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Article

Vertebral shape and spinal osteoarthritis in humans: A 3D analysis

Dean Anthony Arcega[1,2,*], Kimberly Anne Plomp[1], Mark Collard[2,*]

[1] School of Archaeology, University of the Philippines Diliman, Albert Hall, Lakandula Street, Quezon City, Manila, 1101, Philippines
[2] Laboratory of Human Evolutionary Studies, Department of Archaeology, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6, Canada
[*] Corresponding authors: dbarcega@up.edu.ph; mcollard@sfu.ca

With 3 figures and 1 table

Abstract: Spinal osteoarthritis (SOA) is an important contributor to back pain, but the factors that lead to its development are poorly understood. Here, we report a study designed to test the idea that vertebral shape influences the probability of developing SOA. We used geometric morphometrics to compare the 3D shape of the last thoracic (T12) and the first lumbar vertebrae (L1) of adults with and without SOA. The sample was drawn from archaeological and documented skeletons, consisting of 143 T12s and 136 L1s. Two linked hypotheses were tested. The first was that there is an association between vertebral shape and SOA. The second was that the association between in the first hypothesis exists because the risk of SOA is increased by a morphotype that includes more sagittal zygapophyseal facets and smaller interfacet distances. This hypothesis was informed by the results of two previous studies. The analyses supported the first hypothesis. MANOVAs and DFAs indicated that the vertebrae of individuals with SOA tend to have a significantly different morphotype to unaffected individuals. In contrast, the results of the analyses only partially supported the second hypothesis. PCA-derived wireframes upheld only one of the predicted differences, smaller interfacet distances. The other predicted difference – more sagittal facets in affected individuals – was not supported. Unexpectedly, the analyses identified several other traits that distinguish the vertebrae of individuals with SOA. All of these traits can be plausibly linked to suboptimal biomechanics for the spine. Overall, the study supports the idea that vertebral shape can increase the probability of developing SOA.

Keywords: spinal osteoarthritis; eburnation; vertebral shape; 3D Geometric Morphometrics

1 Introduction

Back pain is a significant health issue. It is both common and consequential. In high-income countries, more than 60% of people experience back pain at some point in their lives, while low- and middle-income countries are projected to experience a rapid growth in cases of back pain due to the greying of their populations (Ferreira et al. 2023). Globally, years lived with disability caused by back pain are estimated to have increased by 56% in the past 30 years (Hartvigsen et al. 2018). Despite the fact that back pain is a significant health issue, we still do not fully understand its causes. Thus, investigating possible aetiological factors of diseases that contribute to back pain is an important endeavor.

Spinal osteoarthritis (SOA) is an important contributor to back pain (Egloff et al. 2012). SOA primarily affects the zygapophyseal or facet joints, which are synovial joints formed by the articulation of the superior and inferior articular processes of adjacent vertebrae. SOA involves inflammation, cartilage degradation, and changes to the bone of the superior and inferior articular processes. The regions of the spine differ in their likelihood of experiencing SOA. The lumbar region is the most frequently affected, followed by the cervical and lower thoracic regions, and lastly the upper thoracic region (Spector & MacGregor 2004). SOA affects many individuals living today (Battié et al. 2004), and archaeological evidence indicates that it was also common in the past (Lovell 1994; Jurmain & Kilgore 1995). Estimated prevalence rates range from 3% to 85%, with the disorder being more common in older adults (Battié et al. 2004; Gellhorn et al. 2012).

As with many other spinal diseases, the etiology of SOA is poorly understood. Multiple contributory factors have been proposed including genetics, weight, age, and obesity (Kalichman & Hunter 2007; Weiss & Jurmain 2007). The morphology and condition (e.g., inflammation) of spine-related soft tissues such as the intervertebral discs, back muscles, and

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fascia also seem to contribute to SOA, by accelerating breakdown of cartilage (e.g., Yu et al. 2017). In the study reported here, we focused on the possibility that vertebral shape may contribute to SOA too, following Fujiwara et al. (2001), Eubanks et al. (2009), and Gellhorn et al. (2012).

To date, two studies have investigated vertebral shape as a possible factor in the development of the condition. The first used linear measurements of lumbar articular facets recorded on radiographs and magnetic resonance imaging (MRI) scans of 111 living patients (Fujiwara et al. 2001). The authors diagnosed SOA with Kellgren & Lawrence's (1957) method, which focuses on the presence of osteophytes and joint space narrowing. The findings suggest that individuals with SOA tend to have lumbar vertebrae with more sagittally oriented facets. The second study used linear measurements of interfacet distance of lumbar vertebrae from 444 adults in the Hamman-Todd Collection (Eubanks et al. 2009). The authors found a statistically significant association between smaller interfacet distances and SOA, and proposed that this association was due to smaller interfacet distances disrupting the pyramidal configuration of the lumbar spine. The latter is thought to dissipate load by transferring stress to the more caudal lumbar facets, which are better adapted to withstand mechanical forces. Consequently, Eubanks et al. (2009) argued that smaller interfacet distances lead to a greater risk of SOA because they decrease the ability of the lumbar spine to cope with mechanical stress.

Although the studies of Fujiwara et al. (2001) and Eubanks et al. (2009) identified vertebral traits that may be related to spinal SOA, they have a number of limitations. First, both studies used two-dimensional (2D) measurements to represent vertebral shape, which may have resulted in the loss of important information. Second, they only measured the zygapophyseal facets and interfacet distances, thereby missing potentially important anatomical variation from the rest of the vertebrae. Third, the samples analysed in the two studies were mostly of people of European and East Asian ancestry who died in the last 150 years. Differences between populations, such as genetics, stature, level of physical activity, and life expectancy can influence both vertebral shape (Castillo & Lieberman 2018; Williams et al. 2022) and the prevalence of spinal disorders (Felson et al. 2002; Merbs 2002; Wallace et al. 2021). Thus, inter-population differences could limit the relevance of these studies for other populations. Fourth, the diagnosis of SOA was based on the presence of osteophytes and joint space narrowing. While this approach can identify individuals with mild forms of SOA, it can also introduce more false-positives compared to other diagnostic methods (Rojas-Sepúlveda et al. 2008). As such, the studies may have misidentified some cases of SOA, which calls into question the reliability of their results.

The study we report here was designed to investigate the relationship between SOA and the shape of vertebrae while avoiding the most important of these limitations. In the study, we employed a suite of techniques called Geometric Morphometrics (GM) to compare the three-dimensional (3D) shapes of last thoracic (T12) and first lumbar (L1) vertebrae of individuals with and without osteoarthritis. We focused on these vertebrae because they are the ones most often affected by SOA (Battié et al. 2004; Jurmain & Kilgore 1995; Sparrey et al. 2014). Employing 3D GM allowed us to analyse the whole shape of vertebrae, unlike 2D measurements. Significantly, in previous studies KAP and MC have found associations between 3D vertebral shape and spinal disorders using 3D GM (Plomp et al. 2019a, 2020). We also used a more globally representative sample than Fujiwara et al. (2001) and Eubanks et al. (2009). Like them, we included individuals of European and East Asian ancestry in our sample, but we also measured individuals of African, South Asian, and North American ancestry. Lastly, we used a more conservative approach to the diagnosis of SOA than Fujiwara et al. (2001) and Eubanks et al. (2009). We diagnosed SOA on the basis of the presence of eburnation on the articular surfaces of the zygapophyseal facets. Eburnation refers to dense, polished, ivory-like patches on the joint surface (Waldron & Rogers 1991). These patches result from chronic friction and wear following the loss of protective cartilage and consequent direct bone-on-bone contact. In both clinical radiology and palaeopathology, eburnation is considered pathognomonic for osteoarthritis, making it a reliable diagnostic trait (Waldron & Rogers 1991).

In the study we tested two linked hypotheses. The first contends that there is a significant association between vertebral shape and SOA. The second hypothesis builds on the first. It states that the association between vertebral shape and SOA exists because the risk of SOA is significantly increased by a vertebral morphotype that includes more sagittally-oriented zygapophyseal facets and smaller interfacet distances. This hypothesis is informed by the findings of Fujiwara et al. (2001) and Eubanks et al. (2009) discussed earlier.

2 Material and methods

The study was carried out in accordance with guidelines of Simon Fraser University's Research Ethics Board. The data used in the study can be downloaded from Dryad (https://datadryad.org/). All of the analyses described in this section were performed in *R* version 4.4.0 (R Core Team 2024), with version 4.0.7 of the *geomorph* package (Baken et al. 2021).

2.1 Primary datasets

The study was based on two datasets. The 3D shape data included in the first dataset were collected by KAP and have been employed in two previous studies (Plomp et al. 2019a, 2019b). The dataset also includes SOA assessments undertaken by KAP. These have not been previously published. The second dataset was collected by DAA. This dataset was collected specifically for the present study. Hereinafter, we will refer to the two datasets as the KAP dataset and DAA dataset, respectively.

The sample measured by KAP comprised the last thoracic and first lumbar vertebrae of 80 *Homo sapiens*. The skeletal remains are curated at the Cleveland Museum of Natural History; the Natural History Museum, Vienna; the Museum of Natural History, Berlin; the University of Copenhagen; the University of Zurich; and the Smithsonian Institution National Museum of Natural History. Fifty-six of the individuals were male and 24 female. Sex was taken from collection records where possible. If the sex of an individual was not recorded, it was estimated on the basis of pelvic morphology and, secondarily, cranial traits (Buikstra & Ubelaker 1994; Walker 2008). Only adults were included in the sample to avoid the confounding effects of ontogeny. Some of the individuals had documented ages; others did not. In the absence of a documented age, age was estimated on the basis of dental wear and the state of the surface of the pubic symphysis (Todd 1920). Following Buikstra & Ubelaker (1994), individuals between 17 and 35 were classified as 'young adult', while those between 35 and 50 were classified as 'middle-aged adult'. Individuals who were 50 or older were classified as 'old adult'. The combined totals for the age categories were 28 young adults, 24 middle-aged adults, and 16 old adults. It was not possible to assign the remaining 12 individuals to an age category. The 80 individuals measured by KAP were of a range of ancestries, including African, East Asian, European, and North American. Ancestry was taken from museum records.

KAP identified T12s based on the orientation of the zygapophyseal facets (Shapiro & Jungers 1994). She focused on facet orientation rather than the presence of costal articulations, because facet orientation affects spinal dorsomobility and therefore has more biomechanical significance than the presence of costal articulations (Shapiro 1993). L1s were identified on the basis of articulation with T12s.

To capture vertebral shape, KAP used 54 landmarks (see Fig. 1 and Supporting Information). According to Bookstein's (1992) classification scheme, 32 of landmarks are Type II and 22 are Type III. Type II landmarks are characterised by homology caused by geometric properties and are not directly related to anatomical features. Type III landmarks are dependent on the location of other landmarks and/or the orientation of the whole specimen. KAP recorded the landmarks with a MicroScribe digitising arm. Intraobserver error was evaluated in Plomp et al. (2019a) and found to be within the recommended limit.

KAP relied on macroscopic identification of eburnation to diagnose SOA (Rogers & Waldron 1995). All available vertebrae for an individual were inspected, not just the T12 and L1. In other words, an individual was deemed to have SOA if any of their vertebrae exhibited eburnation. Such individuals will be referred to hereinafter as 'affected' or 'osteoarthritic'. The other individuals in KAP's sample lacked macroscopic signs of any spinal condition, not just SOA. We will refer to these individuals as 'unaffected' or 'healthy'.

The sample measured by DAA comprised the T12s and L1s of 63 *H. sapiens*. These skeletal remains are curated at the University of Alberta and the University of Toronto. DAA used the same methods of identifying T12s and L1s, and of assigning sex, age group, and ancestry, as KAP. Twelve of the individuals measured by DAA were female and 44 were male. It was not possible to determine the sex of the other seven. The totals for the age categories were nine young adults, 13 middle-aged adults, and 33 old adults. It was not possible to assign the remaining eight individuals to an age category. Some of the individuals were of European ancestry; the rest were of South Asian ancestry.

DAA used photogrammetry to collect the shape data. Photogrammetry was preferred to the digitising arm method because recent studies have shown that it is more precise and less prone to interobserver error (Collard et al. 2022a). The protocol utilised by DAA was developed by Evin et al. (2016). For each vertebra, 144 images were shot at approximately 10° intervals using a 24.1 megapixel digital single-lens reflex camera with a 58 mm lens, in conjunction with a Palaeopi TablePi2 turntable. The images were imported into *Agisoft Metashape* (Agisoft LLC 2025) and aligned at the high accuracy setting, and then 3D depth maps were generated. Next, the depth maps were used to build mesh models. Thereafter, the mesh models were imported into MorphoDig (Lebrun 2018) and 54 landmarks recorded. The landmarks were the same as those used to create the shape data included in the KAP Dataset. The landmarks were recorded twice and averaged to minimise recording error (Arnqvist & Mårtensson 1998).

To evaluate intraobserver error for the photogrammetry-derived shape data, a single observer (DAA) recorded the 54 landmarks ten times on one 3D model of an L1. Then, the 10 sets of replicated coordinates were combined with the coordinates for the 64 L1s included in the DAA dataset. Next, all the coordinates (i.e., both the replicated and original coordinates) were reflected and averaged to remove asymmetry (Klingenberg 2016). Thereafter, the averaged coordinates were subjected to generalised Procrustes analysis (GPA), which is designed to remove translational and rotational 'noise' and to minimise the impact of size differences between specimens (Slice 2007). Subsequently, we calculated the Procrustes distance between every set of replicate coordinates and between every set of original coordinates. After this, we compared the greatest Procrustes distance yielded by the replicate coordinates to the smallest Procrustes distance derived from the original coordinates. The former was half the size of the latter, which indicates that intraobserver error is not a significant issue (Neubauer et al. 2010).

DAA diagnosed SOA in the same way as KAP. All available vertebrae for an individual were inspected for macroscopic signs of eburnation on the articular surfaces of the zygapophyseal facet. Individuals were deemed to have SOA if any of their vertebrae exhibited eburnation. When DAA encountered a case he was uncertain about, he consulted with KAP to ensure consistency.

After assembling the KAP and DAA datasets, we checked that KAP and DAA had recorded the landmarks in a similar

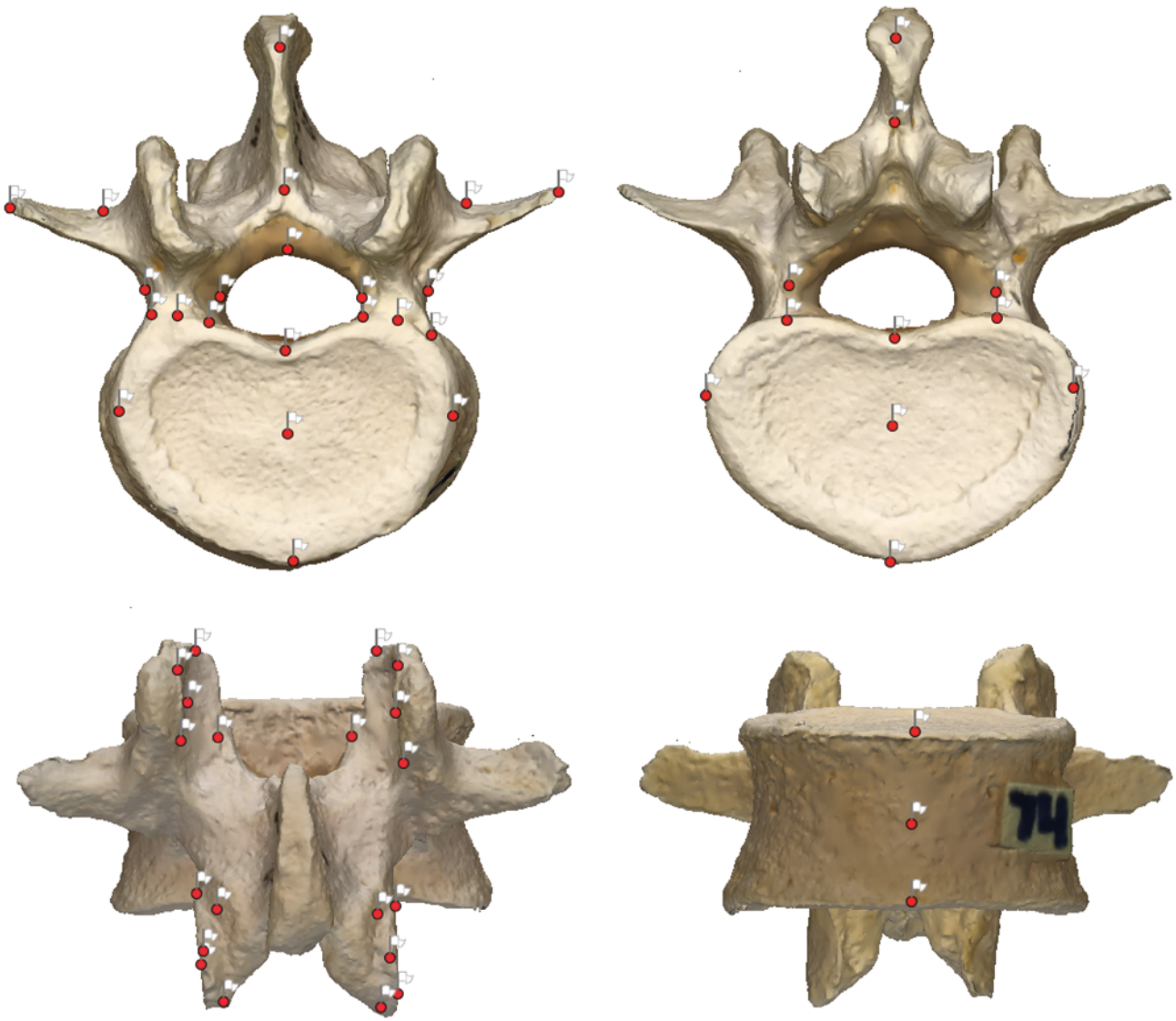

Fig. 1. Landmarks used to capture the 3D shape of a first lumbar vertebrae. Fifty-four landmarks were used in total. Further details of their locations can be found in the Supporting Information.

way. To do this, we selected a photogrammetry-derived 3D model of one of the L1s. Then, KAP and DAA recorded the 54 landmarks on the model ten times each. Next, the two sets of replicate coordinates were combined with the coordinates for the L1s included in both the KAP dataset and the DAA dataset. Thereafter, all the coordinates (i.e., both the replicated and original coordinates) were reflected and averaged to remove asymmetry (Klingenberg 2016). Subsequently, the averaged coordinates were subjected to GPA. After this, we calculated all the Procrustes distances between KAP's replicates and DAA's replicates. That is, we calculated the Procrustes distance between one of KAP's sets of replicates and one of DAA's sets of replicates and repeated the exercise until we had a Procrustes distance for every possible combination of KAP and DAA replicates. We also calculated the Procrustes distance between every two sets of original coordinates. Lastly, we compared the largest Procrustes distance between KAP's and DAA's replicates to the smallest Procrustes distance derived from the original coordinates. We found that the greatest Procrustes distance between the replicates was approximately half the size of the smallest Procrustes distance between the original coordinates. This is a low level of interobserver error (Neubauer et al. 2010), indicating that KAP and DAA recorded the landmarks in a similar way.

2.2 Vertebra-specific datasets

The next step in the study was to reorganise data into two new, vertebrae-specific datasets, which we will refer to as

the T12 dataset and the L1 dataset. The T12 dataset was produced by combining the landmark coordinates and SOA assessments for the T12s from the KAP dataset with the equivalent data from the DAA dataset. The L1 dataset was generated by combining the landmark coordinates and SOA assessments for the L1s from the KAP dataset with the equivalent data from the DAA dataset.

Due to differences in preservation, the samples on which the T12 and L1 datasets were based were not identical. The T12 dataset included 3D coordinates and SOA assessments for 143 T12s. Sixty-seven of the vertebrae were male and 53 were female. The sex of the remaining 23 could not be estimated with confidence. Thirty-four of the T12s were deemed 'young adult', 31 'middle-aged adult', and 40 'old adult'. The age of the remaining 38 could not be estimated with confidence. Forty-seven of the T12s were classified as affected; 96 were deemed unaffected.

The L1 dataset included 3D coordinates and SOA assessments for 136 L1s. Fifty-two of the L1s were female and 65 were male. The sex of the remaining 19 could not be estimated with confidence. Thirty-five of the L1s were deemed 'young adult', 25 'middle-aged adult', and 36 'old adult'. The age of the other 40 could not be estimated with confidence. Thirty-five of the L1s were classified as pathological and 101 were judged to be healthy.

Next, we removed asymmetry from the two sets of coordinate data. We did this by reflecting the coordinates and then averaging the original and reflected coordinates (Klingenberg 2016). This procedure was carried out separately for the two datasets.

Thereafter, we subjected the two sets of averaged coordinates to GPA to remove 'noise' introduced by translation and rotation and to minimise the effects of size differences among the vertebrae (Slice 2007). This procedure was also carried out separately for the two datasets.

Lastly, we transformed the GPA-adjusted coordinates to control for systematic error due to the use of different methods of data collection. Recent studies indicate that combining data obtained with a digitising arm and photogrammetry can be problematic (Collard et al. 2022a). We addressed this possibility by adding a binary variable to each dataset. This variable indicated which data collection technique was used on each vertebra. The Procrustes coordinates were then regressed on this variable (T12: $r^2 = 0.16$, $p < 0.001$; L1: $r^2 = 0.14$, $p < 0.001$), and the residuals were retained for use in subsequent analyses. Details of an assessment of this approach to removing methodological error can be found in the Supporting Information.

2.3 Investigating potential confounding factors

We began this section of the study by ensuring that the regression-based transformation had removed methodological error, as intended. First, a single observer (DAA) recorded the 54 landmarks on six L1s twice, once with a digitising arm and once with photogrammetry. Then, the coordinates were used to create two datasets. In one, the coordinates were left 'raw'. In the other, the coordinates were regressed on the type of data collection method in the manner outlined in the last paragraph. In each dataset, the two replicates per vertebrae were averaged to minimise recording error (Arnqvist & Mårtensson 1998). To remove asymmetry from the data, the coordinates were reflected and relabelled, and the average coordinates between the original and reflected landmarks calculated (Klingenberg et al. 2002). Then, translational and rotational 'noise' was removed, and scaling effects minimised, by running each dataset through a GPA (Slice 2007). Subsequently, the two sets of GPA-adjusted data were analysed with principal component analysis (PCA). To reduce the effects of 'noise', only the principal components (PCs) that accounted for 5% or more of the variance were retained (Zelditch 2004). After this, the retained PCs were then subjected to a Multivariate Analysis of Variance (MANOVA) with the instrument type used as the grouping variable. The MANOVA of the raw dataset was significant ($\lambda = 0.016$, $F = 69.557$, $p < 0.001$). In contrast, the MANOVA of the transformed dataset was not significant ($\lambda = 1$, $F = 0$, $p = 1$). This difference indicates that the regression-based transformation had minimised the methodological error.

Next, we tested for sexual dimorphism. We began by subjecting the T12 dataset to PCA. Then, we reduced 'noise' by removing low information PCs with the procedure outlined by Baylac & Frieß (2005). This involved iteratively adding PCs to a discriminant function analysis (DFA) until the cross validation percentage (CVP) for sex dropped, and retaining only the PCs that contributed positively to the CVP. Next, we performed MANOVAs on the retained PCs to compare vertebral shape between males and females. We repeated these steps with the L1 dataset. Neither MANOVA was significant (T12: $\lambda = 0.951$, $F = 1.461$, $p = 0.2$; L1: $\lambda = 0.974$, $F = 0.724$, $p = 0.5$), which indicates that sexual dimorphism does not influence vertebral shape in the two datasets. All subsequent analyses were therefore performed with pooled-sex data.

The final potential confounding factor we investigated is age. To assess whether age influenced vertebral shape, we replicated the preceding analysis but with age group (young adult, middle-aged adult, old adult) in place of sex. Both MANOVAs were significant (T12: $\lambda = 0.222$, $F = 1.754$, $p < 0.001$; L1: $\lambda = 0.281$, $F = 1.37$, $p = 0.01$), which indicates that there is an association between vertebral shape and age in the two datasets. Subsequently, we investigated whether this association confounds comparisons of vertebral shape in individuals with and without SOA. We accomplished this by subjecting the T12 dataset to PCA and then implementing Baylac & Frieß' (2005) noise reduction procedure with presence/absence of SOA as the grouping variable. Next, we divided the retained PC scores according to age group. Thereafter, we tested for significant shape differences between affected and unaffected individuals in each age group-specific dataset. We used a combination of MANOVA and Benjamini-Hochberg's (1995) correction for multiple comparisons to do this. None

of the MANOVAs was significant (Table 1). The implication of this is that, while vertebral shape changes with age, the age-related alterations are independent of SOA. Accordingly, age was not considered in subsequent analyses.

2.4 Testing the focal hypotheses

After ruling out methodological error, sexual dimorphism, and age as confounding factors, we moved on to evaluating the focal hypotheses. To reiterate, the first of the hypotheses posits that there is an association between vertebral shape and SOA, while the second contends that the association exists because the risk of SOA is significantly increased by a vertebral morphotype that includes more sagittally-oriented zygapophyseal facets and smaller interfacet distances.

The first hypothesis predicts that the average shape of the vertebrae of individuals with SOA should differ significantly from the average shape of the vertebrae of unaffected individuals. To test this prediction, we subjected the residuals in the T12 dataset to PCA and then implemented Baylac & Frieß' (2005) noise reduction procedure with the presence/absence of SOA as the grouping variable. Next, we subjected the retained PCs to MANOVA. The presence/absence of SOA was used as the grouping variable in this analysis too. Thereafter, we carried out a DFA to assess the ability of vertebral shape to predict the presence of SOA. Subsequently, we repeated these steps with the residuals in the L1 dataset.

The second hypothesis predicts that the vertebrae of individuals affected by SOA generally should have more sagittally-oriented zygapophyseal facets and smaller interfacet distances than the vertebrae of unaffected individuals. We tested this prediction by first generating PCA scatter plots illustrating the shape variance captured by the residuals included in the T12 dataset. We then identified the combination of PCs that best separated the affected and unaffected vertebrae on the plots. After this, we generated 3D wireframes to illustrate the shape differences captured by the retained PCs and used these wireframes to identify shape traits associated with the presence of SOA. Thereafter, we repeated these steps with the L1 dataset.

Table 1. Results of MANOVAs comparing T12 and L1 vertebrae of individuals with and without SOA assigned to the three age categories used in the study. Young adults = young adults with SOA *vs* young adults without SOA. Middle-aged adults = middle-aged adults with SOA *vs* middle-aged adults without SOA. Old adults = Old adults with SOA *vs* old adults without SOA.

	T12	L1
Young adults	$\lambda = 0.032$, $F = -1.56$, $p = 0.9$	$\lambda = 0.034$, $F = -2.30$, $p = 0.9$
Middle-aged adults	$\lambda = 0.038$, $F = 0.6$, $p = 0.9$	$\lambda = 0.045$, $F = 0.33$, $p = 0.9$
Old adults	$\lambda = 0.031$, $F = 0.57$, $p = 0.9$	$\lambda = 0.049$, $F = 2.65$, $p = 0.03$

3 Results

3.1 Tests of the first hypothesis

For the T12 dataset, 34 PCs were retained after Baylac & Frieß' (2005) noise reduction procedure was implemented. Together, these PCs accounted for 93% of the shape variance. The MANOVA returned a significant result when affected vertebrae were compared to unaffected vertebrae ($\lambda = 0.562$, $F = 2.472$, $p < 0.001$), while the DFA correctly classified 81% of individuals as either affected or unaffected. Both of these findings are in line with the prediction that the average shape of the vertebrae of individuals with SOA should differ significantly from the average shape of the vertebrae of unaffected individuals.

For the L1 dataset, 37 PCs were retained after we implemented the Baylac & Frieß (2005) noise reduction procedure. Collectively, these PCs accounted for 95% of the shape variance. The MANOVA was significant when affected vertebrae were compared to unaffected vertebrae ($\lambda = 0.470$, $F = 2.979$, $p < 0.001$), and the DFA correctly classified 90% of individuals according to their SOA status. These results are also consistent with the test prediction.

Thus, the two sets of analyses carried out to test the first hypothesis that there is an association between vertebral shape and SOA, supported it.

3.2 Tests of the second hypothesis

For the T12 dataset, the greatest separation between affected and unaffected vertebrae was found when PC3 (8% of shape variance) was plotted against PC5 (6% of shape variance). The plot is shown in Fig. 2. On both PCs, affected vertebrae tend to plot more negatively than unaffected vertebrae. The wireframes indicate that, compared to unaffected vertebrae, affected vertebrae tend to have (1) craniocaudally shorter and dorsoventrally shallower bodies; (2) smaller foramina; (3) more obliquely oriented articular facets; (4) narrower interpedicle distances; (5) narrower neural arches; (6) smaller interfacet distances; (7) longer, more laterally projecting transverse processes; (8) longer, more cranially oriented spinous processes; and (9) cranio-caudally taller spinous process tips. These findings only partially support the second hypothesis. They are consistent with the prediction that affected individuals will have smaller interfacet distances than unaffected individuals, but they are inconsistent with the prediction that affected individuals will have more sagittally oriented articular facets than unaffected ones.

For the L1 dataset, the greatest separation between affected and unaffected vertebrae was found when PC3 (9% of shape variance) was plotted against PC5 (6% of shape variance). The plot is reproduced in Fig. 3. On PC3, affected individuals tend to score more positively than unaffected individuals. In contrast, affected individuals tend to plot more negatively than unaffected individuals on PC5. The wireframes indicate that the traits that differentiate affected L1s from unaffected ones are the same as

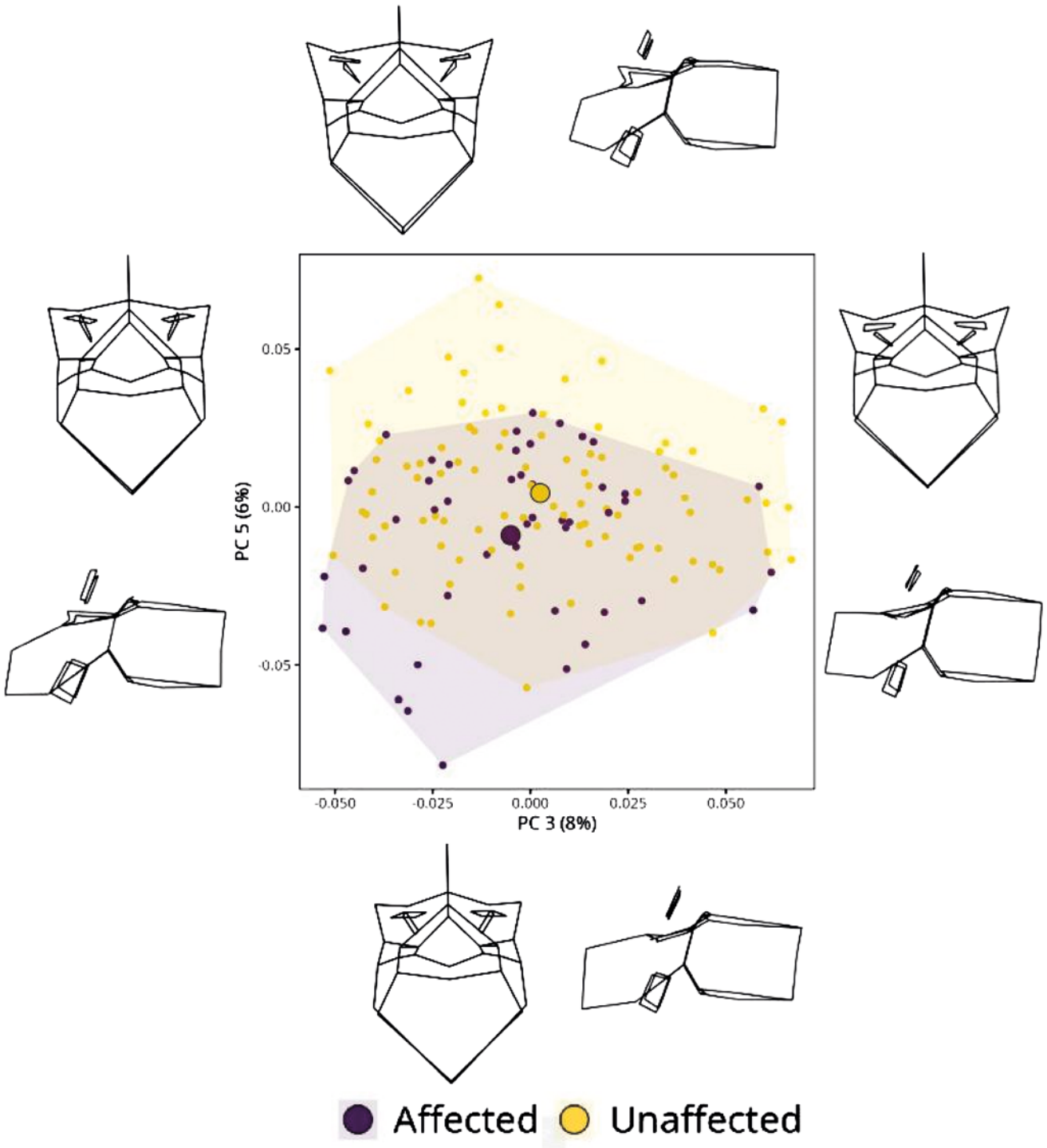

Fig. 2. Plot of principal component (PC) scores comparing the shapes of the last thoracic vertebrae of individuals with and without spinal osteoarthritis (PC3 vs PC5). The large circles are the average shapes. The wireframes illustrate the morphotypes at the extremes of the PCs.

those that differentiate affected and unaffected T12s. Thus, this set of analyses also only partially supports the second hypothesis. The analyses are consistent with the part of the hypothesis that asserts that affected individuals have smaller interfacet distances than unaffected individuals is supported by the analyses, but they are not consistent with the part of the hypothesis that states that affected individuals also have more sagittally oriented articular facets than unaffected individuals.

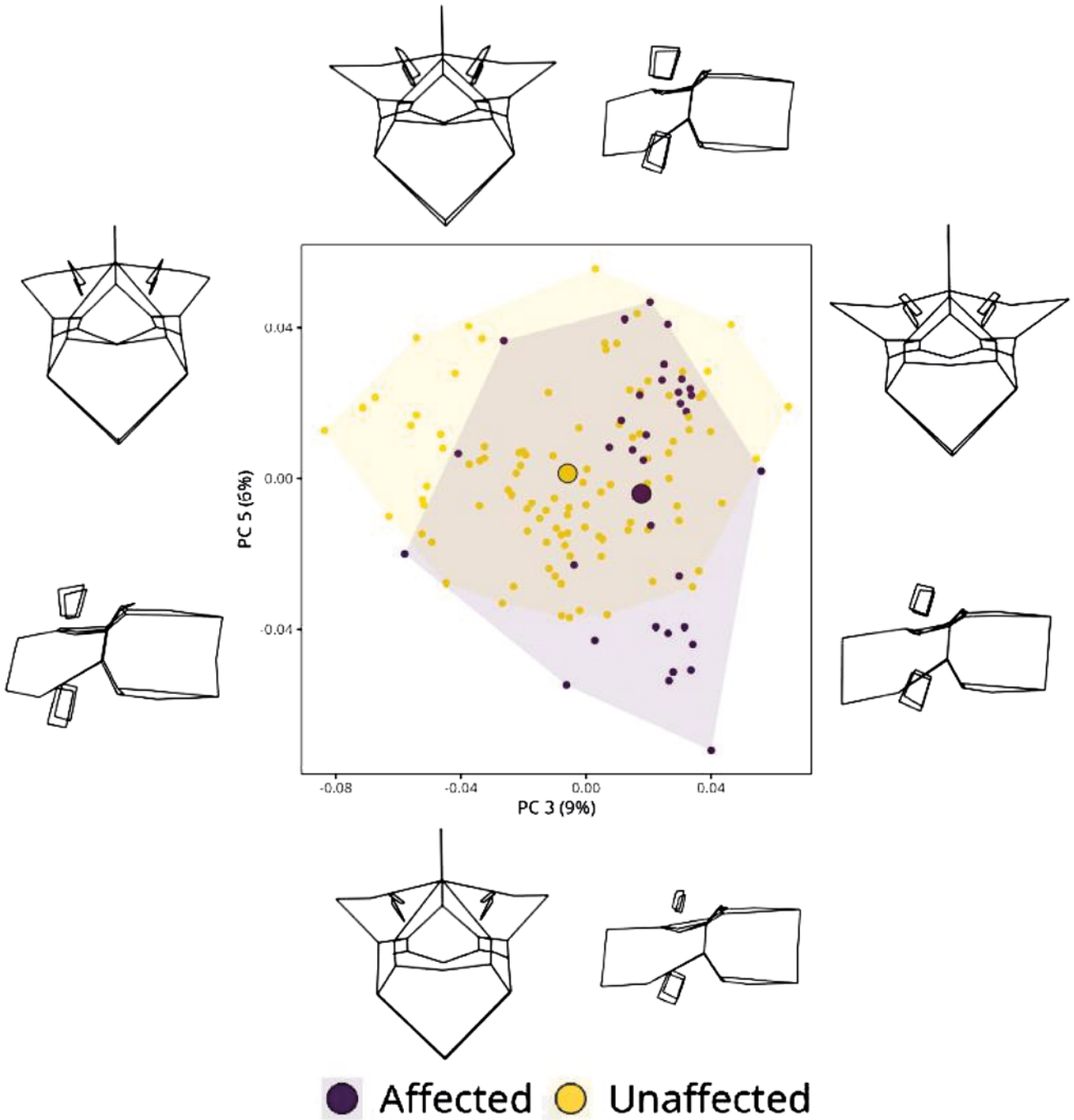

Fig. 3. Plot of principal component (PC) scores comparing the shapes of the first lumbar vertebrae of individuals with and without spinal osteoarthritis (PC3 vs PC5). The large circles are the average shapes. The wireframes illustrate the morphotypes at the extremes of the PCs.

4 Discussion

The study reported here explored the possibility that there is a relationship between vertebral shape and spinal osteoarthritis (SOA) by comparing the 3D shape of T12 and L1 vertebrae of people with and without SOA. Two hypotheses were tested in the study. The first was that there is an association between vertebral shape and SOA. The second hypothesis was that the association exists because the risk of SOA is increased by a vertebral morphotype that includes more sagittally-oriented zygapophyseal facets and smaller interfacet distances. This hypothesis was informed by the findings of two previous studies (Fujiwara et al. 2001; Eubanks et al. 2009;).

Our results supported the first hypothesis. MANOVAs and DFAs indicated that the vertebrae of individuals with SOA have a significantly different morphotype to the vertebrae of unaffected individuals.

In contrast, the results only partially supported the second hypothesis. Our comparisons of PCA-derived wireframes indicated that there are several differences between the average shape of vertebrae of individuals with and without SOA, but these differences only include one of those predicted by the hypothesis, smaller interfacet distances. The other predicted difference – more sagittally oriented articular facets in affected individuals – was not supported by the analyses. To our knowledge, none of the other shape differences between the vertebrae of individuals with and without SOA identified in the analyses has been linked to SOA in previous work. So, they represent a third important finding of the study. The traits in question are (1) craniocaudally shorter and dorsoventrally shallower bodies; (2) smaller foramina; (3) more obliquely oriented articular facets; (4) narrower interpedicle distances; (5) narrower neural arches; (6) smaller interfacet distances; (7) longer, more laterally projecting transverse processes; (8) longer, more cranially oriented spinous processes; and (9) cranio-caudally taller spinous process tips.

There is an important point to make here. While our results indicate that, on average, vertebrae from individuals with SOA are statistically different from those without SOA, the PCs shown in the scatterplots account for a relatively small amount of the shape variance (14% for the T12 plot and 15% for the L1 plot). Moreover, there is considerable overlap between the two groups of vertebrae in both scatterplots. Thus, the traits associated with SOA are subtle and not found exclusively in the vertebrae of individuals with SOA. This is not surprising. There are two reasons for this. One is that SOA is a degenerative disease and therefore some of the individuals assigned to the healthy group in our study may have developed SOA later in life if they had survived. The other is that, as we explained earlier, the development of SOA is generally accepted to be multifactorial. One corollary of this is that it is likely that some individuals with SOA in our sample developed it for reasons unrelated to vertebral shape. Given that our healthy sample likely included individuals who would have gone on to develop SOA due to the shape of their vertebrae if they had not died, and the fact that SOA has multiple causes, we think it is remarkable that our analyses identified a significant difference between the shapes of the vertebrae of individuals with and without SOA, let alone identifying several specific traits that may predispose for SOA. This speaks to the analytical power of 3D GM, in our view.

There are two main potential explanations for there being an association between 3D vertebral shape and SOA. One is that the development of SOA systematically alters vertebral shape via restrictions on posture and movement and bone remodeling, resulting in a morphotype that is distinct from the average morphotype of non-affected individuals. The other potential explanation is that a particular vertebral morphotype predisposes individuals to developing SOA, most likely as a result of a mismatch between vertebral shape and the biomechanical demands placed on the spine.

We are skeptical about the first of these hypotheses. Our sample included the vertebrae of people of a wide variety of lifestyles and ancestries, and it seems unlikely that their posture and movement would have been sufficiently similar for them to converge on shared vertebral morphotypes via remodelling induced by SOA. Another reason we are skeptical about the hypothesis concerns the way we assigned individuals to the affected category. To reiterate, we classified an individual as 'affected' if *any* of their vertebrae exhibited eburnation, not just their T12 and L1. Thus, the affected subsamples include vertebrae that have the SOA-linked shape traits in absence of the key indicator of SOA, which was identified on other vertebrae of the individual. The obvious corollary of this is that SOA is very unlikely to have given rise to the shape traits. There is a third reason why we are skeptical about the hypothesis. As we explained earlier, in the part of the study in which we investigated potential confounding factors, we found a relationship between vertebral shape and age, but this relationship was independent of SOA. This is not what we would expect to see if SOA leads to change in vertebral shape. Because SOA is a progressive condition that worsens as one ages, if the hypothesis were correct, we would expect the association between SOA and vertebral shape to be mediated by age.

The other hypothesis – that a particular vertebral morphotype predisposes for SOA due to a mismatch between the shape traits and the biomechanical demands placed on the spine – is more compelling, in our view. The reason for this is that it is relatively easy to explain how having several of the traits we found to be associated with SOA can affect the biomechanics of the spine in such a way that the risk of SOA increases. The traits in question are (1) craniocaudally shorter and dorsoventrally shallower bodies; (2) smaller foramina; (3) more obliquely oriented articular facets; (4) narrower interpedicle distances; (5) narrower neural arches; (6) smaller interfacet distances; (7) longer, more laterally projecting transverse processes; (8) longer, more cranially oriented spinous processes; and (9) cranio-caudally taller spinous process tips.

A vertebra with a relatively short and shallow body will have a relatively small cross-sectional area, and there is evidence that vertebrae with relatively small cross-sectional areas are a problem from a biomechanical perspective. This evidence comprises studies that have examined vertebral fractures in women (Mazess et al. 1994; Myers & Wilson 1997). These studies indicate that women with vertebrae with relatively small cross-sectional areas have an elevated risk of vertebral fractures, independent of age, height, weight, and bone mineral density. Additionally, there is a potential mechanistic link between having vertebrae with relatively small cross-sectional areas and SOA. This link involves the vertebral facets. If the axial loading capacity of a vertebra

is reduced, then more of the axial load will be transferred to the neural arch and vertebral facets. Increasing the axial load on the vertebral facets will increase the risk of overloading the facets (Latimer & Ward 1993; Shapiro 1993) and this can be expected to accelerate degeneration of the zygapophyseal joints (Sun 2010; Chen et al. 2024). This in turn can be expected to increase the risk of SOA. Thus, there are two reasons to think that having vertebrae with relatively short and shallow bodies will predispose an individual to develop SOA.

Foramen size is hypothesised to be causally related to interfacet distance such that smaller distances between the zygapophyseal facets of adjoining vertebrae lead to smaller foramina while larger distances result in larger foramina (Latimer & Ward 1993; Plomp et al. 2019b). Smaller interfacet distances increase the risk of impingement between facets (Ward et al. 2007). The friction and abnormal axial loading resulting from impingement can be expected to accelerate the degeneration of the facet joints (Inoue et al. 2019), which in turn can be expected to increase the risk of facet-on-facet contact and eventually SOA. Thus, there is also a biomechanical explanation for our finding that individuals with SOA tend to have smaller foramina than unaffected individuals.

The orientation of the zygapophyseal facet joints in the thoracolumbar junction has been linked to resisting rotation, likely to protect the intervertebral discs and spinal cord, and to help maintain lumbar lordosis (Ahmed et al. 1990; Shapiro 1993; Masharawi et al. 2004). Thus, more sagittally oriented facets fulfill this function, as we identified in the vertebrae of unaffected individuals relative to affected ones. In contrast, the vertebrae of affected individuals have relatively more oblique facet orientation. This could make the joints less able to appropriately restrict rotation, which could result in increased stress on the facets (Inoue et al. 2019). This in turn accelerates joint degeneration (Sun 2010; Chen et al. 2024), which is expected to increase risk for developing SOA. Thus, more obliquely oriented facets in T12 and L1 could increase the risk for SOA by restricting rotation.

Smaller interpedicle distances result in mediolaterally narrower neural arches and therefore smaller interfacet distances (Ward et al. 2007). Reduced interfacet distances can lead to direct contact between the zygapophyseal facets of consecutive vertebrae (Ward et al. 2007) and reduce the pyramidal configuration of the facets in the lumbar region. The pyramidal configuration of the facets in the lumbar region is thought to dissipate load by transferring a greater amount of the stress to the more caudal lumbar facets (Masharawi & Salame 2011). Thus, smaller interpedicle distances can be expected to reduce the efficiency of the facets in dissipating mechanical forces (Eubanks et al. 2009) and result in impingement of the facets of adjoining vertebrae (Ward et al. 2007). Reduced loading capacity and facet impingement may lead to the acceleration of joint degeneration and the development of SOA (Sun 2010; Chen et al. 2024).

The transverse processes of the lower thoracic and lumbar vertebrae are the attachment sites for the *erector spinae* muscles. These muscles control the sagittal and lateral flexibility of the spine (Shapiro 1993), and thus the length and orientation of the transverse processes influence the flexibility of the spine (Latimer & Ward 1993). Shorter transverse processes in the lower vertebrae are thought to restrict lateral flexion in the lower spine (Latimer & Ward 1993; Shapiro 1993). More dorsally projecting transverse processes have been hypothesised to increase spinal extension, resist lateral flexion, and maintain lumbar lordosis during bipedal posture and gait (Latimer & Ward 1993; Shapiro 1993). Thus, longer and more laterally projecting transverse processes increase the risk of excessive lateral flexion and result in a less stable spine (Takahashi et al. 2006), which in turn could accelerate degenerative changes such as synovial hypertrophy and SOA (Laplante & DePalma 2012).

Longer, more cranially oriented spinous processes may increase risk of SOA through reduced spinal stability. The shape of the spinous process is thought to be a compromise between spinal mobility and stability (Shapiro 1993; Shapiro & Jungers 1994, 1988). Longer, more cranially-oriented spinous processes are thought to allow for greater dorsal mobility in the spine, while shorter, more caudally-oriented spinous processes are associated with more dorsal stability (Shapiro 1993). Thus, affected individuals can be expected to have lumbar spines that are relatively less stable. And less stable lumbar spines can be expected to be less able to withstand axial loading and compressive forces (Latimer & Ward 1993; Shapiro 1993). This in turn can be expected to accelerate facet joint degeneration and increase the risk of SOA (Sun 2010; Chen et al. 2024).

The height of spinous process tips in humans has been linked to bipedalism. Specifically, relatively short (i.e. vertically 'pinched') spinous process tips of the lower thoracic and lumbar vertebrae has been hypothesised to ensure that there is sufficient space between the processes of adjoining vertebrae in the lumbar curve of the spine (Plomp et al. 2019b). This hypothesis was developed in light of the presence of vertically-pinched spinous process tips in the antelope species known as the gerenuk (*Litocranius walleri)*, which feeds on leaves of trees while standing on its hind legs. It is thought that the gerenuk's vertically pinched spinous processes allow it to have a small amount of lumbar lordosis without the processes impinging on one another (Cartmill & Brown 2017). One corollary of this hypothesis is that the relatively tall spinous process tips of SOA-affected humans can be expected to result in smaller inter-process spacing, thereby increasing risk of impingement in the lower back. Impingement of the facet joints in the ischiofemoral region has been found to limit extension and increase load on the lumbar facets (Gómez-Hoyos et al. 2017). We suspect that a similar mechanism may be involved in spinous process impingement and that this leads to increased inter-facet contact and joint wear, which in turn lead to SOA.

In sum, then, all of the traits we found to be associated with SOA can be argued to affect the biomechanics for the spine in ways that may increase risk for SOA. Accordingly, we suggest that the morphotype associated with SOA in our analyses could increase risk for SOA through suboptimal biomechanics. More specifically, we suggest that the morphotype is composed of traits that likely increase the loading, compression, and shearing forces acting on the facets, resulting in joint degeneration and eventually SOA.

With regard to future research possibilities, an obvious target is the difference between the results of our study and those of Fujiwara et al. (2001). To reiterate, our analysis returned an association between obliquely oriented articular facets and SOA, while Fujiwara et al. (2001) found an association between sagittally oriented facets and SOA. There are two potential explanations for this discrepancy. Fujiwara et al. (2001) focused on living people of East Asian ancestry, while we studied archaeological and documented individuals of several different ancestries. Thus, it is possible that the two sets of results differ due to regional variation in SOA and the factors that cause it. Alternatively, it is possible that the difference in results is due to temporal variation in SOA and the factors that cause it. Ascertaining which of these hypotheses is correct – if either is – will require analysis of a more geographically and temporally representative sample than the one used in the present study.

Another possibility for future research concerns the criteria used to diagnose SOA. These often differ between studies – compare, for example, Rogers & Waldron (1995) and Rojas-Sepúlveda et al. (2008). Thus, it would also be useful to investigate if eburnation is the only lesion that correlates with vertebral shape or if other SOA-linked lesions, such as osteophytes, have a relationship with vertebral shape. Such a study could use the methods employed in the present study to compare the 3D shapes of vertebrae grouped by types of lesions and combinations thereof.

The study reported here revealed a link between the shape of the vertebrae of the lower thoracic and lumbar regions of the spine and SOA, but the situation elsewhere in the vertebral column is unclear. Thus, a third possibility for future research is to adapt the present research protocol to examine the 3D shape of vertebrae in the other regions of the spine and its relationship to SOA. Results reported by Sahin et al. (2015) and Stemper et al. (2011) justify such a study. These authors found associations between vertebral shape and SOA on the atlantoaxial and lumbosacral junctions.

Lastly, it would be useful to place the relationship between vertebral shape and SOA in an evolutionary context by comparing the vertebrae of humans with and without SOA to the vertebrae of our closest living relatives, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). This approach has been used in connection with two other spinal conditions – intervertebral disc herniation and spondylolysis – and yielded interesting results (Plomp et al. 2015, 2019a, 2020). Humans with vertical intervertebral disc herniation were found to have vertebrae that are more similar in shape to those of chimpanzees than are healthy humans (Plomp et al. 2015, 2019a), whereas humans with spondylolysis were found to have vertebrae that are more different in shape to those of chimpanzees than are healthy humans (Plomp et al. 2020). These findings suggest that intervertebral disc herniation and spondylolysis can be partly explained as byproducts of our species' evolutionary history (Collard et al. 2022b). It would be useful to know whether the same holds for SOA.

5 Conclusions

The study reported here sought to shed further light on the role played by vertebral shape in the development of spinal osteoarthritis (SOA). Using 3D shape comparisons of last thoracic and first lumbar vertebrae, it tested two hypotheses. The first was that there is an association between vertebral shape and SOA. The second hypothesis was formulated based on findings from previous studies and contends that the association between vertebral shape and SOA exists because the risk of SOA is significantly increased by a vertebral morphotype that includes more sagittally-oriented zygapophyseal facets and smaller interfacet distances.

The study's results fully supported the first hypothesis because they indicated that there are significant differences in shape between the vertebrae of individuals with and without SOA. In contrast, the analyses only partially supported the second hypothesis. They indicated that the vertebrae of individuals with SOA do indeed tend to have smaller interfacet distances. However, the analyses did not support the idea that the vertebrae of individuals with SOA tend to have articular facets that are more obliquely oriented. Instead, the analyses indicated that individuals with SOA tend to have articular facets that are more sagittally oriented.

The analyses identified a number of other traits that distinguish vertebrae of affected individuals from those of unaffected individuals. Compared to the last thoracic and first lumbar vertebrae of individuals without SOA, those of individuals with SOA tended to have: (1) craniocaudally shorter and dorsoventrally shallower bodies; (2) smaller foramina; (3) more obliquely oriented articular facets; (4) narrower interpedicle distances; (5) narrower neural arches; (6) smaller interfacet distances; (7) longer, more laterally projecting transverse processes; (8) longer, more cranially oriented spinous processes; and (9) cranio-caudally taller spinous process tips. To the best of our knowledge, these traits have not previously been associated with SOA.

There are two main potential explanations for the association between 3D vertebral shape and SOA identified in the analyses. One is that the development of SOA affects posture and movement, resulting in bone remodeling that systematically alters vertebral shape. The second potential explanation is that the identified vertebral morphotype predisposes individuals to developing SOA, most likely as a result of a

mismatch between the shape of the vertebrae and the biomechanical demands placed on the spine. We believe the latter hypothesis is more likely to be correct than the former. We do so primarily because all of the traits we found to be associated with SOA can be linked to the biomechanics of the spine in ways that could induce the development of SOA.

More generally, the study adds weight to the idea that vertebral shape is one of factors that increases the probability of an individual developing SOA. We stress the "one of the factors" in the preceding sentence. We are convinced that SOA has multiple causes. As we pointed out earlier, studies have indicated that the morphology and condition of spine-related soft tissues, including the intervertebral discs, back muscles, and fascia can also contribute to SOA (e.g., Yu et al. 2017). Thus, we are not claiming that vertebral shape is the only cause of SOA. What we are suggesting is that vertebral shape is one of several factors that increases an individual's susceptibility to developing SOA.

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