

1 **Potential adaptations for bipedalism in modern human thoracic and lumbar vertebrae: A**  
2 **3D comparative analysis**

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## 24 **Abstract**

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

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

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## 46 **1. Introduction**

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

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

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

71 In the present paper, we report a study in which we used 3D shape analysis techniques  
72 (O'Higgins and Jones, 1998; Adams et al., 2004; Slice, 2005, 2007) to compare thoracic and  
73 lumbar vertebrae of *H. sapiens* with those of chimpanzees (*Pan troglodytes*), gorillas (*Gorilla*  
74 *gorilla*), and orangutans (*Pongo pygmaeus*). Our investigation was motivated by the fact that  
75 while a number of traits have been reported to distinguish the thoracic and lumbar vertebrae of  
76 *H. sapiens* from their great ape counterparts, all the relevant studies relied on 2D data. 3D shape  
77 analysis techniques have been used to compare the cervical vertebrae of *H. sapiens* to those of  
78 their close relatives (Manfreda et al., 2006; Arlegi et al., 2017, 2018; Nalley and Grider-Potter,  
79 2017), but so far they have not been employed to identify traits that distinguish the thoracic and  
80 lumbar vertebrae of *H. sapiens* from their great ape homologues. This is potentially a problem  
81 because analyzing 3D anatomical structures with 2D methods can result in traits being  
82 mischaracterized or even missed entirely, especially when the structures are complex, as is the  
83 case with the vertebrae of primates.

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

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

92 Schultz, 1961; Shapiro, 1993a; Abitbol, 1995; Ward and Latimer, 2005). The former results in  
93 thoracic kyphosis, which is a backward curvature of the thoracic part of the spine; the latter gives  
94 rise to lumbar lordosis, which is a forward curvature of the lumbar part of the spine. Together,  
95 thoracic kyphosis and lumbar lordosis produce an S-shaped spine. In contrast, the spine of great  
96 apes is often described as C-shaped (Ward and Latimer, 2005; Whitcome et al., 2007). This is a  
97 result of their lower thoracic and upper lumbar vertebrae being more ventrally wedged than in  
98 humans, and their lower lumbar lacking the dorsal wedging that creates lumbar lordosis (Schultz,  
99 1961; Abitbol, 1995; Ward and Latimer, 2005; Whitcome et al., 2007; Been et al., 2010a, 2017).  
100 Three other traits have been reported to distinguish the vertebral bodies of the thoracic and  
101 lumbar vertebrae of *H. sapiens* from those of the great apes: greater height in the craniocaudal  
102 direction (Latimer and Ward 1993; Hernandez et al., 2009), greater depth in the dorsoventral  
103 direction (Robinson, 1972; Latimer and Ward, 1993; Hernandez et al., 2009; Plomp et al., 2015;  
104 Meyer and Williams, 2019), and gradually increasing mediolateral width as one moves down the  
105 spine (Schultz, 1953, 1961; Rose, 1975).

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

115 Another set of traits we sought to verify relate to the zygapophyseal facets. Previous  
116 studies have found that in *H. sapiens* the superior and inferior zygapophyseal facets are coronally  
117 oriented in all thoracic vertebrae except the final one, while in great apes these zygapophyseal  
118 facets are obliquely oriented (Latimer and Ward, 1993; Shapiro, 1993a; Williams and Russo,  
119 2015; Meyer, 2017). The superior and inferior zygapophyseal facets of the final thoracic  
120 vertebrae of *H. sapiens* have been reported to be coronally and sagittally oriented, respectively.  
121 The homologous facets in the great apes are coronally and obliquely oriented, respectively,  
122 according to several previous studies (Latimer and Ward, 1993; Shapiro, 1993a; Russo, 2010;  
123 Williams and Russo, 2015; Meyer, 2017). Differences in orientation in the zygapophyseal facets  
124 of the lumbar vertebrae have also been reported. Several authors have found that the superior and  
125 inferior facets of the lumbar vertebrae of *H. sapiens* are sagittally oriented, while those of the  
126 great apes are more obliquely oriented (Latimer and Ward, 1993; Shapiro, 1993a; Russo, 2010;  
127 Williams and Russo, 2015; Meyer, 2017).

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

138 project more caudally than those of the great apes (Latimer and Ward, 1993; Gómez-Olivencia et  
139 al., 2013).

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## 141 **2. Materials and methods**

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

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

155 To distinguish between thoracic and lumbar vertebrae, we followed the lead of Washburn and  
156 Buettner-Janusch (1952) and Shapiro (1993a, 1995) and used the orientation of the  
157 zygapophyseal facets rather than the presence and absence of costal articulations (Schultz, 1930;  
158 Haeusler et al., 2002, 2011; Williams et al., 2016). We chose this approach because the  
159 orientation and curvature of the zygapophyseal facets of primate vertebrae are important for  
160 locomotion (Ankel, 1972; Shapiro, 1991, 1993a; Boszczyk et al., 2001; Bogduk and Twomey,

161 2005; Whitcome et al., 2007, 2012; Russo, 2010). Additionally, this approach allows for the  
162 analysis of subtle differences in zygapophyseal shape rather than having results impacted by the  
163 substantial differences in orientation between thoracic and lumbar facets. An important corollary  
164 of using the zygapophyseal facet-based approach to distinguishing between thoracic and lumbar  
165 vertebrae is that the term ‘last thoracic’ refers to the diaphragmatic or transitional vertebra,  
166 which has coronally oriented superior zygapophyseal facets and sagittally oriented inferior facets  
167 (Washburn and Buettner-Janusch, 1952; Shapiro, 1993a, 1995).

168 Table 1 provides a breakdown of the sample. The numbers of specimens per vertebral type  
169 varies within each taxon partly because some skeletons did not preserve all vertebral types, and  
170 partly because the modal number of thoracic and lumbar vertebrae varies among the taxa  
171 (Rosenberg, 1876; Keith, 1902, 1923; Benton, 1967; Whitcome, 2012; Williams, 2012a;  
172 Williams et al., 2016; Thompson and Almécija, 2017). Modern humans usually have 12 thoracic  
173 and five lumbar vertebrae, while *Po. pygmaeus* typically has 12 thoracic and four lumbar  
174 vertebrae. *Pan troglodytes* and *G. gorilla* usually have 13 thoracic vertebrae and either three or  
175 four lumbar vertebrae. This makes comparisons between lower thoracic and lumbar vertebrae  
176 difficult in terms of ensuring positional homology. For example, the last thoracic in *H. sapiens*  
177 and *Po. pygmaeus* is normally the 19<sup>th</sup> vertebra, while in *P. troglodytes* and *G. gorilla* it is  
178 usually the 20<sup>th</sup>. While we acknowledge that this is an issue in terms of positional homology, we  
179 contend that the last thoracic vertebrae is functionally homologous in all four species, and  
180 therefore, comparing these vertebrae is appropriate for the purposes of the present study. A  
181 related issue is that *P. troglodytes* and *G. gorilla* can have three or four lumbar vertebrae, which  
182 means that in these species the second lumbar vertebra can also be the penultimate lumbar  
183 vertebra. We addressed this problem by including the second lumbar vertebra of *P. troglodytes*



184 and *G. gorilla* specimens only when the specimens had four lumbar vertebrae. Although this  
 185 procedure reduced the number of second lumbar vertebrae of *P. troglodytes* and *G. gorilla* that  
 186 could be included in the analyses, it ensured that their second lumbar vertebra was not also their  
 187 penultimate lumbar vertebra, minimizing any functional differences between penultimate and  
 188 non-penultimate lumbar vertebrae.

189

190 **Table 1**

191 Number of vertebrae examined.

Vertebra	<i>Homo sapiens</i>	<i>Pan troglodytes</i>	<i>Gorilla gorilla</i>	<i>Pongo pygmaeus</i>
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

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194 We employed a total of 54 landmarks (Fig. 1; SOM Table S2). Thirty-two of them were type  
 195 II and 22 were type III (Bookstein, 1997). We selected the landmarks to capture the entire  
 196 vertebra, including the shape of the body, neural arch, zygapophyseal facets, and the spinous and  
 197 transverse processes. Although the landmarks were chosen specifically for this study, some of  
 198 them correspond to those used in Bastir et al. (2017). In an effort to counter the effects of

199 recording error, we digitized each vertebra twice and then averaged the coordinates for each  
200 landmark (Arnquist and Martensson, 1998).

201 After collecting the data, we used the approach developed by Klingenberg et al. (2002) to  
202 reduce the confounding effects of translation, rotation, size, and asymmetry on the data. The  
203 procedure was performed on each dataset separately. We began by reflecting and relabeling the  
204 landmark coordinates. We then subjected the two sets of landmark coordinates to generalized  
205 Procrustes analysis (GPA) in Morphologika (O'Higgins and Jones, 1996). GPA removes  
206 translational and rotational effects and scales landmark configurations to centroid size (Slice,  
207 2007). Lastly, we calculated the average Procrustes coordinates for each pair of original and  
208 reflected landmarks.

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

218 Investigating the inter-taxa shape variation involved several steps. First, we subjected each  
219 dataset to the Procrustes coordinates to principal component analysis (PCA) to visualize the  
220 shape variance of vertebrae. Next, we implemented the principal component (PC) reduction  
221 procedure outlined by Baylac and Frieß (2005) and Evin et al. (2013). This procedure aims to

222 reduce noise from PCs that account for little variance, while still retaining all relevant shape  
223 information. It tackles this optimization problem by progressively adding PCs into the analyses  
224 until the cross-validation percentage (CVP) begins to drop. Thereafter, the retained PCs were  
225 subjected to multivariate analysis of variance (MANOVA) to assess the statistical significance of  
226 the inter-taxon shape differences. Subsequently, the PC scores were subjected to discriminant  
227 function analysis (DFA) with cross-validation to determine the accuracy of using vertebral shape  
228 to distinguish the four taxa. The method we used was outlined by Evin et al. (2013). To reduce  
229 the redundancy of data, only the DFA scores that corresponded to the PCs with the highest CVP  
230 were considered (White and Rutenberg, 2007; Kimmerle et al., 2008; Cardini et al., 2009). The  
231 five types of vertebrae were analyzed separately.

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

236

### 237 **3. Results**

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

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245 **Table 2**

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

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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

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

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261 **Table 3**

262 Results of pairwise multivariate analysis of variance (MANOVA) on the cross-validated

263 percentages principal components for each vertebra.

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

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266 **Table 4**

267 Percentage of correctly classified specimens in cross-validated discriminant function analyses

268 based on the cross-validated percentages principal components for each vertebra.

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

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271 The traits that will be used to describe the vertebral shape are illustrated in Figure 2. Figures  
 272 3–7 plot the scores for PC1 against those for PC2 for the five vertebral types. The PC1s account  
 273 for 22–35% of the shape variance, while the PC2s account for 11–20%. The wireframe images  
 274 illustrate the shape differences between the positive and negative extremes of each PC.

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

282 direction); and 7) spinous processes that are relatively short, more caudally directed, and more  
283 craniocaudally pinched at the tip.

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

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

303

#### 304 **4. Discussion**

305 4.1. Traits that distinguish *H. sapiens* vertebrae from those of the great apes

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

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

319 As expected, the majority of the traits have previously been described. This is the case for all  
320 the traits of the vertebral body. A number of studies, including Keith (1923), Latimer and Ward  
321 (1993), and Hernandez et al. (2009) have reported that bodies of the vertebrae are craniocaudally  
322 taller in *H. sapiens* than in the great apes, while Schultz (1953, 1961) and Rose (1975) noted that  
323 the bodies of the upper thoracic vertebrae of *H. sapiens* are mediolaterally wider than those of  
324 the great apes. Several authors, including Schultz (1961), Abitbol (1995), Ward and Latimer  
325 (2005), Shapiro (1993a), Whitcome et al. (2007), and Been et al. (2010a, 2017), have observed  
326 that, although variable, the bodies of the lower thoracic vertebrae of *H. sapiens* generally exhibit  
327 less ventral wedging than do those of the great apes. That the bodies of the lower thoracic



328 vertebrae of *H. sapiens* are dorsoventrally longer than those of the great apes was noted by  
329 Robinson (1972) and Plomp et al. (2015). These authors also noted that the superior endplates of  
330 the last thoracic and first and second lumbar vertebrae of *H. sapiens* are more heart-shaped than  
331 those of great apes. Lastly, a number of scholars have noted that the bodies of the first and  
332 second lumbar vertebrae of *H. sapiens* lack the ventral wedging seen in their great ape  
333 homologues (Schultz, 1961; Abitbol, 1995; Ward and Latimer, 2005; Shapiro, 1993a; Whitcome  
334 et al., 2007; Been et al., 2010a, 2017).

335 The traits related to the vertebral foramina have also been identified in previous studies. The  
336 greater mediolateral width of the vertebral foramina of the thoracic and lumbar vertebrae of *H.*  
337 *sapiens* compared to those of great apes was highlighted by Schultz (1930), MacLarnon (1987),  
338 MacLarnon and Hewitt (1999), Sanders and Bodenbender (1994), and Meyer and Haeusler  
339 (2015). Among the researchers who have noted the greater dorsoventral size of the vertebral  
340 foramina of the last thoracic and first two lumbar vertebrae of *H. sapiens* are MacLarnon (1987),  
341 Latimer and Ward (1993), Sanders and Bodenbender (1994), and MacLarnon and Hewitt (1999).

342 Two of the three pedicle traits have been highlighted before. That the pedicles of the last  
343 thoracic and the first and second lumbar vertebrae of *H. sapiens* are dorsoventrally longer than  
344 those of the great apes was pointed out recently by both Plomp et al. (2015) and Williams et al.  
345 (2017). These authors also noted that the pedicles of the last thoracic and the first and second  
346 lumbar vertebrae of *H. sapiens* are mediolaterally narrower than those of the great apes.

347 All the traits pertaining to the articular facets have been discussed in the past. Several authors  
348 have noted that the superior articular facets of the thoracic vertebrae of *H. sapiens* are more  
349 coronally oriented than are those of the great apes, and that the superior articular facets of  
350 modern human first and second lumbar vertebrae are more sagittally oriented than those of great

351 apes (Latimer and Ward, 1993; Shapiro, 1993a; Williams and Russo, 2015; Meyer, 2017). The  
352 same authors have also noted that the inferior articular facets of the upper thoracic vertebrae of  
353 *H. sapiens* are more coronally oriented than those of the great apes, and that the inferior articular  
354 facets of the last thoracic and upper lumbar vertebrae of *H. sapiens* are more sagittally oriented  
355 than their great ape equivalents.

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

363 Previous work has highlighted two of the three spinous process traits. That the spinous  
364 processes of *H. sapiens* are shorter than those of the great apes has been pointed out by Schultz  
365 (1961), Ward (1991), Latimer and Ward (1993), Gómez-Olivencia et al. (2013), Meyer (2016,  
366 2017), Shapiro and Kemp (2019), among others. Latimer and Ward (1993) and Gómez-Olivencia  
367 et al. (2013) have previously reported that the spinous processes of the upper thoracic vertebrae  
368 of *H. sapiens* project more caudally than their homologues in the great apes.

369 Our analyses failed to confirm three traits that previous studies found to distinguish the  
370 thoracic and lumbar vertebrae of *H. sapiens* from their great ape counterparts. Schultz (1953,  
371 1961) and Rose (1975) reported that there is an increase in the mediolateral width of the  
372 vertebral body as one moves down the thoracic and lumbar regions of the spine in *H. sapiens* but  
373 not in the great apes. Our analyses did not support the existence of this difference. We found that

374 the first and second thoracic vertebrae of *H. sapiens* are wider than those of great apes but we did  
375 not find a difference in the width of the last thoracic and the first and second lumbar vertebrae.  
376 To check this finding, we created a dataset that included all three lower vertebrae and subjected  
377 it to PCA. Again, we were unable to identify the putative increase in mediolateral width (SOM  
378 Fig. S1). It seems likely that this discrepancy is due to the fact that we scaled our data to remove  
379 the effects of centroid size, because when the raw distances between the landmarks on either side  
380 of the vertebral body are measured, there is a progressive increase in distance from the last  
381 thoracic to the second lumbar vertebrae in *H. sapiens* (interlandmark distances: last thoracic =  
382 37; first lumbar = 38; second lumbar = 41).

383 The second trait that our analyses failed to confirm relates to the wedging of the lumbar  
384 vertebral bodies. Whitcome et al. (2007) and Been et al. (2010a) found that the upper lumbar  
385 vertebrae of *H. sapiens* are ventrally wedged. In contrast, we found dorsal wedging in these  
386 vertebrae. The reason for this difference is not entirely clear, but we suspect it may be due to the  
387 methods used. Whitcome et al. (2007) and Been et al. (2012) employed 2D data obtained from in  
388 vivo images of living humans whereas we utilized 3D data recorded on dry bone specimens.  
389 Hence, the difference between our results and those of Whitcome et al. (2007) and Been et al.  
390 (2012) could be due to a difference in measurement accuracy between 2D and 3D methods, or a  
391 difference in measurement accuracy between in vivo and skeletal data. Alternatively, it is  
392 possible that vertebral wedging is a trait that varies intraspecifically and that the difference  
393 between the studies is caused by the difference in samples (Zloliniski et al. 2019). Ascertaining  
394 which of these hypotheses is correct will require further research.

395 The third trait that our analyses failed to confirm is one that Shapiro (1993b) reported—the  
396 pedicles of the lower thoracic and the upper lumbar vertebrae of *H. sapiens* are craniocaudally

397 shorter than those of the great apes. We suspect the issue here is landmark choice. While our  
398 analyses did indicate that the pedicles of *H. sapiens* lower vertebrae are longer in the  
399 dorsoventral direction and narrower in the mediolateral direction, our decision to place only one  
400 landmark on the inferior border of the pedicle meant that we were unable to capture any other  
401 shape differences. In hindsight, it is clear that we should have included additional landmarks.

402

#### 403 *4.2. Bipedalism and the traits of that distinguish H. sapiens thoracic and lumbar vertebrae from* 404 *those of the great apes*

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

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

419 Abitbol, 1995; Ward and Latimer, 2005; Shapiro, 1993a; Whitcome et al., 2007; Been et al.,  
420 2012, 2017).

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

435 The two traits that are specific to the bodies of the last thoracic and upper lumbar vertebrae  
436 may also be adaptations for resisting the compressive loads associated with bipedalism. Their  
437 greater dorsoventral length means that they have a relatively larger surface area, and this has  
438 been hypothesized to enable them to withstand the higher compressive loads that act on the  
439 lower spine of *H. sapiens* as a consequence of bipedalism (Davis, 1961; Rose, 1975; Shapiro,  
440 1991, 1993a; Latimer and Ward, 1993; Hernandez et al., 2009). Their heart-shaped outline has  
441 been linked to compressive loading via the shape of the intervertebral disc, which is necessarily

442 also heart-shaped (Harrington et al. 2001). It has been suggested a disc of this shape is able to  
443 withstand compressive forces better than a more ovoid one because it has a shorter radius  
444 (Harrington et al. 2001; Letic, 2012). This hypothesis is based on LaPlace's Law, which states  
445 that the ability of a fluid-filled tube like the intervertebral disc to withstand compression  
446 decreases with an increase in the tube's radius (Harrington et al. 2001; Letić, 2012). The  
447 possibility that the development of more heart-shaped bodies in the last thoracic and upper  
448 lumbar vertebrae of *H. sapiens* is an adaptation to withstand the compressive loading associated  
449 with bipedalism is supported by studies in which modern human vertebrae with signs of  
450 intervertebral disc herniation were found to be less heart-shaped than healthy specimens  
451 (Harrington et al. 2001; Plomp et al., 2012, 2015a, b).

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

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

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

482 A number of hypotheses that link the enlarged vertebral foramina of *H. sapiens* with  
483 bipedalism have been proposed (MacLarnon, 1987; Latimer and Ward, 1993; Sanders and  
484 Bodenbender, 1994; MacLarnon and Hewitt, 1999). Two of these hypotheses have yet to be  
485 refuted. Sanders and Bodenbender (1994) suggested that the vertebral foramina of the lumbar  
486 vertebrae of *H. sapiens* are larger than those of other primates because bipedalism requires  
487 exceptional control of muscle movements in the lower limbs. This necessitates large lumbar

488 spinal nerves and spinal nerve roots and therefore large vertebral foramina. Sanders and  
489 Bodenbender (1994) based this hypothesis on previous work that had identified an association  
490 between vertebral foramina size and the nerves for limb motor control in a number of species,  
491 including *H. sapiens* (e.g., Thomas and Combs, 1962, 1965; O'Higgins et al., 1989).

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

498 Latimer and Ward's (1993) explanation for the enlarged vertebral foramina in the vertebrae of  
499 *H. sapiens* appears more compelling than the hypothesis suggested by Sanders and Bodenbender  
500 (1994) because greater foramen size continues to the fourth and fifth lumbar vertebrae, which are  
501 both lower than the terminus of the spinal cord in *H. sapiens* (Noback and Harting, 1971).

502 It is believed that, in addition to protecting the spinal cord, the neural arches play a role in  
503 load bearing during bipedalism (Adams and Hutton, 1980; 1985; Shapiro, 1993a,b; Hongo et al.,  
504 1999; Bogduk and Twomey, 2005). Specifically, the laminae and pedicles are thought to transmit  
505 loads between the articular facets and the vertebral body (El-Khoury and Whitten, 1993; Pal and  
506 Routal, 1987; Whyne et al., 1998). This hypothesis is hard to reconcile with the finding that the  
507 pedicles and laminae of the thoracic and lumbar vertebrae of *H. sapiens* are dorsoventrally  
508 longer than those of the great apes. Without an increase in thickness, a longer structure can be  
509 expected to be less capable of withstanding loading than a shorter one. Thus, the difference in  
510 length between the pedicles and laminae of *H. sapiens* and great apes is contrary to what we



511 would expect to see if the pedicles and laminae of *H. sapiens* were adapted to the additional  
512 compressive loading associated with bipedalism. While the biomechanical significance of the  
513 shape of pedicles and laminae deserves further investigation, it seems reasonable to conclude for  
514 now that their greater relative size in *H. sapiens* compared to the great apes is only indirectly  
515 linked to bipedalism via the size of the spinal cord.

516 Articular facets Our analyses confirmed that the articular facets of the first and second thoracic  
517 vertebrae of *H. sapiens* are more coronally oriented than those of the great apes, and that the  
518 articular facets of the first and second lumbar vertebrae of *H. sapiens* are more sagittally oriented  
519 than their great ape counterparts. These differences in facet orientation have been linked to  
520 vertebral slippage and rotation in the context of posture and gait (Shapiro, 1993a; Whitcome,  
521 2012). Because the great apes' centre of mass is located higher in the torso than it is in humans,  
522 their spines experience a ventral gravitational pull. As a consequence of this, the facets of their  
523 lumbar vertebrae need to resist both slippage and rotation. The facets' oblique orientation is  
524 thought to be a solution to this problem (Bogduk and Twomey, 2005; Shapiro, 1991, 1993a;  
525 Ward and Latimer, 1991, 2005; Masharawi et al., 2008; Russo and Shapiro, 2013; Williams and  
526 Russo, 2015). The situation is hypothesized to be different for modern humans because they are  
527 bipedal. It has been argued that the articular facets of the thoracic vertebrae of *H. sapiens* are  
528 oriented towards the coronal plane because this stops the vertebrae from slipping forward when  
529 standing upright (Shapiro, 1993a; Been et al., 2010a). Conversely, the articular facets of the  
530 lumbar vertebrae of *H. sapiens* are oriented towards the sagittal plane in order to resist rotation,  
531 which likely helps protect the intervertebral discs and spinal cord from injury, as well as  
532 maintaining lumbar lordosis (Ahmed et al., 1990; Shapiro, 1993a; Been et al., 2010a, Jaumard et  
533 al., 2011).

534 Transverse processes Like a number of other scholars, we found that the transverse processes of  
535 the last thoracic and the first and second lumbar vertebrae of *H. sapiens* are, on average, shorter  
536 from base to tip than those of the great apes (Latimer and Ward, 1993; Jellema et al., 1993;  
537 Sanders, 1998; Been et al., 2012). The transverse processes of the lower thoracic and lumbar  
538 vertebrae are attachment sites for the erector spinae muscles, which control the sagittal and  
539 lateral flexibility of the lower spine (Shapiro and Jungers, 1988, 1994; Shapiro, 1993a; Been et  
540 al., 2010a). Accordingly, their length is thought to be linked to posture and locomotion in  
541 primates (Benton, 1967; Sanders and Bodenbender, 1994; Shapiro, 1993a; Ward, 1993; Shapiro,  
542 1995; Johnson and Shapiro, 1998). Specifically, short transverse processes in the lower vertebrae  
543 are believed to restrict the moment arm of the erector spinae muscles and therefore limit the  
544 amount of lateral flexion that can occur in the lower spine (Shapiro, 1993a; Sanders, 1998;  
545 Argot, 2003; Been et al., 2010a).

546 Our identification of a more dorsal orientation of the transverse processes in the last thoracic  
547 and first and second lumbar vertebrae of *H. sapiens* is likely related to bipedalism via  
548 invagination of the vertebral column (Jellema et al., 1993; Latimer and Ward, 1993; Ward et al.,  
549 2012; Williams and Russo, 2015; Bastir et al., 2017). One of the effects of invagination, which  
550 positions the vertebral column forward in the thorax, is to increase the length of the lever arms of  
551 the epaxial muscles (Bogduk et al., 1992; Shapiro, 1993a, 2007; Sanders, 1998; Filler et al.,  
552 2007; Whitcome et al., 2007; Been et al., 2010a; Gómez-Olivencia et al., 2017). This in turn  
553 increases the muscles' ability to extend the spine, resist lateral flexion, and maintain lumbar  
554 lordosis during bipedal posture and gait (Benton, 1967; Jellema et al., 1993; Latimer and Ward,  
555 1993, 2005; Sanders and Bodenbender, 1994; Shapiro, 1993a, 1995; Ward, 1993; Sanders, 1998;  
556 Argot, 2003; Been et al., 2010a; Ward et al., 2012; Gómez-Olivencia et al., 2017).

557 The relatively long transverse processes of the first and second thoracic vertebrae of *H.*  
558 *sapiens* may also be linked with bipedalism. Because the functional morphology of the thoracic  
559 region of the spine has not received much attention to date (Shapiro, 1993a), the possible  
560 functional significance of this trait must be assessed on the basis of what has been proposed in  
561 connection with other spinal regions. As discussed above, the short transverse processes of the  
562 lumbar vertebrae of *H. sapiens* are thought to restrict lateral flexion in the lower spine (Shapiro,  
563 1993a; Sanders, 1998; Argot, 2003; Been et al., 2010a). An obvious implication of this is that the  
564 relatively long transverse processes of the upper thoracic vertebrae of *H. sapiens* allow some  
565 lateral flexion in the upper spine (Shapiro, 1993a). Lateral flexion in the thoracic spine has been  
566 proposed to be related to throwing (Atwater, 1979; Young et al., 1996), but it could also be  
567 advantageous in walking and running since both involve rotation of the torso (Thorstensson et al.  
568 1984; Schache et al., 2002). Of course, it is also possible that the long transverse processes of the  
569 first and second thoracic vertebrae of *H. sapiens* may not be functionally significant.  
570 Experimental research into the biomechanical role of transverse process length in the upper spine  
571 of humans is needed to assess these possibilities.

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

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

582 Spinous process Three of the traits identified in our analyses relate to the spinous processes. A  
583 spinous process that is short from base to tip, was present in all five vertebral types we analyzed.  
584 Body mass has been hypothesized to influence the variation in spinous process length among  
585 primate species (Shapiro and Simons, 2002). However, the shortness of the spinous processes of  
586 *H. sapiens* compared to those of *P. troglodytes*, *G. gorilla*, and *Po. pygmaeus* cannot be  
587 explained by body size. This is because *H. sapiens* is neither the largest nor the smallest of the  
588 four taxa. With an average body mass of 59 kg (Jungers, 1988), *H. sapiens* is markedly smaller  
589 than *G. gorilla*, whose average body mass is 121 kg (Smith and Jungers 1997), and a few  
590 kilograms larger than *P. troglodytes*, whose average body mass is 53 kg (Smith and Jungers  
591 1997).

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

603 previous suggestion that the ‘tallness’ of the thoracic and lumbar vertebral bodies in *H. sapiens* is  
604 likely not an adaptation for dorsomobility.

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

618 The new spinous process feature revealed by our analyses—a craniocaudal ‘pinching’ of the  
619 spinous process tip in all the vertebrae examined—may also be linked with bipedalism. This trait  
620 has been identified in the lumbar vertebrae of some non-hominin species and two different  
621 hypotheses have been put forward to account for it. First, based on their presence in the lumbar  
622 vertebrae of ateline monkeys and certain carnivoran species, craniocaudally ‘pinched’ spinous  
623 process tips have been suggested to allow for more sagittal flexibility and motion due to  
624 expansion of the interspinal distance available for the supraspinous and interspinous ligaments  
625 (Erikson, 1963; Gambaryan, 1974; Shapiro, 1993a). The second hypothesis was developed to

626 explain the presence of craniocaudally pinched process tips in the lumbar vertebrae of the  
627 gerenuk (*Litocranius walleri*), a species of gazelle that often stands on its rear legs when feeding  
628 on the leaves of trees. It was suggested that the craniocaudally ‘pinched’ process tips provide  
629 more space between the processes of adjoining vertebrae, which allows for a small amount of  
630 lumbar lordosis without the processes impinging on one another (Ritcher, 1970; Cartmill and  
631 Brown, 2017). Given that the other spinous process traits of *H. sapiens* appear to be involved in  
632 stabilizing the spine in the sagittal plane, we propose that the second of these hypotheses may be  
633 more accurate. That is, we suggest that the pinched spinous process tips of the thoracic and  
634 lumbar vertebrae of *H. sapiens* may ensure adequate spacing between processes in relation to the  
635 thoracic and lumbar curves of the S-shaped modern human spine play a crucial role in  
636 bipedalism (Erikson, 1963; Ritcher, 1970; Gambaryan, 1974; Shapiro, 1993a; Cartmill and  
637 Brown, 2017).

638

#### 639 *4.3. Additional observations*

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

649 lower vertebrae would have undergone more evolutionary change than the upper vertebrae.  
650 Evaluating this hypothesis will require further research, including comparisons of fossil ape and  
651 hominin vertebrae.

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## 653 **5. Conclusions**

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

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

667 Most of the traits that distinguish modern human thoracic and lumbar vertebrae from their  
668 homologues in the great apes can plausibly be linked to bipedalism. This includes three of the  
669 four new traits. There is reason to think that the dorsoventrally longer laminae may increase the  
670 size of the vertebral foramina so that it can accommodate the nerves required for bipedalism. The  
671 pinched spinous process tips may help maintain lumbar lordosis, while the long transverse

672 processes of the upper thoracic vertebrae may allow for some lateral flexion, which may be  
673 advantageous in walking and running since both involve rotation of the torso.

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

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695 **Table 5**

696 Traits that distinguish modern human thoracic and lumbar vertebrae from their great ape  
 697 homologues, according to the results of the present study. The traits are arranged according to  
 698 where they occur on the vertebra, starting with the vertebral body and moving backwards. Where  
 699 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 <i>H. sapiens</i> than in the great apes.	Yes	Latimer and Ward (1993), Hernandez et al. (2009)
The bodies of the 1 <sup>st</sup> and 2 <sup>nd</sup> thoracic vertebrae are wider (i.e., larger in the mediolateral direction) in <i>H. sapiens</i> than in the great apes.	Yes	Schultz (1953, 1961), Rose (1975)

The body of the final thoracic vertebra exhibits less ventral wedging in <i>H. sapiens</i> 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 1 <sup>st</sup> and 2 <sup>nd</sup> lumbar vertebrae are deeper (i.e., larger in the dorsoventral direction) in <i>H. sapiens</i> than in the great apes.	Yes	Robinson (1972), Plomp et al. (2015)
The bodies of the final thoracic and 1 <sup>st</sup> and 2 <sup>nd</sup> lumbar vertebrae are more heart-shaped in the transverse plane in <i>H. sapiens</i> than in the great apes.	Yes	Robinson (1972), Plomp et al. (2015)

The bodies of the 1<sup>st</sup> and 2<sup>nd</sup> 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)

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

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

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

The transverse processes of the final thoracic and 1 <sup>st</sup> and 2 <sup>nd</sup> lumbar vertebrae project more dorsally in <i>H. sapiens</i> than in the great apes.	Yes	Jellema et al. (1993), Latimer and Ward (1993), Been et al. (2012)
The transverse processes of the 1 <sup>st</sup> and 2 <sup>nd</sup> thoracic vertebrae are longer from base to tip in <i>H. sapiens</i> than in the great apes.	No	
The spinous processes of all the vertebrae examined are shorter from base to tip in <i>H. sapiens</i> 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 1 <sup>st</sup> and 2 <sup>nd</sup> thoracic vertebrae project more caudally in <i>H. sapiens</i> 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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1074 **Figures**

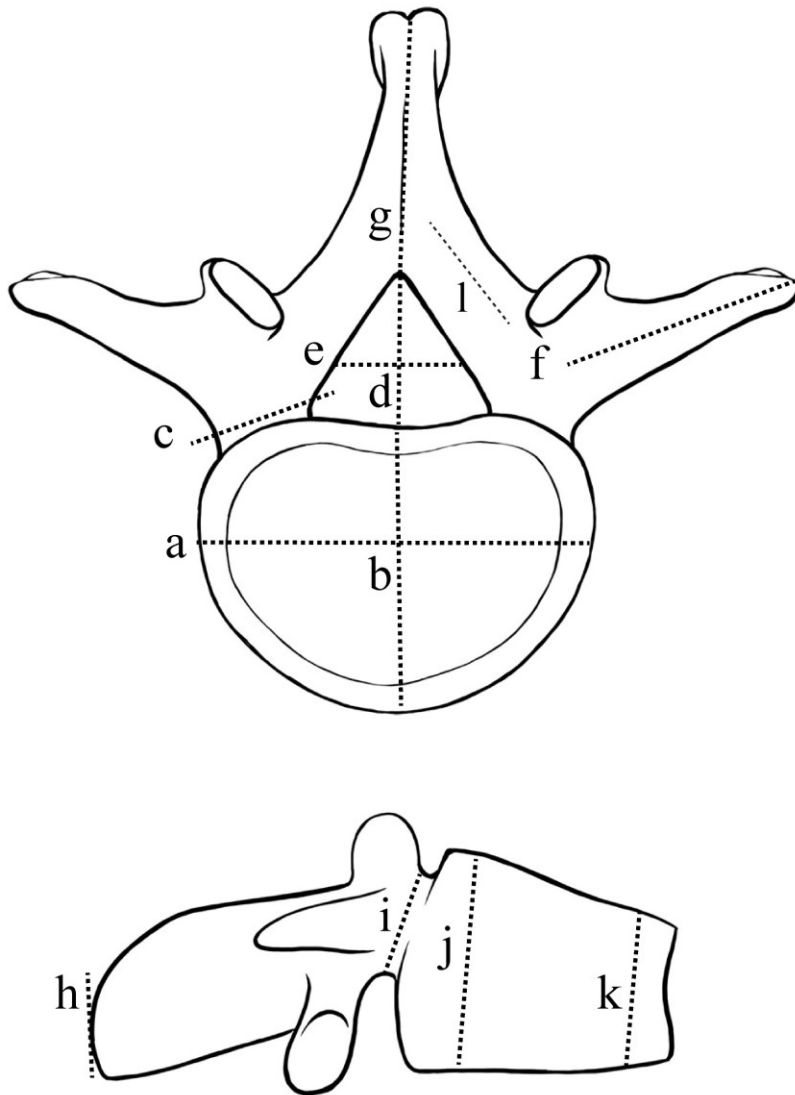


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1076 **Figure 1.** Location of the 54 landmarks used to capture the shapes of the vertebrae.

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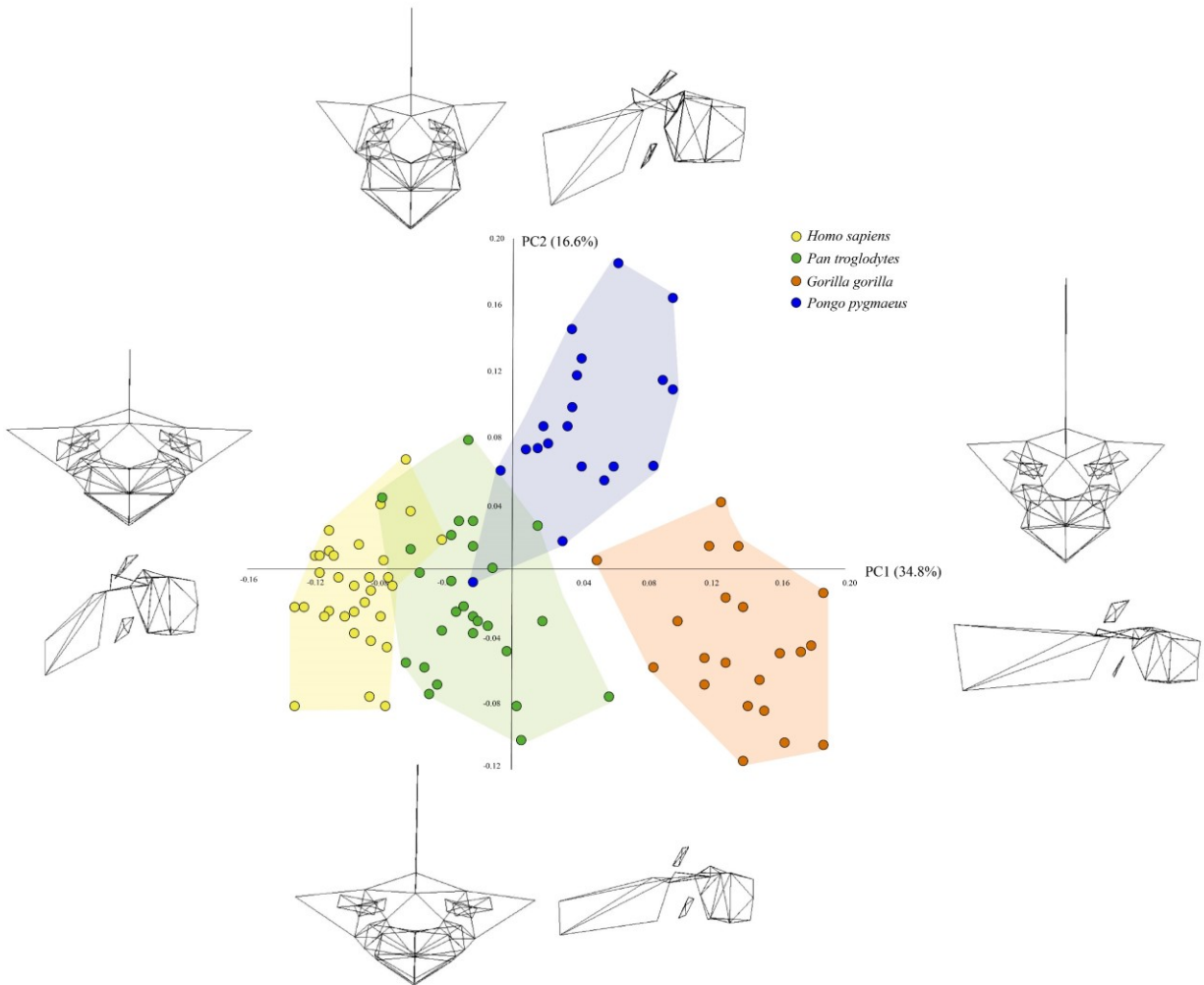
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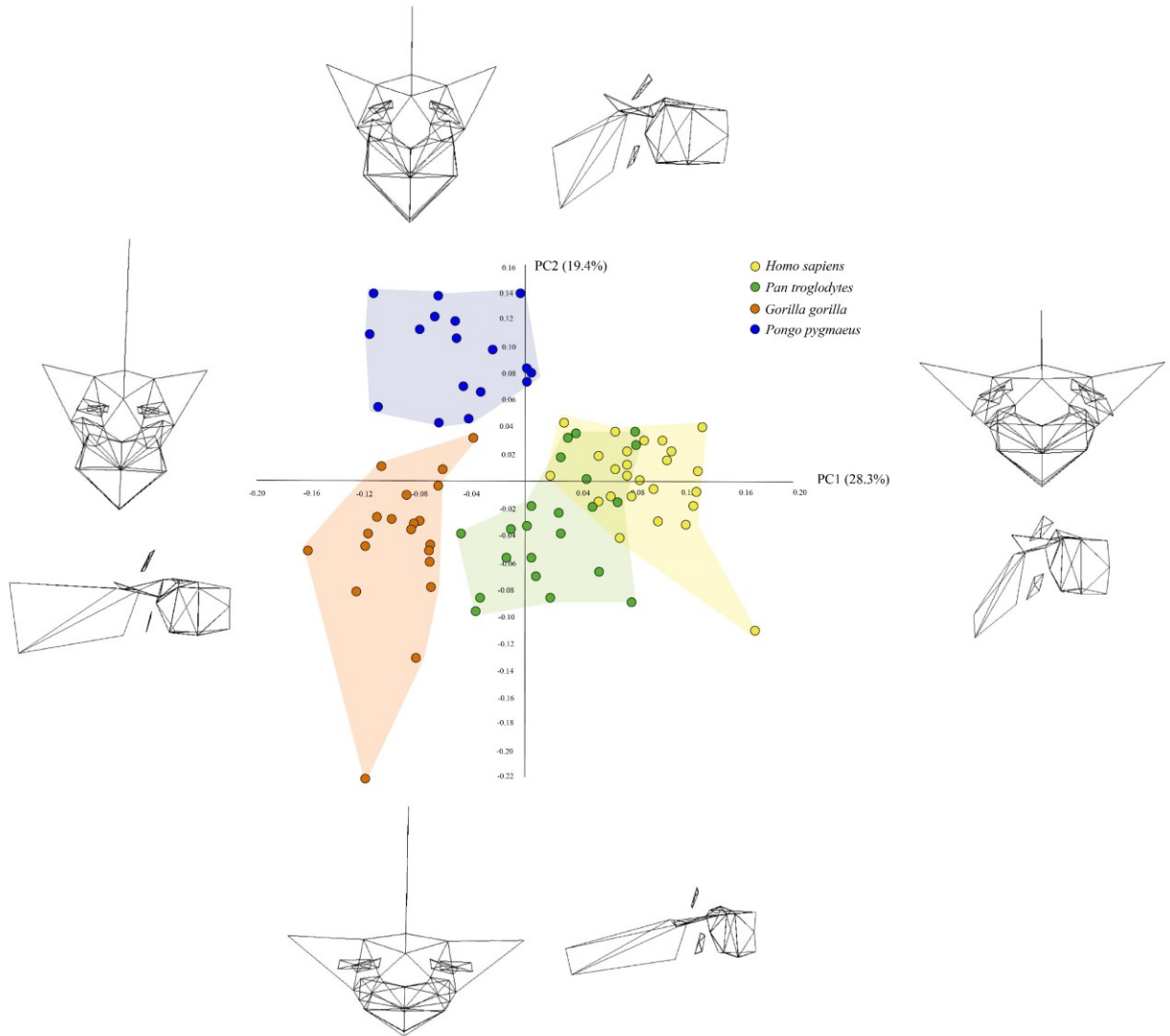
1080 **Figure 2.** Illustration outlining the terminology used to describe the vertebral traits throughout  
 1081 this paper: a) mediolateral width of the vertebral body; b) dorsoventral length of the vertebral  
 1082 body; c) mediolateral width of the pedicle; d) dorsoventral length of the vertebral foramen; e)  
 1083 mediolateral width of the vertebral foramen; f) length from base to tip of the transverse process;  
 1084 g) length from base to tip of the spinous process; h) craniocaudal height of spinous process tip; i)  
 1085 craniocaudal height of pedicle; j) craniocaudal height of the dorsal portion of the vertebral body;

1086 k) craniocaudal height of the ventral portion of the vertebral body; l) dorsoventral length of the  
1087 lamina.



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1089 **Figure 3.** Principal components analysis scatterplot illustrating the shape variance on principal  
1090 component 1 (PC1) and principal component 2 (PC2) of the first thoracic vertebrae of *H. sapiens*  
1091 (*yellow*), *P. troglodytes* (*green*), *G. gorilla* (*orange*), and *Po. pygmaeus* (*blue*) vertebrae pooled  
1092 together. The wireframes depict the shape changes occurring along each PC.

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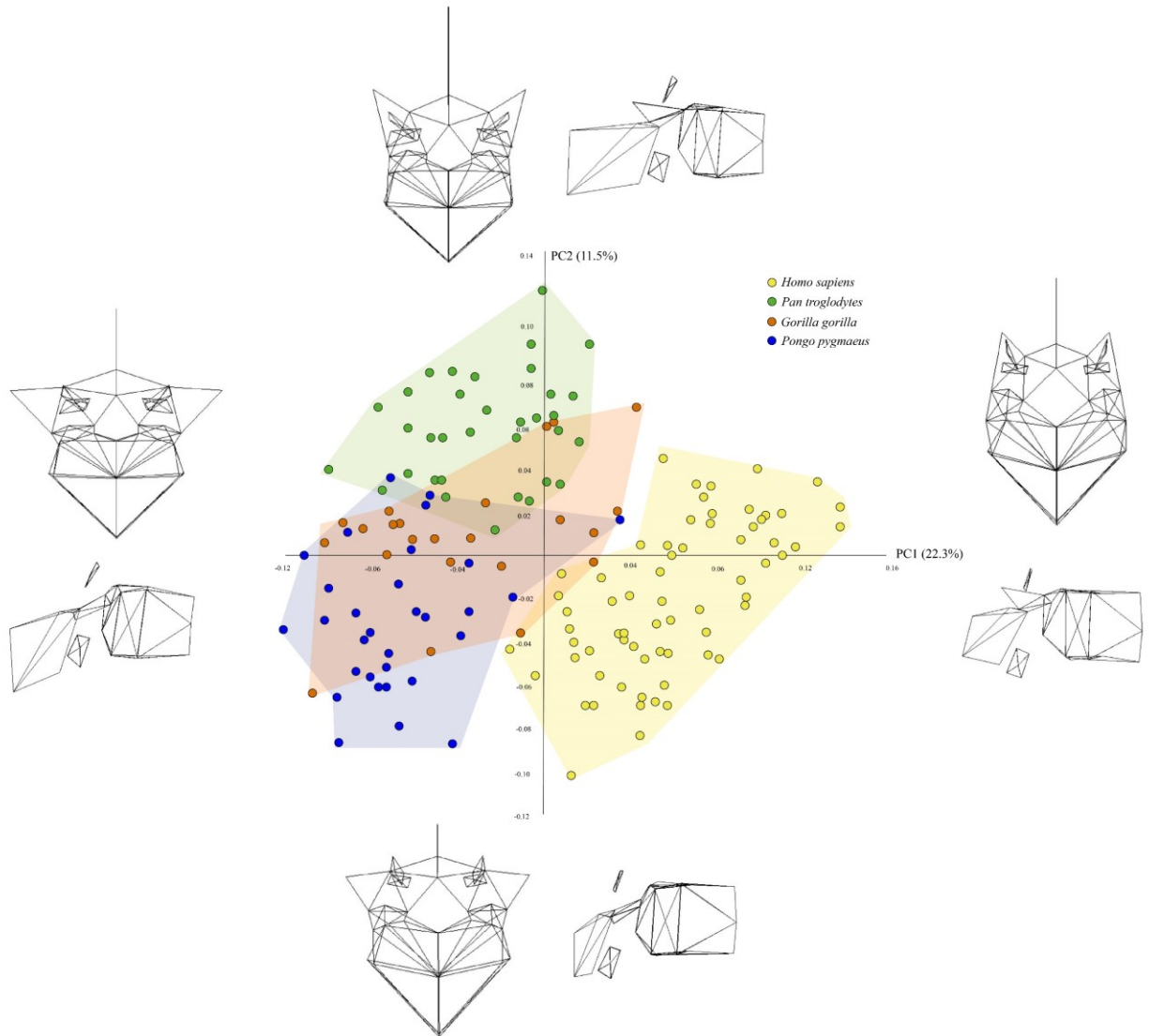


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1099 **Figure 4.** Principal components analysis scatterplot illustrating the shape variance on principal  
 1100 component 1 (PC1) and principal component 2 (PC2) of the second thoracic vertebrae of *H.*  
 1101 *sapiens* (yellow), *P. troglodytes* (green), *G. gorilla* (orange), and *Po. pygmaeus* (blue) vertebrae  
 1102 pooled together. The wireframes depict the shape changes occurring along each PC.

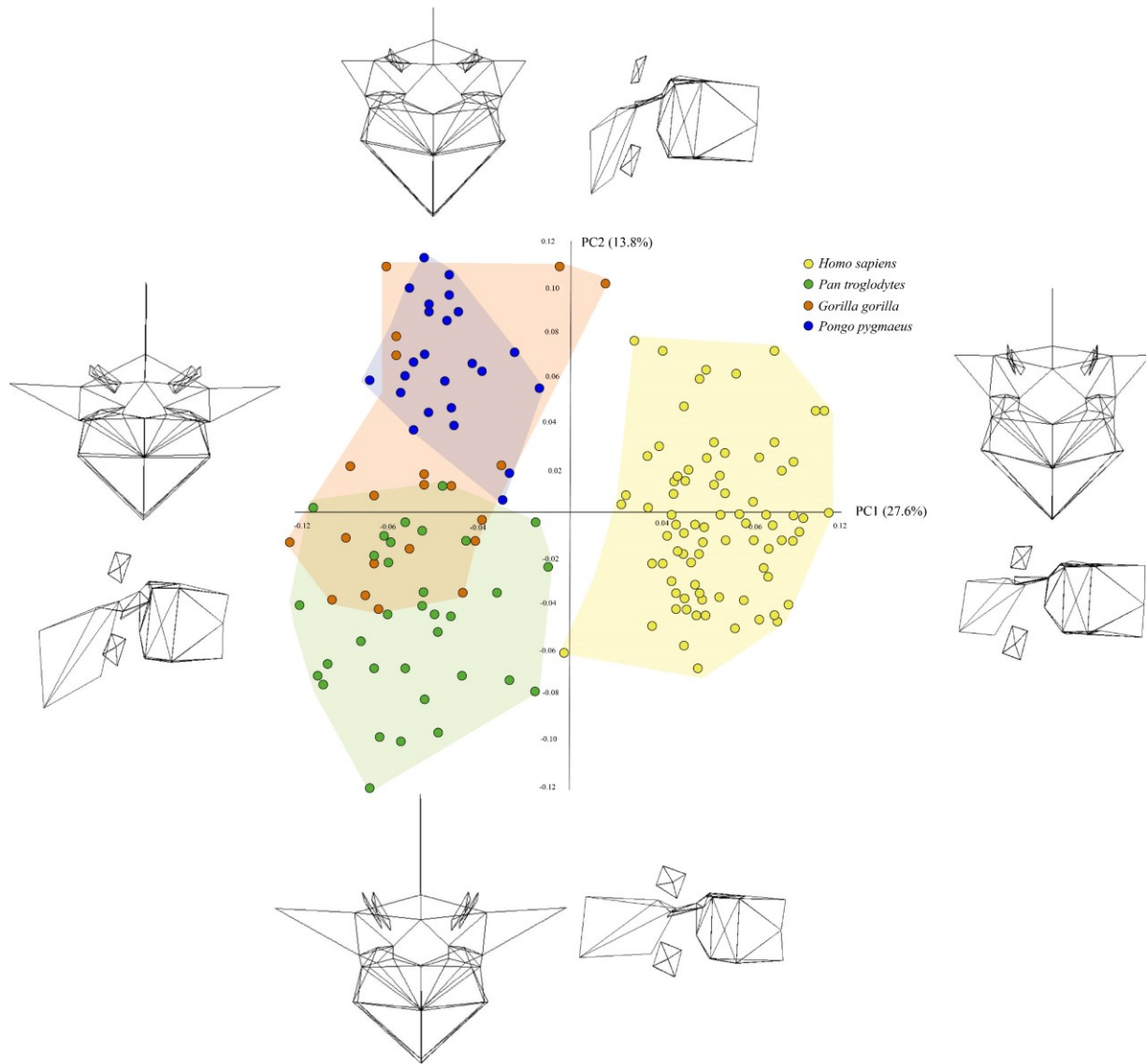
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 1106 **Figure 5.** Principal components analysis scatterplot illustrating the shape variance on principal  
 1107 component 1 (PC1) and principal component 2 (PC2) of the last thoracic vertebrae of *H. sapiens*  
 1108 (yellow), *P. troglodytes* (green), *G. gorilla* (orange), and *Po. pygmaeus* (blue) vertebrae pooled  
 1109 together. The wireframes depict the shape changes occurring along each PC.

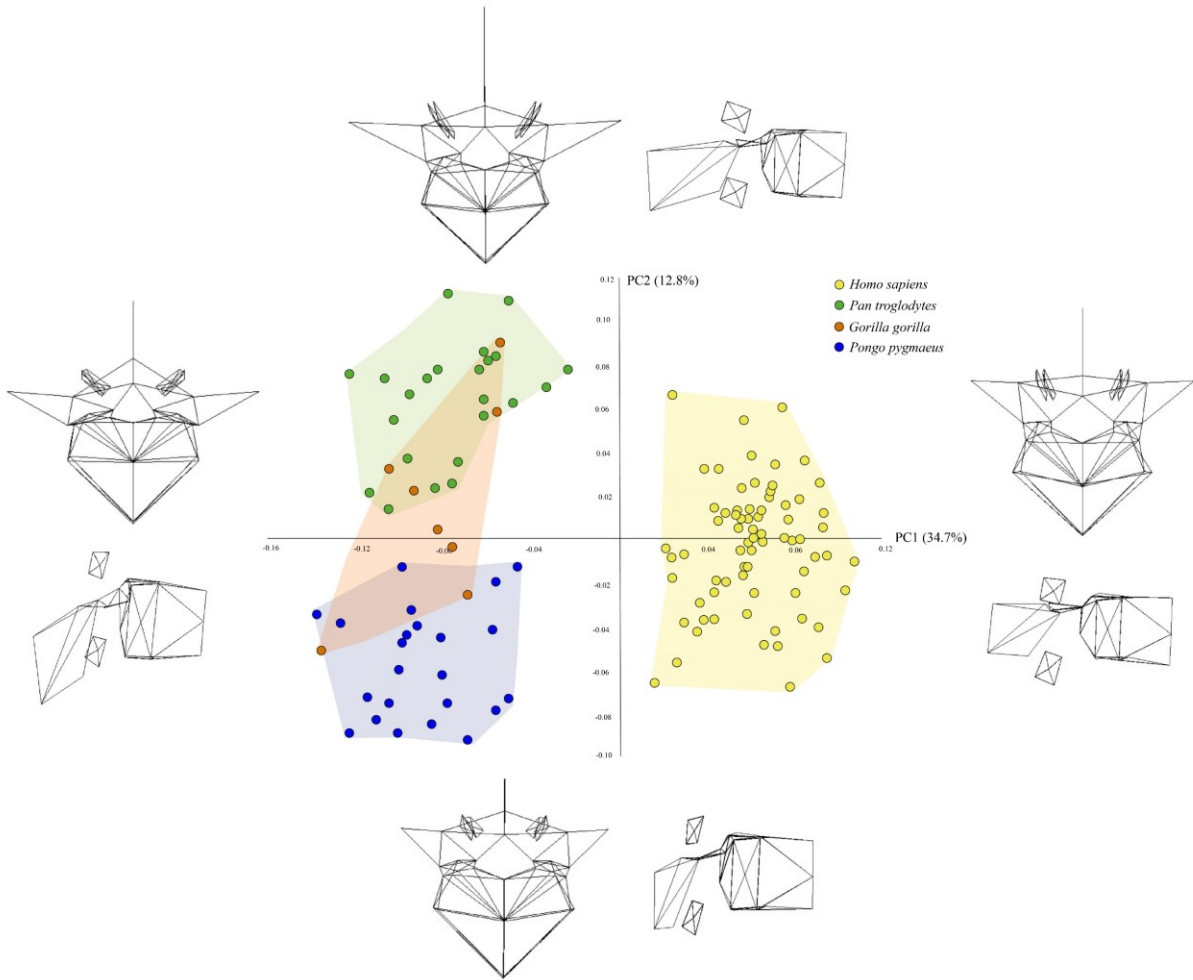
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 1113 **Figure 6.** Principal components analysis scatterplot illustrating the shape variance on principal  
 1114 component 1 (PC1) and principal component 2 (PC2) of the first lumbar vertebrae of *H. sapiens*  
 1115 (*yellow*), *P. troglodytes* (*green*), *G. gorilla* (*orange*), and *Po. pygmaeus* (*blue*) vertebrae pooled  
 1116 together. The wireframes depict the shape changes occurring along each PC.

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1120 **Figure 7.** Principal components analysis scatterplot illustrating the shape variance on principal  
 1121 component 1 (PC1) and principal component 2 (PC2) of the second lumbar vertebrae of *H.*  
 1122 *sapiens* (yellow), *P. troglodytes* (green), *G. gorilla* (orange), and *Po. pygmaeus* (blue) vertebrae  
 1123 pooled together. The wireframes depict the shape changes occurring along each PC.