Potential adaptations for bipedalism in modern human thoracic and lumbar vertebrae: A 3D comparative analysis

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Abstract

A number of putative adaptations for bipedalism have been identified in the hominin spine. However, it is possible that some have been overlooked, because only a few studies have employed 3D data and these studies have focused on cervical vertebrae. With this in mind, we used geometric morphometric techniques to compare the 3D shapes of three thoracic and two lumbar vertebrae of *Homo sapiens*, *Pan troglodytes, Gorilla gorilla*, and *Pongo pygmaeus*. The study had two goals. One was to confirm the existence of traits previously reported to distinguish the thoracic and lumbar vertebrae of *H. sapiens* from those of the great apes. The other was to, if possible, identify hitherto undescribed traits that differentiate *H. sapiens* thoracic and lumbar vertebrae from those of the great apes. Both goals were accomplished. Our analyses not only substantiated a number of traits that have previously been discussed in the literature but also identified four traits that have not been described before: 1) dorsoventrally shorter pedicles in the upper thoracic vertebrae; 2) dorsoventrally longer laminae in all five of the vertebrae examined; 3) longer transverse processes in the upper thoracic vertebrae; and 4) craniocaudally 'pinched' spinous processes tips in all of the vertebrae examined. A review of the biomechanical literature suggests that most of the traits highlighted by our analyses can be plausibly linked to bipedalism, including three of the four new ones. As such, the present study not only sheds further light on the differences between the spines of *H. sapiens* and great apes, but also enhances our understanding of how the shift to bipedalism affected the hominin vertebral column.

Keywords: Vertebrae; Bipedalism; Chimpanzee; Human; Gorilla; Orangutan

1. Introduction

It is now widely accepted that bipedalism is one of the most important adaptations that distinguishes hominins from other taxa (Wood and Richmond, 2000; Richmond et al., 2001; Ackermann and Smith, 2007; Harcourt-Smith, 2015). Beyond this, however, there is little agreement regarding the evolution of hominin bipedalism. Researchers disagree about when it first appeared (Haile-Selassie, 2001; Brunet et al., 2002; Pickford et al., 2002), its adaptive significance (Snyder, 1967; Chaplin et al., 1994; Videan and McGrew, 2002; Bramble and Lieberman, 2004; Sockol et al., 2007), and the locomotor behavior that preceded it (Richmond et al., 2001; Crompton et al., 2008; Lovejoy et al., 2009). They also differ over the extent to which bipedalism varied among extinct hominin species, with some arguing that all of the species employed essentially modern human-like bipedalism (e.g., Latimer and Lovejoy, 1989; Bennett et al., 2009; Raichlen et al., 2010), and others suggesting that there have in fact been several different forms of hominin bipedalism (e.g., Susman et al., 1984; Richmond et al., 2001; Harcourt-Smith and Aiello, 2004; Lovejoy et al., 2009; Prang, 2019).

Paleoanthropologists have long recognized that one way of reducing the amount of uncertainty regarding the evolution of bipedalism is to pinpoint potential adaptations for bipedalism in the skeleton of *Homo sapiens* through comparative analysis. The idea here is that identifying locomotion-related skeletal features that distinguish *H. sapiens* from other primate species will make it easier to recognize bipedal taxa in the fossil record. Not surprisingly, given the centrality of bipedalism to human evolution, this endeavor has been a major focus of the paleoanthropological community and a considerable amount of excellent work has been published (e.g., Keith, 1923; Schultz, 1938; Davis, 1961; Day and Wood, 1968; Robinson, 1972; Rose, 1975; Oxnard, 1983; Latimer and Lovejoy, 1989; Ward et al., 2011; Williams et al., 2013).

However, some parts of the skeleton require further investigation. The spine is one of these, as Williams and Russo (2015) have recently pointed out.

In the present paper, we report a study in which we used 3D shape analysis techniques (O'Higgins and Jones, 1998; Adams et al., 2004; Slice, 2005, 2007) to compare thoracic and lumbar vertebrae of *H. sapiens* with those of chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla*), and orangutans (*Pongo pygmaeus*). Our investigation was motivated by the fact that while a number of traits have been reported to distinguish the thoracic and lumbar vertebrae of *H. sapiens* from their great ape counterparts, all the relevant studies relied on 2D data. 3D shape analysis techniques have been used to compare the cervical vertebrae of *H. sapiens* to those of their close relatives (Manfreda et al., 2006; Arlegi et al., 2017, 2018; Nalley and Grider-Potter, 2017), but so far they have not been employed to identify traits that distinguish the thoracic and lumbar vertebrae of *H. sapiens* from their great ape homologues. This is potentially a problem because analyzing 3D anatomical structures with 2D methods can result in traits being mischaracterized or even missed entirely, especially when the structures are complex, as is the case with the vertebrae of primates.

The study had two goals. One was to determine whether 3D data support the existence of the traits previously reported to separate the thoracic and lumbar vertebrae of *H. sapiens* from those of the great apes. The other goal of the study was to, if possible, identify new traits that distinguish the thoracic and lumbar vertebrae of *H. sapiens* from their great ape counterparts—traits that have not been identified before because of the reliance on 2D data in previous studies.

Several of the traits we aimed to confirm relate to the vertebral body. A number of studies have found that in *H. sapiens* the bodies of the thoracic and upper lumbar vertebrae are ventrally wedged while the bodies of the lower lumbar vertebrae are dorsally wedged (e.g., Keith, 1923;

Schultz, 1961; Shapiro, 1993a; Abitbol, 1995; Ward and Latimer, 2005). The former results in thoracic kyphosis, which is a backward curvature of the thoracic part of the spine; the latter gives rise to lumbar lordosis, which is a forward curvature of the lumbar part of the spine. Together, thoracic kyphosis and lumbar lordosis produce an S-shaped spine. In contrast, the spine of great apes is often described as C-shaped (Ward and Latimer, 2005; Whitcome et al., 2007). This is a result of their lower thoracic and upper lumbar vertebrae being more ventrally wedged than in humans, and their lower lumbar lacking the dorsal wedging that creates lumbar lordosis (Schultz, 1961; Abitbol, 1995; Ward and Latimer, 2005; Whitcome et al., 2007; Been et al., 2010a, 2017). Three other traits have been reported to distinguish the vertebral bodies of the thoracic and lumbar vertebrae of *H. sapiens* from those of the great apes: greater height in the craniocaudal direction (Latimer and Ward 1993; Hernandez et al., 2009), greater depth in the dorsoventral direction (Robinson, 1972; Latimer and Ward, 1993; Hernandez et al., 2009; Plomp et al., 2015; Meyer and Williams, 2019), and gradually increasing mediolateral width as one moves down the spine (Schultz, 1953, 1961; Rose, 1975).

We also sought to confirm traits relating to the neural arch and vertebral foramina. These include dorsoventrally longer, mediolaterally narrower, and craniocaudally shorter pedicles in the lower thoracic and upper lumbar vertebrae (Shapiro, 1993b; Plomp et al., 2015; Williams et al., 2017), and mediolaterally wider pedicles in the penultimate and final lumbar vertebrae (Davis, 1961; Panjabi et al., 1993; Shapiro, 1993a,b; El-Khoury and Whitten, 1993; Sanders and Bodenbender, 1994; Whyne et al., 1998; Briggs et al., 2004; Been et al., 2010b). We also sought to confirm that the thoracic and lumbar vertebrae of *H. sapiens* have mediolaterally wider vertebral foramina than those of the great apes (Schultz, 1930; MacLarnon, 1987; MacLarnon and Hewitt, 1999; Sanders and Bodenbender, 1994; Meyer and Haeusler, 2015).

Another set of traits we sought to verify relate to the zygapophyseal facets. Previous studies have found that in *H. sapiens* the superior and inferior zygapophyseal facets are coronally oriented in all thoracic vertebrae except the final one, while in great apes these zygapophyseal facets are obliquely oriented (Latimer and Ward, 1993; Shapiro, 1993a; Williams and Russo, 2015; Meyer, 2017). The superior and inferior zygapophyseal facets of the final thoracic vertebrae of *H. sapiens* have been reported to be coronally and sagittally oriented, respectively. The homologous facets in the great apes are coronally and obliquely oriented, respectively, according to several previous studies (Latimer and Ward, 1993; Shapiro, 1993a; Russo, 2010; Williams and Russo, 2015; Meyer, 2017). Differences in orientation in the zygapophyseal facets of the lumbar vertebrae have also been reported. Several authors have found that the superior and inferior facets of the lumbar vertebrae of *H. sapiens* are sagittally oriented, while those of the great apes are more obliquely oriented (Latimer and Ward, 1993; Shapiro, 1993a; Russo, 2010; Williams and Russo, 2015; Meyer, 2017).

The remaining traits we targeted relate to the processes of the vertebrae. The transverse processes of the upper thoracic vertebrae of *H. sapiens* have been found to project cranially and laterally, while their homologues in the great apes project more dorsally (Jellema et al., 1993; Latimer and Ward, 1993; Been et al., 2012; Bastir et al., 2014, 2017). In the lower thoracic and lumbar vertebrae, the transverse processes of *H. sapiens* are reported to be shorter and to project more dorsally than those of the great apes (Jellema et al., 1993; Latimer and Ward, 1993; Been et al., 2012). Differences in the spinous processes have also been reported. The spinous processes of all the vertebrae are shorter from base to tip in *H. sapiens* than in great apes (Schultz, 1961; Ward, 1991; Latimer and Ward, 1993; Gómez-Olivencia et al., 2013; Meyer, 2016, 2017). In addition, the spinous processes of the upper thoracic vertebrae of *H. sapiens* have been found to project more caudally than those of the great apes (Latimer and Ward, 1993; Gómez-Olivencia et al., 2013).

2. Materials and methods

We used a Microscribe digitizing arm to record landmark data on vertebrae from 80 *H. sapiens*, 34 *P. troglodytes*, 27 *G. gorilla*, and 25 *Po. pygmaeus* (Table 1). The specimens are curated at the Cleveland Museum of Natural History, USA; the Natural History Museum Vienna, Austria; the Museum of Natural History Berlin, Germany; the University of Copenhagen, Denmark; the University of Zurich, Switzerland; and the Smithsonian Institution National Museum of Natural History, USA. Detailed specimen information is available in Supplementary Online Material (SOM) Table S1. Only adult specimens were included in the sample; adult status was determined on the basis of epiphyseal fusion. None of the specimens exhibited signs of pathology. Most of the great ape specimens were wild-shot, but some died in captivity.

We digitized up to five vertebrae for each specimen—first, second, and last thoracic, and the first and second lumbar. These vertebrae were selected to provide an overview of vertebral shape in the thoracic and upper lumbar spine, as well as to gain insight into the shape of vertebrae at both the upper and lower transitional ends of the thoracic spine.

To distinguish between thoracic and lumbar vertebrae, we followed the lead of Washburn and Buettner-Janusch (1952) and Shapiro (1993a, 1995) and used the orientation of the zygapophyseal facets rather than the presence and absence of costal articulations (Schultz, 1930; Haeusler et al., 2002, 2011; Williams et al., 2016). We chose this approach because the orientation and curvature of the zygapophyseal facets of primate vertebrae are important for locomotion (Ankel, 1972; Shapiro, 1991, 1993a; Boszcyyk et al., 2001; Bogduk and Twomey, 2005; Whitcome et al., 2007, 2012; Russo, 2010). Additionally, this approach allows for the analysis of subtle differences in zygapophyseal shape rather than having results impacted by the substantial differences in orientation between thoracic and lumbar facets. An important corollary of using the zygapophyseal facet-based approach to distinguishing between thoracic and lumbar vertebrae is that the term ‘last thoracic’ refers to the diaphragmatic or transitional vertebra, which has coronally oriented superior zygapophyseal facets and sagittally oriented inferior facets (Washburn and Buettner-Janusch, 1952; Shapiro, 1993a, 1995).

Table 1 provides a breakdown of the sample. The numbers of specimens per vertebral type varies within each taxon partly because some skeletons did not preserve all vertebral types, and partly because the modal number of thoracic and lumbar vertebrae varies among the taxa (Rosenberg, 1876; Keith, 1902, 1923; Benton, 1967; Whitcome, 2012; Williams, 2012a; Williams et al., 2016; Thompson and Almécija, 2017). Modern humans usually have 12 thoracic and five lumbar vertebrae, while *Po. pygmaeus* typically has 12 thoracic and four lumbar vertebrae. *Pan troglodytes* and *G. gorilla* usually have 13 thoracic vertebrae and either three or four lumbar vertebrae. This makes comparisons between lower thoracic and lumbar vertebrae difficult in terms of ensuring positional homology. For example, the last thoracic in *H. sapiens* and *Po. pygmaeus* is normally the 19th vertebra, while in *P. troglodytes* and *G. gorilla* it is usually the 20th. While we acknowledge that this is an issue in terms of positional homology, we contend that the last thoracic vertebrae is functionally homologous in all four species, and therefore, comparing these vertebrae is appropriate for the purposes of the present study. A related issue is that *P. troglodytes* and *G. gorilla* can have three or four lumbar vertebrae, which means that in these species the second lumbar vertebra can also be the penultimate lumbar vertebra. We addressed this problem by including the second lumbar vertebra of *P. troglodytes* and *G. gorilla* specimens only when the specimens had four lumbar vertebrae. Although this procedure reduced the number of second lumbar vertebrae of *P. troglodytes* and *G. gorilla* that could be included in the analyses, it ensured that their second lumbar vertebra was not also their penultimate lumbar vertebra, minimizing any functional differences between penultimate and non-penultimate lumbar vertebrae.

Table 1

Number of vertebrae examined.

Vertebra	*Homo sapiens*	*Pan troglodytes*	*Gorilla gorilla*	*Pongo pygmaeus*
First thoracic	32	27	21	21
Second thoracic	25	22	20	17
Final thoracic	66	34	24	32
First lumbar	80	33	21	25
Second lumbar	75	23	8	24

We employed a total of 54 landmarks (Fig. 1; SOM Table S2). Thirty-two of them were type II and 22 were type III (Bookstein, 1997). We selected the landmarks to capture the entire vertebra, including the shape of the body, neural arch, zygapophyseal facets, and the spinous and transverse processes. Although the landmarks were chosen specifically for this study, some of them correspond to those used in Bastir et al. (2017). In an effort to counter the effects of recording error, we digitized each vertebra twice and then averaged the coordinates for each landmark (Arnquist and Martensson, 1998).

After collecting the data, we used the approach developed by Klingenberg et al. (2002) to reduce the confounding effects of translation, rotation, size, and asymmetry on the data. The procedure was performed on each dataset separately. We began by reflecting and relabeling the landmark coordinates. We then subjected the two sets of landmark coordinates to generalized Procrustes analysis (GPA) in Morphologika (O'Higgins and Jones, 1996). GPA removes translational and rotational effects and scales landmark configurations to centroid size (Slice, 2007). Lastly, we calculated the average Procrustes coordinates for each pair of original and reflected landmarks.

Having removed the effects of asymmetry, we assessed the impact of intra-observer error on the data. To do so, we used the approach outlined by Neubauer et al. (2009, 2010). This entailed digitizing a single first lumbar vertebra ten times and then using Morphologika to compare the greatest Procrustes distance between the ten-replicated landmark configurations with the smallest Procrustes distance between the non-replicated landmark configurations of all first lumbar vertebrae. The smallest distance between the non-replicated vertebrae was almost twice the greatest distance between the repeated vertebrae. According to Neubauer et al. (2009, 2010), this amount of intra-observer error is unlikely to undermine the analysis of shape variation in a sample of the type used in the present study.

Investigating the inter-taxa shape variation involved several steps. First, we subjected each dataset to the Procrustes coordinates to principal component analysis (PCA) to visualize the shape variance of vertebrae. Next, we implemented the principal component (PC) reduction procedure outlined by Baylac and Frieβ (2005) and Evin et al. (2013). This procedure aims to reduce noise from PCs that account for little variance, while still retaining all relevant shape information. It tackles this optimization problem by progressively adding PCs into the analyses until the cross-validation percentage (CVP) begins to drop. Thereafter, the retained PCs were subjected to multivariate analysis of variance (MANOVA) to assess the statistical significance of the inter-taxon shape differences. Subsequently, the PC scores were subjected to discriminant function analysis (DFA) with cross-validation to determine the accuracy of using vertebral shape to distinguish the four taxa. The method we used was outlined by Evin et al. (2013). To reduce the redundancy of data, only the DFA scores that corresponded to the PCs with the highest CVP were considered (White and Ruttenberg, 2007; Kimmerle et al., 2008; Cardini et al., 2009). The five types of vertebrae were analyzed separately.

The data used in the study can be downloaded from Mendeley Data (https://doi.org/10.17632/8r25v762vd.1). The PCAs were performed in Morphologika (O'Higgins and Jones, 1996), the DFAs and Procrustes distances analyses in R (R Development Core Team, 2017), and the MANOVAs in SPSS (IBM Inc, 2017).

3. Results

Table 2 shows the number of PCs that yielded the highest cross-validation percentage for each type of vertebra. The number of PCs included in the analyses ranged from 10 to 28. The retained PCs accounted for 78–92% of the shape variance.

Table 2

Results of the principal components analysis, including the principal components (PCs) that yielded the highest cross-validated percentages for each dataset and the total amount of variance for which they account.

Vertebra	PCs	% variance
First thoracic	1–10	78.8
Second thoracic	1–13	78.4
Final thoracic	1–27	91.2
First lumbar	1–28	92.3
Second lumbar	1–22	90.6

The MANOVAs and DFAs indicate that there are marked differences between *H. sapiens* and the great apes in the vertebrae under consideration. *Homo sapiens* is significantly different from *P. troglodytes, G. gorilla*, and *Po. pygmaeus* in all five vertebrae, according to the MANOVAs (Table 3). Consistent with this, 100% of the *H. sapiens* vertebrae were correctly classified in the DFAs (Table 4). The great ape vertebrae were also correctly classified at a high rate, with DFA results of 95–100% for *P. troglodytes* vertebrae, 95–100% for *G. gorilla* vertebrae, and 100% for *Po. pygmaeus* vertebrae.

Table 3

Results of pairwise multivariate analysis of variance (MANOVA) on the cross-validated percentages principal components for each vertebra.

Vertebra	Comparison	MANOVA results
First thoracic	*H. sapiens–P. troglodytes*	$\lambda = 0.049$, $F = 92.792$, $p < 0.0001$
	H. sapiens–Po. pygmaeus	$\lambda = 0.054$, $F = 73.855$, $p < 0.0001$
	H. sapiens–G. gorilla	$\lambda = 0.035$, $F = 114.217$, $p < 0.0001$
Second thoracic	*H. sapiens–P. troglodytes*	$\lambda = 0.095$, $F = 24.208$, $\underline{\mathrm{p}} < 0.0001$
	H. sapiens–Po. pygmaeus	$\lambda = 0.026$, $F = 81.353$, $p < 0.0001$
	H. sapiens–G. gorilla	$\lambda = 0.051$, $F = 44.602$, $p < 0.0001$
Last thoracic	*H. sapiens–P. troglodytes*	$\lambda = 0.099$, $F = 24.332$, $p < 0.0001$
	H. sapiens–Po. pygmaeus	$\lambda = 0.085$, $F = 27.867$, $p < 0.0001$
	H. sapiens–G. gorilla	$\lambda = 0.048$, $F = 50.709$, $p < 0.0001$
First lumbar	*H. sapiens–P. troglodytes*	$\lambda = 0.091$, $F = 29.820$, $p < 0.0001$
	H. sapiens–Po. pygmaeus	$\lambda = 0.070$, $F = 36.013$, $p < 0.0001$
	H. sapiens–G. gorilla	$\lambda = 0.095$, $F = 25.996$, $p < 0.0001$
Second lumbar	*H. sapiens–P. troglodytes*	$\lambda = 0.120$, $F=24.946$, $p < 0.0001$
	H. sapiens–Po. pygmaeus	$\lambda = 0.171$, $F=16.775$, $p < 0.0001$
	H. sapiens–G. gorilla	$\lambda = 0.130$, $F=12.973$, $p < 0.0001$

Table 4

Percentage of correctly classified specimens in cross-validated discriminant function analyses based on the cross-validated percentages principal components for each vertebra.

Taxon	First thoracic	Second thoracic	Last thoracic	First lumbar	Second lumbar
Homo sapiens	100.0%	100.0%	100.0%	100.0%	100.0%
Pan troglodytes	100.0%	95.4%	97.0%	99.0%	100.0%
Gorilla gorilla	100.0%	95.0%	95.8%	95.2%	100.0%
Pongo pygmaeus	100.0%	100.0%	100.0%	100.0%	100.0%

The traits that will be used to describe the vertebral shape are illustrated in Figure 2. Figures 3–7 plot the scores for PC1 against those for PC2 for the five vertebral types. The PC1s account for 22–35% of the shape variance, while the PC2s account for 11–20%. The wireframe images illustrate the shape differences between the positive and negative extremes of each PC.

Figures 3 and 4 show that the first and second thoracic vertebrae of *H. sapiens* differ from those of *P. troglodytes, G. gorilla*, and *Po. pygmaeus* in several ways (Figs. 3 and 4). Compared to their great ape counterparts, modern human upper thoracic vertebrae tend to have 1) bodies that are relatively tall and wide; 2) transverse processes that are relatively long and project more cranially and laterally; 3) vertebral foramina that are relatively wide; 4) pedicles that are relatively shallow (i.e., small in the dorsoventral direction); 5) articular facets that are more coronally oriented; 6) laminae that are relatively deep (i.e., relatively large in the dorsoventral direction); and 7) spinous processes that are relatively short, more caudally directed, and more craniocaudally pinched at the tip.

Figure 5 indicates that the final thoracic vertebrae of *H. sapiens* also differ from those of the great apes (Fig. 5), but the pattern diverges from that observed in the two upper thoracic vertebrae. In comparison to those of the great apes, the final thoracic vertebrae of *H. sapiens* tend to have 1) vertebral bodies that are longer in the craniocaudal and dorsoventral directions, more heart-shaped superior endplates, and exhibit less ventral wedging; 2) transverse processes that are shorter from base to tip and more dorsally oriented; 3) vertebral foramina that are dorsoventrally longer and mediolaterally wider; 4) pedicles that are longer in the dorsoventral direction and narrower in the mediolateral direction; 5) laminae that are longer in the dorsoventral direction; and 6) spinous processes that are dorsoventrally shorter and have craniocaudally pinched tips. In contrast to the situation with the first and second thoracic vertebrae, there are no obvious differences between the articular facets of the final thoracic vertebrae of modern humans and those of the great apes.

The shape differences between the lumbar vertebrae of *H. sapiens* and those of great apes are the same as those observed with the final thoracic vertebrae, but there are two additional ones (Figs. 6 and 7). One is that the bodies of lumbar vertebrae in *H. sapiens* tend to exhibit dorsal wedging (i.e., the ventral border of the vertebral body is noticeably craniocaudally longer than the dorsal border) while those of the great apes do not. The other is that the superior and inferior articular facets of the lumbar vertebrae of *H. sapiens* are more sagittally oriented than those of great apes.

4. Discussion

4.1. Traits that distinguish H. sapiens *vertebrae from those of the great apes*

In this study, we used 3D morphometric methods to identify traits distinguishing human thoracic and lumbar vertebrae from those of great apes. Table 5 summarizes the traits that our analyses suggest tend to distinguish *H. sapiens* vertebrae from those of the great apes and indicates whether the traits have been identified previously. The traits are arranged according to where they occur on the vertebra, starting with the vertebral body and moving backwards.

Our analyses identified four traits that, to the best of our knowledge, have not previously been recognized. Two of these traits are present in all the vertebral types we analyzed. In all five vertebrae, the laminae of *H. sapiens* tend to be relatively long in the dorsoventral direction compared to those of the great apes, and the spinous processes of *H. sapiens* tend to have more pinched tips than their great ape counterparts. The other two new traits are present only in the first and second thoracic vertebrae. One is that the pedicles of *H. sapiens* are reduced in length in the dorsoventral direction whereas those of the great apes are not. The other is that the transverse processes of *H. sapiens* tend to be relatively longer from base to tip than those of the great apes.

As expected, the majority of the traits have previously been described. This is the case for all the traits of the vertebral body. A number of studies, including Keith (1923), Latimer and Ward (1993), and Hernandez et al. (2009) have reported that bodies of the vertebrae are craniocaudally taller in *H. sapiens* than in the great apes, while Schultz (1953, 1961) and Rose (1975) noted that the bodies of the upper thoracic vertebrae of *H. sapiens* are mediolaterally wider than those of the great apes. Several authors, including Schultz (1961), Abitbol (1995), Ward and Latimer (2005), Shapiro (1993a), Whitcome et al. (2007), and Been et al. (2010a, 2017), have observed that, although variable, the bodies of the lower thoracic vertebrae of *H. sapiens* generally exhibit less ventral wedging than do those of the great apes. That the bodies of the lower thoracic vertebrae of *H. sapiens* are dorsoventrally longer than those of the great apes was noted by Robinson (1972) and Plomp et al. (2015). These authors also noted that the superior endplates of the last thoracic and first and second lumbar vertebrae of *H. sapiens* are more heart-shaped than those of great apes. Lastly, a number of scholars have noted that the bodies of the first and second lumbar vertebrae of *H. sapiens* lack the ventral wedging seen in their great ape homologues (Schultz, 1961; Abitbol, 1995; Ward and Latimer, 2005; Shapiro, 1993a; Whitcome et al., 2007; Been et al., 2010a, 2017).

The traits related to the vertebral foramina have also been identified in previous studies. The greater mediolateral width of the vertebral foramina of the thoracic and lumbar vertebrae of *H. sapiens* compared to those of great apes was highlighted by Schultz (1930), MacLarnon (1987), MacLarnon and Hewitt (1999), Sanders and Bodenbender (1994), and Meyer and Haeusler (2015). Among the researchers who have noted the greater dorsoventral size of the vertebral foramina of the last thoracic and first two lumbar vertebrae of *H. sapiens* are MacLarnon (1987), Latimer and Ward (1993), Sanders and Bodenbender (1994), and MacLarnon and Hewitt (1999).

Two of the three pedicle traits have been highlighted before. That the pedicles of the last thoracic and the first and second lumbar vertebrae of *H. sapiens* are dorsoventrally longer than those of the great apes was pointed out recently by both Plomp et al. (2015) and Williams et al. (2017). These authors also noted that the pedicles of the last thoracic and the first and second lumbar vertebrae of *H. sapiens* are mediolaterally narrower than those of the great apes.

All the traits pertaining to the articular facets have been discussed in the past. Several authors have noted that the superior articular facets of the thoracic vertebrae of *H. sapiens* are more coronally oriented than are those of the great apes, and that the superior articular facets of modern human first and second lumbar vertebrae are more sagitally oriented than those of great apes (Latimer and Ward, 1993; Shapiro, 1993a; Williams and Russo, 2015; Meyer, 2017). The same authors have also noted that the inferior articular facets of the upper thoracic vertebrae of *H. sapiens* are more coronally oriented than those of the great apes, and that the inferior articular facets of the last thoracic and upper lumbar vertebrae of *H. sapiens* are more sagitally oriented than their great ape equivalents.

Three of the four traits relating to the transverse processes have been noted before. Several authors have pointed out that the transverse processes of *H. sapiens* upper thoracic vertebrae project more cranially and laterally than their great ape equivalents (Jellema et al., 1993; Latimer and Ward, 1993; Been et al., 2012; Bastir et al., 2014, 2017). Some of these authors have also noted that the transverse processes of the last thoracic and first and second lumbar vertebrae tend to be both shorter from base to tip and more dorsally oriented (Latimer and Ward, 1993; Jellema et al., 1993; Sanders, 1998; Been et al., 2012).

Previous work has highlighted two of the three spinous process traits. That the spinous processes of *H. sapiens* are shorter than those of the great apes has been pointed out by Schultz (1961), Ward (1991), Latimer and Ward (1993), Gómez-Olivencia et al. (2013), Meyer (2016, 2017), Shapiro and Kemp (2019), among others. Latimer and Ward (1993) and Gómez-Olivencia et al. (2013) have previously reported that the spinous processes of the upper thoracic vertebrae of *H. sapiens* project more caudally than their homologues in the great apes.

Our analyses failed to confirm three traits that previous studies found to distinguish the thoracic and lumbar vertebrae of *H. sapiens* from their great ape counterparts. Schultz (1953, 1961) and Rose (1975) reported that there is an increase in the mediolateral width of the vertebral body as one moves down the thoracic and lumbar regions of the spine in *H. sapiens* but not in the great apes. Our analyses did not support the existence of this difference. We found that the first and second thoracic vertebrae of *H. sapiens* are wider than those of great apes but we did not find a difference in the width of the last thoracic and the first and second lumbar vertebrae. To check this finding, we created a dataset that included all three lower vertebrae and subjected it to PCA. Again, we were unable to identify the putative increase in mediolateral width (SOM Fig. S1). It seems likely that this discrepancy is due to the fact that we scaled our data to remove the effects of centroid size, because when the raw distances between the landmarks on either side of the vertebral body are measured, there is a progressive increase in distance from the last thoracic to the second lumbar vertebrae in *H. sapiens* (interlandmark distances: last thoracic = 37; first lumbar = 38; second lumbar = 41).

The second trait that our analyses failed to confirm relates to the wedging of the lumbar vertebral bodies. Whitcome et al. (2007) and Been et al. (2010a) found that the upper lumbar vertebrae of *H. sapiens* are ventrally wedged. In contrast, we found dorsal wedging in these vertebrae. The reason for this difference is not entirely clear, but we suspect it may be due to the methods used. Whitcome et al. (2007) and Been et al. (2012) employed 2D data obtained from in vivo images of living humans whereas we utilized 3D data recorded on dry bone specimens. Hence, the difference between our results and those of Whitcome et al. (2007) and Been et al. (2012) could be due to a difference in measurement accuracy between 2D and 3D methods, or a difference in measurement accuracy between in vivo and skeletal data. Alternatively, it is possible that vertebral wedging is a trait that varies intraspecifically and that the difference between the studies is caused by the difference in samples (Zlolniski et al. 2019). Ascertaining which of these hypotheses is correct will require further research.

The third trait that our analyses failed to confirm is one that Shapiro (1993b) reported—the pedicles of the lower thoracic and the upper lumbar vertebrae of *H. sapiens* are craniocaudally shorter than those of the great apes. We suspect the issue here is landmark choice. While our analyses did indicate that the pedicles of *H. sapiens* lower vertebrae are longer in the dorsoventral direction and narrower in the mediolateral direction, our decision to place only one landmark on the inferior border of the pedicle meant that we were unable to capture any other shape differences. In hindsight, it is clear that we should have included additional landmarks.

4.2. Bipedalism and the traits of that distinguish H. sapiens *thoracic and lumbar vertebrae from those of the great apes*

Most of the traits listed in Table 5 have been posited to be adaptations for bipedalism in previous studies. In this section, we will discuss these hypotheses and also consider whether the four newly identified traits can be linked to bipedal posture and gait. Before we do so, it is important to point out that very few hypotheses have been tested with comparative analyses in which phylogenetic effects have been controlled let alone experimentally tested. As such, they should be treated with caution as not all vertebral traits unique to humans are necessarily adaptations to bipedalism.

<u>Vertebral body</u> Several of the traits relate to the vertebral body. The ones that can be most easily linked to bipedalism involve wedging of the vertebral body. To reiterate, like a number of other researchers, we found that the last thoracic vertebra of *H. sapiens* exhibits less ventral wedging than its counterparts in the great apes. We also found that the first and second lumbar vertebrae of *H. sapiens* display more dorsal wedging than their great ape equivalents. This pattern of wedging results in the unique S-shape of the *H. sapiens* spine, which brings the centre of mass over the hips and therefore plays a crucial role in bipedal posture and gait (Schultz, 1961;

Abitbol, 1995; Ward and Latimer, 2005; Shapiro, 1993a; Whitcome et al., 2007; Been et al., 2012, 2017).

The greater mediolateral width of the bodies of the first and second thoracic vertebrae of *H. sapiens* can also potentially be linked to bipedalism. Wide vertebral bodies have been hypothesized to better withstand compressive loads than narrow ones (Davis, 1961; Rose, 1975; Shapiro, 1991, 1993a; Latimer and Ward, 1993; Hernandez et al., 2009) and there is reason to think that the bipedal posture and gait of *H. sapiens* results in its upper thoracic vertebrae experiencing higher compressive loads than those of the great apes. Although there is not a marked difference in the weight of the crania of modern humans and great apes (Schultz, 1942), the head is positioned more directly above the neck in the former and this can be expected to result in a greater compressive load on the upper thoracic vertebrae (Meyer et al., 2017). In addition to this, the upper thoracic vertebrae of *H. sapiens* always have to support the entire weight of the arms during locomotion whereas those of the great apes do so only occasionally (Nimbarte et al. 2010). Thus, the compressive loads on the upper thoracic vertebrae of *H. sapiens* and great apes likely differ in a way that is consistent with the hypothesis that the comparatively greater width of the upper thoracic vertebrae of *H. sapiens* is an adaptation for bipedalism.

The two traits that are specific to the bodies of the last thoracic and upper lumbar vertebrae may also be adaptations for resisting the compressive loads associated with bipedalism. Their greater dorsoventral length means that they have a relatively larger surface area, and this has been hypothesized to enable them to withstand the higher compressive loads that act on the lower spine of *H. sapiens* as a consequence of bipedalism (Davis, 1961; Rose, 1975; Shapiro, 1991, 1993a; Latimer and Ward, 1993; Hernandez et al., 2009). Their heart-shaped outline has been linked to compressive loading via the shape of the intervertebral disc, which is necessarily also heart-shaped (Harrington et al. 2001). It has been suggested a disc of this shape is able to withstand compressive forces better than a more ovoid one because it has a shorter radius (Harrington et al. 2001; Letic, 2012). This hypothesis is based on LaPlace's Law, which states that the ability of a fluid-filled tube like the intervertebral disc to withstand compression decreases with an increase in the tube's radius (Harrington et al. 2001; Letić, 2012). The possibility that the development of more heart-shaped bodies in the last thoracic and upper lumbar vertebrae of *H. sapiens* is an adaptation to withstand the compressive loading associated with bipedalism is supported by studies in which modern human vertebrae with signs of intervertebral disc herniation were found to be less heart-shaped than healthy specimens (Harrington et al. 2001; Plomp et al., 2012, 2015a, b).

Currently it is unclear whether the remaining vertebral body trait—their greater relative craniocaudal height in all of the vertebrae examined—is related to bipedalism. Living great apes have shorter lumbar spines than other primates due to a reduction in the number and height of the lumbar vertebrae (Shapiro, 1993a; Williams, 2012b; Whitcome, 2012, 2017) and this has been argued to result in a stiffer lower back (Rose, 1975; Jungers, 1984; Latimer and Ward, 1993; Shapiro, 1993a; Ward, 1993; Williams, 2012b). An obvious corollary of this hypothesis is that species with more vertebrae and/or craniocaudally taller vertebral bodies can be expected to have more flexible spines (Rose, 1975; Ward, 1993; Sanders and Bodenbender, 1994; Williams and Russo, 2015). However, a recent study by Thompson et al. (2015) found that the range of motion is similar during bipedal walking in both chimpanzees and modern humans, which suggests that the greater height of the vertebrae of *H. sapiens* may not in fact give rise to greater spinal flexibility. At the moment, then, it seems best to conclude that, if the larger craniocaudal size of the thoracic and lumbar vertebrae of *H. sapiens* has a function, that function is uncertain.

Neural arch and vertebral foramen Our analyses identified several traits that relate to the neural arch and vertebral foramen. These include the traits concerning the size of the laminae and pedicles, which contribute to the neural arch and delineate the sides of the vertebral foramen. They also include the two traits that reference the dimensions of the vertebral foramina.

Taken together, these traits indicate that in all the vertebrae examined, the vertebral foramen of *H. sapiens* is larger than those of the great apes, but the difference is greater in the lower thoracic and upper lumbar vertebrae than in the upper thoracic vertebrae. In the latter vertebrae the vertebral foramina are only larger in a mediolateral direction, whereas in the lower thoracic and upper lumbar vertebrae the vertebral foramina are larger in both mediolateral and dorsoventral directions. The laminae of *H. sapiens* are relatively dorsoventrally longer than those of the great apes in all five vertebrae examined, so this difference between the two sets of vertebrae does not seem to be due to the laminae. Rather, it appears to be a consequence of a difference in the pedicles. The pedicles of *H. sapiens* are dorsoventrally shorter than those of the great apes in the upper thoracic vertebrae but longer in the lower thoracic and upper lumbar vertebrae. In addition, the pedicles of the lower thoracic and upper lumbar vertebrae of *H. sapiens* are mediolaterally narrower than their great ape counterparts, which further increases the size of the relevant vertebral foramina.

A number of hypotheses that link the enlarged vertebral foramina of *H. sapiens* with bipedalism have been proposed (MacLarnon, 1987; Latimer and Ward, 1993; Sanders and Bodenbender, 1994; MacLarnon and Hewitt, 1999). Two of these hypotheses have yet to be refuted. Sanders and Bodenbender (1994) suggested that the vertebral foramina of the lumbar vertebrae of *H. sapiens* are larger than those of other primates because bipedalism requires exceptional control of muscle movements in the lower limbs. This necessitates large lumbar spinal nerves and spinal nerve roots and therefore large vertebral foramina. Sanders and Bodenbender (1994) based this hypothesis on previous work that had identified an association between vertebral foramina size and the nerves for limb motor control in a number of species, including *H. sapiens* (e.g., Thomas and Combs, 1962, 1965; O'Higgins et al., 1989).

Latimer and Ward (1993) noted that the vertebral foramina of *H. sapiens* are larger than those of great apes and posited that this is a byproduct of caudally increasing inter-facet distances in the thoracic and lumbar spine, which they argued is an important adaptation for bipedalism. The idea here is that without the increase in inter-facet distance, lumbar lordosis would result in the impingement of the articular facets of adjoining lumbar vertebrae, potentially causing trauma to the posterior vertebral elements (Ward and Latimer, 2005; Ward et al., 2007).

Latimer and Ward's (1993) explanation for the enlarged vertebral foramina in the vertebrae of *H. sapiens* appears more compelling than the hypothesis suggested by Sanders and Bodenbender (1994) because greater foramen size continues to the foruth and fifth lumbar vertebrae, which are both lower than the terminus of the spinal cord in *H. sapiens* (Noback and Harting, 1971).

It is believed that, in addition to protecting the spinal cord, the neural arches play a role in load bearing during bipedalism (Adams and Hutton, 1980; 1985; Shapiro, 1993a,b; Hongo et al., 1999; Bogduk and Twomey, 2005). Specifically, the laminae and pedicles are thought to transmit loads between the articular facets and the vertebral body (El-Khoury and Whitten, 1993; Pal and Routal, 1987; Whyne et al., 1998). This hypothesis is hard to reconcile with the finding that the pedicles and laminae of the thoracic and lumbar vertebrae of *H. sapiens* are dorsoventrally longer than those of the great apes. Without an increase in thickness, a longer structure can be expected to be less capable of withstanding loading than a shorter one. Thus, the difference in length between the pedicles and laminae of *H. sapiens* and great apes is contrary to what we would expect to see if the pedicles and laminae of *H. sapiens* were adapted to the additional compressive loading associated with bipedalism. While the biomechanical significance of the shape of pedicles and laminae deserves further investigation, it seems reasonable to conclude for now that their greater relative size in *H. sapiens* compared to the great apes is only indirectly linked to bipedalism via the size of the spinal cord.

<u>Articular facets</u> Our analyses confirmed that the articular facets of the first and second thoracic vertebrae of *H. sapiens* are more coronally oriented than those of the great apes, and that the articular facets of the first and second lumbar vertebrae of *H. sapiens* are more sagitally oriented than their great ape counterparts. These differences in facet orientation have been linked to vertebral slippage and rotation in the context of posture and gait (Shapiro, 1993a; Whitcome, 2012). Because the great apes' centre of mass is located higher in the torso than it is in humans, their spines experience a ventral gravitational pull. As a consequence of this, the facets of their lumbar vertebrae need to resist both slippage and rotation. The facets' oblique orientation is thought to be a solution to this problem (Bogduk and Twomey, 2005; Shapiro, 1991, 1993a; Ward and Latimer, 1991, 2005; Masharawi et al., 2008; Russo and Shapiro, 2013; Williams and Russo, 2015). The situation is hypothesized to be different for modern humans because they are bipedal. It has been argued that the articular facets of the thoracic vertebrae of *H. sapiens* are oriented towards the coronal plane because this stops the vertebrae from slipping forward when standing upright (Shapiro, 1993a; Been et al., 2010a). Conversely, the articular facets of the lumbar vertebrae of *H. sapiens* are oriented towards the sagittal plane in order to resist rotation, which likely helps protect the intervertebral discs and spinal cord from injury, as well as maintaining lumbar lordosis (Ahmed et al., 1990; Shapiro, 1993a; Been et al., 2010a, Jaumard et al., 2011).

Transverse processes Like a number of other scholars, we found that the transverse processes of the last thoracic and the first and second lumbar vertebrae of *H. sapiens* are, on average, shorter from base to tip than those of the great apes (Latimer and Ward, 1993; Jellema et al., 1993; Sanders, 1998; Been et al., 2012). The transverse processes of the lower thoracic and lumbar vertebrae are attachment sites for the erector spinae muscles, which control the sagittal and lateral flexibility of the lower spine (Shapiro and Jungers, 1988, 1994; Shapiro, 1993a; Been et al., 2010a). Accordingly, their length is thought to be linked to posture and locomotion in primates (Benton, 1967; Sanders and Bodenbender, 1994; Shapiro, 1993a; Ward, 1993; Shapiro, 1995; Johnson and Shapiro, 1998). Specifically, short transverse processes in the lower vertebrae are believed to restrict the moment arm of the erector spinae muscles and therefore limit the amount of lateral flexion that can occur in the lower spine (Shapiro, 1993a; Sanders, 1998; Argot, 2003; Been et al., 2010a).

Our identification of a more dorsal orientation of the transverse processes in the last thoracic and first and second lumbar vertebrae of *H. sapiens* is likely related to bipedalism via invagination of the vertebral column (Jellema et al., 1993; Latimer and Ward, 1993; Ward et al., 2012; Williams and Russo, 2015; Bastir et al., 2017). One of the effects of invagination, which positions the vertebral column forward in the thorax, is to increase the length of the lever arms of the epaxial muscles (Bogduk et al., 1992; Shapiro, 1993a, 2007; Sanders, 1998; Filler et al., 2007; Whitcome et al., 2007; Been et al., 2010a; Gómez-Olivencia et al., 2017). This in turn increases the muscles' ability to extend the spine, resist lateral flexion, and maintain lumbar lordosis during bipedal posture and gait (Benton, 1967; Jellema et al., 1993; Latimer and Ward, 1993, 2005; Sanders and Bodenbender, 1994; Shapiro, 1993a, 1995; Ward, 1993; Sanders, 1998; Argot, 2003; Been et al., 2010a; Ward et al., 2012; Gómez-Olivencia et al., 2017).

The relatively long transverse processes of the first and second thoracic vertebrae of *H. sapiens* may also be linked with bipedalism. Because the functional morphology of the thoracic region of the spine has not received much attention to date (Shapiro, 1993a), the possible functional significance of this trait must be assessed on the basis of what has been proposed in connection with other spinal regions. As discussed above, the short transverse processes of the lumbar vertebrae of *H. sapiens* are thought to restrict lateral flexion in the lower spine (Shapiro, 1993a; Sanders, 1998; Argot, 2003; Been et al., 2010a). An obvious implication of this is that the relatively long transverse processes of the upper thoracic vertebrae of *H. sapiens* allow some lateral flexion in the upper spine (Shapiro, 1993a). Lateral flexion in the thoracic spine has been proposed to be related to throwing (Atwater, 1979; Young et al., 1996), but it could also be advantageous in walking and running since both involve rotation of the torso (Thorstensson et al. 1984; Schache et al., 2002). Of course, it is also possible that the long transverse processes of the first and second thoracic vertebrae of *H. sapiens* may not be functionally significant. Experimental research into the biomechanical role of transverse process length in the upper spine of humans is needed to assess these possibilities.

The more cranial and lateral projection of modern human transverse processes may also allow for some lateral flexion of the upper spine. Studies of the primate lumbar spine have suggested that cranially and laterally projecting transverse processes increase lateral flexion by moving the erector spinae and quadratus lumborum muscles farther from the axis of lateral flexion motion (Gambaryan, 1974; Shapiro, 1993a, 2007; Sanders, 1998; Filler, 2007; Been et al., 2010a). Given this, it seems plausible that the orientation of the transverse processes of the upper thoracic vertebrae of *H. sapiens* may increase the leverage of the longissimus subdivision of the erector spinae muscles, thereby allowing lateral flexion in the thoracic spine (Shapiro, 1993a, 2007;

Sanders, 1998). Thus, the transverse processes' more cranial and lateral projection may also be functionally related to bipedalism.

Spinous process Three of the traits identified in our analyses relate to the spinous processes. A spinous process that is short from base to tip, was present in all five vertebral types we analyzed. Body mass has been hypothesized to influence the variation in spinous process length among primate species (Shapiro and Simons, 2002). However, the shortness of the spinous processes of *H. sapiens* compared to those of *P. troglodytes, G. gorilla*, and *Po. pygmaeus* cannot be explained by body size. This is because *H. sapiens* is neither the largest nor the smallest of the four taxa. With an average body mass of 59 kg (Jungers, 1988), *H. sapiens* is markedly smaller than *G. gorilla*, whose average body mass is 121 kg (Smith and Jungers 1997), and a few kilograms larger than *P. troglodytes*, whose average body mass is 53 kg (Smith and Jungers 1997).

Because body mass cannot explain the shortness of the spinous processes in *H. sapiens*, a number of researchers have proposed that this trait is related to the biomechanical demands of bipedalism (Ritcher, 1970; Ward, 1991; Ward and Latimer, 1993; Meyer, 2016, 2017). Their argument focuses on the multifidus muscle, which inserts on the spinous processes and helps stabilize the spine by controlling movement in the sagittal plane (Waters and Morris, 1972; Shapiro and Jungers, 1988, 1994; Panjabi et al., 1989; Shapiro, 1993a; Shapiro et al., 2005). The relatively short spinous processes in the lower thoracic and lumbar vertebrae of *H. sapiens* are argued to decrease the lever arms for the spinal extensor muscles and limit the sagittal mobility of the spine (Ward, 1991; Shapiro, 1993a, 2007; Sanders, 1998; Argot, 2003; Meyer, 2016; Gómez-Olivencia et al., 2017; Shapiro and Kemp, 2019). Needless to say, the presence of a trait that likely limits the mobility of the modern human spine in the sagittal plane adds weight to our previous suggestion that the 'tallness' of the thoracic and lumbar vertebral bodies in *H. sapiens* is likely not an adaptation for dorsomobility.

Turning now to the caudally projecting spinous processes of the first and second thoracic vertebrae of *H. sapiens*, hypotheses linking this trait with bipedalism have been proposed by Shapiro (1993a, 1995, 2007; see also Shapiro et al., 2005) and Latimer and Ward (1993). Shapiro argued that caudally projecting spinous processes stabilize the spine in the sagittal plane by reducing the lever arm of the extensor muscles in orthograde posture. Latimer and Ward (1993) suggested that the greater caudal projection of the spinous processes in *H. sapiens* compared to *P. troglodytes* is linked to modern humans' thoracic kyphosis. The greater caudal projection, they proposed, ensures that the processes do not impinge on each other in the lordotic curves while also allowing consistent spacing between each process throughout the spine. These hypotheses are not necessarily mutually exclusive. It is possible that the greater caudal projection of the spinous processes stabilizes the spine while also ensuring adequate spacing between adjacent processes (Latimer and Ward, 1993; Shapiro, 1993a, 1995, 2007; Sanders and Bodenbender, 1994; Shapiro et al., 2005; Shapiro, 2007; Gómez-Olivencia et al., 2013).

The new spinous process feature revealed by our analyses—a craniocaudal 'pinching' of the spinous process tip in all the vertebrae examined—may also be linked with bipedalism. This trait has been identified in the lumbar vertebrae of some non-hominin species and two different hypotheses have been put forward to account for it. First, based on their presence in the lumbar vertebrae of ateline monkeys and certain carnivoran species, craniocaudally 'pinched' spinous process tips have been suggested to allow for more sagittal flexibility and motion due to expansion of the interspinal distance available for the supraspinous and interspinous ligaments (Erikson, 1963; Gambaryan, 1974; Shapiro, 1993a). The second hypothesis was developed to explain the presence of craniocaudally pinched process tips in the lumbar vertebrae of the gerenuk (*Litocranius walleri*), a species of gazelle that often stands on its rear legs when feeding on the leaves of trees. It was suggested that the craniocaudally 'pinched' process tips provide more space between the processes of adjoining vertebrae, which allows for a small amount of lumbar lordosis without the processes impinging on one another (Ritcher, 1970; Cartmill and Brown, 2017). Given that the other spinous process traits of *H. sapiens* appear to be involved in stabilizing the spine in the sagittal plane, we propose that the second of these hypotheses may be more accurate. That is, we suggest that the pinched spinous process tips of the thoracic and lumbar vertebrae of *H. sapiens* may ensure adequate spacing between processes in relation to the thoracic and lumbar curves of the S-shaped modern human spine play a crucial role in bipedalism (Erikson, 1963; Ritcher, 1970; Gambaryan, 1974; Shapiro, 1993a; Cartmill and Brown, 2017).

4.3. Additional observations

Lastly, it is worth highlighting the fact that there was more overlap between *H. sapiens* and *Pa. troglodytes* in the plots generated for the first and second thoracic vertebrae than in those for the lower vertebrae (Figs. 3 and 4) and that as one moves down the spine, *H. sapiens* is located increasingly farther from the great apes (Fig. 3–7). Given that *Pan* and *Homo* share a common ancestor to the exclusion of *Gorilla* and *Pongo* but have different locomotor behaviors, this pattern suggests that the upper vertebrae of modern humans have retained more ancestral traits than their lower vertebrae. This in turn suggests that the upper vertebrae have undergone less change than the lower vertebrae during the evolution of bipedalism in the lineage leading to modern humans. The development of lumbar lordosis is an obvious potential reason why the lower vertebrae would have undergone more evolutionary change than the upper vertebrae. Evaluating this hypothesis will require further research, including comparisons of fossil ape and hominin vertebrae.

5. Conclusions

The study reported here compared the 3D shapes of three thoracic and two lumbar vertebrae of *H. sapiens* and the great apes with a view to: 1) confirming the existence of traits previously reported to distinguish the thoracic and lumbar vertebrae of *H. sapiens* from those of the great apes and to create descriptive models of how the traits covary both within individual vertebrae and between the different regions; and 2) identifying new traits that distinguish the thoracic and lumbar vertebrae of *H. sapiens* from their great ape counterparts.

Our analyses supported the existence of several traits suggested by earlier studies to distinguish modern human vertebrae from those of great apes. In addition, we identified four traits that differentiate *H. sapiens* from the great apes and, to the best of our knowledge, have not been identified previously; these are: 1) dorsoventrally shorter pedicles in the first and second thoracic vertebrae; 2) dorsoventrally longer laminae in all of the vertebrae examined; 3) longer transverse processes in the first and second thoracic vertebrae; and 4) craniocaudally pinched spinous process tips in all the vertebrae examined.

Most of the traits that distinguish modern human thoracic and lumbar vertebrae from their homologues in the great apes can plausibly be linked to bipedalism. This includes three of the four new traits. There is reason to think that the dorsoventrally longer laminae may increase the size of the vertebral foramina so that it can accommodate the nerves required for bipedalism. The pinched spinous process tips may help maintain lumbar lordosis, while the long transverse processes of the upper thoracic vertebrae may allow for some lateral flexion, which may be advantageous in walking and running since both involve rotation of the torso.

The identification of four new traits that distinguish modern human thoracic and lumbar vertebrae from their great ape homologues highlights the power of 3D morphometric techniques relative to traditional, 2D methods. Applying the same approach to additional vertebrae of modern humans and great apes and extending the sample to include extinct hominins and apes is an obvious next step.

Table 5

Traits that distinguish modern human thoracic and lumbar vertebrae from their great ape homologues, according to the results of the present study. The traits are arranged according to where they occur on the vertebra, starting with the vertebral body and moving backwards. Where the second column indicates that a trait has been recognized previously.

Trait	Previously noted?	Sources
The bodies of all the vertebrae examined are taller (i.e., larger in the craniocaudal direction) in *H. sapiens* than in the great apes.	Yes	Latimer and Ward (1993), Hernandez et al. (2009)
The bodies of the 1st and 2nd thoracic vertebrae are wider (i.e., larger in the mediolateral direction) in *H. sapiens* than in the great apes.	Yes	Schultz (1953, 1961), Rose (1975)

The body of the final thoracic vertebra exhibits less ventral wedging in *H. sapiens* than in the great apes.	Yes	Keith (1923), Schultz (1961), Abitbol (1995), Ward and Latimer (2005), Shapiro (1993a), Whitcome et al. (2007), Been et al. (2010a, 2017)
The bodies of the final thoracic and 1st and 2nd lumbar vertebrae are deeper (i.e., larger in the dorsoventral direction) in *H. sapiens* than in the great apes.	Yes	Robinson (1972), Plomp et al. (2015)
The bodies of the final thoracic and 1st and 2nd lumbar vertebrae are more heart-shaped in the transverse plane in *H. sapiens* than in the great apes.	Yes	Robinson (1972), Plomp et al. (2015)

The bodies of the 1st and 2nd lumbar vertebrae are dorsally wedged in *H. sapiens* but not in the great apes.	Yes	Keith (1923), Schultz (1961), Abitbol (1995), Ward and Latimer (2005), Shapiro (1993a), Whitcome et al. (2007), Been et al. (2010a, 2017)
The vertebral foramina of all the vertebrae examined are wider (i.e., larger in the mediolateral direction) in *H. sapiens* than in the great apes.	Yes	Schultz (1930), MacLarnon (1987), MacLarnon and Hewitt, (1999) Sanders and Bodenbender (1994), Meyer and Hausler (2015)

The vertebral foramina of the final thoracic and 1st and 2nd lumbar vertebrae are dorsoventrally larger in *H. sapiens* than in the great apes.	Yes	Schultz (1930), MacLarnon (1987), MacLarnon and Hewitt, (1999) Sanders and Bodenbender (1994), Meyer and Hausler (2015)
The pedicles of the final thoracic and 1st and 2nd lumbar vertebrae are dorsoventrally larger in *H. sapiens* than in the great apes.	Yes	Plomp et al. (2015), Williams et al. (2017)
The pedicles of the final thoracic and 1st and 2nd lumbar vertebrae are narrower (i.e., smaller in the mediolateral direction) in *H. sapiens* than in the great apes.	Yes	Plomp et al. (2015), Williams et al. (2017)
The pedicles of the 1st and 2nd thoracic vertebrae are dorsoventrally smaller in *H. sapiens* than in the great apes.	No	

The superior articular facets of the 1st, 2nd, and final thoracic vertebrae are more coronally oriented in *H. sapiens* than in the great apes.	Yes	Latimer and Ward (1993), Shapiro (1993a), Williams and Russo (2015), Meyer (2017)
The superior articular facets of the 1st and 2nd lumbar vertebrae are more sagittally oriented in *H. sapiens* than in the great apes.	Yes	Latimer and Ward (1993), Shapiro (1993a), Williams and Russo (2015), Meyer (2017)
The inferior articular facets of the 1st and 2nd thoracic vertebrae are more coronally oriented in *H. sapiens* than in the great apes.	Yes	Latimer and Ward (1993), Shapiro (1993a), Williams and Russo (2015), Meyer (2017)

The inferior articular facets of the final thoracic and 1st and 2nd lumbar vertebrae are more sagittally oriented in *H. sapiens* than in the great apes.	Yes	Latimer and Ward (1993), Shapiro (1993a), Williams and Russo (2015), Meyer (2017)
The laminae of all the vertebrae examined are dorsoventrally larger in *H. sapiens* than in the great apes.	No	
The transverse processes of the 1st and 2nd thoracic vertebrae project more cranially and laterally in *H. sapiens* than in the great apes.	Yes	Jellema et al. (1993), Latimer and Ward (1993), Been et al. (2012), Bastir et al. (2014, 2017)
The transverse processes of the final thoracic and 1st and 2nd lumbar vertebrae are shorter from base to tip in *H. sapiens* than in the great apes.	Yes	Jellema et al. (1993), Latimer and Ward (1993), Been et al. (2012)

The transverse processes of the final thoracic and 1st and 2nd lumbar vertebrae project more dorsally in *H. sapiens* than in the great apes.	Yes	Jellema et al. (1993), Latimer and Ward (1993), Been et al. (2012)
The transverse processes of the 1st and 2nd thoracic vertebrae are longer from base to tip in *H. sapiens* than in the great apes.	No	
The spinous processes of all the vertebrae examined are shorter from base to tip in *H. sapiens* than in the great apes.	Yes	Ward (1991), Latimer and Ward (1993), Gómez-Olivencia et al. (2013), Meyer (2016, 2017)
The spinous processes of the 1st and 2nd thoracic vertebrae project more caudally in *H. sapiens* than in the great apes.	Yes	Latimer and Ward (1993), Gómez-Olivencia et al. (2013)

The tips of the spinous processes of all vertebrae examined are flatter (i.e. smaller in the craniocaudal direction) in *H. sapiens* than in the great apes.	No

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Figures

Figure 1. Location of the 54 landmarks used to capture the shapes of the vertebrae.

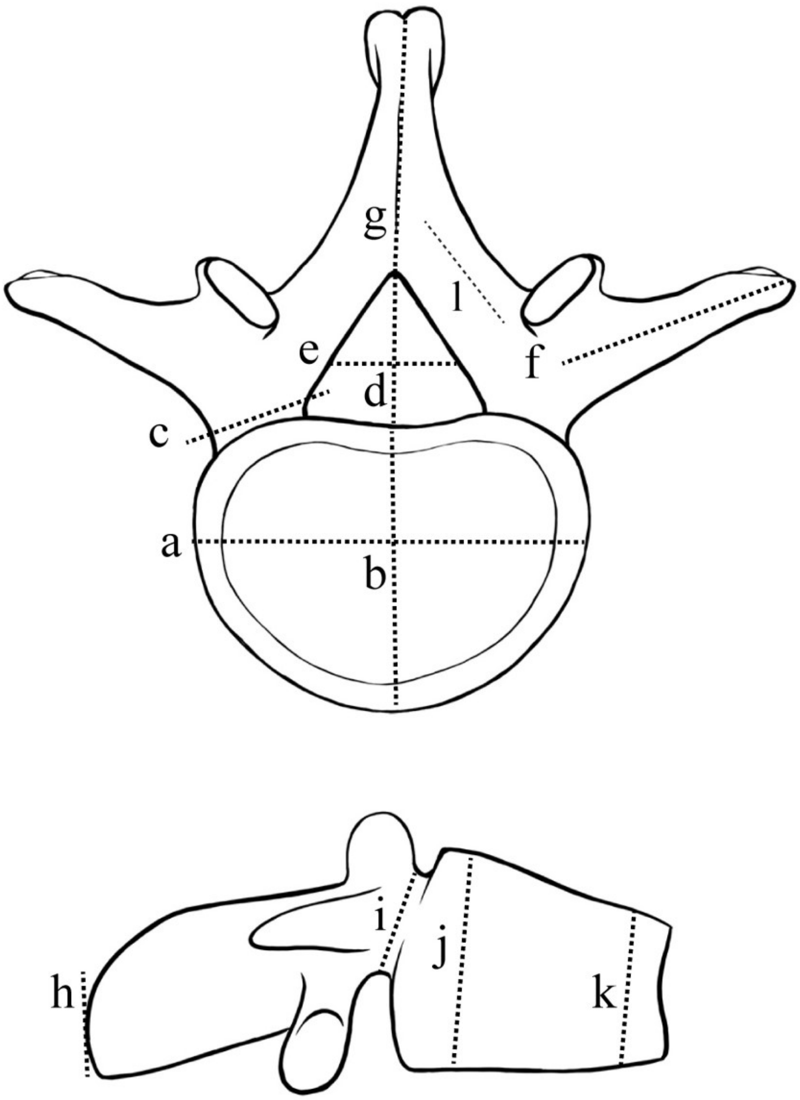

Figure 2. Illustration outlining the terminology used to describe the vertebral traits throughout this paper: a) mediolateral width of the vertebral body; b) dorsoventral length of the vertebral body; c) mediolateral width of the pedicle; d) dorsoventral length of the vertebral foramen; e) mediolateral width of the vertebral foramen; f) length from base to tip of the transverse process; g) length from base to tip of the spinous process; h) craniocaudal height of spinous process tip; i) craniocaudal height of pedicle; j) craniocaudal height of the dorsal portion of the vertebral body;

k) craniocaudal height of the ventral portion of the vertebral body; l) dorsoventral length of the lamina.

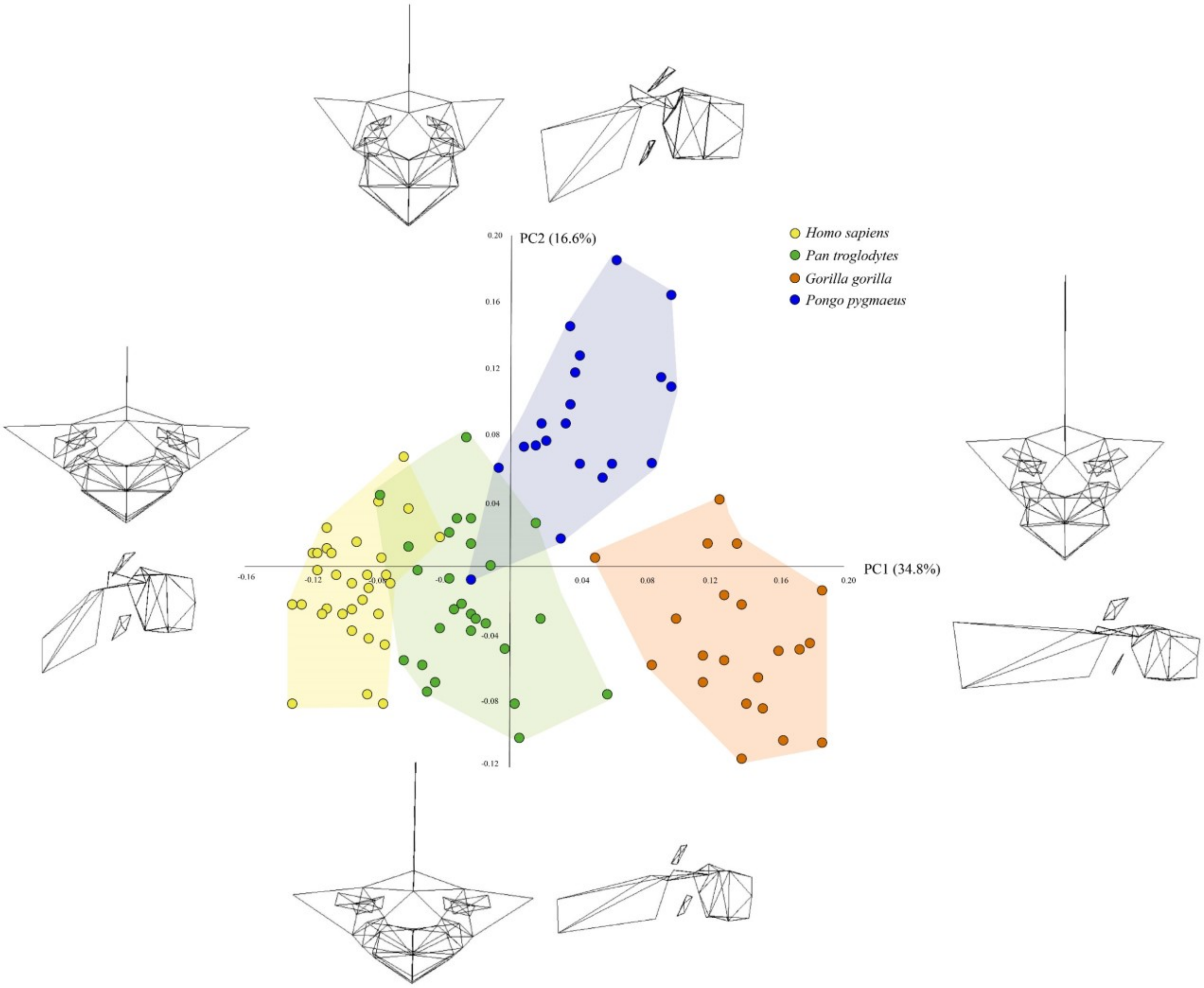

Figure 3. Principal components analysis scatterplot illustrating the shape variance on principal component 1 (PC1) and principal component 2 (PC2) of the first thoracic vertebrae of *H. sapiens* (yellow), *P. troglodytes* (green), *G. gorilla* (orange), and *Po. pygmaeus* (blue) vertebrae pooled together. The wireframes depict the shape changes occurring along each PC.

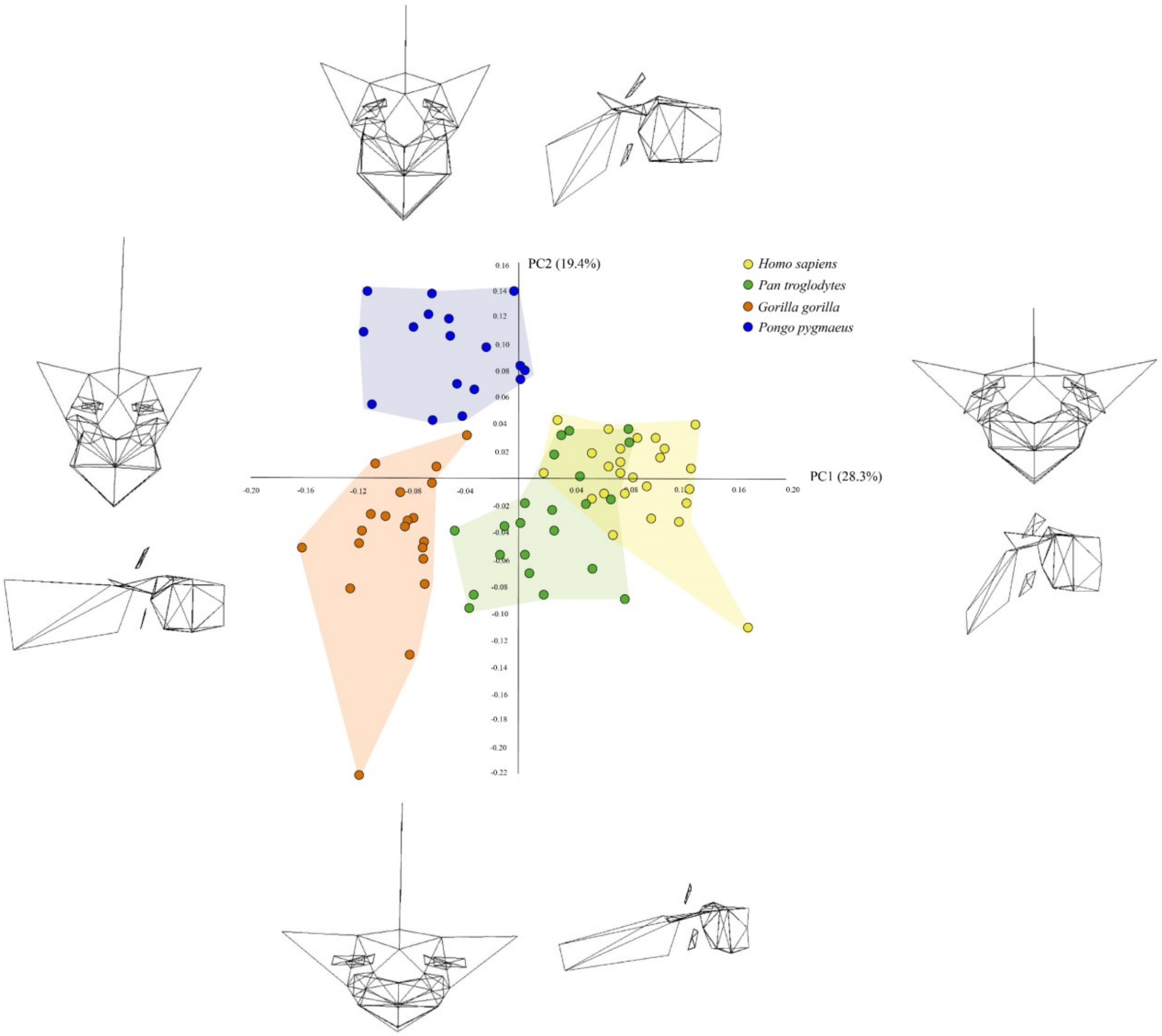

Figure 4. Principal components analysis scatterplot illustrating the shape variance on principal component 1 (PC1) and principal component 2 (PC2) of the second thoracic vertebrae of *H. sapiens* (yellow), *P. troglodytes* (green), *G. gorilla* (orange), and *Po. pygmaeus* (blue) vertebrae pooled together. The wireframes depict the shape changes occurring along each PC.

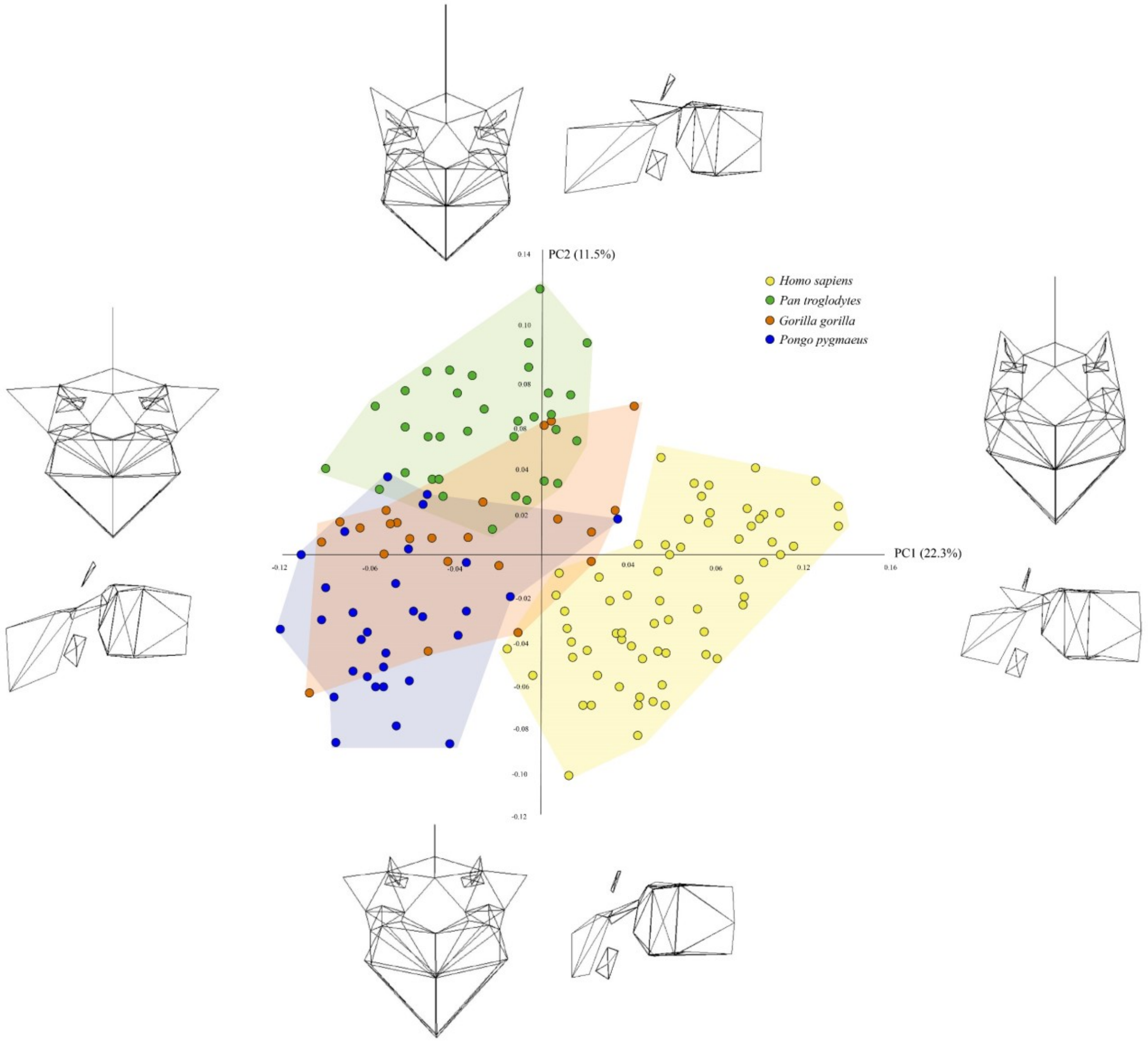

Figure 5. Principal components analysis scatterplot illustrating the shape variance on principal component 1 (PC1) and principal component 2 (PC2) of the last thoracic vertebrae of *H. sapiens* (yellow), *P. troglodytes* (green), *G. gorilla* (orange), and *Po. pygmaeus* (blue) vertebrae pooled together. The wireframes depict the shape changes occurring along each PC.

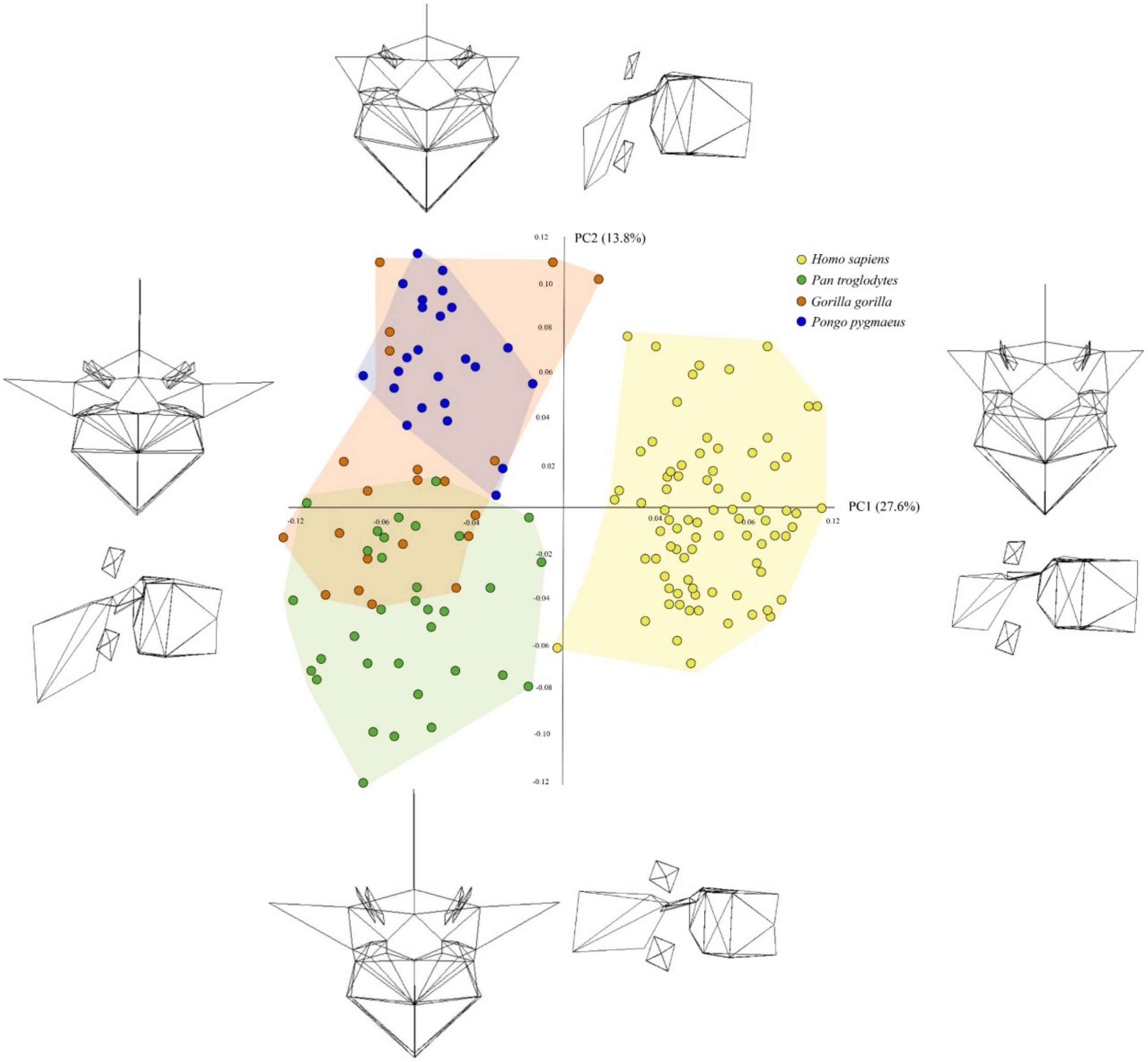

Figure 6. Principal components analysis scatterplot illustrating the shape variance on principal component 1 (PC1) and principal component 2 (PC2) of the first lumbar vertebrae of *H. sapiens* (yellow), *P. troglodytes* (green), *G. gorilla* (orange), and *Po. pygmaeus* (blue) vertebrae pooled together. The wireframes depict the shape changes occurring along each PC.

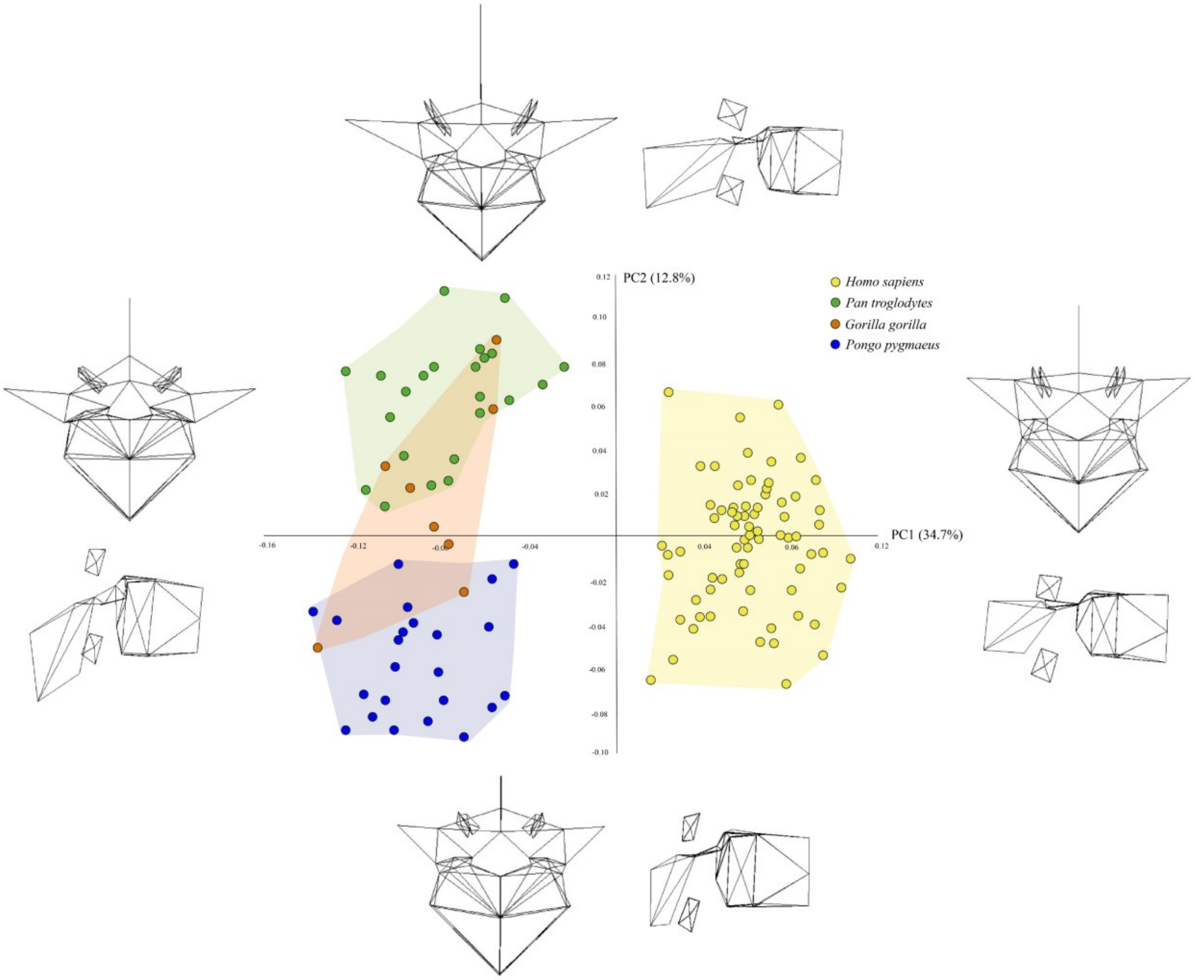

Figure 7. Principal components analysis scatterplot illustrating the shape variance on principal component 1 (PC1) and principal component 2 (PC2) of the second lumbar vertebrae of *H. sapiens* (yellow), *P. troglodytes* (green), *G. gorilla* (orange), and *Po. pygmaeus* (blue) vertebrae pooled together. The wireframes depict the shape changes occurring along each PC.