples are necessary to properly test the hypothesis and to support these conclusions.

DATA SHARING STATEMENT

This study largely benefits from the availability of CT data and 3D models of chimpanzees in online open repositories such as Digital Morphology Museum (KUPRI) (http://dmm.pri.kyoto-u.ac.jp/dmm/) and Morphosource (www.Morphosource.org). The authors appreciate transparency and reproducibility in science and agree with the policy of data sharing recently implemented by the American Journal of Physical Anthropology. The landmark coordinates and R-code used in this study have been uploaded to the Open Science Framework (OSF) platform (https://osf.io/zrgbf/?view_only=ffd87b50e6744ca780d43a758403d05a) and allow researchers to reproduce the findings of the current study. Additional data such as linear measurements can be found in the Supplementary Information of the paper. Because of ethical and legal reasons, the CT scans and 3D models of the human sample used in this study must remain confidential and cannot be shared. These data are deposited in GIAVAL Research Group, Department of Anatomy and Human Embryology, University of Valencia, Av. Blasco Ibanez, 15. E-46010, Valencia, Spain. For requesting access to these data, please, contact JAS-G.

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AUTHOR CONTRIBUTIONS

Nicole Torres-Tamayo: Conceptualization; formal analysis; investigation; methodology; visualization; writing-original draft; writing-review and editing. **Sandra Martelli**: Writing-review and editing. **Stefan Schlager:** Formal analysis; methodology; software; validation; writing-original draft; writing-review and editing. **Daniel García-Martínez:** Writing-review and editing. **Juan Alberto Sanchis-Gimeno**: Data curation; writing-review and editing. **Federico Mata-Escolano.** Data curation. **Shahed Nalla:** writing-review and editing. **Naomichi Ogihara**: Data curation; writing-review and editing. **Motoharu Oishi:** Data curation; writing-review and editing. **Markus Bastir:** Conceptualization; funding acquisition; project administration; resources; supervision; writing-review and editing.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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FIGURE LEGENDS

Figure 1. Landmarks, semilandmarks and linear measurements collected on a human torso 3D model (a) and on a chimpanzee torso 3D model (b) (red: true landmarks, green: curve semilandmarks, purple: suface semilandmarks). (c) Linear measurements collected on the human torso 3D models [I.a = Thorax mediolateral (ML) width at seventh rib level, II.a = Thorax ML width at eighth rib level, III.a = Thorax ML width at ninth rib level, IV.a = Thorax ML width at tenth rib level, V.a = Pelvic width]. (d) Linear measurements collected on the chimpanzee torso 3D models (I.b = Thorax ML width at seventh rib level, II.b = Thorax ML width at eighth rib level, III.b = Thorax ML width at ninth rib level, IV.b = Pelvic width). Note that figures are scaled to show the same distance between the most caudal cervical vertebra and the lowest point of the ischium.

Figure 2. Procrustes mean shape comparison (frontal view) of the torso morphology of *H. sapiens* (a and b) and *P. troglodytes* (c and d). Light colors indicate female mean shapes (a and c) and dark colors indicate male mean shapes (b and d). Note that figures are scaled to show the same distance between the most caudal cervical vertebra and the lowest point of the ischium. No landmarks and semilandmarks were digitized on the lumbar and sacral vertebrae, so they were not involved in the warping.

Figure 3. Results of regression of Procrustes shape coordinates on size (allometry) (a) and of allometric regression residuals on sex (b) in *H. sapiens*. (a) Allometric regression (12.77% explained; $p<0.05$) shows that smaller torsos mainly belong to females and exhibit relatively narrower torsos than pelves, while larger torsos mainly belong to males and show relatively wider thoraces than pelves. Plot of regression scores suggests the same allometric pattern for males and females, with the former being a scaled version of the latter. (b) Regression of allometric residuals on sex (6% explained; $p=0.06$) shows a statistically non-significant effect of sexual dimorphism in torso shape variation so that shape differences need to be magnified by 1.5 times to be somehow noticeable. Note that figures are scaled to show the same distance between the most caudal cervical vertebra and the lowest point of the ischium. No landmarks and semilandmarks were digitized on the lumbar and sacral vertebrae, so they were not involved in the warping.

Figure 4. Results of regression of Procrustes shape coordinates on size (allometry) in *P. troglodytes*. Allometric regression (14% explained; $p=0.22$) shows non-significant allometric signal in this data. Important: Because there is no statistically significant allometric signal in this data, one cannot expect to interpret the morphological visualizations in biological terms as they are not different from what it is expected by chance. Note that figures are scaled to show the same distance between the most caudal cervical vertebra and the lowest point of the ischium. No landmarks and semilandmarks were digitized on the lumbar and sacral vertebrae, so they were not involved in the warping.

Figure 5. Plot of PLS scores in LV1 (a), LV2 (b) and LV3 (c) of the 2B-PLS analysis combining *H. sapiens* and *P. troglodytes,* and associated shape deformations (frontal and left lateral view) at -2 standard deviations (left) and +2 standard deviations (right) of each axis' PLS scores distribution. (a) Negative values of LV1 show ribcages relatively narrow at the top and relatively wide at the bottom ('funnel-shape'), whereas positive values show the opposite morphologies ('barrel-shape'). In addition, ribcages at negative scores are also relatively cranio-caudally longer compared to ribcages at positive scores. In lateral view, negative values are characterized by ribcages without any rib torsion and little thoracic kyphosis ('C-shape' overall spine curvature), and strong rib torsion and spine kyphosis ('S-shape' overall spine curvature) are observed in positive values. Regarding the pelvis, negative scores show relatively tall iliac body, tall and coronally oriented iliac blades and a sagittaly oval pelvic inlet, whereas positive values show short iliac body, short and sagittaly oriented iliac blade and a less sagittaly oval pelvic inlet. Also, in negative values the iliocostal space is relatively smaller than in positive values. (b) LV2 shows relatively narrower torsos with 'S-shaped' spines, relatively short iliac bodies and sagittaly oriented iliac blades towards negative PLS scores, and relatively wider torsos with 'C-shaped' spines, relatively tall iliac bodies and coronally oriented iliac blades towards positive PLS scores. (c) In the LV3, PLS vector indicates that negative PLS scores show narrow torsos with flattened thoraces, relatively taller pelves, more kyphotic thoracic spines and a relatively small iliocostal space, while positive PLS scores show wider torsos with deeper thoraces, relatively shorter pelves, less kyphotic thoracic spines and a relatively greater iliocostal space. But also, in the LV3 point distributions of the two species have different slopes (Supporting Information Table S6), suggesting different aspects in the covariation patterns between species: *P. troglodytes* that have "barrel-shaped" and dorsoventrally flattened ribcages have an even narrower pelvis than *H. sapiens* with a similar ribcage shape, while *P. troglodytes* that have "funnel-shaped" and dorsoventrally deeper thoraces display an even broader more flaring pelvis than *H. sapiens* with similar ribcage morphology. Note that figures are scaled to show the same distance between the most caudal cervical vertebra and the most caudal point of the ischium. No landmarks and semilandmarks were digitized on the lumbar and sacral vertebrae, so they were not involved in the warping.

Figure 6. Plot of PLS scores in LV1 (a) and LV2 (b) of the 2B-PLS analysis based on the covariance matrix of *N*=30 adult *H. sapiens* and associated shape deformations (frontal and left lateral view) at -2 standard deviations (left) and +2 standard deviations (right) of each axis' PLS scores distribution. (a) LV1 shows that males plot towards negative PLS scores and show relatively wider (lower) thoraces and narrower (upper) pelves, while females plot towards positive PLS scores and have narrower (lower) thoraces and wider (upper) pelves. Also, negative values show a much deeper ribcage compared to the positive values. (b) LV2 of the 2B-PLS analysis shows a similar but more subtle sex-related covariation: males tend to plot towards negative PLS scores and females tend to plot towards positive PLS scores. Note that figures are scaled to show the same distance between the most caudal cervical vertebra and the lowest point of the ischium. No landmarks and semilandmarks were digitized on the lumbar and sacral vertebrae, so they were not involved in the warping.

Figure 7. Plot of PLS scores in the LV1 (a) and LV2 (b) of the 2B-PLS analysis based on the covariance matrix of allometric regression residuals in *N*=30 adult *H. sapiens* and associated shape deformations (frontal and left lateral view) at -2 standard deviations (left) and +2 standard deviations (right) of each axis' PLS scores distribution. (a) LV1 of the 2B-PLS analysis shows relatively wide thoraces and wide pelves that lead to wide trunks towards negative PLS scores, while positive PLS scores show relatively narrow thoraces and narrow pelves that lead to narrow trunks. Also, lateral views show that negative PLS scores display more thoracic spine kyphosis and ribs with less torsion than positive PLS scores. (b) LV2 of the 2B-PLS analysis shows still some sexually-dimorphic features: males tend to plot towards negative PLS scores and have slightly more horizontal rib orientation, smaller subpubic angles and more sagittaly oval pelvic inlets than females towards positive PLS scores. Note that figures are scaled to show the same distance between the most caudal cervical vertebra and the lowest point of the ischium. No landmarks and semilandmarks were digitized on the lumbar and sacral vertebrae, so they were not involved in the warping.

Figure 8. Plot of PLS scores in the LV1 (a) and LV2 (b) of the 2B-PLS analysis based on the covariance matrix of *N*=10 adult *P. troglodytes* and associated shape deformations (frontal and left lateral view) at -2 standard deviations (left) and +2 standard deviations (right) of each axis' PLS scores distribution. Important: Because of the lack of significant results in the covariance explained by the singular values (Table 7), one cannot expect to interpret these shape deformations in biological terms as they are not different from what it is expected by chance. Note that figures are scaled to show the same distance between the most caudal cervical vertebra and the most caudal point of the ischium. No landmarks and semilandmarks were digitized on the lumbar and sacral vertebrae, so they are not involved in the warping.