Stuebner, Victoria (2022) *Lumbar vertebral body and disc variation in modern humans with implications for reconstructing lumbar lordosis in fossil hominins.* Master of Science by Research (MScRes) thesis, University of Kent,.

Lumbar vertebral body and disc variation in modern humans with implications for reconstructing lumbar lordosis in fossil hominins

Victoria H. Stuebner

Masters by research in Biological Anthropology

Year of submission: 2022

School of Anthropology and Conservation

University of Kent, Canterbury

Supervisors: Profs Tracy Kivell and Matthew Skinner

Word Count: 26,473

Number of Pages:138

Abstract

Lumbar lordosis plays a significant role in the vertebral column because it supports the weight of the torso during bipedal locomotion (Aeillo and Dean, 2002). In previous studies, vertebral body wedging (VBW) patterns (Williams et al. 2013; García-Martínez et al. 2020) and multiple linear regression formulas have been used to study lordosis in hominins (Been et al. 2010a; Been, Gómez-Olivencia and Kramer, 2012). This project evaluates the accuracy of current methods used for reconstructing lumbar lordosis in hominins through an analysis of how age, sexual dimorphism, VBW and intervertebral disc wedging (IVDW) influences lordosis. This study was the first to investigate the correlation between individual IVDW and VBW in detail and introduces the idea of reconstructing lordosis using the lumbolumbar angle. This study used a sample of modern humans, comprised of individuals between 25 and 50 years of age from the University of New Mexico Decedent Image Database (UNMDID) (n=112) and living South African adults (n=27), to study lordosis (Edgar et al. 2020). Reconstructions of lordosis were reported for fossil specimens Oberkassel 1, Oberkassel 2, Kebara 2, and StS 14. VBW, IVDW, the Cobb and lumbolumbar angle were measured digitally from CT scans. The results revealed that within the sample lordosis did not vary significantly based on age but did show signs of sexual dimorphism. Comparisons between IVDW and VBW demonstrated that IVDW contributed the most to lordotic curvature, but VBW had a stronger correlation with the Cobb and lumbolumbar angles. The relationship between VBW and IVDW was consistently negative. The reconstructed lordosis of fossil specimens was within the range of modern humans. Lordosis reconstructions varied based on methods but suggest that reconstructing the lumbolumbar angle, as opposed to the Cobb angle, could increase the accuracy of future reconstructions.

Acknowledgements

First, I would like to express my appreciation to my primary supervisor, Dr Tracy Kivell, for providing me with guidance on this research project, allowing me to participate in her lab, and always finding time to meet and communicate with me. I would also like to thank Dr Matt Skinner for providing essential information and advice on the UNMDID, data collection, and my results. Further, I would like to thank everyone in the Kivell/Skinner lab group, but especially Dr Chris Dunmore, Dr Marine Cazenave, and Dr Zewdi Tsegai, for helping me navigate Avizo and Image J.

Marine also reached out to Dr Zarina Lockhat, Dr Farhanah Suleman, and Dr Anna Oettlé to request CT scans of the South African sample on my behalf. I am grateful for the opportunity to work with this sample thanks to these academics. I want to express thanks to the curators of the UNMDID who granted me access to their decedent population as well (Edgar et al. 2020).

Dr Ella Been also offered helpful advice and took time to meet with me to discuss the samples and measurements used in this thesis.

The academics at the University of Roehampton, specifically Dr Lia Betti, and Dr Todd Rae who continue to provide encouragement during my journey through graduate school.

Finally, my father, John, and partner, Joel, have provided me with encouragement and emotional support that has helped me immensely during this time.

Table of Contents

List of Figures

List of Tables

1. Introduction

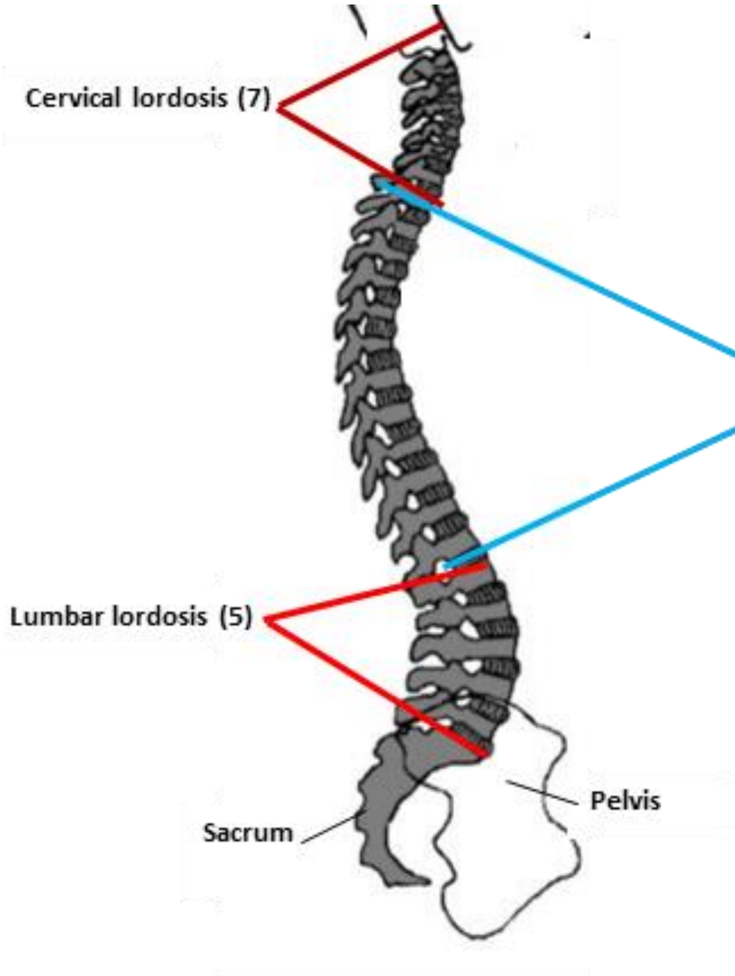
Lumbar lordosis is a crucial adaptation for bipedalism that has developed to support the upper body over the lower limbs while in motion (Aiello and Dean, 2002). Nevertheless, as a trait, lumbar lordosis is highly variable between individuals, and current research lacks a common consensus on what could cause such variability (Jackson and MacManus, 1994; Cheng et al. 1998; Damasceno et al. 2006; Been et al. 2010b, 2010d; Kalichman et al. 2011). Previous research suggests that morphology found in both the vertebrae and intervertebral discs explains most of the variability found in the lumbar lordosis, however, lordosis reconstructions of past hominins must try to adapt and overcome the absence of intervertebral discs in the fossil record(Been et al. 2007; 2010a; Been, Gómez-Olivencia and Kramer, 2012). It can be argued, however, that reconstructing lordosis with vertebral body morphology alone ignores the intervertebral discs, which some studies have shown, contribute a much larger proportion of lordotic wedging to the lumbar region (Jackson and McManus, 1994; Damasceno et al. 2006; Masharawi et al. 2008, Been et al. 2010d). There are also other factors that have been associated with variation in lordosis, like lifestyle (Williams et al. 2022), geography (Lois-Zlolniski et al. 2019; García-Martínez, 2020), aging (Jackson and McManus, 1994; Gelb et al. 1995; Masharawi et al. 2008; Hansen et al. 2015) and sex (Cheng et al. 1998; Vialle et al. 2005; Damasceno et al. 2006; Whitcome, Shapiro and Lieberman, 2007; Bailey et al. 2016) but, these studies yield mixed results and are often excluded as contributing factors for fossil lordosis reconstructions (Been et al. 2010a; Been, Gómez-Olivencia and Kramer, 2012). This study aims to evaluate the reliability of predicting lumbar lordosis in hominins from vertebral body morphology, while also studying the impact of other factors like age, sex, and intervertebral disc morphology. The study has been conducted on samples of modern human CT scans from both the UNMDID and South Africa (Edgar et al. 2020).

1.1. Human lumbar morphology and adaptations for bipedalism

The vertebral column of modern *Homo sapiens* has developed a distinctive ‘S’ like shape to maintain balance while bipedal (Figure 1) (Tardieu, Hasegawa and Haeusler, 2017:912). The human vertebral column consists of vertebrae and intervertebral discs that create a lordosis (convexly curved ventrally) in the cervical and lumbar regions and kyphosis in the thoracic region (convexly curved dorsally) (Figure 1) (Aeillo and Dean, 2002; Lovejoy, 2005; Pilbeam, 2004). Coinciding with the shape of the vertebral column, humans have a narrow torso and a short pelvis with wide ilia relative to other extant hominids (Aiello and Dean, 2002; Sparrey et al. 2014). The shape of the human vertebral column, ribs, and pelvis work together to ensure that the body moves efficiently without excess energy expenditure (Nakatsukasa, 2004; Prueshoft, 2004; Lovejoy, 2005; Sparrey et al. 2014; Tardieu, Hasegawa and Haeusler, 2017).

Figure 1.

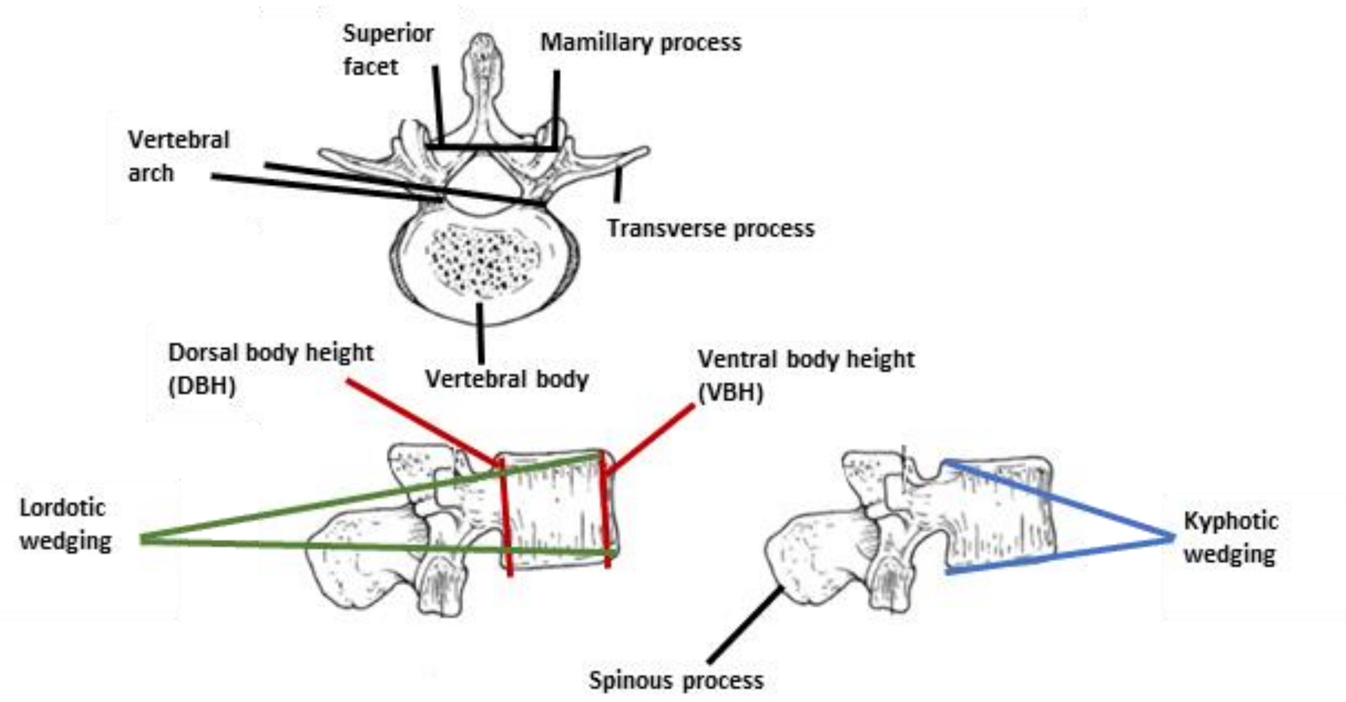
Human vertebral column, outlining the different anatomical regions of the vertebrae and curvature. The number of vertebrae assigned to each region is in parentheses. Image adapted from (Kroemer Elbert, Kroemer, and Kroemer Hoffman, 2018) .



While the human vertebral column has many distinctive features, the lumbar lordosis is a feature that is derived in humans relative to other hominins (Aeillo and Dean, 2002; Rose, 1975; Martelli, 2019). Lumbar lordosis is composed of lordotic wedging in the lumbar region's vertebral bodies and intervertebral discs (Aeillo and Dean, 2002; Lovejoy, 2005). Ventral or kyphotic wedging occurs when the body of the vertebra or intervertebral disc has a greater height posteriorly than it does superiorly, and dorsal or lordotic wedging occurs when the vertebral body has a greater superior height (Figure 2) (Abitbol, 1987; Digiovanni et al. 1989; Scoles et al. 1991; Stokes and Aronsson, 2001; Aeillo and Dean, 2002). The range of lordotic curvature found amongst humans is diverse, but the pattern of wedging is consistent, with more cranially positioned vertebrae and intervertebral discs wedged ventrally, while the caudally positioned vertebrae and intervertebral discs are wedged dorsally (Rose, 1975; Jackson and McManus, 1994; Cheng et al. 1998; Damasceno et al. 2006; Been et al. 2010a). Within the lumbar region kyphotic wedging provides stability, while lordotic wedging provides flexibility to the spine to support upright posture,increase strides and walking speed (Been and Bailey, 2019) and the lordotic curvature helps to safely attenuate, or absorb, shock when running (Castillo and Lieberman, 2018)

Figure 2.

The anatomy of a typical human lumbar vertebra, the L3, different components of the vertebra are labelled in black and the dorsal and ventral vertebral body heights are pointed out in red. Lordotic wedging is outlined in green while kyphotic wedging is outlined in blue. Image adapted from Aiello and Dean (2002).



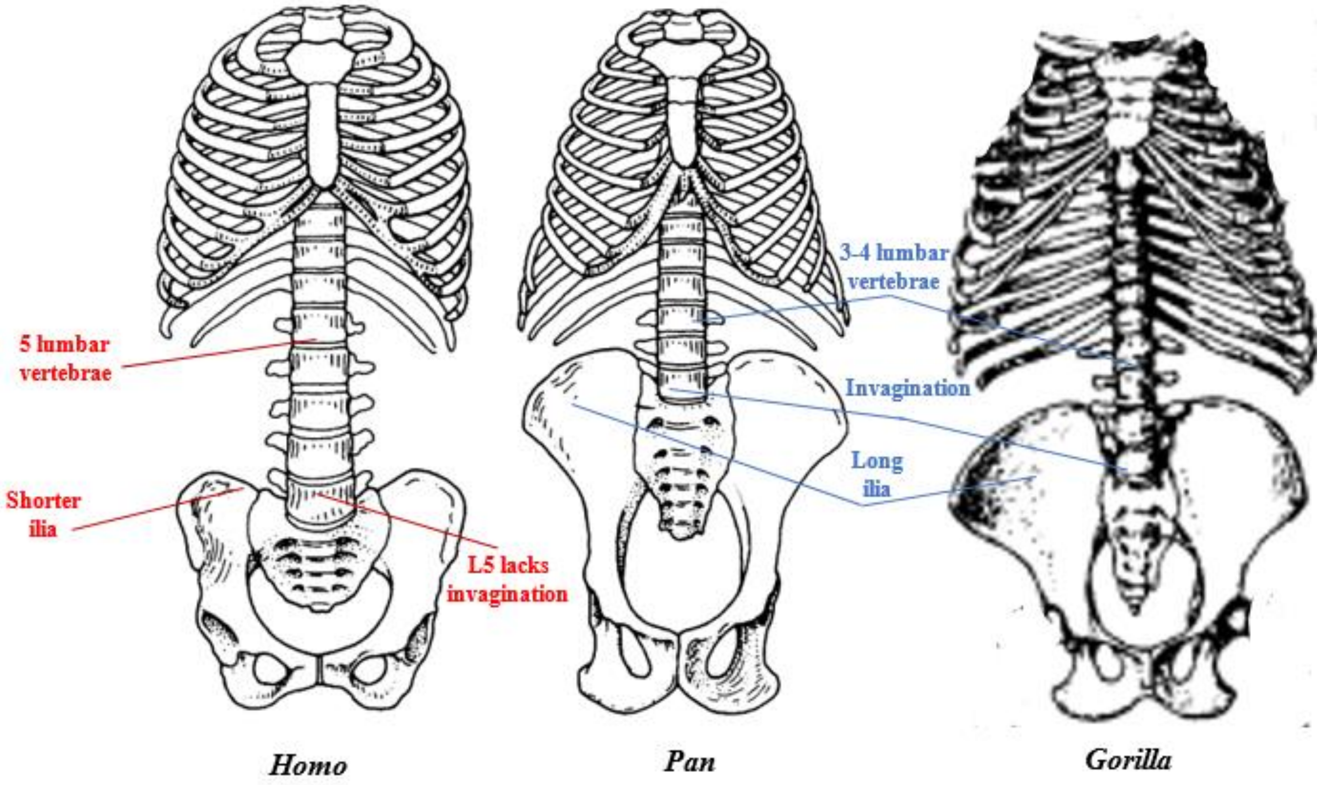
1.2. Comparative anatomy within the lumbar regions of African apes

The genus *Pan* is the most closely related to *Homo* of all extant primates and it is important to compare the anatomy of both to understand what morphology their last common ancestor (LCA) may have possessed (Aiello and Dean, 2002; Lovejoy, 2005; Lovejoy et al. 2009; Sparrey et al. 2014). To investigate the morphology present in the torso of the LCA, the genera were compared with the closest related genus, *Gorilla* (Aiello and Dean, 2002; Lovejoy, 2005; Lovejoy et al. 2009; Sparrey et al. 2014). Relative to modern humans, *Pan* and *Gorilla* share several features. This includes a short lumbar region, with three to four lumbar vertebrae (Pilbeam, 2004; Williams, 2012), a broad trunk, narrow pelvis, and invagination, where the last lumbar vertebra is surrounded by the pelvis (Figure 3) (Aeillo and Dean, 2002; Lovejoy, 2005; Lovejoy et al. 2009; Sparrey et al. 2014). There is also evidence of a slight lumbar lordosis in *Gorilla* and *Pan* (Martelli, 2005; Martelli, 2019), but they have far less lordotic wedging in the lumbar region than modern humans (Rose, 1975). The slight lordosis, from increased vertebral body wedging (Been et al., 2010b), can be explained by adaptations for orthograde posture, which is characteristic of extant hominoids, including humans (Martelli, 2005; Martelli, 2019). The most frequent method of locomotion for both *Gorilla* and *Pan* is knuckle-walking, so it makes sense that their torsos would share similar morphological features respective to humans (Aeillo and Dean, 2002; Lovejoy, 2005; Lovejoy et al. 2009; Sparrey et al. 2014).

:

Figure 3.

The derived features of the human torso are labeled in red, and the features shared between G*orilla* and *Pan* are labeled in blue. The image of *Homo* and *Pan* was adapted from Aeillo and Dean (2002) and Schultz (1950). The image of the *Gorilla* torso was adapted from Begun (2004) and Schultz (1969). The images are not in proportion to one another.



Since bipedalism is a characteristic distinctive to hominins, the *Pan* and *Homo* LCA likely lacked a lumbar lordosis like that of modern humans (Been et al. 2010a). *Pan* shares a lot of similarities to *Gorilla,* a genus of more distant ancestry, so it is likely that the axial skeleton of the LCA resembles these two genera more than modern humans (Pilbeam, 2004; Lovejoy, 2005; Lovejoy et al. 2009; Williams et al. 2012; Williams and Pilbeam, 2021). Even so, the length and flexibility of the LCA's lumbar region has been heavily debated by those suggesting that the LCA was 'short-backed' like *Pan* with three to four vertebrae (Pilbeam, 2004; Williams et al. 2012:135; Williams and Pilbeam, 2021) or 'long-backed' like early hominins with six vertebrae (Lovejoy et al. 2009; McCollum et al. 2010:7). This presents an issue for this study, because depending on how lumbar vertebrae is defined *Australopithecus africanus* specimen StS 14 could either be understood to possess five (Haeusler, Martelli and Boeni, 2002) or six lumbar vertebrae (Robinson, 1972). Research favouring a long-backed LCA argues that StS 14 retained the vertebral formula of the LCA (Lovejoy et al. 2009; McCollum et al. 2010), while supporters of the short-back hypothesis argue that the most parsimonious hypothesis is that a short and stiff lumbar region evolved once in the LCA of *Pan*, *Gorilla*, and *Homo*, and then became more flexible and elongated in hominins like StS 14 to support bipedality (Pilbeam, 2004; Williams et al. 2012; Williams and Pilbeam., 2021). Regardless, the flexibility and curved nature of the human lumbar region are traits that have been beneficial for the development of bipedalism and are visible in the fossil record.

This study does measure all six lumbar vertebrae from STS 14 (see Appendix-A), but follows methods used to investigate lordosis in the fossil record which compares the first five presacral vertebrae (Been, Gómez-Olivencia and Kramer, 2012; Williams et al. 2013; Williams et al. 2018; Williams et al. 2021). Presacral vertebrae (PS), or vertebrae superior to the sacrum, is a term used to describe the order at which a vertebra sits in the vertebral column without giving it a label, like thoracic or lumbar (Haeusler, Martelli and Boeni, 2002; Been, Gómez-Olivencia and Kramer, 2012; Williams et al. 2012; Williams et al. 2013; Williams et al. 2018; Williams et al. 2021). In lordosis reconstructions comparing PS1 to PS5 in fossils is analogous to comparing L1 to L5 in humans but mitigates the debate around vertebral formula in hominins.

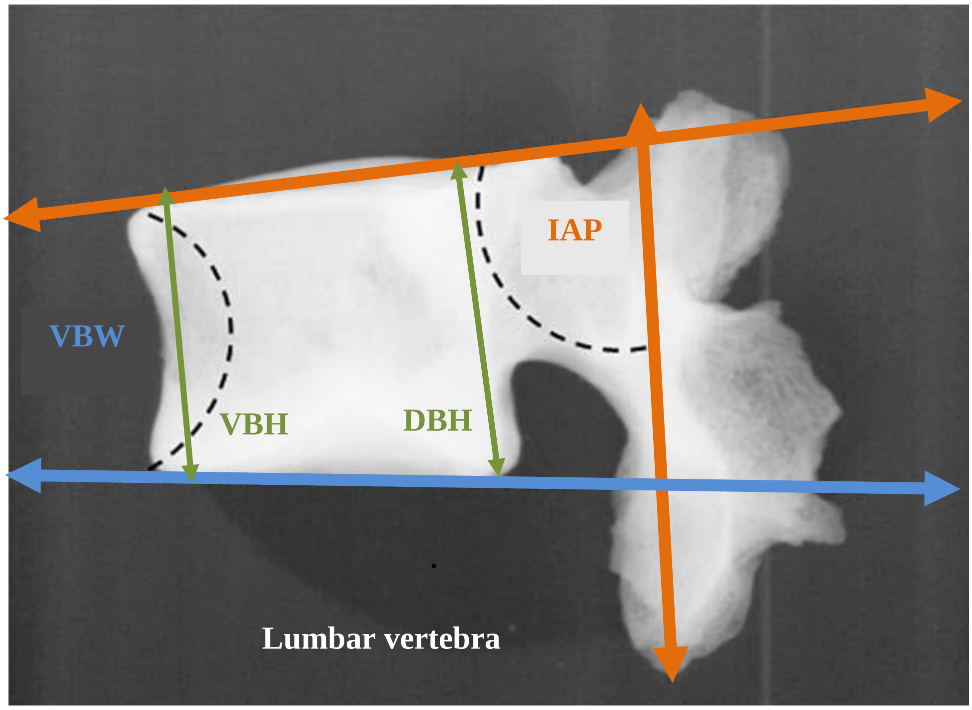
1.3. Typical methods of reconstructing lumbar lordosis from fossil and skeletal remains

Typically, only hard tissue is preserved in the fossil record, so palaeoanthropologists have developed different methods to study the evolution of the hominin lumbar region without the intervertebral discs. One such method is by measuring each vertebral body's anterior and posterior heights, and summing them together (Cunningham, 1886; DiGiovanni et al. 1989; Scoles et al. 1991; Williams et al. 2013; Williams et al; 2018; Williams et al. 2021). This method was designed for use in the medical field to study Scheuermann's kyphosis, a pathology characterised by exceptional ventral wedging in the thoracic region of the spine (DiGiovanni et al. 1989; Scoles et al. 1991). Since cartilage does not preserve in the fossil record, identifying and summing the wedging pattern of fossil hominins is a common way to compare specimens without making any assumptions about the intervertebral discs (Williams et al. 2013; Williams et al. 2018; García-Martínez et al. 2020. Williams et al. 2021). If all vertebrae are present in a fossil, then the wedging of each vertebra, typically kyphotic or lordotic, can be described as a wedging pattern and can be compared to the patterns found in modern humans and other hominins (Williams et al. 2013; Williams et al. 2018; García-Martínez et al. 2020; Williams et al. 2021). This method also allows for comparisons between individual vertebrae, which is useful when studying fossils as the complete vertebral column is rarely present (Williams et al. 2013). However, vertebral body wedging only forms a small percentage of the lordotic curvature relative to the intervertebral discs (Jackson and McManus, 1994; Damasceno et al. 2006; Been et al. 2010d), limiting the accuracy with which one can estimate lordosis in fossil hominins.

An alternative method used to study lordotic curvature in fossils reconstructs lordotic curvature based on data from modern humans. Been, Gómez-Olivencia and Kramer (2012) measured the Cobb angle, from the sacrum to the PS5 (Stokes and Aronsson, 2001) of living humans and primates, along with the inferior articular process angle (Been et al. 2007) from each lumbar vertebrae to predict lordotic curvature in the absence of soft tissue. The inferior articular process (IAP) angle is the angle between the inferior articular process and the cranial endplate of the desired vertebra (Figure 4) (Been et al. 2007). Been et al. (2007) compared the correlation of the Cobb angle, IAP, and VBW angles, which revealed that relative to VBW, the IAP explained most of the variability found within the Cobb angle. This method requires at least three well preserved vertebrae with inferior articular processes to be successful which can be hard to find in the fossil record (Been et al. 2010a; Been, Gómez-Olivencia and Kramer, 2012). Another concern with using IAP to reconstruct lordosis, is its reliance on a linear regression line which bases predictions of the Cobb angle on the IAP, VBW, and Cobb angle from a variety of extant primates including humans (Been et al. 2007; Been et al. 2010a; Been, Gómez-Olivencia and Kramer 2012). To clarify, when studying fossil hominins, modern humans are the best extant species to which to compare, and like VBW, the IAP does not completely explain the variation in the lordotic curvature found in modern humans. In this project VBW and IVDW are measured, and the lordosis of fossils are reconstructed using multiple linear regression. IAP could not be examined because this study used CT data which does not yield appropriate images for the IAP to be measured.

Figure 4.

The IAP angle is depicted in orange on a single lumbar vertebra, the VBW angle is depicted in blue, and the VBH and DBH are depicted in green on the lumbar vertebra. Image adapted from Been, Gómez-Olivencia, and Kramer (2012).

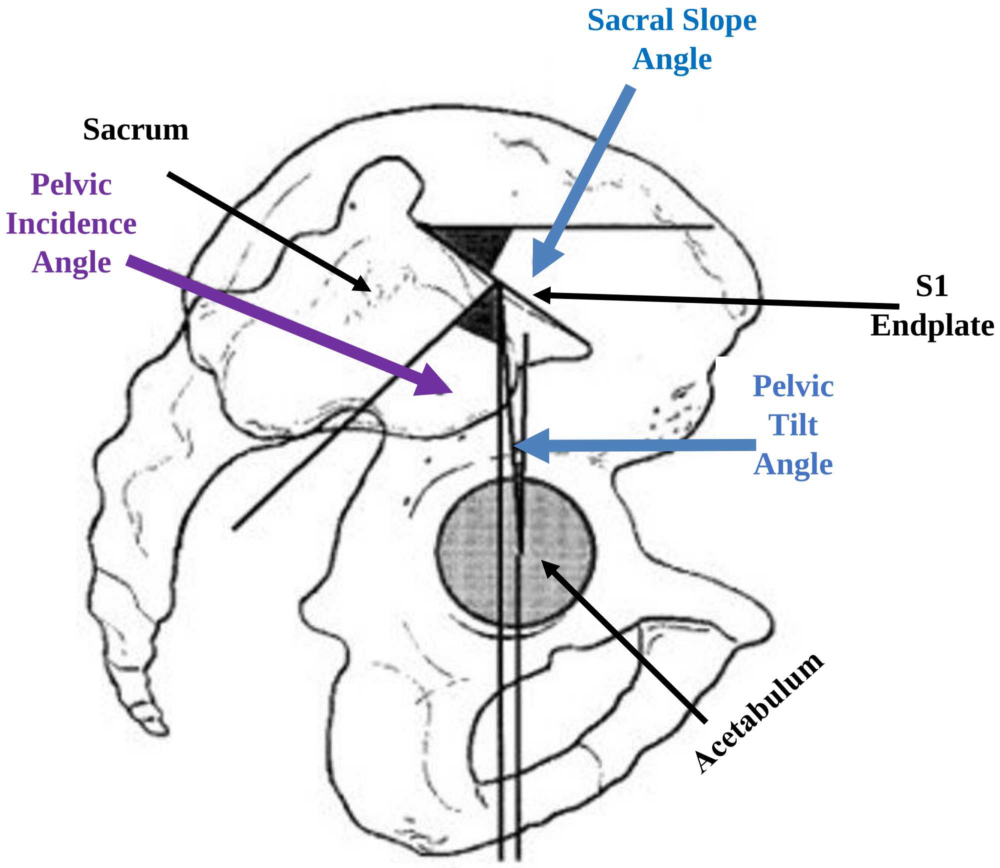


1.4. Earliest evidence of lumbar lordosis in hominins

When a fossil does not have any of their lumbar vertebrae, then the sacrum and pelvis, if present, can be used to predict the presence of a lordotic curvature (Legaye et al. 1998; Ward, 2002; Lovejoy, 2005, Lovejoy et al. 2009; Been, Gómez-Olivencia, and Kramer, 2014; Tardieu, Hasegawa and Haeusler, 2017; Haeusler et al. 2019). The pelvic incidence angle evaluates how the sacrum is oriented inside the pelvis by measuring the cranial endplate of the first sacral vertebra to the fifth sacral vertebra alongside its relationship to the acetabulum (Figure 5) (Legaye et al. 1998; Been, Gómez-Olivencia and Kramer, 2014; Haeusler et al. 2019). This method has been used to evaluate the presence of lordosis in earlier hominins (e.g., *Australopithecus sediba*, *Australopithecus afarensis*) that only have poorly preserved or absent vertebral columns (Been, Gómez-Olivencia and Kramer, 2014; Sparrey et al. 2014). Using the pelvis to predict lumbar lordosis has its constraints, as it cannot provide information on the pattern of wedging found within the lumbar region but can support the idea that a human-like lordosis was present in earlier fossil hominins (Legaye et al. 1998; Been, Gómez-Olivencia and Kramer, 2014; Tardieu, Hasegawa and Haeusler, 2017; Haeusler et al. 2019). This project investigates the accuracy of predicting lordotic curvature in hominins based on the lordosis of modern humans, relative to the information provided by the vertebral body wedging pattern.

Figure 5.

An example of the pelvic incidence, labeled in purple, on a modern human pelvis. Other relevant angles are in blue, and important aspects of the pelvis in relationship to pelvic incidence are labeled in black. This figure is adapted from Legaye et al. (1998).

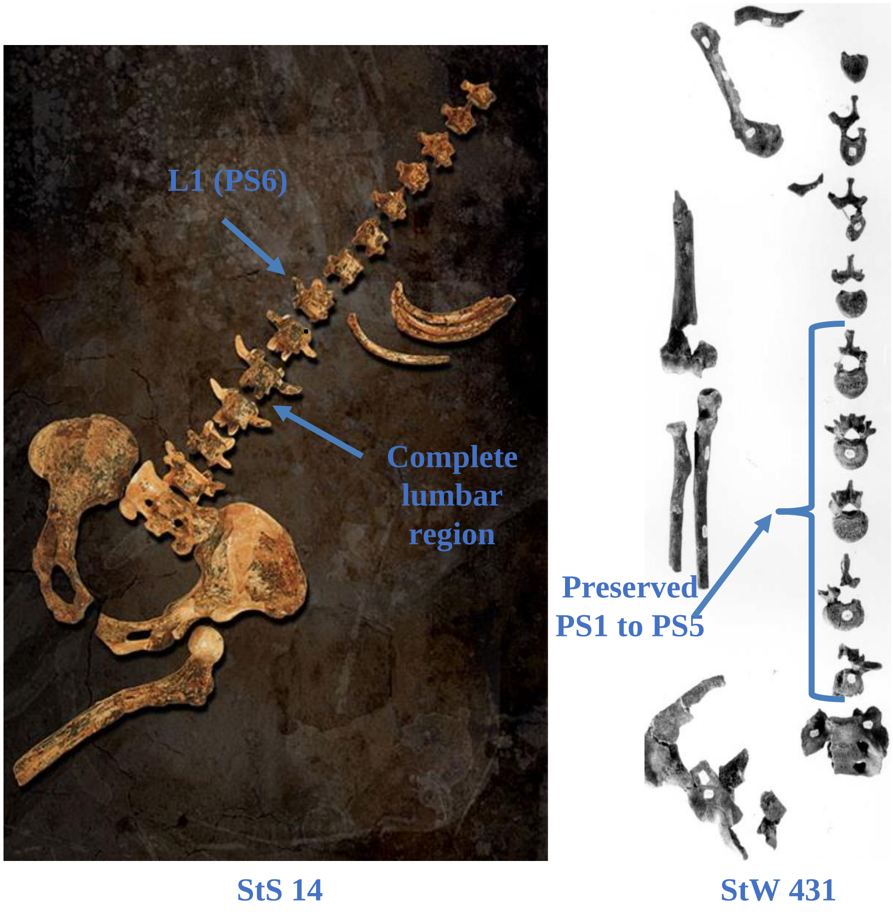


Currently, the oldest evidence of a possible lumbar lordosis within the fossil record is from *Ar. ramidus,* approximately 4.4 million years ago (Ma) (Lovejoy et al. 2005; Lovejoy et al. 2009). While *Ar. ramidus* does not have any lumbar vertebrae or a sacrum preserved to measure VBW or pelvic incidence angle, the pelvis was preserved well enough to show ilia with morphology similar to modern humans which suggests that lordosis was already present in this species (Lovejoy et al. 2005; Lovejoy et al. 2009). *Au. Afarensis* fossil, A. L. 288-1, estimated at 3.2 Ma (Johanson, 2004), has a preserved pelvis, but only a few lumbar vertebrae, and shows signs of Scheuermann's kyphosis in the thoracic region (Meyers et al. 2015). Further, one of the seven thoracic vertebrae was misidentified and belonged to a large cercopithecoid, but T7-T11 and L2-3 are still present in assorted degrees of preservation (Meyers et al. 2015). With only a complete L3, and a spinous process fragment of the L2, a reconstruction of lumbar lordosis is far more difficult in this specimen, like *Ar. ramidus* (Meyers et al. 2015). Fortunately, based on the pelvis and pelvic incidence angle of A. L. 288-1 suggests that *Au. afarensis* likely had a lordotic curvature (Ward, 2002; Been, Gómez-Olivencia and Kramer, 2014). Using the pelvic incidence angle of *Au. afarensis* and the morphology present in *Ar. ramidus* as a reference it is likely that the lordotic curvature existed prior to *Au. africanus*.

The most complete lumbar regions in early hominins are found in *Au. africanus* specimens StS 14 and StW 431 which are dated from 2.5 to 3 Ma (Figure 6) (Sanders, 1998; Whitcome, Shapiro and Lieberman, 2007; Been, Gómez-Olivencia and Kramer, 2012; Williams et al. 2013; Sparrey et al. 2014; Williams et al. 2018; Ward et al., 2020; Williams et al. 2021). As mentioned previously, *Au. africanus* is reported to have six lumbar vertebrae, i.e., six presacral vertebrae without articular facets for the ribs, with a PS6 that has qualities found in both thoracic and lumbar vertebrae (Haeusler, Martelli and Boeni, 2002). Based on the vertebral body wedging pattern and IAP angle of StS 14 and StW 431, they both have a predicted lumbar lordosis that is low, but still within the range of modern humans (Been, Gómez-Olivencia and Kramer, 2012; Williams et al. 2013; Williams et al. 2018; Williams et al. 2021). Since the lordotic curvature of modern humans is so variable, the same variation of lordotic curvature may have occurred in *Au. africanus* but this cannot be uncovered with only a few fossil specimens (Damasceno et al. 2006; Been et al. 2007; Masharawi et al. 2008; Been et al. 2010a;2010b;2010d; Been, Gómez-Olivencia and Kramer, 2012).

Figure 6.

The remains of *Au. Africanus* specimens StS 14 (left) and StW 431 (Right). The lumbar vertebrae are referenced in each image. StS 14 image adapted from MSU Hominid Fossil Repository (2017) and StW 431 image adapted from Toussaint et al. (2003).



Au. sediba specimens preserve two lumbar vertebrae assigned to MH1 and five assigned to MH2 (Williams et al. 2013; Williams et al. 2018; Williams et al. 2021). An initial analysis by Williams et al. (2013) found that MH1 had a ventrally wedged PS5 and a dorsally wedged PS3, while MH2 had a dorsally wedged PS1 and PS2 which they interpreted as hyper lordosis in the lumbar region based on the wedging of present vertebral bodies. In contrast, Been, Gómez-Olivencia and Kramer (2014) predicted that the lumbar region of *Au. sediba* had a lordosis that was within the lower range of modern humans based on the pelvic incidence angle from the reconstructed pelvis of MH2 (Kibii et al. 2011). Recently, a partial PS5, and nearly complete PS4 and PS3 were discovered in association with MH2 (Williams et al. 2021) which showed that this specimen had a less lordoticlumbar region than expected which corroborates Been, Gómez-Olivencia, and Kramer, (2014). The pelvic incidence angle of MH2 was based on a pelvic reconstruction (Kibii et al. 2011), thus adding additional error into estimation of lumbar lordosis in this specimen. The interpretations extracted from fossil lumbar vertebrae in australopiths can clearly vary based on the methods used, so it is important for this thesis to evaluate current methods of studying posture in paleoanthropology.

1.5. Lordosis in fossil *Homo*

The earliest lumbar vertebrae found from *Homo* is associated with sub-adults, including a L1 from post crania associated with the Dmanisi subadult skull D2700/D2735, estimated at 15 years of age or younger (Lordkipanze et al. 2007), and several lumbar vertebrae from *Homo ergaster (s.s.)* skeleton, KNM-WT 15000 (Haeusler, Schiess and Boeni, 2011; Been, Gómez-Olivencia and Kramer, 2012; Sparrey et al. 2014; Williams et al. 2013; Williams et al. 2018). KNM-WT 15000 is estimated between 11 to 15 years of age (Haeusler, Schiess and Boeni, 2011) and has 16 vertebrae preserved, including all lumbar vertebrae, of which they could debatably possess five or six (Hausler, Martelli and Boeni, 2002; Lovejoy, 2005; Haeusler, Schiess, and Boeni, 2011). KNM-WT 15000 has greater lordotic wedging in their lumbar vertebrae than current australopith specimens, but less lordotic wedging than the average modern human (Been, Gómez-Olivencia and Kramer, 2012; Been, Gómez-Olivencia and Kramer, 2014; Sparrey et al. 2014; Williams et al. 2013; Williams et al. 2018; Williams et al., 2021). Since KNM-WT 15000 is relatively young and shows signs of scoliosis, using them could skew reconstructions of the lumbar curvature for *H. ergaster (s.s.)* as a species (Lovejoy, 2005; Haeusler, Schiess and Boeni, 2011; Schiess and Haeusler, 2013). Current understanding of lordosis in fossil hominins reveals an increase in lordosis from australopiths to *Homo*, however these fossils fall within the modern human range of lordosis and may not depict the full variability of lordosis that transpired within these species.

Neanderthals and early *H. sapiens* have more recent fossil specimens with all their lumbar vertebrae preserved. Fossil *H. sapiens* generally have a predicted lumbar lordosis and VBW that is like that of contemporary humans (Been, Gómez-Olivencia and Kramer, 2012; Gómez- Olivencia et al. 2017; García-Martínez et al. 2020). In contrast, the degree of lordosis found in Neanderthals is contentious, with many arguing that fossils Kebara 2 and Shanidar 3 would have a straighter lumbar region where L1 to L4 are kyphotic and L5 is hyper lordotic (Been et al. 2010a; Been et al. 2010c; Been, Gómez-Olivencia and Kramer, 2012; Been, Gómez-Olivencia and Kramer, 2014; Williams et al. 2013; Gómez-Olivencia et al. 2017; García-Martínez et al. 2020; Williams et al. 2022). On the contrary, one analysis on Neanderthal lumbar vertebrae, revealed that their lumbar vertebrae have a similar pattern to humans, but that their degree of wedging for each vertebra is more exaggerated (García-Martínez et al. 2020). Some of the fossil vertebra associated with Neanderthals are described with pathological changes which could lead researchers to falsely predict a straighter lordotic curvature (Haeusler et al. 2019). It is difficult to decipher lumbar lordosis in *Homo* because there are many cases of pathologies within these specimens and a variety of methods used for reconstructions. This project evaluates if it is possible to predict the lordosis of Neanderthals and other hominins with a limited sample size, pathologies, and varying methods.

1.6. Variability and function in the lumbar region of modern humans

The lordotic curvature of contemporary humans is highly variable (Damasceno et al. 2006; Been et al., 2007; Been et al. 2010d), but the relationship the lumbar vertebrae and intervertebral discs have with the variance and function of lordosis is still under deliberation (Jackson and MacManus, 1994; Cheng et al. 1998; Damasceno et al. 2006; Been et al. 2010b; Kalichman et al. 2011). Table 1 provides reported ranges of lumbar lordosis in modern human samples, these ranges appear so different because each sample is subject to different conditions (e.g., posture, age range, ancestry, methods) that can impact the morphology of the vertebral bodies and discs (Jackson and MacManus, 1994; Cheng et al. 1998; Damasceno et al. 2006; Been et al. 2010b, Been et al. 2010d; Kalichman et al. 2011). These studies concluded that relative to vertebrae, the intervertebral discs contribute the most dorsal wedging to lordosis (Jackson and McManus, 1994; Damasceno et al. 2006; Been et al. 2010d). When variability is studied in the vertebral column, however, the summed VBW and IVDW share a similar correlation to lordosis (Been et al. 2010d). Therefore, summed IVDW constitutes most of the lordotic curvature (Jackson and McManus, 1994; Damasceno et al. 2006; Been et al. 2010d) but summed VBW has a significant influence on the vertebral column's variability. To an extent, variability within the lumbar region can be explained by wedging, but there are other factors that can influence variability like age and sex which also need to be considered.

Table 1:

The range of lordotic curvature found in current literature with details on the methods and samples used.

Source	Range	Scans	Posture	Age (years)	Sample type	Sex (n)
Amonoo-Kuofi, 1992:375	7.1° to 74.6°	Lateral radiograph	Lateral recumbent position with hips and knees flexed	9-61	Patients with abdominal and genital related concerns, provenance of sample unknown.	250 males and 235 females
Been et al. 2010b:1014	30° to 75°	Lateral radiograph	Standing	20-50	Patients at spinal clinic in Israel	53 males and 48 females
Fernand and Fox, 1985:800	13° to 85°	Lateral radiograph	Lateral recumbent position one group flexed, the other not flexed	17-84	Patients from New York and New Jersey	426 males and 536 females
Damasceno et al. 2006:195-196	33° to 89°	Lateral radiograph	Standing	18-50	Asymptomatic patients from Brazil	143 males and 207 females
Jackson and McManus,1994:1613	31° to 88°	Lateral radiograph	Standing	20-65	Asymptomatic patients from Missouri	50 males and 50 females
Vialle et al. 2005:262	30° to 89°	Lateral radiograph	Standing	20-70	Asymptomatic volunteers from France	190 males and 110 females

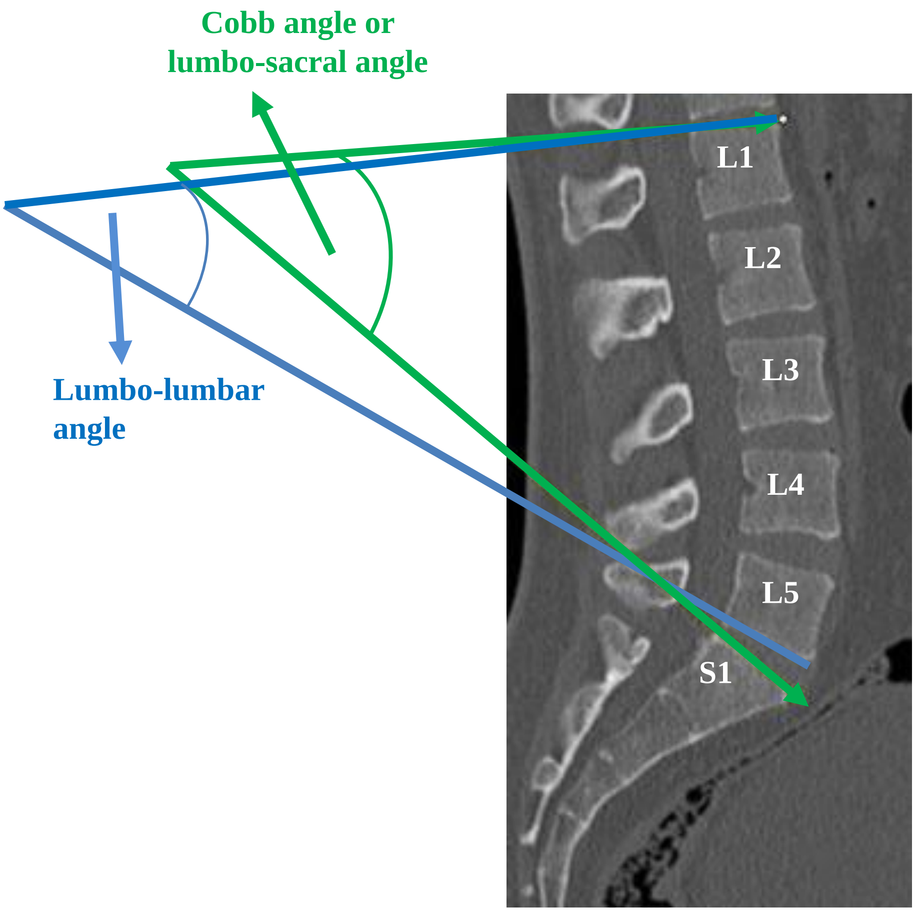
Like the combined wedging of the vertebral bodies and intervertebral discs, the individual vertebra and discs that explain the variability within lordotic curvature, is distinct from how each element contributes lordosis. For instance, wedging of the L2 (Been et al. 2007; Been et al. 2010d) and L4 (Cheng et al. 1998) have a stronger correlation with lumbar lordosis than the other vertebrae and intervertebral discs, but do not contribute as much wedging to lordosis as the ultimate vertebrae and intervertebral disc. A breakdown of the lumbar region found that the caudal section, between the L4 and S1, contains two thirds of the total lordosis (Jackson and McManus, 1994; Damasceno et al. 2006). The caudal portion of the lordotic curvature, particularly the intervertebral discs may have to contend with more compressive pressure than other areas of the spine, which has led to more lordotic wedging (Cassidy, 1988; Farhan, 1995; Filler, 2007; Shymon et al. 2014).

Additional analysis comparing the individual vertebrae and discs with each other also uncovers interesting information about the biomechanics of the lumbar region. For example, there is a stronger correlation between the central lumbar segments (includes vertebrae and intervertebral discs) than between the first and last lumbar segments (Been et al. 2007; Been et al. 2010d.). This implies that the portions of the curvature subjected to greater functional constraints, like the caudal elements, are less variable than the central elements because they must remain constant to maintain an adequate posture (Cassidy, 1988; Farhan, 1995; Filler, 2007; Shymon et al. 2014). The variability found in the center of the curvature also suggests that the central vertebrae are more important for lordosis reconstructions. Within the lumbar region a negative correlation between the vertebral bodies and intervertebral discs has been discovered (Been et al. 2010d) but has not been explored too much in current literature. This may be true of the wedging of intervertebral discs and bodies in other areas of the vertebral column, as there was a correlation between summed VBW and IVDW in the cervical lordosis (Tao et al. 2021). A negative correlation between the wedging of the intervertebral discs and vertebral bodies suggests that there is a relationship between these two variables that could impact lordotic curvature. The individual VBW and IVDW and the correlative relationships between them provide a deeper understanding of variability in the lumbar region.

The values reported in Table 1 could be impacted by different methods used to define and measure lordotic curvature. While the Cobb angle has commonly been used as the standard measurement of lordotic curvature (Jackson and MacManus, 1994; Cheng et al. 1998; Been et al. 2010b, Been et al. 2010c; Kalichman et al. 2011) many researchers have measured lumbar lordosis utilising different angles. For instance, Vialle et al. (2005) and Damasceno et al. (2006) use two different measurements of lordosis in the lumbar region, the Cobb angle, from L1-S1, and the lumbolumbar angle, from L1-L5 (Figure 7). Lumbar lordosis has also been described as an angle from L3-S1 (Abitbol., 1987) and L2- S1 in other literature (Fernand and Fox, 1985). This can make comparisons between studies more difficult. The Cobb angle is more widely used as a measurement of lordosis in modern humans because the last intervertebral disc plays a significant role in the construction and function of the lordotic curvature (Farfan, 1995; Shymon et al. 2014), but it may not be the best measurement for lordosis reconstructions. This study measures the lumbolumbar angle and the Cobb angle so that the results can be compared to see which angle improves the accuracy of lordosis reconstructions in fossil hominins.

Figure 7.

Common measurements of lordotic curvature are depicted with the Cobb angle labeled in green and the lumbolumbar angle labeled in blue. The images are of an individual from UNMDID sample Edgar et al. (2020).



1.7. Sex and age variation

Many studies confirm that females have a greater total lordosis than males (Vialle et al. 2005; Damasceno et al. 2006; Bailey et al. 2016; but see Jackson and McManus, 1994), which is associated with the changes to the center of mass that occur while pregnant which requires females to extend their lower back to maintain an upright walking posture (Whitcome, Shapiro, and Lieberman, 2007). The presence of sexual dimorphism in the Cobb angle is largely dependent on what posture, supine (laying horizontally), or standing, the samples are in. Sexual dimorphism is only present in the Cobb angle when the measurements are taken from a sample that is standing (Hansen et al. 2015; Bailey et al. 2016). However, some studies (Jackson and McManus, 1994; Been et al. 2010c) have utilised standing posture and still found that males and females had a similar lordosis, so it is unclear if another variable like lifestyle would impact sexual dimorphism in the lumbar region (Lois-Zlolniski et al. 2019; García-Martínez et al. 2020; Williams et al. 2022). This means that it is important for this project and many others to replicate these studies with different samples and methods to truly understand how lordosis varies between the sexes.

While there is a strong consensus that sexual dimorphism impacts lordotic curvature, there are conflicting reports on the impact sexual dimorphism has on the individual vertebrae and intervertebral discs (Gelb et al. 1995; Cheng et al. 1998; Vialle et al. 2005; Damasceno et al. 2006; Whitcome, Shapiro and Lieberman, 2007; Been et al. 2010d; Kalichman et al. 2011; Hansen et al. 2015; Bailey et al. 2016). Females often have a more dorsally wedged L3 than males, so they have three dorsally wedged vertebrae as opposed to males who often only showcase dorsal wedging on one or two vertebrae (Whitcome, Shapiro, and Lieberman, 2007). Further, some reports suggest the L3 and L4 of females are more lordotic than males, but that the last lumbar vertebra has similar wedging in both sexes (Gelb et al. 1995; Cheng et al. 1998; Masharawi et al. 2008; Been et al. 2010c). Additionally, males can have intervertebral discs with greater lordotic wedging than females, but this primarily occurs while in the supine position (Been et al. 2010d; Kalichman et al. 2011; Bailey et al. 2016). Only one study has found that males have more lordotic intervertebral discs while standing, but this was not statistically significant (Damasceno et al. 2006). Females may have more lordotic vertebrae rather than intervertebral discs to avoid placing pressure on their intervertebral discs during pregnancy (Bailey et al. 2016). Since sex can influence variability in lordotic curvature and wedging, it is important to evaluate this phenomenon within the UNMDID and South African samples.

The impact age has on the lumbar region has differing results based on the research currently available. A positive but weak correlation between age and lordosis has been found in several studies, suggesting lordosis increases as age advances (Gelb et al. 1995; Vialle; 2005; Damasceno et al. 2006; Been et al. 2010c.; Kalichman et al. 2011; Hansen et al. 2015; Williams et al. 2022). When looking at individual vertebrae, age has a positive correlation with the L3 and L4 (Gelb et al. 1995). In contrast, intervertebral disc thinning is a sign of aging in humans which has been thought to lead to a ‘flatback syndrome’ or a straight lordotic curvature, but many studies on older individuals have showed that disc thinning had little impact on lumbar lordosis (Gelb et al. 1995:1351; Kalichman et al. 2011; Hansen et al. 2015). Generally lumbar lordosis appears to increase over an individual's lifetime, particularly for women, with a slight decrease in lordosis at age 50 before increasing again (Amonoo-Kuofi, 1992). This research suggests more testing is needed to confirm results from previous studies and is relevant for this study's sample from the UNMDID with information on age at death (Edgar et al., 2020).

1.8. Geographic variation

Lumbar lordosis may be influenced by geographic variation in modern humans. Research focusing on vertebral body wedging in individuals with African, European, and Asian ancestry, found that lordotic curvature varied more between these geographic and ethnicity-based samples than between males and females (García-Martínez et al. 2020). The European sample was more dorsally wedged, while the Asian sample had more ventral wedging (García-Martínez et al. 2020). Multiple methods were used to evaluate vertebral body wedging for this study with osteological and digital specimens which could impact the variability found in the results because different methods can yield different results. Additionally, vertebral body wedging is not equitable to lordosis, so it is not clear how these samples varied in overall lordosis (García-Martínez et al. 2020). In comparison, Williams et al. (2022) found no differences in vertebral body wedging based on ancestry, and used the same method, with callipers, across all samples. This could suggest a lifestyle or cultural element that would influence variation in posture but is difficult to determine without the preserved intervertebral discs. Ethnicity will be excluded from the analysis in this study because both the deceased UNMDID sample (Edgar et al., 2020), and the living South African sample contain people from different African, European, and Indigenous American ancestry which could not be precisely defined. Most recently, it has been suggested that humans of different ancestries do not vary in vertebral body wedging (Williams et al., 2022), which suggests that ancestry will not impact the results between the living and deceased samples of this study.

1.9. Experimental data on lumbar lordosis in living species

The wedging of lumbar vertebrae and intervertebral disc can change morphologically over a lifetime in non-human animals if they are introduced to bipedal posture artificially, which uncovers a functional relationship between wedging and bipedalism (Yamada et al. 1960; Nathan et al. 1964; Cassidy, 1988; Prueschoft, Hayama and Hunter, 1998). For instance, rodents forced to engage in bipedalism show more lordotic wedging in the caudal vertebrae than the controls (Yamada et al. 1960, Cassidy, 1988; Russo, Marsh and Forrester, 2020). Dorsal wedging on the caudal vertebrae appears to increase as bipedal activity increases (Russo, Marsh and Foster, 2020). The intervertebral discs of rodents, however, do not respond positively to bipedal locomotion with many subjects developing herniated discs, particularly in the caudal region (Yamada et al. 1960; Cassidy, 1988). These injuries imply that the caudal elements of lordotic curvature are under the greatest stress from bipedalism and could help explain the intervertebral discs' role within the wedging pattern of modern humans.

Similar studies have even focused on other, typically straight-backed, and pronograde, catarrhines (Nathan et al. 1964; Prueschoft, Hayama and Hunter, 1998). For example, the lumbar region of wild Japanese macaques was analyzed alongside macaques who had been trained to walk bipedally by humans. The bipedal macaques developed more dorsal wedging in their lower lumbar vertebrae and intervertebral discs than the wild ones (Preuschoft, Hayama, and Hunter, 1998). Similar results have been produced with baboons (Nathan et al. 1964). These studies demonstrate how walking bipedally can lead to an increase in lordotic wedging amongst primates. There also appears to be less complications like intervertebral disc herniations in samples of primate than samples of rodents (Yamada et al. 1960, Cassidy, 1988). These experiments reveal that function plays a greater role on wedging in the caudal lumbar vertebrae and intervertebral discs, so this area of the lumbar region would be more likely to show dorsal wedging in humans than in other areas.

The human vertebral column's morphology and its relationship to the morphology found within the human skeleton has allowed them to walk bipedally with far less energetic costs than other primates (Taylor and Rowentree, 1973; Duval-Beaupère, Schmidt and Cosson, 1992; Tardieu, Hasegawa, and Haeusler, 2017). Based on the geometry of the pelvis and vertebral column, the pelvic tilt, lumbar lordosis, and thoracic kyphosis angles share significant correlations between one another in modern humans (Tardieu, Hasegawa and Haeusler, 2017). All the elements of the torso work together to maintain an upright walking posture without expending to much energy (Duval-Beaupère, Schmidt and Cosson, 1992; Tardieu, Hasegawa and Haeusler, 2017). Moreover, another experiment on bipedal macaques demonstrated that, even with lumbar lordosis, the macaques still respirated more as bipeds than in their natural state as quadrupeds (Nakatsukasa, 2004; but see Taylor and Rowentree, 1973). Since the trained bipedal macaques with lordotic wedging continued to perform better as quadrupeds, it is fair to assume that dorsal vertebral body wedging is not the only factor in sufficiently walking as a biped. Rather, it proves that bipedalism relies on other morphological adaptations in addition to lumbar lordosis.

1.10. Hypotheses and predictions for current investigation on lordosis

The above summary demonstrates the morphological variation documented in the human lumbar region, the lack of consensus on the contributing factors to lumbar lordosis, and the impact this variation and uncertainty has on estimating lordosis in fossil hominins. This project aims to test previous hypotheses about lumbar lordosis in hominins and methods used to quantify lordosis and wedging on a novel human sample. The Cobb angle, lumbolumbar angle, vertebral body, and intervertebral disc wedging angles are measured from a series of modern humans to evaluate sexual dimorphism and intraspecific variation, utilising samples from the UNMDID and South Africa. Fossil *H. sapiens*, Oberkassel 1 and 2, the Kebara 2 Neanderthal, and *Au. africanus* specimen, StS 14 are included to analyse the reliability of reconstructing lordosis in fossil hominins based on the vertebral bodies.

This project uses a novel sample of deceased individuals from the UNMDID (Edgar et al. 2020), which is not the norm for other studies on lordosis that are typically based on *in-vivo* lateral radiographs (Been et al. 2007; Been et al. 2010a; 2010b;2010d; Been Gómez-Olivencia, and Kramer, 2012). The UNMDID sample (Edgar et al. 2020) of deceased individuals must be compared against an *in-vivo* sample, the South Africans, to evaluate the validity of using deceased individuals to study lordosis. If both human samples yield similar results, then the pooled human sample will be used to study the lordotic curvature in modern humans. This study hypothesises that the living South African sample and the deceased UNMDID sample will have similar lordotic curvatures. This study predicts (1) the intervertebral discs will show more dorsal wedging than the vertebral bodies; (2) the intervertebral discs and vertebral bodies will explain a similar degree of variability in the lordotic curvature; (3) the variability found in the wedging of each vertebral body and intervertebral disc can be partially explained by the vertebrae and intervertebral discs in closest proximity to one another; (4) There will be a negative correlation between VBW and IVDW; (5) The caudal vertebrae and discs will have more lordotic wedging than the cranial ones; (6) the lumbar lordosis and wedging will vary by sex; and (7) lordotic curvature will not vary significantly by age.

That latter portion of this thesis focuses on reconstructing lordosis in fossil hominins. Based on comparisons made between the modern human sample and fossil hominins the study hypothesises that (8) fossil hominins will have vertebral body wedging that is within range of the modern human samples. Furthermore, this study proposes that (9) species that share a closer relationship evolutionarily like *H. sapiens* and Neanderthals will have a similar predicted lumbar lordosis relative to StS-14 which is more distant evolutionarily; and (10) the lumbolumbar angle will be a more accurate measurement to use for lordosis reconstructions than the Cobb angle because it has a stronger relationship with the vertebral bodies. Ultimately, this project does not expect to reveal definitive predictions of posture or lumbar lordosis in Kebara 2 or StS-14 based solely on vertebral body wedging but does expect to find consistent evidence of dorsal wedging as a functional response to bipedalism which may vary between species.

2. Study Materials and Methods

2.1. Modern *Homo sapiens* samples

This study includes two samples of modern *H. sapiens* CT scans. The first sample is from the University of New Mexico Decedent Image Database (UNMDID) which is a forensic anthropology database of full body DICOM scans from recently deceased individuals (Edgar et al. 2020). All scans were taken at the University of New Mexico, in Albuquerque, New Mexico, United States (Edgar et al. 2020). Access to the UNMDID can be granted to any individual with an academic email by requesting access to specific scans and stating the purpose of the request (Edgar et al. 2020). The UNMDID has detailed information on each individual, including their medical history, cause of death, age, socioeconomic status, ethnicity, height, and weight (Edgar et al. 2020). This study originally requested 184 CT scans (Edgar et al. 2020) based on profiles of healthy males and females without noticeable signs of spinal pathologies (Jackson and McManus, 1994; Kalichman et al. 2011; Hansen et al. 2015), between the ages of 25 and 50 (Amonoo-Kuofi, 1992; Cheng et al. 1998; Vialle et al. 2005; Damasceno et al. 2006; Been et al. 2007; Been et al. 2010a; 2010b; 2010d; Been Gómez-Olivencia, and Kramer, 2012; Hsu Castillo and Lieberman et al. 2015; Hansen et al., 2015; Bailey et al. 2016) and a weight of 50 to 90 Kg to avoid higher risk spinal degeneration or other pathologies (Kalichman et al. 2011; Al Rassy et al. 2018; Parenteau et al. 2021). All scans were taken according to the University of New Mexico's CT scanning protocol with the individual in the supine posture with arms above the head to avoid obscuring the torso (Edgar et al. 2020).

Once the scans were requested the lumbar regions of n=112 (58 males and 54 females) individuals were evaluated for wedging on the vertebral bodies and discs, and lordosis (Edgar et al., 2020) (Table 2). One male and three females with an irregular number of lumbar vertebrae were only included in the analysis in the appendix, these individuals were excluded from the primary UNMDID sample n=108 (57 males and 51 females) (Edgar et al. 2020). Age and sex were recorded with vertebral measurements to see if these factors affected variability in lordotic curvature. Analysis based on ethnic background (Lois-Zlolniski et al. 2019; García-Martínez et al. 2020; Williams et al. 2022) was not possible because the sample consisted mostly of people of European and Indigenous American descent (Edgar et al. 2020) which could not be identified precisely enough to draw any meaningful conclusions about variation in lordotic curvature.

Most analyses on lordosis and wedging in modern humans use radiographs of living subjects in standing posture which avoids any concerns about deterioration of the intervertebral discs when using cadavers (Fernand and Fox, 1985; Amonoo-Kuofi, 1992; Jackson and McManus, 1994; Vialle et al. 2005; Damasceno et al. 2006; Been et al. 2007; Masharawi et al. 2008; Been et al. 2010a; 2010b; 2010d; Been, Gómez-Olivencia and Kramer, 2012; Hansen et al. 2015; Bailey et al. 2016). Since this study includes a sample of deceased individuals, it was important to compare this sample to a living sample from South Africa to investigate the degree of deterioration in the cadaveric sample which could impact the results (Edgar et al., 2020). The intervertebral discs of cadavers have been used to study wedging in orthopedic literature, so there is already some precedent to study wedging in the UNMDID sample (Adams and Hutton, 1985; Twomey and Taylor, 1985; Pooni et al. 1986; O'Connell et al. 2007). Since both samples were CT scanned in the supine position, they will also need to be compared with other studies on lordosis that are taken from samples where individuals were standing.

The sample of CT scans from living South African individuals were taken at the Steve Biko Academic Hospital in Pretoria. A sample of n=56 CT scans were originally shared, but n=27 (12 males and 15 females) was ultimately selected due to spinal pathologies in the remaining specimens (Table 2) (Jackson and McManus, 1994; Kalichman et al. 2011; Hansen et al. 2015). The scans also did not come with information on ethnicity, but it is believed that most of the scans are from people of South African and European descent. Since age is unknown, it is not estimated or compared with the deceased sample for analysis.

Permissions and ethical approval to access the South African sample was granted by Profs Zarina Lockhat, Farhanah Suleman, and Anna Oettlé, who originally collected the CT scans. Ethical approval for the complete project was granted by The University of Kent (#04-PGR-21/22).

2.2. Fossil Hominin Specimens

Fossils specimens include micro CT scans of fossil *H. sapiens*, Oberkassel 1 and Oberkassel 2 (Nobis, 1986), *H. neanderthalensis* specimen Kebara 2 (Arensburg et al. 1983; Vallada et al, 1987), and *Au. africanus* specimen StS 14 (Table 2) (Broom and Robinson, 1947; Thackeray, Gommery, and Braga, 2002; Ward et al. 2020). Unlike the UNMDID (Edgar et al. 2020) and South African samples which had whole torso scans, the scans provided of each fossil specimen were of each individual disarticulated vertebra. The fossils were excluded from general analysis, and measurements that would require the presence of intervertebral discs, like the Cobb angle. All fossils were compared with the modern human sample, but only Oberkassel 2, Kebara 2, and StS 14 had their lordosis calculated with a regression line based on vertebral body wedging.

StS 14, dated to 2.5 Ma, is a partial skeleton attributed to, *Au. africanus* that preserves a relatively complete lumbar region (Broom and Robinson, 1947; Ward et al. 2020). StS 14 was discovered in Sterkfontein cave in Gauteng, South Africa in 1947 (Broom and Robinson, 1947; Thackeray, Gommery, and Braga et al. 2002). StS 14 has been identified as a juvenile, because their sacrum is not fully fused (Thackery, Gommery, and Braga, 2002). The first six presacral vertebrae are measured for comparisons in this study (see Appendix-A) and a prediction of lordosis from PS1 to PS5 will be included to reconstruct the lordotic curvature for comparison of results with similar studies (Been, Gómez-Olivencia and Kramer, 2012; Williams et al. 2013; Williams et al. 2018; Williams et al., 2021). There are some signs of thoracic kyphosis on this specimen, but the lumbar vertebrae appear fine (Haeusler, 2019). Any well-preserved lumbar vertebrae were measured, so in the case of StS 14, which plausibly has six lumbar vertebrae (Robinson, 1972), all six were measured. This study only includes the first five presacral vertebrae for reconstructions, but included L6 in the appendix

(Haeusler, Martelli, and Boeni, 2002). StS 14 is one of two fossils with a complete lumbar region in the study.

Kebara 2 is a Neanderthal specimen found in the Kebara Cave located in Mt Carmel, Israel from excavations in 1983 (Arensburg et al. 1983; Valladas et al. 1987). Like StS 14, Kebara 2 has a complete lumbar region which has been used in other analyses of lordosis in hominins (Been et al. 2010c; Been, Gómez-Olivencia and Kramer, 2012; Williams et al. 2013; Gómez-Olivencia et al. 2017; García-Martínez et al. 2020; Williams et al. 2022). Kebara cave is a Middle Paleolithic site with the Kebara 2 fossil estimated to be 60,000 years old (Arensburg et al. 1983; Valladas et al. 1987). Kebara 2 is identified as male and was recognized in this project as a male Neanderthal to compare with males from the contemporary human sample (Arensburg et al. 1983**).** Vertebrae associated with Kebara 2 have some pathologies, the specimen likely has Scheuermann's kyphosis, the spinous processes of L2 to L5 are not fully developed, and Schmorl's nodes are present on the L2 (Haeusler, 2019) but these vertebrae were still included in the analysis.

The *H. sapiens* Oberkassel 1 and 2 were found in Bohn, Germany (Nobis, 1986). The human burials are estimated to be around 12,000 years old (Nobis, 1986; Friedline, 2012). Oberkassel 1 is sexed as male and Oberkassel 2 is sexed as female (Nobis, 1986) which allows the vertebrae to be compared to humans via sex. However, the micro CT scans of these vertebrae are notably less well preserved than the older fossils. L1 and L3 to L5 are present in Oberkassel 1, and L1, L2, and L4 are present in Oberkassel 2. Of these vertebrae, only the L1 from both specimens and the L2 from Oberkassel 2 were preserved adequately for comparisons with other fossils and the modern human sample.

Table 2:

The samples used in this project with total sample size and sample size divided by sex.

Sample	**Male**	**Female**	**N**
UNMDID (Edgar et al. 2020)	58	54	112
South African	12	15	27
Fossil *H. sapiens*	1	1	2
H. neanderthalensis	1	0	1
Au. Africanus	?	?	1

2.3. Methods of lordosis and wedging measurements

Table 3 describes the measurements taken for this study. Medical CT scans were opened in Avizo 6.3 (FEI Visualization Sciences Group), and several standardized images were taken for morphometric measurements (Hsu, Castillo and Lieberman, 2015). The torso was cropped to show only the lumbar region and sacrum, and an oblique slice was placed in the sagittal midline of each vertebral body, so dorsal and ventral measurements were comparable to those taken from radiographs in previous studies (Jackson and McManus, 1994; Gelb et al. 1995; Cheng et al. 1998; Vialle et al. 2005; Damasceno et al. 2006; Been et al. 2007; 2010a; 2010b; 2010d; Kalichman et al. 2011; Been, Gómez-Olivencia and Kramer, 2012; Bailey et al. 2016; García-Martínez et al. 2020). Sometimes several vertebrae were aligned, and one oblique slice could be taken for multiple vertebrae, but each individual could have as many as six oblique slices created to ensure each slice was positioned at the sagittal midline of the vertebral body. The position of the oblique slice in each vertebra was also documented photographically with dorsal and ventral images of the vertebra that corresponds with each slice.

Table 3:

Lordosis and wedging measurements included in this project with definitions. The way these measurements will be refered to in text are in bold.

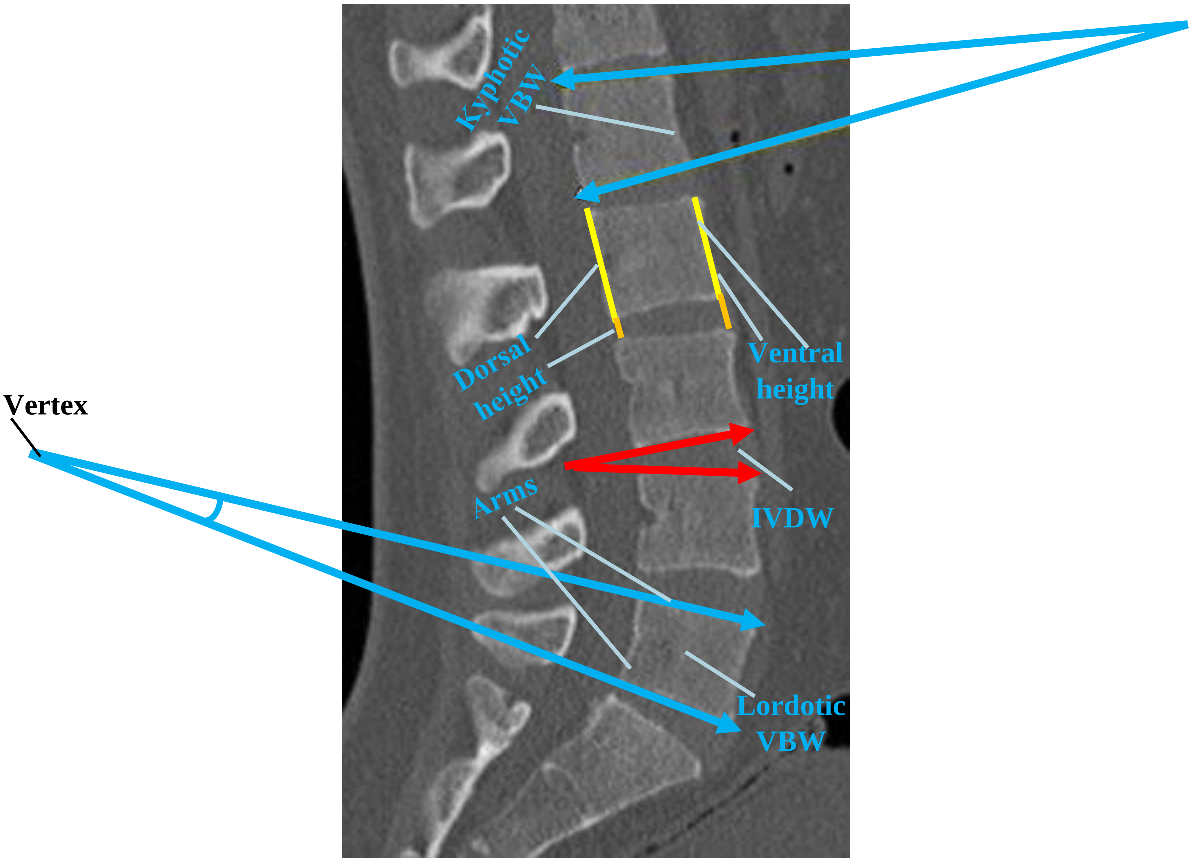
Measurements	**Description**
Cobb angle (°) (Stokes and Aronsson, 2001)	Lumbar lordosis measured from the superior endplates of L1 to S1.
Lumbolumbar angle (°) (Cheng et al., 1998; Vialle et al. 2005; Damasceno et al. 2006)	Lumbar lordosis measured from the superior endplate of L1 to the anterior endplate of L5, which excluded the lumber regions ultimate intervertebral disc.
Total wedging angle (**TW**) **(°)** (Damasceno et al. 2006; Been et al. 2007; Been et al. 2010a; 2010b; 2010d; Been, Gómez-Olivencia and Kramer, 2012)	The summed individual wedging angles from the L1 vertebral body to the ultimate intervertebral disc.
Summed **L1-5** angle **(°)**	The summed individual wedging angles from the L1 vertebral body to the L5 vertebral body. Excludes ultimate intervertebral disc.
Dorsal and ventral height Ventral intervertebral disc height (**VIDH**) (mm) dorsal intervertebral disc height (**DIVDH**)(mm) ventral body height (**VBH**)(mm) dorsal body height (**DBH**)(mm) (Digiovanni et al. 1989; Scoles et al, 1991; Stokes and Aronsson, 2001; Been et al. 2010c)	Ventral and dorsal heights for the intervertebral discs and vertebral bodies.
Individual wedging angle (Digiovanni et al. 1989; Scoles et al, 1991; Stokes and Aronsson, 2001): **VBW (°)** and **IVDW (°)**	Measures the wedging angle of a single vertebral body or intervertebral disc. When the ventral height was greater than the dorsal height the measurement was taken with the vertex of the angle facing dorsally (lordotic), and when the dorsal height was greater than the ventral height the vertex of the angle was ventral (kyphotic).
Total vertebral body wedging (**TVBW**) **(°)** (Damasceno et al. 2006; Been et al. 2007; Been et al. 2010a; 2010b; 2010d; Been, Gómez-Olivencia and Kramer, 2012)	The summed individual wedging angles from all the vertebral bodies in the lumbar region.
Total intervertebral disc wedging (**TIVDW**) **(°)** (Damasceno et al. 2006; Been et al. 2007; Been et al. 2010a; 2010b; 2010d;	The summed individual wedging angles from all the intervertebral discs in the lumbar region.

Been, Gómez-Olivencia and Kramer, 2012)	

The lumbar region was measured digitally using Image J (Rasband, 2018) following similar methods to Hsu, Castillo, and Lieberman (2015). Lordotic and kyphotic wedging was determined by the dorsal and ventral height of each vertebral element (Table 3) (Digiovanni et al.1989; Scoles et al. 1991; Stokes and Aronsson, 2001; Been et al., 2010c). This study follows the standard set by Been and colleagues (Been et al. 2007; Been et al. 2010a; 2010b; 2010d; Been, Gómez-Olivencia and Kramer, 2012) who marked lordosis as positive wedging, and kyphosis as negative wedging. Individual VBW was measured with the arms of the angle placed one the vertebrae superiorly and posteriorly at the highest point laterally, with the vertex placed to a point where the angle encompassed the whole vertebra (Figure 8). The IVDW angles were taken from the space in between the two vertebrae using a similar method as the vertebral bodies (Figure 8). Measurements of the vertebrae and intervertebral discs in this study were all taken from Image J based on the direction of the wedging (Figure 8).

Figure 8.

Examples of measurements used for this study. VBW is depicted in blue, IVDW is depicted in red. Dorsal and ventral measurements are depicted in yellow. The anatomy of an angle is labeled Image from UNMDID (Edgar et al. 2020).



The Cobb angle is a measurement of spinal curvature that can be used to evaluate lordosis. When the Cobb angle is used to measure lordotic curvature, it is measured from the superior side of the first lumbar vertebral body to the superior side of the first sacral vertebrae (Table 3, Figure 8) (Stokes and Aronsson, 2001). The Cobb angle is the most prominently used measurement in literature both in evolutionary anthropology (e.g., Been et al. 2007; Been et al. 2010a; 2010b; 2010d) and clinical research (e.g.,Vialle et al. 2005; Damasceno et al. 2006). The lumbolumbar angle is also a measurement of lordotic curvature which is measured from the L1 to the L5 and excludes the last intervertebral disc (Table 3) (Cheng et al., 1998; Vialle et al. 2005; Damasceno et al. 2006). Both measurements of lordosis were included in the current study to determine if either angle has a stronger correlation with VBW for lordosis reconstructions. The oblique slice created for the Cobb and lumbolumbar angle was positioned as close to the sagittal midline of all 5 vertebrae and intervertebral discs. However, it was not always possible to select the midline of all vertebrae based on the cadaver's posture (Figure 7) (Edgar et al., 2020).

2.4. Statistical analysis and intraobserver error

All measurements were taken by a single researcher. Intraobserver error for each measurement was tested on n= 22 individuals selected from both the UNMDID and South African sample. Eleven males and nine females had the same measurements taken and recorded three times, each several weeks apart. The fossil specimens were measured twice with several weeks in-between. Intraobserver error was determined using an intra-class correlation coefficient (ICC).

A Shapiro-Wilks test for normality was performed on the samples and revealed that some of the variables were normally distributed, while others were not. Therefore, both parametric and non-parametric tests were used. All statistical tests were performed in SPSS (SPSS inc., Chicago, Illinois., USA) significance was set at P ≤ 0.05. The mean, standard deviation, SE, and range for all morphological variables were calculated.

Evaluation of differences in the measured variables between each sample (e.g., UNMDID and South African) or between sexes were tested using either a Student’s t-test or, for non-parametric variables, a Mann-Whitney U test. To compare several measured variables, like individual wedging, a One-Way Analysis of Variance (ANOVA) was used with a Tukey’s post-hoc test for parametric data, and non-parametric data required a Kruskal-Wallis test with pair-wise comparisons. Tests on variability between measured variables were performed using a Pearson’s correlation test or a Spearman’s rank correlation test depending on the distribution of data. Correlations were described as strong, when r ≥ 0.8, moderate when between 0.79 ≤ r ≥ 0.50, and weak as r ≤ 0.49 similar to Been et al. (2010c). Lordosis reconstructions for fossil hominins were created from linear regression formulas.

Table 4:

Distribution of variables

Variable	**Distribution**	
Ventral height (mm) (vertebral bodies or intervertebral discs)	Non-parametric: vertebra L4 to L5, and intervertebral disc L2 to L3.	Parametric: All other variables
Dorsal height (mm) (vertebral bodies or intervertebral discs)	Parametric	
Individual VBW **(**°**)**	Non-parametric	
Individual IVDW **(**°**)**	Non-parametric: Disc L2-3	Parametric: All other variables
Summed VBW **(**°**)**	Parametric	
Summed IVDW **(**°**)**	Parametric	
Cobb angle **(**°**)**	Parametric	
Lumbolumbar angle **(**°**)**	Parametric	
Summed Wedging angle **(**°**)**	Parametric	

Summed lumbolumbar angle **(°)**	Parametric

3. <u>Results</u>

3.1. Intraobserver error

All the measurements from the human lumbar region yielded an ICC of $p \geq .90$ for both the UNMDID sample and the South African sample. All the fossils in the study were measured twice, their ICC measurements were $p \geq .9$ as well.

3.2. Summary statistics

The Cobb angle, lumbolumbar angle, TVBW and TIVDW are all normally distributed based on a Shapiro-Wilks test. The mean and standard deviation (SD) for the Cobb angle for the modern human sample combined was 54.04 ± 10.82. The mean, SD, range, and standard error (SE) of lordosis in the lumbar region are depicted in Table 5 for the modern human samples.

Most variables were normally distributed, except for VBW from the individual vertebra, the IVDW of disc L2-3, and the ventral heights of L4, L5, and intervertebral disc L2-L3. The mean, SD, SE, normality, and ranges for the individual vertebra and intervertebral disc wedging are also listed between each population and by sex in Table 6. The wedging patten shows the vertebra and intervertebral disc increase in lordotic wedging cranially to caudally (Table 6).

Table 5:

Lordosis and lordotic wedging in the UNMDID and South African sample by sex with sample size (n). The mean ± the SD, and SE are all depicted in degrees (°). The total of the two modern human samples together is also depicted (Edgar et al., 2020).

Sample	**UNMDID**			**South African**			**Total**		
Sex (n)	m (57)	f (51)	total (108)	m (12)	f (15)	total (27)	m (69)	f (66)	total (135)
Cobb angle mean ± SD (°)	53.58 ± 10.87	54.73 ± 10.10	54.12 ± 10.48	50.18 ± 7.9	56.55 ± 14.57	53.72 ± 12.3	52.99 ± 10.45	55.15 ± 11.17	54.04 ± 10.82
Cobb ange range (°)	23.21 to 76.57	22.90 to 76.57	22.90 to 76.57	36.64 to 62.82	32.05 to 80.49	32.05 to 80.49	23.21 to 76.57	22.90 to 80.49	22.9 to 80.49
Cobb angle SE (°)	1.44	1.41	1.01	2.29	3.76	2.37	1.26	1.37	0.93
TW mean ± SD (°)	53.76 ±11.71	55.98 ± 12.54	54.81 ± 12.10	51.92 ±13.21	57.26 ± 13.39	54.89 ± 13.33	53.44 ± 11.9	56.27 ± 12.64	54.83 ± 12.30
TW range (°)	27.86 to 84.75	14.28 to 89.12	14.28 to 89.12	30.37 to 72.05	32.40 to 76.41	30.37 to 76.41	27.86 to 84.75	14.28 to 89.12	14.28 to 89.12
TW SE (°)	1.55	1.76	1.16	3.81	3.46	2.57	1.43	1.56	1.06
Lumbolumbar angle mean ± SD (°)	37.49 ± 9.84	38.41 ± 9.81	37.93 ± 9.79	34.4 ± 7.73	38.34 ± 14.17	36.59 ± 11.72	36.96 ± 9.53	38.39 ± 10.83	37.66 ± 10.17
Lumbolumbar angle range (°)	10.26 to 60.63	9.05 to 56.53	9.05 to 60.63	24.20 to 53.53	16.03 to 59.0	16.03 to 59.0	10.26 to 60.63	9.05 to 59.00	9.05 to 60.63
Lumbolumbar angle SE (°)	1.3	1.37	0.94	2.23	3.66	2.26	1.15	1.33	0.88
L1-5 mean ± SD (°)	35.99 ± 11.28	38.62 ± 11.95	37.43 ± 11.62	34.24 ± 12.16	36.21 ± 12.78	35.33 ± 12.31	35.68 ± 11.37	38.07 ± 12.08	36.85 ± 11.74
L1-L5 range (°)	15.50 to 65.64	0.15 to 66.04	0.15 to 66.04	14.76 to 54.28	15.97 to 55.80	14.76 to 55.80	14.76 to 65.64	0.15 to 66.04	0.15 to 66.04
L1-5 SE (°)	1.49	1.67	1.12	3.51	3.3	2.37	1.37	1.49	1.01
TVBW mean ± SD (°)	-0.41 ± 12.08	5.99 ± 12.56	2.61 ± 12.67	2.39 ± 8.90	3.21 ± 16.39	2.84 ±13.36	0.08 ± 11.59	5.36 ± 13.44	2.66 ± 12.76
TVBW range (°)	-23.24 to 26.90	25.70 to 33.29	-25.70 to 33.29	-13.15 to 15.47	-19.62 to 30.94	-19.62 to 30.94	-23.24 to 26.90	-25.70 to 33.29	-25.7 to 33.29
TVBW SE (°)	1.6	1.76	1.22	2.57	4.23	2.57	1.39	1.65	1.1
TIVDW mean ± SD (°)	54.17 ± 9.74	49.99 ± 9.59	52.2 ± 9.85	49.53 ± 12.37	54.06 ± 8.59	52.05 ±10.47	53.37 ± 10.29	50.92 ± 9.47	52.17 ± 9.94
TIVDW range (°)	31.97 to 75.79	30.78 to 66.90	30.78 to 75.79	36.32 to 72.92	38.24 to 67.76	36.32 to 72.91	31.97 to 75.79	30.78 to 67.76	30.78 to 75.79
TIVDW *SE* (°)	1.29	1.34	0.95	3.57	2.22	2.02	1.24	1.17	0.86

Table 6:

The mean, SD, SE, and ranges of wedging depicted in degrees (°) for individual lumbar vertebrae and intervertebral disc between the human samples, divided by sex. An asterisk (*) is placed aside nonparametric variables (Edgar et al., 2020).

	UNMDID mean ± SD (°)			UNMDID SE(°)			South African mean ± SD			South African SE (°)			Total mean ± SD (°)			Total SE (°)		
	m (n=57)	f (n=51)	total	m	f	total	m (n=12)	f (n=15)	total (n=27)	m	f	total (n=108)	m (69)	f (n=66)	total (135)	m	f	total
L1*	-6.66 ± 2.58	-6.64 ± 2.70	-6.65 ± 2.63	0.34	0.38	0.25	-5.76 ± 1.82	-5.73 ± 2.88	-5.74 ± 2.42	0.53	0.74	0.47	-6.51 ± 2.48	6.43 ± 2.75	-6.47 ± 2.60	0.30	0.34	0.22
L2*	-3.58 ± 3.51	-2.79 ± 4.00	-3.21 ± 3.75	0.47	0.56	0.36	-4.75 ± 2.38	-2.95 ± 6.24	-3.75 ± 4.92	0.69	1.61	0.95	-3.78 ± 3.36	-2.83 ± 4.55	-3.31 ± 4.0	0.40	0.56	0.34
L3*	-0.32 ± 4.10	1.66 ± 4.44	0.61 ± 4.36	0.54	0.62	0.42	-1.35 ± 3.07	0.37 ± 3.94	0.39 ± 3.62	0.89	1.02	0.7	-1.45 ± 3.94	1.37 ± 4.34	0.411 ± 4.23	0.47	0.53	0.36
L4*	2.04 ± 4.05	4.35 ± 3.94	3.13 ± 4.14	0.54	0.55	0.4	3.57 ± 4.65	3.11 ± 3.70	3.31 ± 4.07	1.34	0.95	0.78	2.31 ± 4.16	4.07 ± 3.89	3.17 ± 4.11	0.50	0.48	0.35
L5*	7.89 ± 3.10	9.53 ± 3.82	8.67 ± 3.54	0.41	0.53	0.34	10.67 ± 3.74	8.41 ± 5.90	9.42 ± 5.10	1.08	1.52	0.98	8.37 ± 3.36	9.28 ± 4.35	8.83 ± 3.89	0.41	0.54	0.33
Disc L1-2	6.83 ± 2.71	5.52 ± 2.43	6.21 ± 2.65	0.36	0.34	0.25	6.24 ± 3.07	6.61 ± 2.17	6.45 ± 2.57	0.89	0.56	0.49	6.72 ± 2.76	5.77 ± 2.4	6.26 ± 2.63	0.33	0.30	0.23
Disc L2-3*	8.01 ± 2.43	7.37 ± 2.83	7.71 ± 2.64	0.32	0.40	0.25	6.77 ± 2.94	6.80 ± 1.96	6.79 ± 2.39	0.85	0.51	0.46	7.79 ± 2.55	7.24 ± 2.65	7.52 ± 2.61	0.31	0.33	0.22
Disc L3-4	9.83 ± 2.96	8.16 ± 3.12	9.04 ± 3.14	0.39	0.44	0.3	7.67 ± 3.68	7.57 ± 2.56	7.62 ± 3.04	1.06	0.66	0.59	9.45 ± 3.18	8.02 ± 2.99	8.75 ± 3.16	0.38	0.37	0.27
Disc L4-5	11.95 ± 2.95	11.46 ± 3.12	11.72 ± 3.03	0.39	0.44	0.29	11.17 ± 2.82	12.02 ± 3.37	11.64 ± 3.11	0.81	0.87	0.6	11.81 ± 2.92	11.58 ± 3.16	11.70 ± 3.03	0.35	0.39	0.26
Disc L5-S1	17.56 ± 4.25	17.48 ± 5.68	17.52 ± 4.95	0.56	0.80	0.48	17.68 ± 4.33	21.05 ± 4.90	19.55 ± 4.87	1.25	1.26	0.94	17.58 ±4.23	18.29 ± 5.68	17.93 ± 4.98	0.51	0.70	0.43

3.3. Comparisons between the deceased UNMDID sample and living South African sample

The two modern human samples were compared to evaluate if lordosis was different between deceased and living individuals. There was no statistically significant difference between the UNMDID and South African samples in the Cobb angle (Student's t-test, p=0.864), lumbolumbar angle (Student's t-test, p=0.543), TVBW (Student's t-test, p=0.934), or TIVDW (Student's t-test, p=0.943) (Table 7).

Table 7:

Results from a Students t-test with the test statistic (t), degrees of freedom (df), and significance value (p) comparing lordosis and lordotic wedging between the South African and UNMDID samples (Edgar et al., 2020). Test results reported as (t(df)=t-value, p= p-value)

Samples	**South African and UNMDID**					
Angles	**Cobb**	**Total Wedging**	**Lumbolumbar**	**L1-L5**	**Total VBW**	**Total IVDW**
t-test results:	t(133)=-0.172, p=0.864	t(133)=0.028, p=0.978	t(133)=-0.609, p=0.543	t(133)=--751, p=0.454	t(133)=0.083, p=0.934	t(133)=-0.071,p=0.943

The wedging of the individual intervertebral disc and vertebral bodies was also compared between the two samples (Table 8). A Mann-Whitney U test was used to compare individual VBW and the IVDW of disc L2-L3, and a Student's t-test was used to compare all other morphological variables. Individual VBW and IVDW were not statistically different between the samples, except for the IVDW of intervertebral disc 3-4 (Table 8). Disc L3-L4 was more dorsally wedged in the UNMDID sample with an average of 9.4° than the South African sample's average of 7.62° (Students t-test, p=0.036) (Table 8).

Table 8: The VBW and IVDW for each vertebra and intervertebral disc was compared between the South African sample and UNMDID sample (Edgar et al., 2020). Variables with an asterisk (*) indicates that a Mann-Whitney U test was performed between the variables (U) is the test statistic, while all other variables were tested using a Student's t-test (t). Significant differences are in red text.

Wedging Angle	**Test Results**
L1*	U=1188.5, p=0.138
L2*	U=1461.5, p=0.985
L3*	U=1623.5, p=0.363
L4*	U=1490.5, p=0.858
L5*	U=1364.0, p=0.605
Disc L1-2	t(133)=0.416, p=0.678
Disc L2-3*	U=1731.5, p=0.132
Disc L3-4	t(133)=-2.212, p=0.036
Disc L4-5	t(133)=-0.122, p=0.903
Disc L5-S1	t(133)=1.912, p=0.058

On average the dorsal and ventral heights of the UNMDID sample's intervertebral disc and vertebral bodies were higher than the South African sample (Table 9 and Table 10). Despite the difference in the dorsal and ventral heights of each vertebra and intervertebral disc, the TVBW and TIVDW, along with most of the individual wedging angles were unaffected. Since there was similarity between the two groups for the Cobb angle, TVBW, and TIVDW (Table 7), both human samples were pooled for future analysis.

Table 9:

Results comparing the differences between ventral body height (VBH) and dorsal body height (DBH) in the vertebrae of the South African and UNMDID samples (Edgar et al., 2020). Most variables were tested using a Student's t-test, but when an asterisk (*) is present the samples were compared using a Mann-Whitney U.

Vertebra	L1		L2		L3		L4		L5	
Variable	VBH	DBH	VBH	DBH	VBH	DBH	VBH*	DBH	VBH*	DBH
df	133	133	133	133	133	133	n/a	133	n/a	133
Test Statistic	-2.016	-3.501	-2.482	-2.548	-2.709	-2.610	1909.0	-3.021	1943.5	-3.515
Sig.	0.046	0.001	0.014	0.012	0.008	0.012	0.013	0.003	0.008	0.001

Table 10:

Results comparing the differences between ventral body height (VBH) and dorsal body height (DBH) in the intervertebral discs of the South African and UNMDID samples (Edgar et al., 2020). Most variables were tested using a Student's t-test, but when an asterisk (*) is present the samples were compared using a Mann-Whitney U.

Disc	L1-L2		L2-L3		L3-L4		L4-L5		L5-S1	
Variable	VBH	DBH	VBH*	DBH	VBH	DBH	VBH	DBH	VBH	DBH
df	133	133	N/A	133	133	133	133	133	133	133
Test Statistic	-2.140	-0.843	2000.5	-1.309	-2.761	.206	-1.574	-.133	1.302	1.387
Sig.	0.034	0.401	0.003	0.193	0.007	0.837	0.118	0.894	0.195	0.171

3.4. The contribution of summed vertebral body wedging and intervertebral disc wedging to lumbar lordosis

The combined modern human sample was used to evaluate how TIVDW and TVBW influence lordotic curvature. A One-Way ANOVA with a Tukey's Post Hoc test revealed that

TIVDW was not significantly different from the Cobb angle (ANOVA, p=0.751) or the TW (ANOVA, p=0.993) but TVBW was significantly different from the other measurements (ANOVA, $p < 0.01$, N=135) (Table 11). The lumbolumbar angle was significantly different from all other angles except the sum of wedging angles between L1-L5 (ANOVA, p=0.992) (Table 11).

Table 11:

One-Way ANOVA results (p-values) with a Tukey's post-hoc test comparing the means between measurements of lumbar lordosis, TVBW, and TIVDW.

Angle	**Cobb**	**TW**	**Lumbolumbar**	**L1-L5**	**TVBW**	**TIVDW**
Cobb						
Total Wedging	0.993					
Lumbolumbar	P＜0.01	P＜0.01				
L1-L5	P＜0.01	P＜0.01	0.992			
Total VBW	P＜0.01	P＜0.01	P＜0.01	P＜0.01		
Total IVDW	0.751	0.387	P＜0.01	P＜0.01	P＜0.01	

The second method used to evaluate how intervertebral discs and vertebral bodies contribute to lordotic curvature is through correlation. As expected, Table 12 depicts a statistically significant positive correlation between the vertebral bodies, intervertebral discs, and lordotic curvature. TVBW has a moderately positive correlation with the Cobb angle (Pearson's Correlation, $r = 0.557$. $p < 0.01$) and TW (Pearson's Correlation, $r = 0.686$, $p < 0.01$), while TIVDW has a weaker correlation with both Cobb angle (Pearson's Correlation, $r = 0.351$, $p < 0.01$) and TW angle (Pearson's Correlation, $r = 0.357$, $p < 0.01$) (Table 12).

Table 12:

Pearson's correlation test comparing several different types of lordosis measurements, TVBW, and vertebral TIVDW. Red text is correlation coefficients where ($p < 0.01$).

Angle	Cobb	Total Wedging	Lumbolumbar	L1-L5	TVBW	TIVDW
Cobb	1					
Total Wedging	0.862	1				
Lumbolumbar	0.881	0.774	1			
L1-L5	0.774	0.915	0.835	1		
Total VBW	0.557	0.686	0.627	0.783	1	
Total IVDW	0.351	0.357	0.153	0.128	-0.434	1

The wedging found in the lumbar vertebrae explains 31.1 % of variability or $r^2(100)$, within the Cobb angle (Figure 9) while the intervertebral discs (Figure 10) explain only 12.4% of the variability $(0.351)^2(100)$. The only negative relationship found was between TVBW and TIVDW (Pearson's Correlation, $r = -0.434$, $p < 0.01$). Additionally, the lumbolumbar angle has a stronger relationship with TVBW (Pearson's Correlation, $r = .627$, $p < 0.01$) than the Cobb angle (Pearson's Correlation, $r = 0.557$, $p < 0.01$).

Figure 9.

Scatter plot depicting a moderately positive correlation between the Cobb angle and TVBW (Pearson's Correlation, r = 0.557. p＜0.01). Kyphotic and lordotic TVBW values for the individuals are distinguished by a dotted red line.

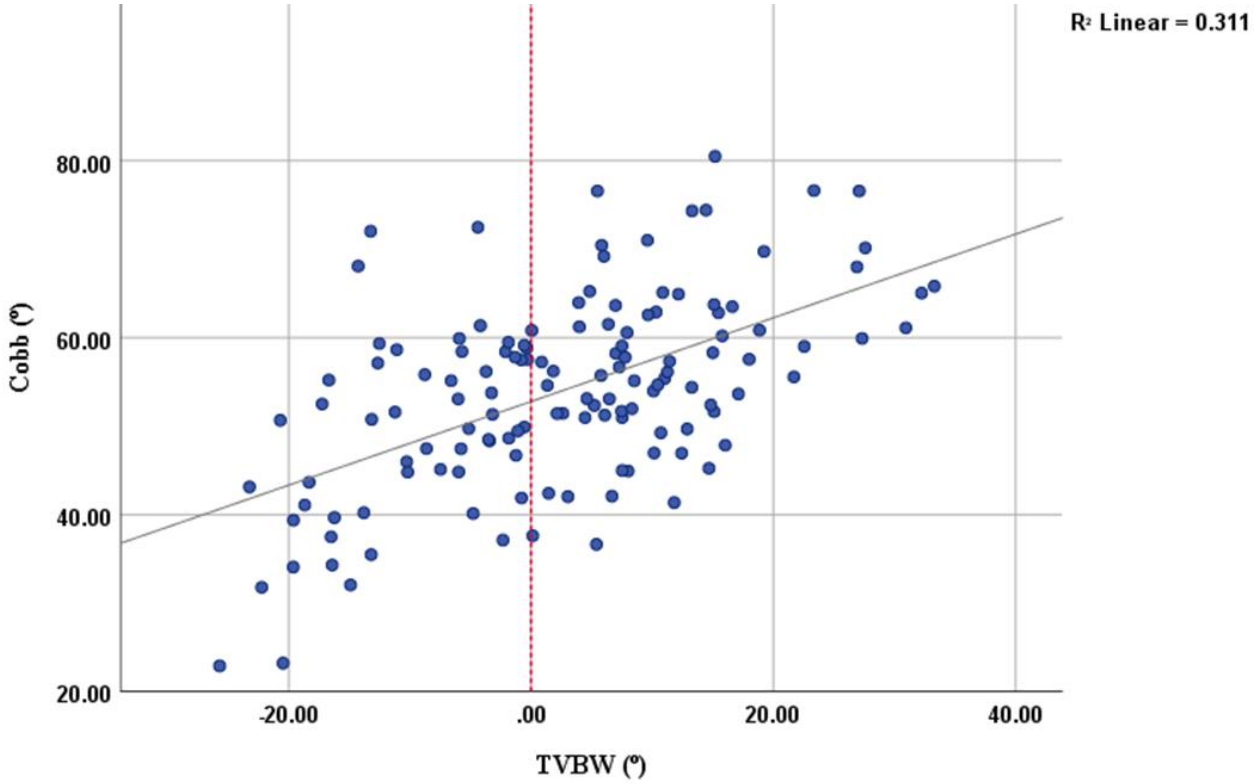
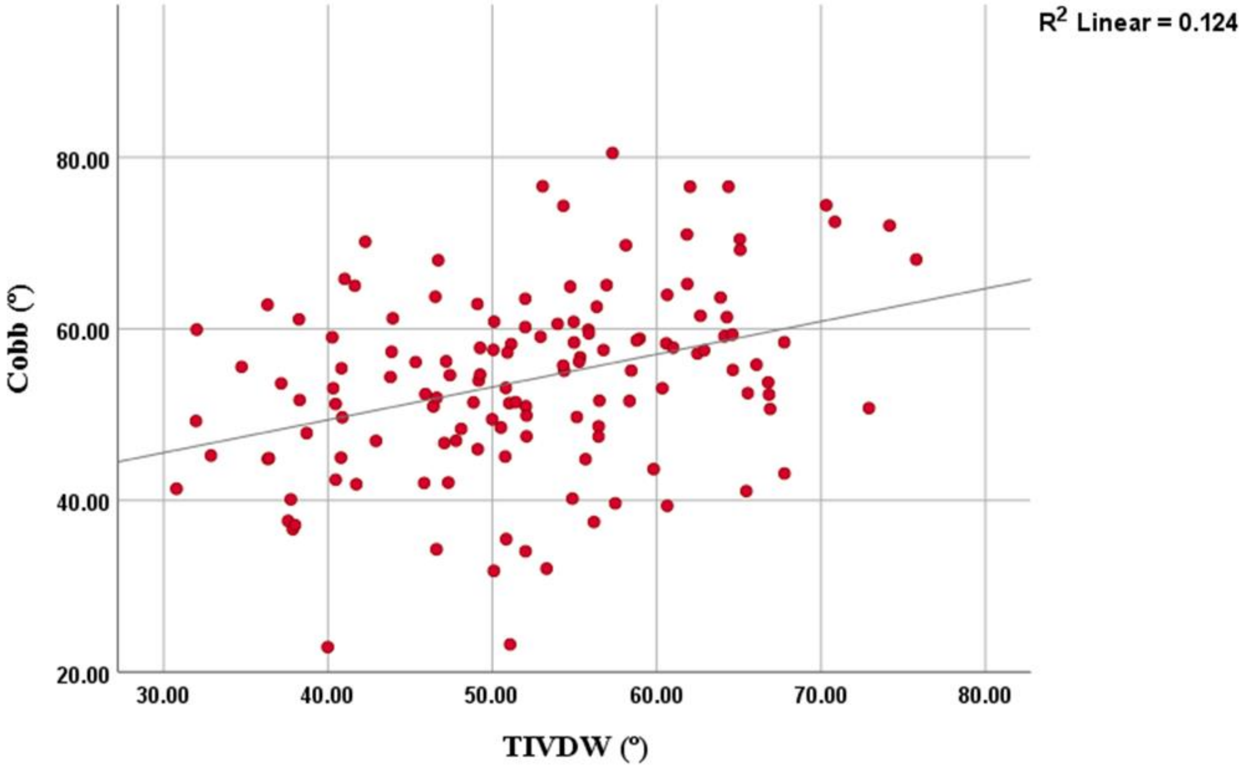


Figure 10.

Scatter plot depicting the positive weak correlation between the Cobb angle and TIVDW (°)

(Pearson's Correlation, r = 0.351, p < 0.01).

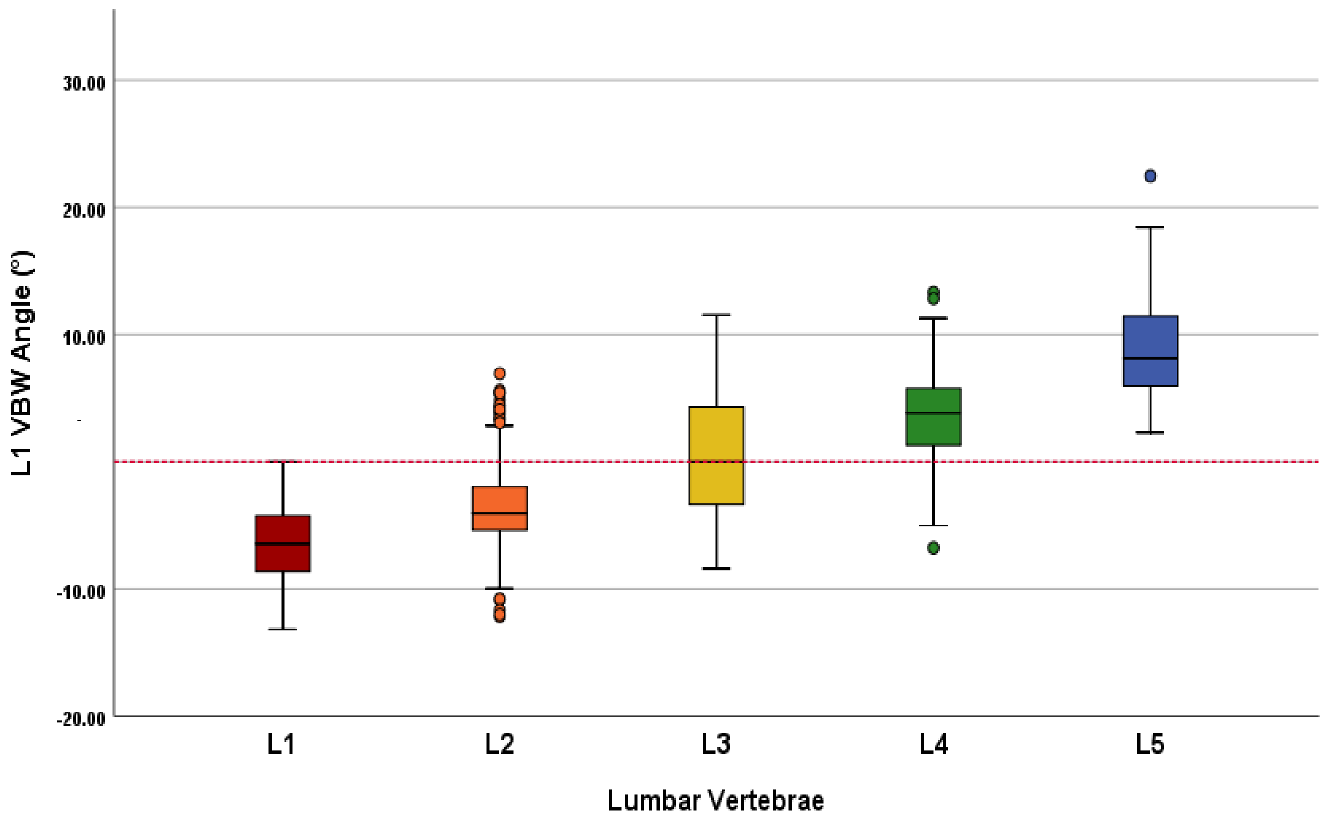


3.5. The wedging pattern in modern humans and individual VBW and IVDW

Individual analysis of each vertebral body within the combined modern human sample shows an increase in lordotic wedging from L1 to L5. The lowest values on average for wedging were found in L1 (-6.47 ± 2.60) and the greatest values in L5 (8.83 ± 3.89). The wedging pattern found clearly ascends from kyphotic to lordotic with L1 spanning from kyphotic to neutral (Range, -13.19 to 0.0), while the VBW of the L5 is only lordotic (Range, 2.31 to 22.46) (Figure 11).

Figure 11.

Box-and-whisker plot depicting the VBW wedging pattern found in the combined modern human sample. The wedging angle is depicted in degrees (°). A dotted red line on the Y-axis separates kyphotic wedging values from lordotic ones.



The lumbar vertebrae show a significant difference (Kruskal-Wallis, $p < 0.01$) in wedging between lumbar vertebrae. A pairwise comparison between each of the vertebral bodies reveals that each one has distinctive wedging (Table 13).

Table 13:

Kruskal Wallace test results (p-values) with pair-wise comparisons between lumbar vertebrae.

Vertebra	L1	L2	L3	L4	L5
L1					
L2	$p < 0.01$				
L3	$p < 0.01$	$p < 0.01$			
L4	$p < 0.01$	$p < 0.01$	0.30		
L5	$p < 0.01$	$p < 0.01$	$p < 0.01$	$p < 0.01$	

A Spearman's Correlation was used to assess how each vertebra influenced variability between each other and the Cobb angle (Table 14). There was a significant correlation (Spearman's correlation, $p < 0.01$) between the Cobb angle and all other variables except for L1 (Spearman's correlation, p= 0.110). The central lumbar vertebrae L2 to L4, have stronger correlations with the other vertebrae than L1 and L5 (Table 14).

Table 14:

Spearman's rho correlation across vertebral bodies. Text is red when statistical significance ($p < 0.05$).

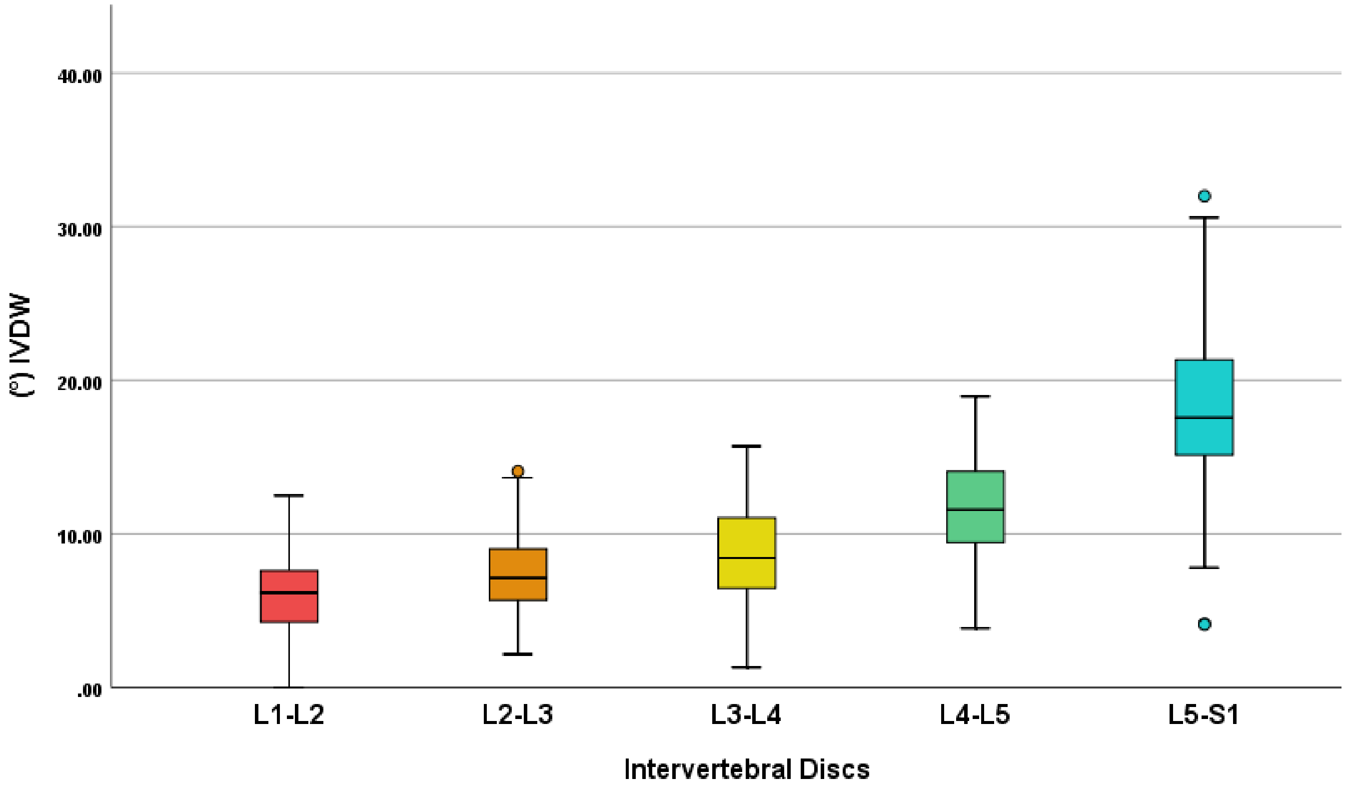
	L1	L2	L3	L4	L5	Cobb
L1 (rho)	1					
L2 (rho)	0.474	1				

L3 (rho)	0.091	0.437	1			
L4 (rho)	0.190	0.413	0.547	1		
L5 (rho)	0.126	0.241	0.174	0.423	1	
Cobb (rho)	0.110	0.391	0.422	0.391	.353	1

The intervertebral discs also had a wedging pattern that ascended from least lordotic to most lordotic, however, unlike the vertebral bodies, the intervertebral discs only have positive wedging angles (Figure 12). Disc L1-2 was the least lordotic on average (6.26 ± 2.63) while disc L5-S1 was the most lordotic (17.93 ± 4.98). Disc L1-L2 ranged from 0.0 to 12.5 and Disc L5-S1 ranged from 4.1 to 31.99 (Figure 12).

Figure 12.

Box-and-whisker plot demonstrating the range of the wedging angles (°) for each of the individual intervertebral discs.



A Kruskal-Wallace test (disc L3-L4) and One-Way ANOVA revealed a significant difference between the degree of wedging in the intervertebral discs (ANOVA, $p < 0.01$) except for L2-L3 and disc L3-L4 (Kruskal Wallace, p=0.094). The comparisons of IVDW are portrayed in Table 15.

Table 15:

The p-values from a One-Way ANOVA and Kruskal-Wallis test labelled with and asterisk (*) comparing the wedging angles of individual intervertebral discs. The p-values that are statistically significant are in red text.

Disc	L1-L2	L2-L3*	L3-L4	L4-L5	L5-S1
L1-L2					
L2-L3*	.119				
L3-L4	$p < 0.01$	.094			
L4-L5	$p < 0.01$	$p < 0.01$	$p < 0.01$		
L5-S1	$p < 0.01$	$p < 0.01$	$p < 0.01$	$p < 0.01$	

While the intervertebral discs play a significant role in the composition of the lordotic curvature, intervertebral discs do not explain much of the variability found within the Cobb angle (Table 16). There is only a significant correlation between the Cobb angle and the intervertebral discs L2-L3 (Spearman's correlation, $p=0.036$), L4-L5 (Pearson's correlation, $p=0.013$), and L5-S1 (Pearson's correlation, $p < 0.01$) (Table 16). The intervertebral discs at the center of the curvature have a stronger correlation with each other than with the first and last intervertebral disc in the lumbar region (Table 16). The last intervertebral disc, L5-S1, impacts variability in the Cobb angle more than any other intervertebral disc (Table 16).

Table 16:

Intervertebral discs wedging correlation coefficients. Coefficients highlighted in red are statistically significant ($p < 0.05$). Disc L2-3 is non-parametric and is marked with an asterisk (*) to indicate that a Spearman's correlation test has been done.

	L1-L2	L2-L3*	L3-L4	L4-L5	L5-S1	Cobb
L1-L2 (r)	1					
L2-L3*	0.392	1				
L3-L4 (r)	0.271	0.467	1			
L4-L5 (r)	0.158	0.222	0.460	1		

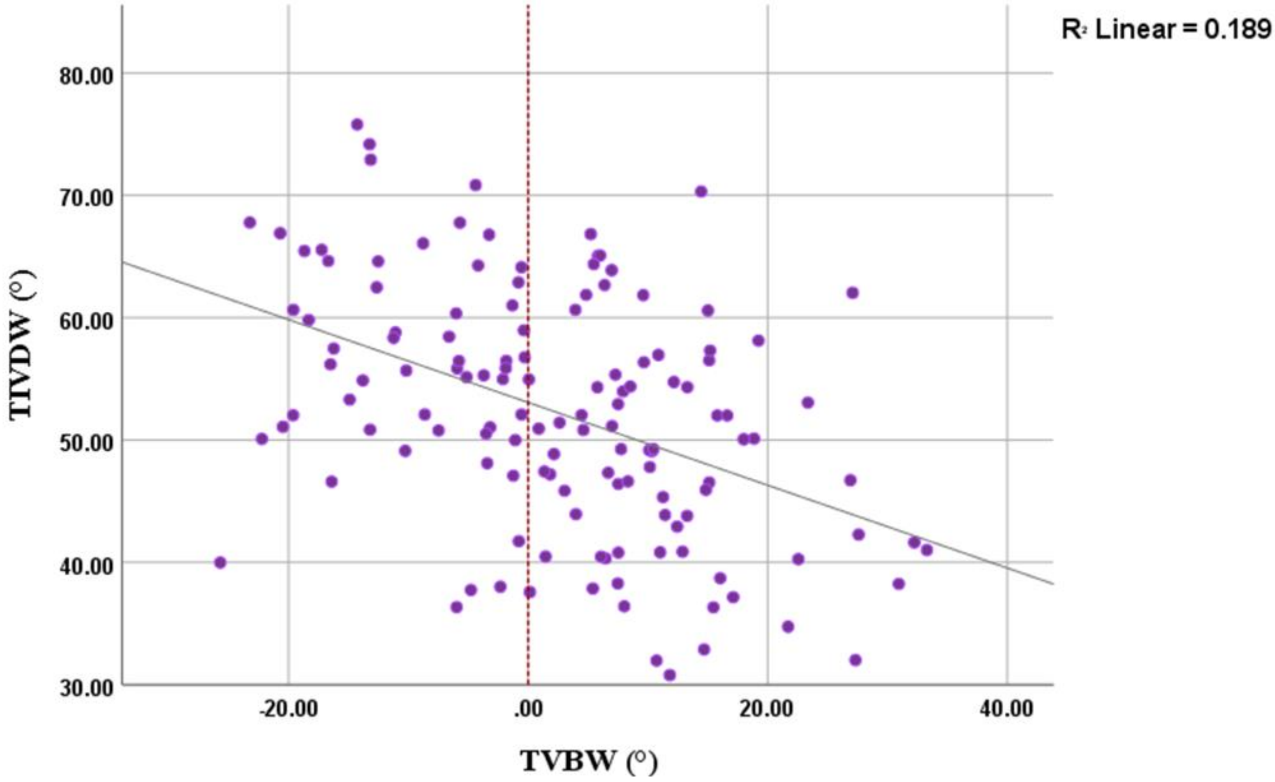
L5-S1 (r)	0.053	-0.017	0.020	0.263	1	
Cobb (r)	0.145	0.180	0.144	0.214	0.312	1

3.6. Exploring the negative relationship between the wedging of the vertebral bodies and intervertebral discs

As mentioned previously, there is a weak, but statistically significant, correlation between TIVDW and TVBW (Figure 13). 18.9% $(-0.434)^2(100)$ of the variability found in the wedging of the vertebral bodies can be explained by the intervertebral discs or vice versa (Figure 13). The individual vertebrae and intervertebral disc were also tested to see if this relationship was consistent throughout the lumbar region (Table 17).

Figure 13.

Scatter plot depicting the negative relationship between TIVDW and TVBW. Kyphotic and lordotic wedging of the vertebral bodies are separated by a dotted red line on the X-axis**.** As TIVDW increase TVBW decreases or vice versa (Pearson's Correlation, r = - 0.434, p ＜0.01).



The relationship between individual VBW and IVDW is consistently negative (Table 17). The strongest correlation is found between L1 and disc L1-2 (Spearman's correlation, r= - 0.392, p＜0.01) but the central intervertebral discs and vertebral bodies generally have stronger correlations between each other than the cranial and caudal lumbar vertebrae (Table 17). The correlation found between the discs and the vertebral bodies is weak, but consistent and often statistically significant (Table 17).

Table 17:

Spearman’s correlation coefficients between IVDW and VBW. Correlation coefficients with statistical significance are in red text (p＜0.05).

	L1	L2	L3	L4	L5
Disc L1-2	-0.392	-0.286	-0.175	-0.179	-0.109
Disc L2-3	-0.253	-0.286	-0.187	-0.100	-0.044
Disc L3-4	-0.148	-0.296	-0.341	-0.374	-0.184
Disc L4-5	-0.205	-0.285	-0.192	-0.272	-0.227
Disc L5-S1	-0.137	-0.100	-0.106	-0.070	-0.124

3.7. Sexual dimorphism in the modern human sample

Table 5 portrays the averages for lordosis, TVBW, and TIVDW divided by sex between the UNMDID sample and the South African sample. Both samples show no difference in the overall lordotic curvature. Each sample was evaluated for sexual dimorphism separately and combined in a Student’s t-test (Table 18). Neither sample shows signs of sexual dimorphism in lordotic curvature, however, the TVBW (Student’s t-test, p=0.008) and TIVDW (Student’s t-test, p=0.027) is significantly different for males and females in the UNMDID sample (Table 18) (Edgar et al., 2020).

Table 18:

Student's t-test results comparing lordosis and lordotic wedging between sex in the UNMDID sample (Edgar et al., 2020), South African sample, and the combined sample totals. Statistically significant values are in red text. Sample size is depicted as (n).

	UNMDID		South African		Total	
	M (57)	F (51)	M (12)	F (15)	M (69)	F (66)
∠Cobb	t(106)=-0.570, p= 0.570		t(25)=-1.359, p=0.186		t(133)= -1.160, p=0.248	
∑ TW	t(106)=-0.950, p= 0.344		t(25)=-1.039, p=0.310		t(133)= -1.340, p=0.183	
∠ LL	t(106)= -0.484, p=0.632		t(25)=-0.929, p=0.367		t(133)= -0.818, p=0.415	
∑ L1-L5	t(106)=-1.178, p= 0.241		t(25)=-0.406, p=0.688		t(133)= -1.184, p=0.239	
∑ VBW	t(106)= -2.696, p=0.008		t(25)= -0.166, p=0.870		t(133)=-2.448, p=0.016	
∑ IVDW	t(106)=2.243, p= 0.027		t(25)=-1.122, p=0.273		t(133)= 1.473, p=0.153	

Within the UNMDID sample (Edgar et al., 2020) females have a greater TVBW (Student's t-test, males, -0.41 ± 12.08, females, 5.99 ± 12.56,p < 0.01) on average while males had greater TIVDW (Student's t-test, males, 54.17 ± 9.74; females, 49.99 ± 9.59, p=.037) (Figure 14 and Figure 15). While males and females from the South African sample look comparable to the UNMDID sample, the South African sample has no statistically significant differences between males and female (Figure 14 and Figure 15). When the samples are combining only the TVBW is different between the sexes (Table 18).

Figure 14.

Box-and-whiskers plot of TVBW (º) and sex. Females have a greater range of VBW and a higher average in the UNMDID sample. Kyphotic and lordotic TVBW values are separated by a dotted red line (Edgar et al., 2020).

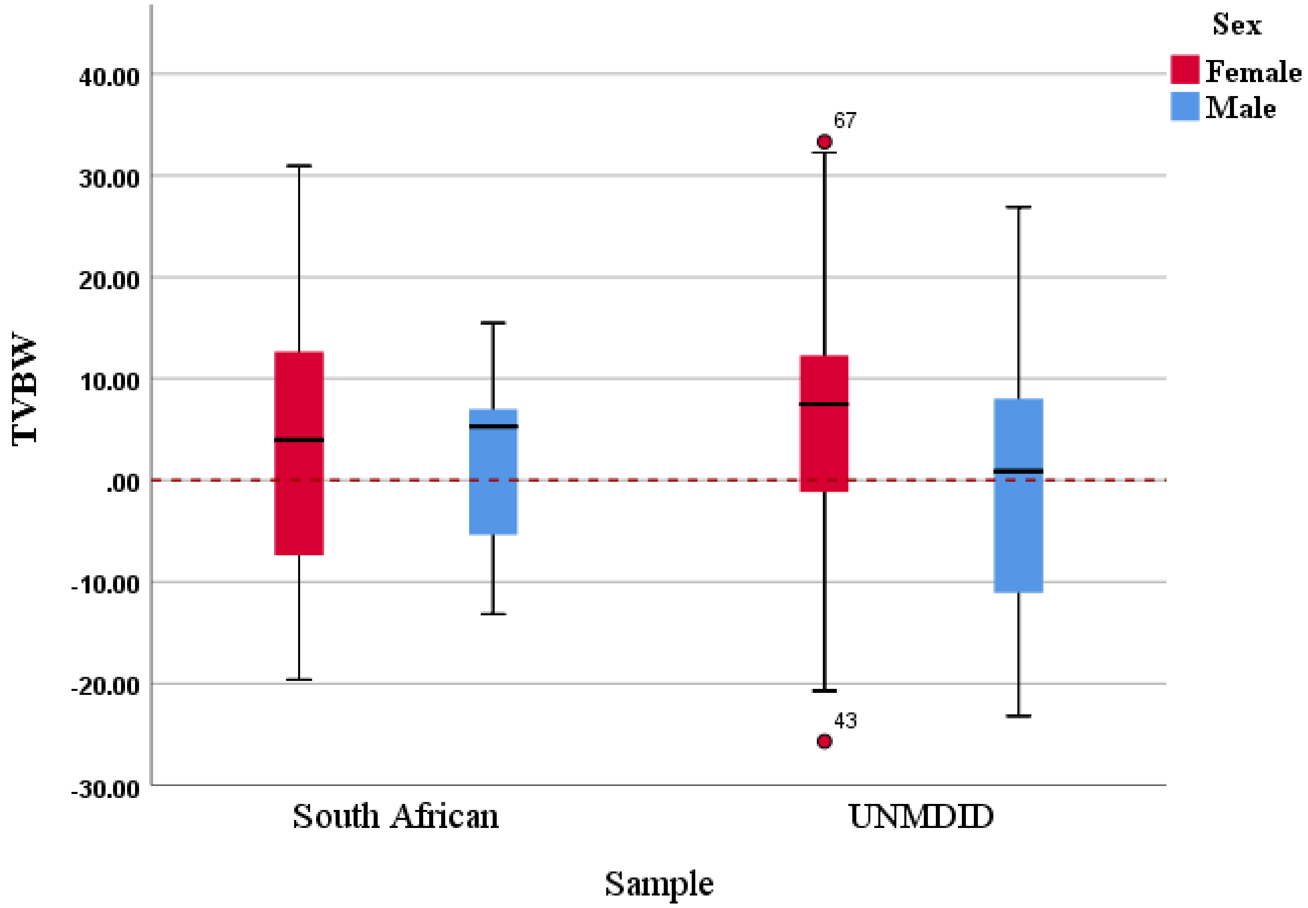
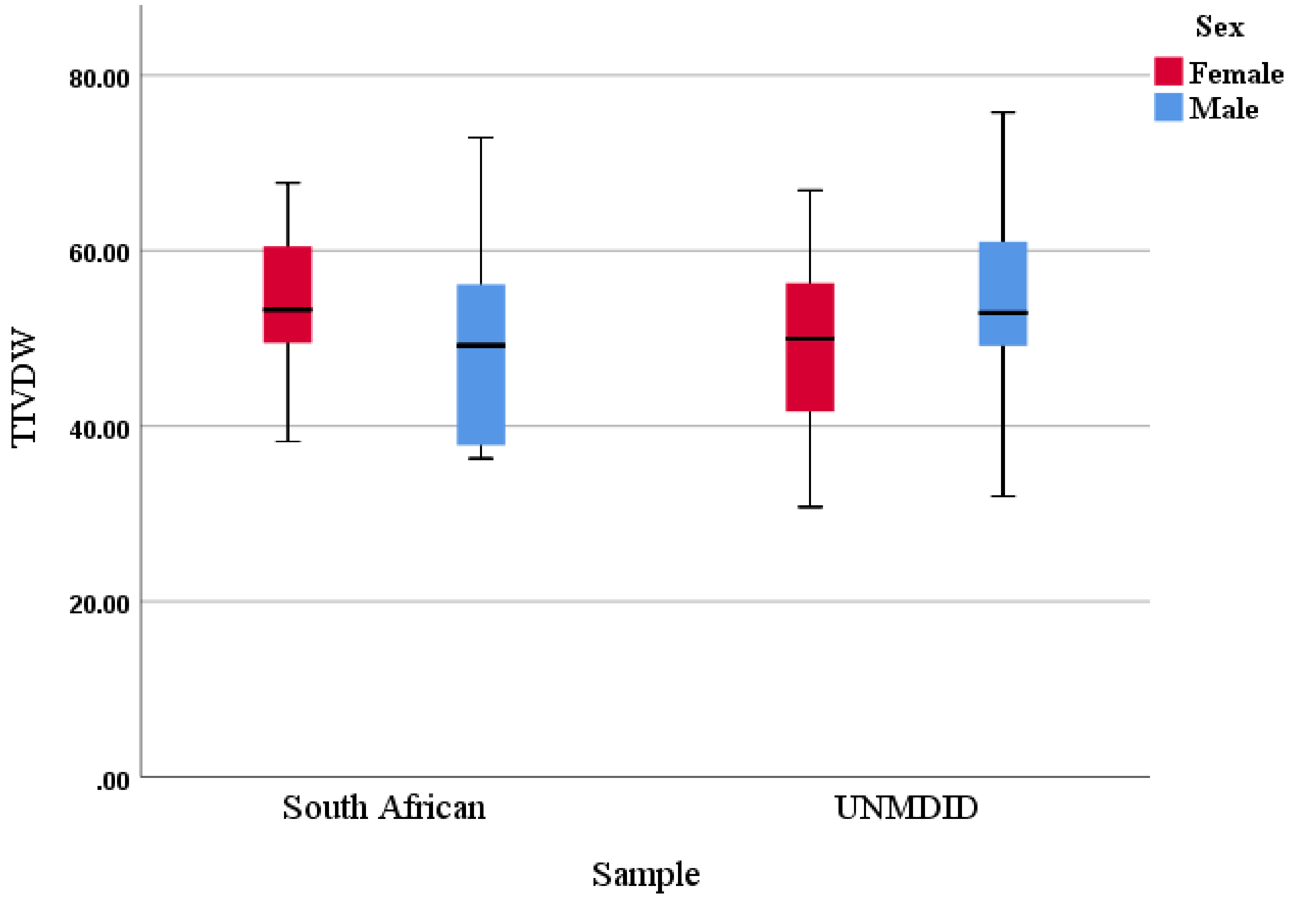


Figure 15.

Box-and-whiskers plot of TIVDW divided by sample and sex. The results for the South African sample were not statically signficant, but males had higher IVDW than females for the UNMDID (Edgar et al., 2020).



The mean wedging angles of individual intervertebral disc and vertebral bodies by sex is depicted in Table 6. In the combined sample females have a significantly more dorsally wedged L3 (Mann-Whitney U test, males, -1.45 ± 12.08; females, 1.37 ± 4.34, $p < 0.01$) and L4 (Mann-Whitney U test, males, 2.31 ± 4.16; females, 4.07 ± 3.89, p= 0.011) while males have more dorsal wedging on disc L1-2 (Student's t-test, males, 6.27 ± 2.76; females, 5.77 ± 2.4, P= 0.035) and disc L3-L4 (Student's t-test, males, 9.45 ± 3.18; females, 8.02 ± 2.99, p= 0.028) (Table 19). Within the UNMDID sample (Edgar et al., 2020) females show additional dorsal wedging on their L5 (Mann-Whitney U test, males, 7.89 ± 3.10; females, 9.53 ± 3.82, P < 0.01) (Table 19). The South African sample did not show any statistically significant signs of dimorphism (Table 19).

Table 19:

The results from Student's t-tests (t) and Man-Whitney U-tests (U) comparing the wedging angles of individual IVDW and VBW between males and females from the UNMDID sample (Edgar et al., 2020), South African sample, and combined. Statistically significant results are in the red text.

	UNMDID Sig.		**South African Sig.**		**Total Sig.**	
	M (57)	**F(51)**	**M (12)**	**F(15)**	**M (69)**	**F(66)**
L1	U=1459.5, p=0.971		t(25)=-0.028, p=0.978		U=2271, p=0.979	
L2	U=1228, p=0.165		t(25)=-1.025, p=0.318		U=1862.5, p=0.068	
L3	U=1058.5, p=0.015		U=64, p=0.217		U=1675, p=0.008	
L4	U=901.5, p=0.001		t(25)=0.288, p=0.776		U=1698.5, p=0.011	
L5	U=1096, p=0.028		t(25)=1.152, p=0.260		U=2036.5, p=0.290	
Disc L1-2	U= 1847, p=0.015		t(25)=-0.371, p=0.714		t(133)=.2.134, p=0.035	
Disc L2-3	U=1678, p=0.167		t(25)=-0.033, p= 0.974		U=25.95.5, p=0.161	
Disc L3-4	U=1894.5, p= 0.007		t(25)=0.178, p=0.933		t(133)=2.684, p=0.008	
Disc L4-5	t(106)= 0.849, p= 0.398		t(25)=-0.695, p=0.493		t(133)=0.44, p=0.658	
Disc L5-S1	t(106)= 0.078, p= 0.938		t(25)=-1.874, p=0.073		t(133)=-0.834, p=0.406	

3.8. The relationship between age and lordotic curvature

The UNMDID is the only sample where information on age is provided, so this sample is the only one used in the age analysis (range 25 to 50, years) (Edgar et al., 2020). There is no statistically significant correlation between age and measurements from the lumbar region depicted in Table 20 (Edgar et al., 2020).

Table 20:

Spearman's correlation test between age, lordosis, and lordotic wedging in the UNMDID sample ages 25-50 (Edgar et al., 2020).

	Age	Cobb angle	Total Wedging	Lumbol umbar	Summed L1-L5	Total VBW	Total IVDW
Age	1.0	.063	.038	.031	.004	-0.085	.125

3.9.Lumbar vertebrae wedging patterns found within the fossil hominin sample

Fossil *H. sapiens*, Oberkassel 1 and 2, *H. neanderthalensis*, Kebara 2, and *Au. Africanus*, StS 14 had the wedging of their vertebral bodies compared with those from the combined modern human sample. All fossil vertebrae stay within the range of the modern human sample with two exceptions, Oberkassel 2, and Kebara 2 (Table 21). Oberkassel 2 has a dorsally wedged L1, while all other L1's within the study is kyphotic or neutrally wedged. Additionally, Kebara 2 has a very kyphotic L3 that falls outside the range of modern humans (Table 21).

Table 21:

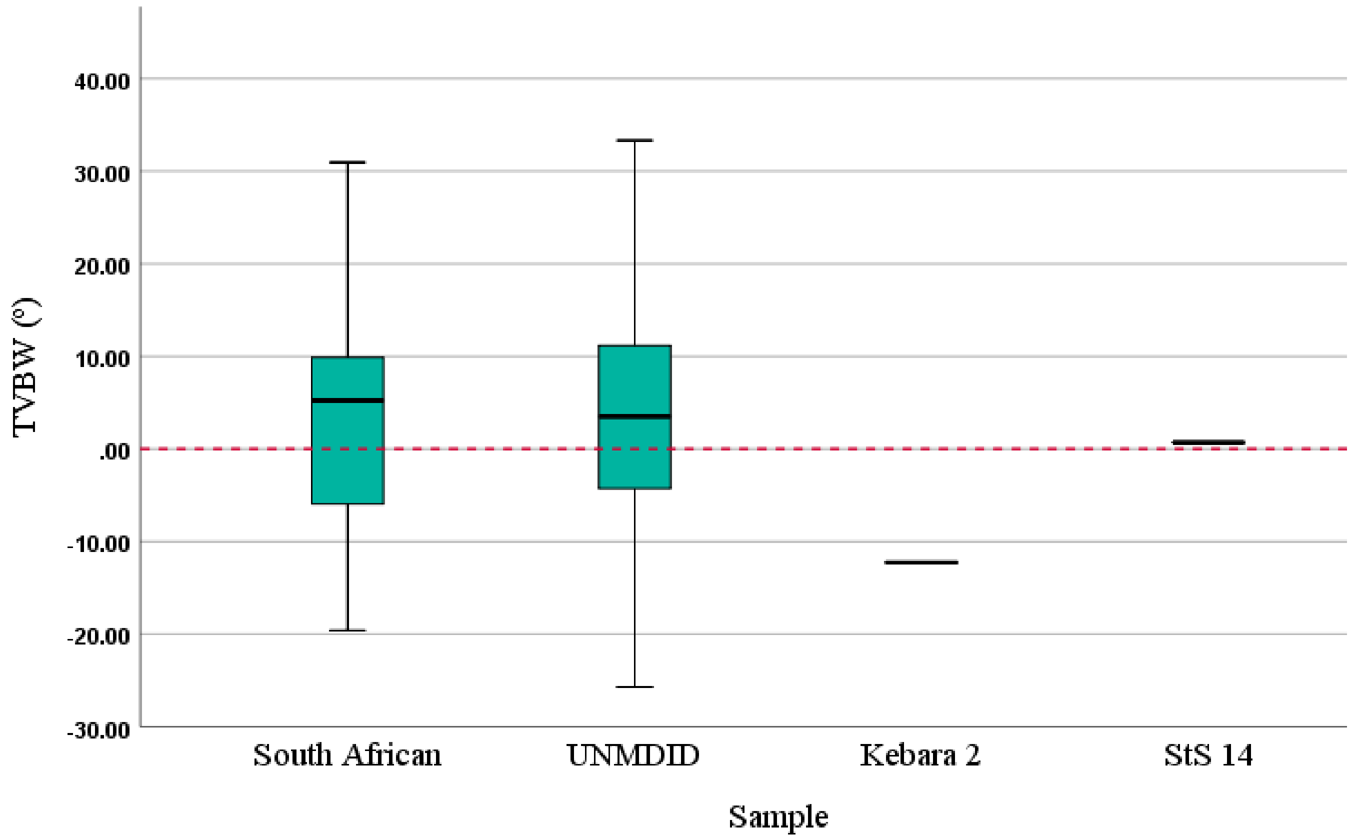
VBW in fossils hominins compared to the modern human average. Wedging that falls outside of the modern human range is in red.

Vertebral bodies	**Modern *Homo sapiens***	**Oberkassel 1**	**Oberkassel 2**	**Kebara 2**	**StS 14**
L1 (PS5)	-6.47 ± 2.60	-11.52	2.28	-5.73	-8.46
L2 (PS4)	-3.31 ± 4.0		3.76	-7.13	-4.17
L3 (PS3)	0.411 ± 4.23			-8.73	-2.87
L4 (PS4)	3.17 ± 4.11			-2.23	4.53
L5 (PS5)	8.83 ± 3.89			11.54	11.66
Total VBW	2.66 ± 12.76			-12.28	0.69

The total vertebral body wedging of Kebara 2 and StS 14 were also compared with modern humans (Table 21). Both fall within the range of the modern human sample, and this is also true when the modern human samples are separated (Figure 16). Both fossils have TVBW angles are less than the modern human average (Figure 16).

Figure 16.

Box-and-Whiskers plot of the total VBW angles (°) between contemporary humans, Kebara 2 and StS 14. A dotted red line is used to distinguish kyphotic and lordotic VBW.

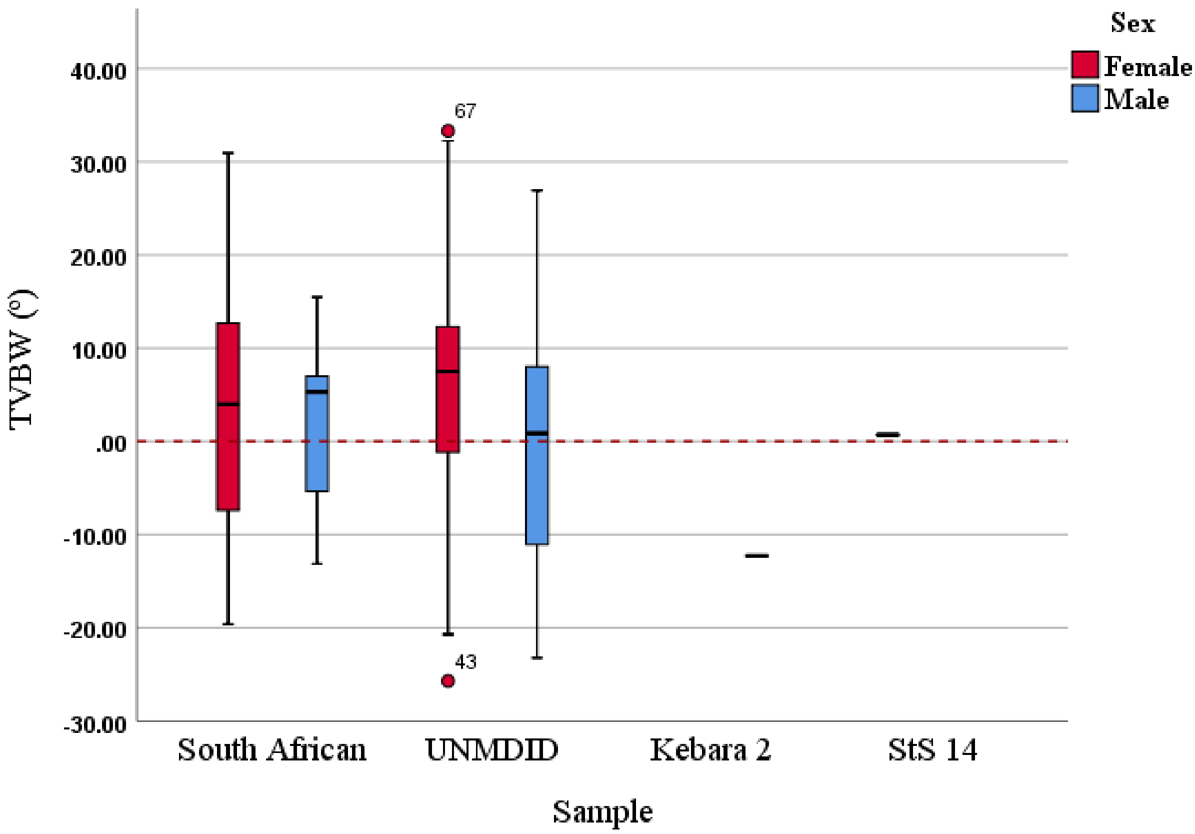


3.10. VBW in fossils based on sex

Fossils were compared with the contemporary human sample based on sex. For example, Kebara 2, was assigned male when found (Arensburg et al. 1983), and already has total VBW that falls within the range of contemporary humans, but when the modern humans are separated by sex it reveals that Kebara 2 has vertebral body wedging that is closer in range with contemporary human males than females (Figure 17). Kebara 2 still has VBW that is lower than the mean for both males and females (Figure 17).

Figure 17.

Box-and-whiskers plot depicting total vertebral body wedging (°) separated by sex between the South African sample, UNMDID sample (Edgar et al., 2020), Kebara 2, and StS 14. Kyphotic VBW is negative, while lordotic wedging is positive and is distinguished b a dotted red line.



Oberkassel 1 and 2 have been assigned male and female respectively (Nobis, 1986). The VBW of L1 (Figure 18) and L2 (Figure 19) from the Oberkassel specimens was also compared separately with the modern humans by sex to investigate the lordotic wedging found in the L1 of Oberkassel 2. Oberkassel 2, a female, (Nobis, 1986; Freidline et al., 2012) has a much higher degree of lordotic wedging than other specimens of either sex (Figure 18). The L2 of Oberkassel 2 is within the range of females from the South African sample but is still much more lordotic than the average for contemporary humans (Figure 19).

Figure 18.

Box-and-whiskers plot depicting the VBW angle of L1 across contemporary humans and fossil specimens. Kyphotic and lordotic wedging are separated by a dotted red line.

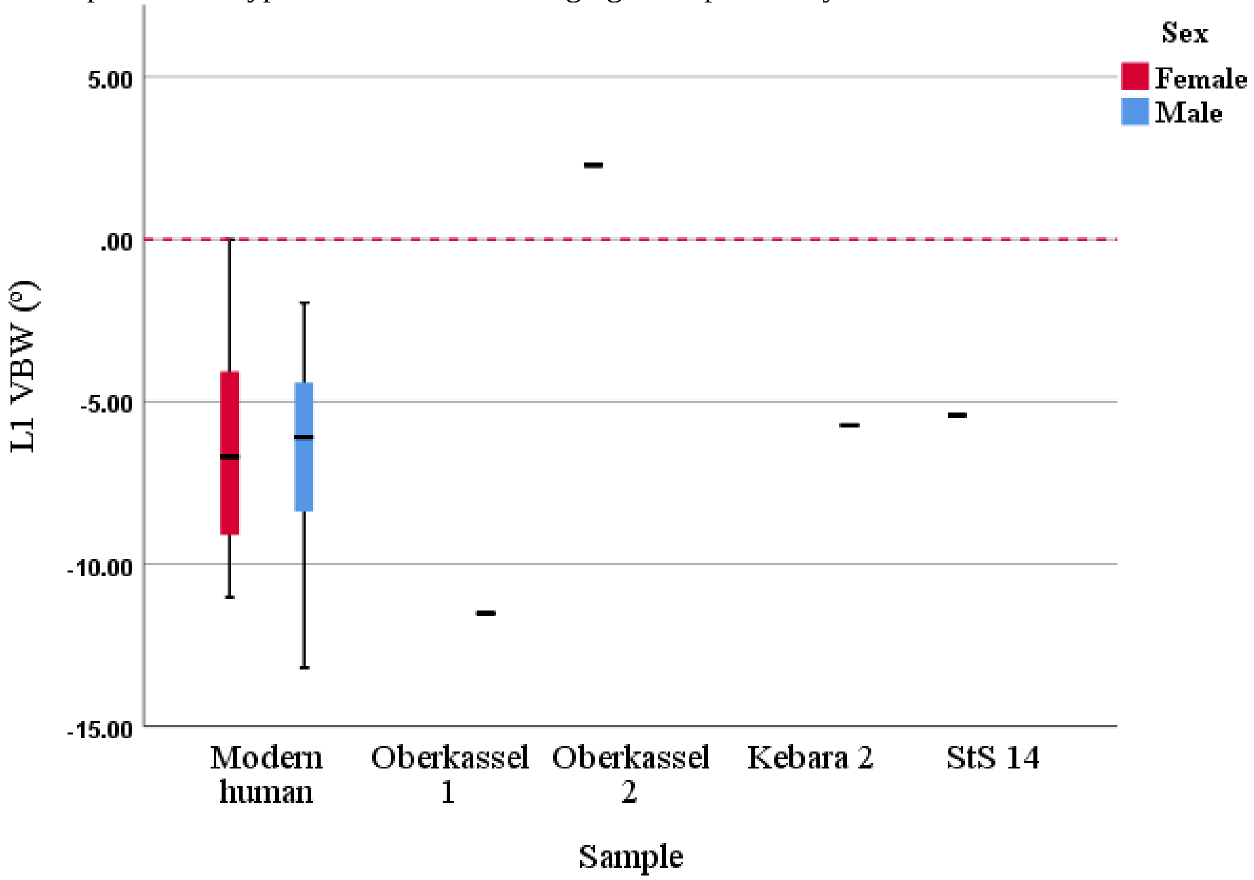
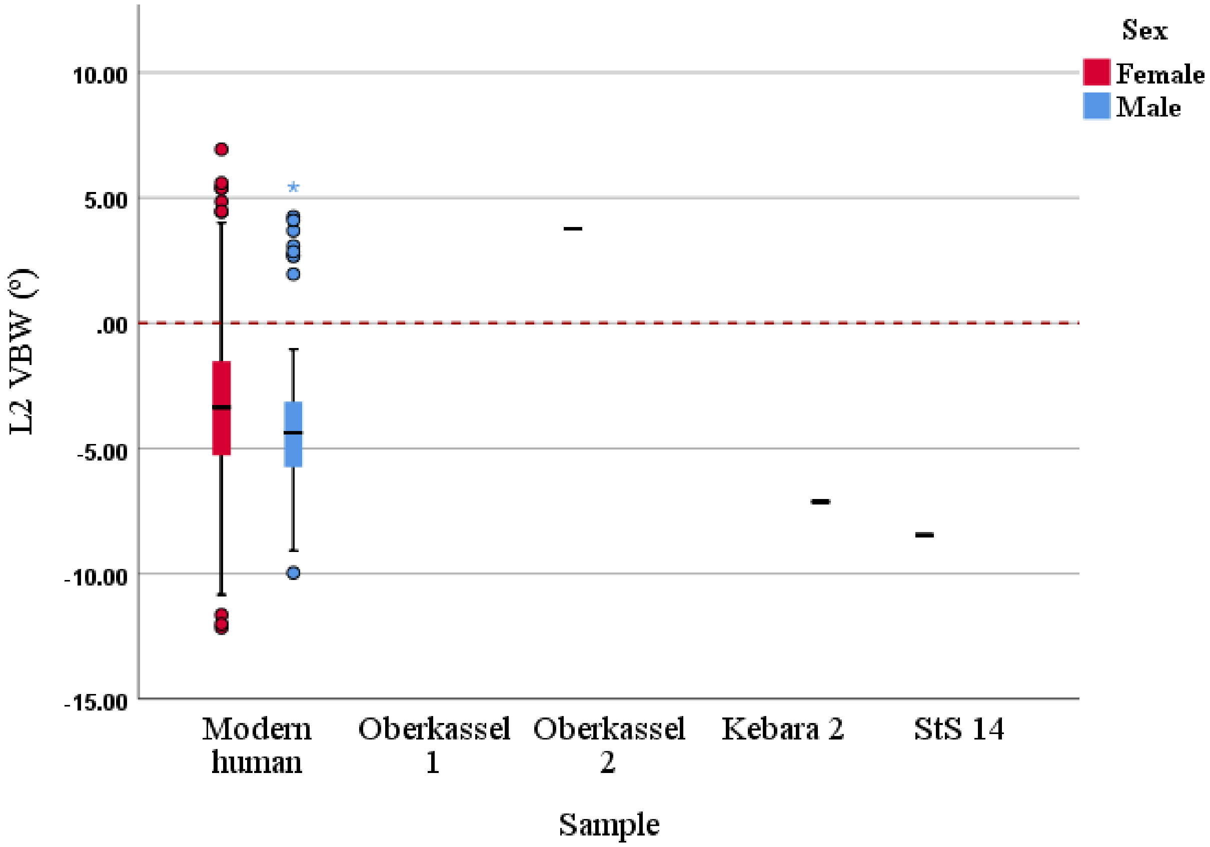


Figure 19.

Box-and-whiskers plot depicting the VBW angle of L2 across contemporary humans and fossils. Kyphotic and lordotic wedging is distinguished by negative and positive values.

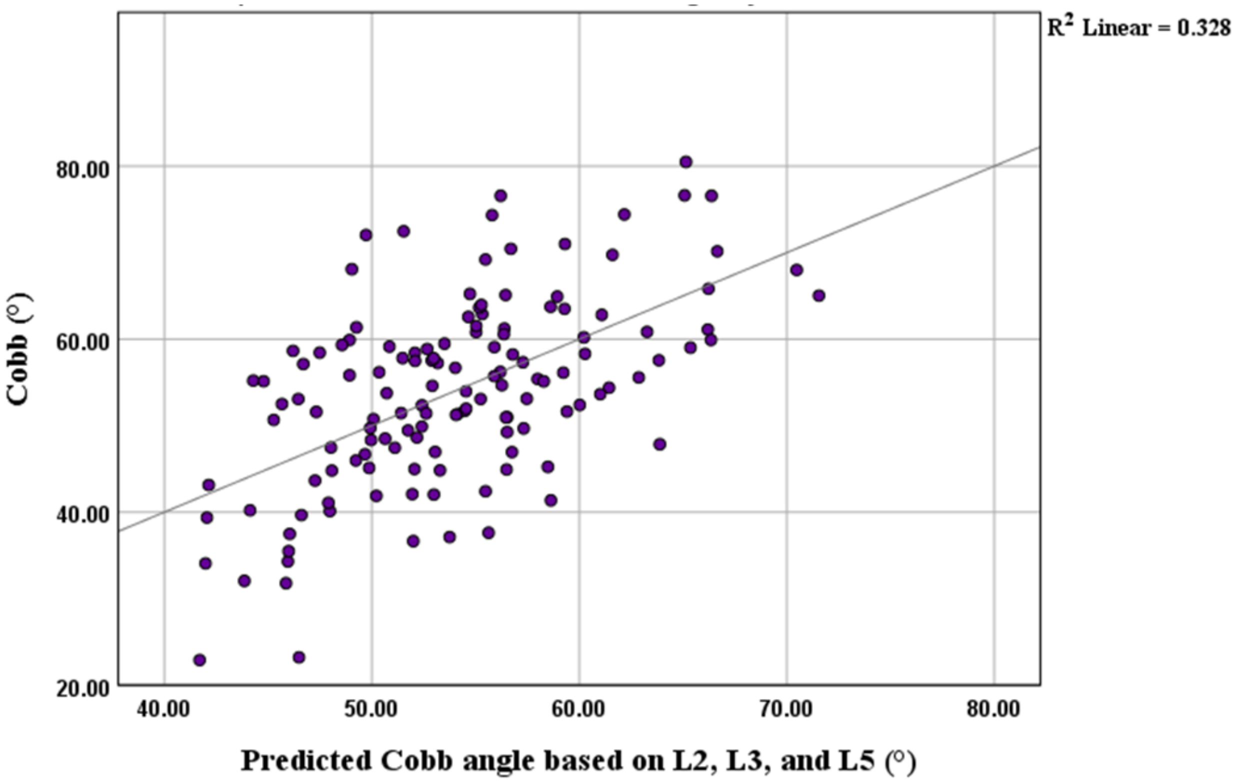


3.11. Predicting lordotic curvature of fossil hominins with vertebral body wedging

Several methods were employed to reconstruct the Cobb and lumbolumbar angles in fossil hominins. A stepwise multiple linear regression line was created to predict the Cobb angle based on the VBW angles of L2, L3, and L5, which were chosen as the most pertinent to predicting variability in the Cobb angle (Figure 20). The wedging of these vertebral bodies explains 32.8% of the variability found in the Cobb angle. A multiple linear regression based on all the vertebral bodies explains 33.6% of the variability found in the lordotic curvature (Figure 21).

Figure 20.

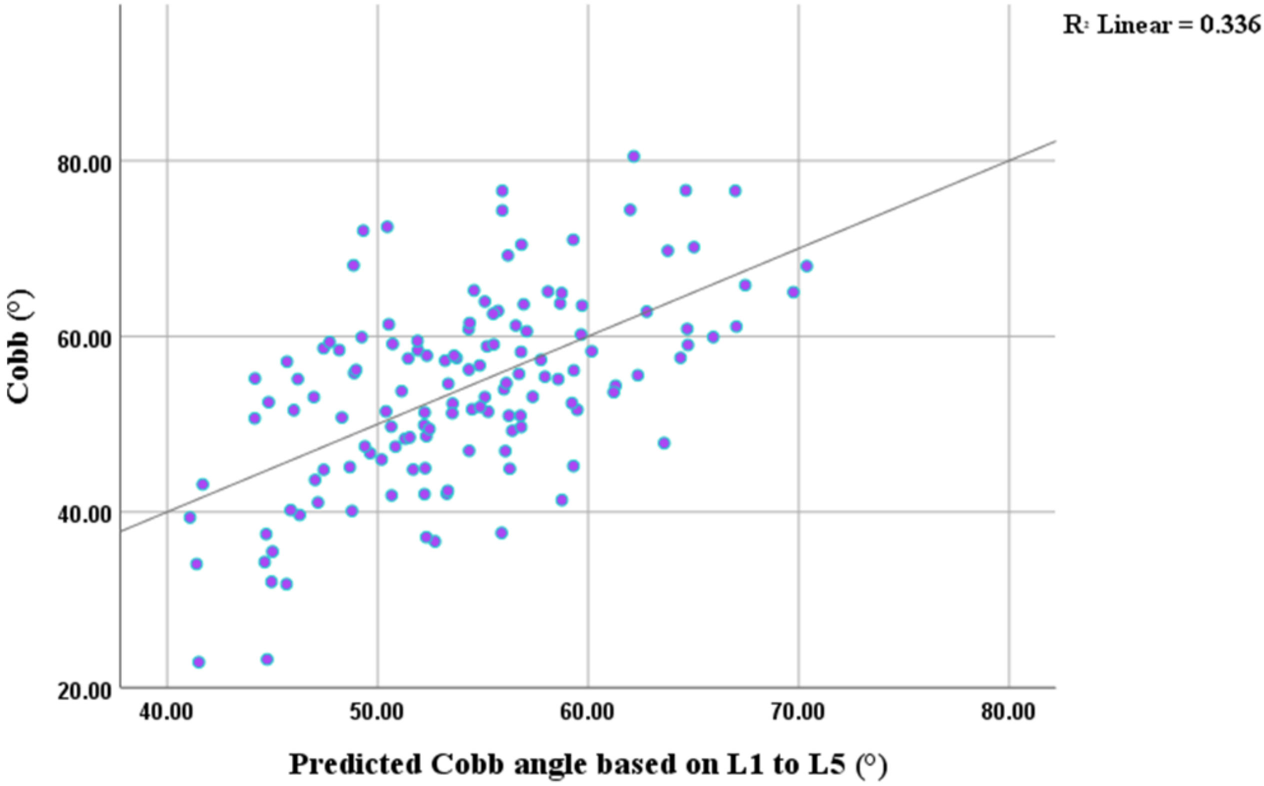
This scatter plot represents the predicted Cobb angle values (º) from a stepwise linear regression formula based on the VBW of L2, L3, and L5 with the values of the actual Cobb angle based on the pooled modern human sample**.**



80

Figure 21.

This scatterplot represents the predicted Cobb angle values based on a multiple linear regression formula of all individual lumbar vertebrae (L1-L5) with the actual values for the Cobb angle from the modern human sample.



The lumbolumbar angle has been presented as an alternative measurement to the Cobb angle as the basis of lordosis reconstruction in fossil hominins because it has a stronger relationship with TVBW. A stepwise multiple linear regression formula based on the L2, L3 and L5 explains 41.3% of the variability in the lumbolumbar angle (Figure 22). Including all vertebral bodies only slightly increases the amount of variability explained by the Cobb angle (Figure 23). The importance of the L2, L3, and L5 to variability in the lumbar region remains unchanged between the lumbolumbar and Cobb angle.

Figure 22.

This scatterplot represents the predicted lumbolumbar angle based on a multiple linear regression formula from the VBW of the L2, l3, and L5 with the actual Cobb angle values from the modern human sample.

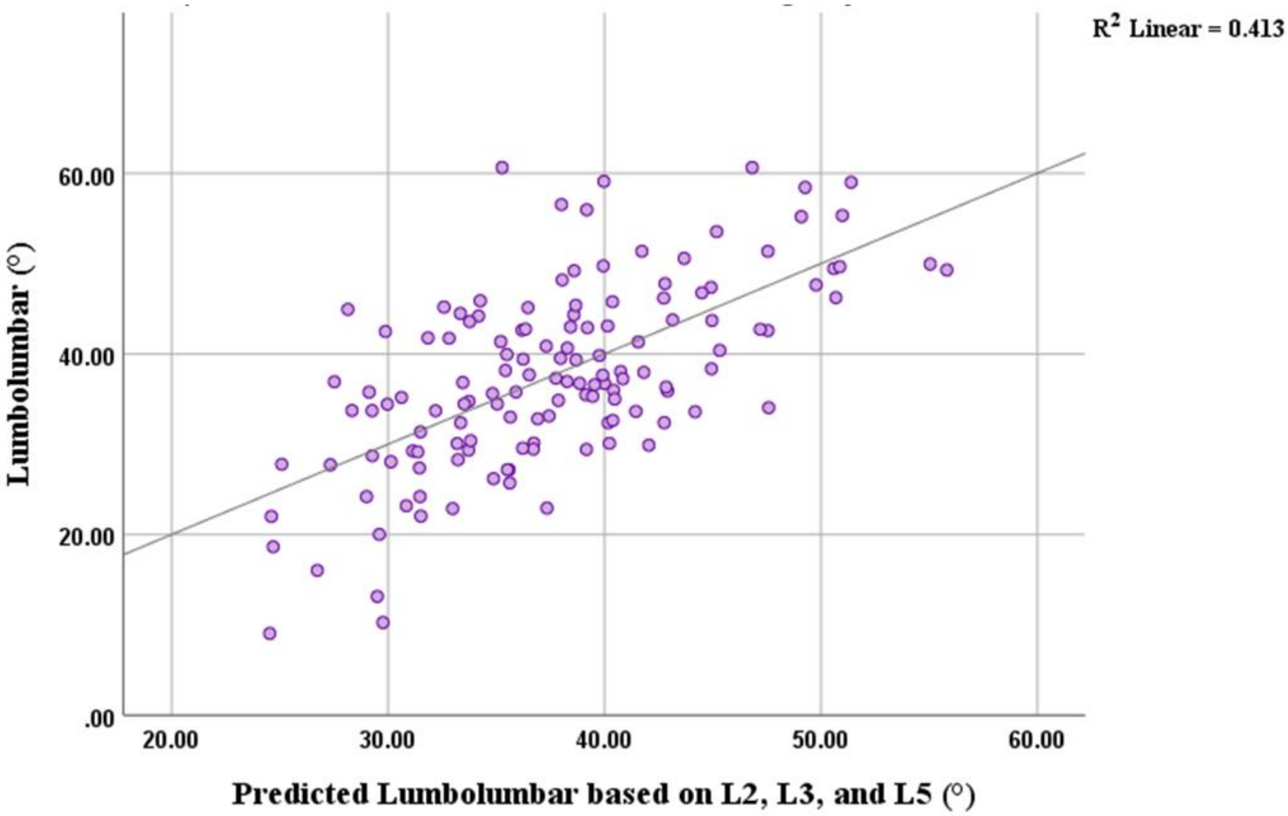
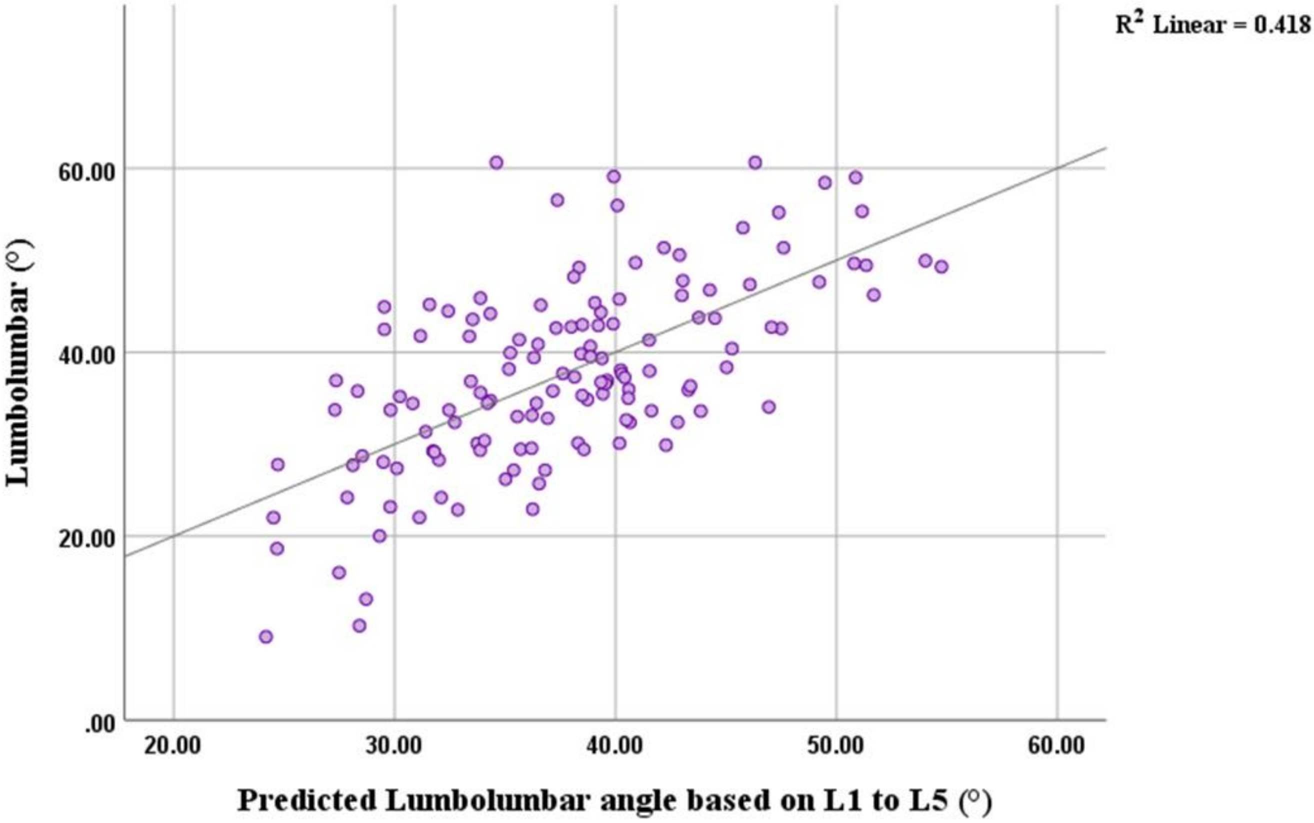


Figure 23.

This scatterplot representing the predicted values of the lumbolumbar angle from a multiple linear regression formula of all the lumbar vertebrae (L1-L5) against the actual values of the lumbolumbar angle from the modern human sample.



The Cobb and lumbolumbar angle of Oberkassel 2, Kebara 2, and StS 14 were predicted based on the linear regression formulas (Table 22). Based on the predicted Cobb and lumbolumbar angle, Oberkassel 2 is expected to have the greatest lordosis out of all the fossils and is followed by StS 14, and Kebara 2 (Table 22). StS 14 has predict values closest to the modern human average (Cobb angle, mean=54.04, lumbolumbar angle, mean =37.66). Kebara 2 has the lowest predicted values (Table 22). The lumbolumbar angle yielded results that were lower than the Cobb angle, which is expected (Table 22).

Table 22:

A series of linear regression formulas based on the contemporary human sample were used to reconstruct lordosis in fossil hominins. Oberkassel 1 was excluded because only the first lumbar vertebra was available, and it does not have a significant association with either the Cobb angle or the lumbolumbar angle. Values that could not be calculated are in grey.

Linear regression equations	**Oberkassel 2**	**Kebara 2**	**StS 14**
Cobb angle = 0.138 **(L1)** +0 .697 **(L2)** + 0.503 **(L3)** + 0.298 **(L4)** + 0.713 **(L5)** + 48.03		45.44	52.18
Cobb angle = 0.699 **(L2)** + 0.791 **(L5)** + 0.644 **(L3)** = 49.12		47.64	53.56
Cobb angle = 1.18 **(L2)** + 57.96	62.40	49.55	53.04
lumbolumbar angle = 0.088 **(L1)** + 0.748 **(L2)** + 0.539 **(L3)** + 0.207 **(L4)** + 0.757 **(L5)** + 33.153		30.88	37.51
lumbolumbar angle = 0.813 **(L2)** + 0.814 **(L5)** + 0.619 **(L3)** + 32.92		31.11	37.24
lumbolumbar angle = 1.29 **(L2)** + 41.935	46.79	32.74	36.56

4. <u>Discussion</u>

The aim of this thesis was to investigate how IVDW, VBW, sex, and age influenced the variability of lumbar lordosis in modern humans alongside how such factors may influence the reconstructed lordosis of fossil hominins. To fully investigate the variability and function of lordosis in the lumbar region, this study included the lordosis and wedging angles from a sample of n=135 modern humans and compared this data with the VBW wedging patterns of fossils StS 14, Kebara 2, Oberkassel 1, and Oberkassel 2. The modern human sample was used as the basis of linear regression formulas depicted in Table 22 which estimated the lordotic curvature of the fossil specimens using only VBW, similar to the methods of Been, Gómez-Olivencia and Kramer (2012).

4.1. Comparing lumbar lordosis in the South African and UNMDID samples

The first hypothesis proposed in this study predicted that lordosis would be the same between the deceased UNMDID sample, and the living South African sample (Edgar et al. 2020). The results revealed that the Cobb angle, lumbolumbar angle, TVBW, and TIVDW were similar between the living and deceased samples (Edgar et al. 2020). The greatest concern over using a cadaveric sample, like the UNMDID (Edgar et al. 2020), stems from the risk that the intervertebral discs, comprised of soft tissue, may have started to decompose prior to the individual being CT scanned (Humzah and Soames, 1988). The results presented in this analysis suggests that the cadavers from the UNMDID were scanned prior to any significant decomposition (Edgar et al. 2020). In other studies, the use of *in-vivo* radiographs is the standard, but the similarity between the deceased and living samples in this study suggests that cadaveric sample can be used in future studies on lordotic curvature (Been et al. 2007;

Whitcome, Shapiro and Lieberman, 2007; Been et al. 2010a.; 2010b.; 2010d; Been, Gómez-Olivencia and Kramer, 2012).

Like TIVDW and TVBW, individual VBW and IVDW were comparable between samples apart from disc L3-L4. Disc L3-L4 was more lordotic in the UNMDID sample than in the South African sample. Since the Cobb angle and TIVDW are not different between these two groups, it seems unlikely that the difference in wedging of the L3-L4 disc could be explained by decomposition. TVBW and individual VBW is similar between the deceased and living samples suggesting that unlike in other studies there is little impact from lifestyle or geographic differences on these variables (Lois-Zlolniski et al. 2019; García-Martínez et al. 2020; Williams et al. 2022). The dorsal and ventral heights of the vertebral bodies and intervertebral discs were higher on average in the deceased sample than the living sample but has not impacted the wedging angles. Considering a previous study has used the VBH and DBH as a measurement of size in humans and fossils, it is possible that the differences in heights are related to a size difference between the samples, especially since they are not sex balanced (Been et al, 2010c).

Recent research on modern humans has compared samples from different geographic and ethnic backgrounds. These studies had information on geographic ancestry (Lois-Zlolniski et al. 2019; García-Martínez et al. 2020) and lifestyle (Williams et al. 2022) which was not available for the South African sample and was not adequately detailed for the UNMDID sample (Edgar et al. 2020). One analysis consisted of a post-industrial sample with individuals of European and African ancestry and a preindustrial sample of individuals with African and South American ancestry the results revealed that pre-industrial and post-industrial samples differed in VBW more than samples based on geographic ancestry

(Williams et al. 2022). This suggests lifestyle differences influence VBW in modern humans while geographic ancestry does not. In contrast, research which used geometric morphometrics to study lordosis also used a sample from South Africa and compared this sample with one of Mediterranean ancestry and found that the South African sample was less lordotic than the Mediterranean one (Zlolniski et al. 2019). It is more likely, in this study's samples that the one intervertebral disc, disc L3-L4, is different because the South African sample is smaller and has a lower ratio of males to females than the UNMDID sample. This study found that males have a slightly more lordotic L3-L4, so the South African sample, with a higher ratio of females, would have a more kyphotic L3-L4 on average relative to the UNMDID sample (Bailey et al. 2016).

The UNMDID has invaluable information on ethnicity, weight, stature, pathology, and socio-economic status (Edgar et al. 2020) which can now be used for further studies on the lumbar region, since it is comparable to an *in-vivo* sample of CT scans. This also could allow for the inclusion of other samples from CT databases, including non-human primates, in future studies on lordosis. The inclusion of cadavers, and scans from CT databases could also be used to increase the statistical power (Biau, Kernéis and Porcher, 2008) of lordosis reconstructions in fossil hominins (Been, Gómez-Olivencia and Kramer, 2012).

4.2. Variability of lordotic curvature within the modern human sample

Both modern human samples were pooled to study the variability of lordotic curvature in the supine position using several different measurements to quantify lordosis including the Cobb angle, lumbolumbar angle, and the TW angle. The lumbar lordosis found amongst modern humans from the current sample was expected to be comparable to the lordotic curvature reported in other studies, especially those conducted in supine posture. The results revealed that the modern human sample had an average Cobb angle that is comparable to other studies in standing (Stagnara et al. 1982; Been et al. 2010d; Been, Gómez-Olivencia and Kramer, 2012) and supine posture (Hansen et al. 2015; Bailey et al. 2016) (Table 23). Some other studies reported a slightly higher mean Cobb angle while standing (Gelb et al. 1995; Vialle et al. 2005; Damasceno et al. 2006; Shymon et al. 2014), but the results from the current study are consistent with the consensus that the average Cobb angle for modern humans is somewhere between 50º to 60º (Table 23). It has been proposed that humans have a 'neutral zone' of lumbar lordosis that is optimal for speed, walking, and avoiding spinal pathologies (Been, Simonovich, and Kalichman, 2019:304). This would be estimated as the middle or mean from the range found in modern humans currently (Table 23) (Been, Simonovich and Kalichman, 2019; Plomp, Been, and Collard, 2022).

Table 23:

Comparing the averages of the Cobb angle from the combined modern human sample to other studies.

Source	**Method**	**Mean ± SD (º)**	**Range (º)**
Current	CT scans, supine posture	54.04 ± 10.82	22.9 to 80.49
Been et al. (2010c):1016	Radiograph, standing	51.3 ± 10.7	N/A
Damasceno et al. (2006):194	Radiograph, standing	60.9 ± 10.65	33 to 89
Hansen et al. (2015):1693 Compares L/A of control and patients with back pain, only the results from the control is presented.	MRI, standing	58.0 ± 10.3	N/A
	MRI, supine	52.0 ± 9.5	N/A
Jackson and McManus (1994):1613. Volunteers and patients with back pain presented.	Radiograph, standing	Volunteers: 60.9 ± N/A	31 to 88
		Patients: 56.3 ± N/A	24 to 84
Vialle et al. 2005:262	Radiograph, standing	60.2 ± 10.3	30 to 89

The range for the Cobb angle presented in this study falls outside of the typical 30º to 75º range identified for a healthy lordotic curvature while standing (Been et al. 2010d: E1014). A very kyphotic or lordotic lumbar region can hinder locomotion to some degree, but these results are also dependent on the lumbar region's relationship to the rest of the vertebral column and pelvis (Bakouny et al. 2017; Been et al. 2017; Been and Bailey, 2019). It is more likely that the ranges for the Cobb angle found in this study stem from measuring curvature of individuals in supine posture instead of standing. The Cobb angle measured in supine is lower than the Cobb angle measured in standing, but the range of the Cobb angle in supine has not been officially reported (Meakin et al. 2009; Hansen et al. 2015; Bailey et al. 2016). It is currently unclear if there is a statistically significant difference between the Cobb angle if it is measured in the supine posture or standing posture, so it is important to acknowledge the posture used in studies on lordotic curvature (Meakin et al. 2009; Bailey et al. 2016). Overall, the range seems comparable to most of the studies reported in the table above, if not a bit broader, and is likely not related to a pathological condition.

It was hypothesised that the lumbolumbar angle would share a stronger correlation with TVBW than the correlation shared between TVBW and the Cobb angle. Like in other studies, the lumbolumbar angle is lower than the Cobb angle (Table 24) (Vialle et al. 2005; Damasceno et al. 2006). The mean lumbolumbar angle for this sample was lower than that of other studies (Table 24) (Cheng et al. 1998; Vialle et al, 2005; Damasceno et al. 2006) which probably relates to the posture in which the lumbolumbar angle was measured for each study (Hansen et al. 2015; Bailey et al. 2016). This study found that the lumbolumbar angle did not perform better than the Cobb angle with correlation coefficients between TW and TIVDW. However, as expected, the lumbolumbar angle did have a moderate relationship with the

TVBW (r =.627) which was stronger than the correlation between the Cobb angle and TVBW (r =.557). Therefore, reconstructing the lordosis angle in fossil hominins based on the lumbolumbar angle and TVBW could have a greater accuracy than reconstructions based on the Cobb angle.

Table 24:

Comparison of the lumbolumbar angle with other studies. Current study is in red text.

Source	**Method**	**Mean ± SD**	**Range**
Current	CT, supine	37.66 ± 10.17	9.05 to 60.63
Damasceno et al. (2006:194	Radiograph, standing	45.1 ± 10.8	15.0 to 78.0
Cheng et al. (1998):381	Radiograph, standing, male sample	41.4 ± 12.3	N/A
	Radiograph standing, female sample	42.5 ± 11.17	N/A
Vialle et al. (2005):262	Radiograph, standing	43 ± 11.2	13.6 to 69

4.3. Vertebral bodies or intervertebral discs: Their variability and functional roles within the lumbar region.

One of the primary goals of this project was to study the different relationships the lumbar vertebrae and discs have with lordosis. It was hypothesised that IVDW and VBW would have a similar impact on the variability found within the Cobb angle, but the IVDW would contribute a greater proportion of wedging to lordotic curvature. The results of this study show that TIVDW makes up a large proportion of the lordotic curvature but, only explains 12.4% of the variability found within the sample. In contrast, TVBW explains 32.8% of the variability within the Cobb angle and 41.3% of the variability found within the lumbolumbar angle. These results contradict previous expectations about the correlation TVBW and

TIVDW share with the Cobb angle which suggested they contributed equally to the variability of lordosis found in humans (Been et al. 2010c). It is widely known that the vertebral bodies play a significant role in variability even though they make up a smaller proportion of the curvature (Jackson and McManus, 1994; Damasceno et al. 2006; Been et al. 2010c; Kalichman et al. 2011). This suggests that the vertebral bodies and intervertebral discs each play distinctive functional roles in lordotic curvature.

The human lumbar region has developed into a curvature to counteract the compressive loading that the vertebral column must bear to support orthograde posture (Farfan, 1995). The discs and bodies are both subjected to these loads, but the intervertebral discs can only withstand compressive loading based on their morphology of a solid perimeter, the anulus fibrosus, and soft interior, the nucleus pulpous (Adams and Hutton, 1985; Humzah and Soames, 1988; Farfan, 1995). The lumbar vertebrae must also contend with shearing forces in the zygopophyses and may be under less rigid constraints to conform to a uniform wedging pattern (Farfan, 1995). In contrast, one of the intervertebral discs primary functions is to act as shock absorbers during locomotion (Been and Bailey, 2019). If the intervertebral discs are subjected to shearing forces, which they have not adapted to, this could lead to intervertebral disc herniation (Plomp, Been, and Collard, 2022). Disc herniation is a pathology where the nucleus pulpous permeates outside the exterior of the intervertebral disc and has been associated with increased kyphosis in the lumbar region (Plomp, Been, and Collard, 2022). This showcases the evolutionary pressure on the intervertebral discs to maintain their wedging angle relative to the lumbar vertebrae and could serve as a functional explanation of why variation is lower in TIVDW than TVBW.

This study expected the wedging pattern of the vertebra and intervertebral discs to increase in lordosis from the first lumbar vertebra to the last intervertebral disc. The wedging pattern found in this study shows that each vertebra and disc increases in dorsal wedging from L1 to S1 which is similar to many other studies on wedging in the lumbar region (Stagnara, 1982; Jackson and McManus,1994; Gelb et al. 1995; Cheng et al. 1998; Vialle et al. 2005; Damasceno et al. 2006; Been et al. 2010a; Bailey et al. 2016; García-Martínez et al, 2020; Williams et al. 2022). As expected, the intervertebral disc was only neutral to dorsally wedged, and possessed a higher degree of lordotic wedging in all the intervertebral discs relative to the vertebral bodies (Jackson and McManus, 1994; Damasceno et al. 2006; Bailey et al. 2016). The difference in mean wedging and variability between each vertebra is significant, affirming that the lumbar region has a distinctive wedging pattern that is consistent regardless of the lordotic angle.

This study expected to find a correlation between the lumbar vertebrae and Cobb angle that was strongest in the center of the curvature, but a higher rate of lordosis in between L4-S1 similar to the predictions of Jackson and McManus (1994). This study found that vertebrae and intervertebral disc in the center of the curvature had a significant relationship with the Cobb angle than the cranial and caudal vertebrae and discs. This continues the trend of the central segments showing a stronger correlation with the Cobb angle, then the primary and ultimate segments (Been et al. 2010d). In line with this study's predictions, the highest degree of wedging can be found in the L5 and the last intervertebral disc like previous study's results (Jackson and McManus, 1994; Damasceno et al., 2006; Been et al., 2010d). The lower elements of the lordotic curvature may face greater functional pressures from bipedalism, so they are the most lordotically wedged, but the least variable relative to the central vertebrae and intervertebral discs (Farfan, 1995; Shymon, 2014).

4.4. Functional explanations for the wedging pattern and variability found in the lumbar region

The presence of the lordotic curvature, as opposed to a straight spine, provides enough flexibility to the spine to maintain an upright posture (Farfan et al. 1995; Been and Bailey, 2019; Plomp, Been and Collard, 2022). A less flexible spine is more stable, but also influence gait (Bakouny et al., 2017) leads to a decreased walking speed and shorter strides (Been and Bailey et al. 2019). The tradeoff between stability and flexibility in the lumbar region may have led to the kyphotic wedging found in the cranial elements, and the dorsal wedging displayed in the caudal elements. The highest proportions of dorsal wedging found in the lumbar region is in the caudal vertebrae and intervertebral discs (Jackson and McManus, 1994, Damasceno et al. 2006, Bailey et al. 2016). A study focused on compressive loading of the lumbar spine, found that the last intervertebral disc was the most impacted by the addition of a backpack to the spine (Shymon et al. 2014). This suggests that disc L5-S1 is more sensitive to compressive loads that other areas of the lumbar region. As the most lordotically wedged element of the vertebral column (Been and Bailey, 2019) and the disc most influenced by gravity (Farfan, 1995), the last intervertebral disc has adapted to withstand the greatest compressive loads from locomotion.

The concept that variability occurs in morphological features under less functional constraints was explored in another study on the vertebral column (Shapiro and Kemp, 2019). The study focused on vertebral body morphology in catarrhines and found less variability in primates like cercopithecoids and humans due to the greater functional demands their locomotion as terrestrial quadrupeds, and bipeds respectively, has on the skeleton (Shapiro and Kemp, 2019). This could also be the case for lordotic wedging. The L5 in humans and in experimental animal models is always lordotic and appears to be a functional response to bipedalism in other mammals (Yamada et al. 1960, Nathan et al. 1964; Cassidy, 1988; Prueschoft, Hayama, and Hunter, 1998; Russo, Marsh, and Forrester, 2020). The high variability in the center of the lumbar region indicates that the central vertebrae would be more important in estimating lordosis than the caudal elements, but that these vertebrae also have a less significant role in the curvatures overall functional relationship with bipedalism.

4.5. The negative relationship between the wedging of lumbar vertebrae and intervertebral discs

The negative relationship between the TIVDW and TVBW has been previously mentioned by two studies (Been et al. 2010d; Tao et al., 2021), but has yet to be explored in detail. This study predicted that there would be a negative relationship between VBW and IVDW and that the vertebra and disc closest in proximity would share a stronger relationship. As expected, the correlation found between IVDW and VBW is consistently negative. This falls inline with the studies that tested TIVDW and TVBW (Been et al. 2010d; Tao et al., 2021). The results unveiled that the strongest negative correlations between IVDW and VBW is in the center of the lordotic curvature. In line with previous predictions, there is a stronger relationship with the vertebral body and intervertebral discs near one another. These results are like those reported on vertebral body wedging which suggests higher variability in the center of the lumbar region (Been et al. 2010d). This means that, while the correlation between IVDW and VBW is negative, it follows a similar pattern to the relationship found within individual VBW and IVDW. The difference in wedging between individual vertebrae and intervertebral discs may have an impact on the composition and variability of the whole lordotic curvature.

Apart from the positive correlation both VBW and IVDW share with the Cobb angle, the negative relationship between VBW and IVDW could help explain why lordosis varies widely in modern humans (Been et al. 2010d; Tao et al. 2021). This phenomenon has been found in the lumbar (Been et al. 2010d) and cervical regions (Tao et al. 2021) of the vertebrae and may occur throughout the whole vertebral column or occur specifically when there is a lordosis. One explanation for the correlation between the intervertebral discs and vertebral bodies is that the vertebral column has adapted either the VBW or IVDW to compensate for an inadequate wedging patern (Barrey et al. 2013; Been and Bailey, 2019). If this is true, adjusting the wedging of the VBW or IVDW curtails the possibility of the vertebral column overloading and developing spinal pathologies (Barrey et al. 2013; Been and Bailey, 2019). The relationship between the intervertebral discs and vertebral bodies may impacts the variability found within the lordotic curvature, but this factor would not be visible by analyzing the two elements separately (Been et al. 2010d) and could affect the accuracy of lordosis reconstructions in fossil material.

4.6. Sexual dimorphism in the lumbar region

Sexual dimorphism in the lumbar region has been detected in many modern human samples (Vialle et al. 2005; Damasceno et al. 2006; Masharawi et al. 2008; Bailey et al. 2016; but see Jackson and McManus, 1994), and explains some of the variability found in lordotic curvature, which, in turn, could impact fossil reconstructions. This study predicted that lordosis, IVDW, and VBW would vary by sex. In contrast, the results revealed that there was no difference found in the Cobb or lumbolumbar angles of males and females in the modern human sample. Moreover, the South African sample did not show any statistically significant difference between VBW or IVDW in the sexes. However, the UNMDID sample (Edgar et al., 2020) does show signs of sexual dimorphism with females having a higher TVBW, and males a greater TIVDW.

The dimorphism found within the UNMDID sample can be dissected further into differences in wedging on specific vertebral bodies and intervertebral discs. For instance, relative to males, females display greater lordotic wedging on the L3, L4, and L5. These results were comparable to Whitcome, Shapiro and Lieberman (2007) who found a similar pattern of VBW in females. Males from this sample have more lordotic intervertebral discs on average. This is statistically significant from disc L1-L2 and L3-L4. Increased lordotic IVDW in males relative to females has only been reported by a few studies (Damasceno et al. 2006; Bailey et al. 2016) and is likely influenced by posture. To clarify, a previous study comparing lordosis by posture and sex found that males had greater lordotic wedging on their intervertebral disc than females while in the supine position, but not standing (Bailey et al. 2016). In many studies where individuals were evaluated from a standing posture, females had a greater lordosis than males, but when placed in supine, the increased IVDW in males lead to similar Cobb angle between the sexes (Damasceno et al. 2006; Whitcome, Shapiro and Lieberman, 2007; Been et al. 2010d; Bailey et al. 2016). When in supine, males appear to offset their more kyphotic vertebrae with an increased lordosis in their intervertebral discs (Bailey et al. 2016). This is likely why there is no difference in the Cobb or lumbolumbar angle of males and females in the current study.

The leading evolutionary explanation for sexual dimorphism in lumbar lordosis is pregnancy (Whitecome, Shapiro and Lieberman, 2007; Masharawi et al. 2008; Hay et al. 2015; Bailey et al. 2016). When a female becomes pregnant there is a greater need to extend the lumbar region to counteract the added ventral force the fetus adds to the center of mass (Whitcome, Shapiro and Lieberman, 2007). This implies that most of the sexual dimorphism found in the lumbar region is associated with the different evolutionary constraints place on the female torso to support pregnancy while supporting upright posture (Whitcome, Shapiro and Lieberman, 2007; Masharawi et al. 2008; Hay et al. 2015). Bailey et al. (2016) have mentioned an alternative explanation which suggests that dimorphism in vertebral body wedging may be a spandrel, side effect, from the sexually dimorphic sacral and pelvic morphology found in humans. Either suggestions implies that obstetric constraints either directly or indirectly lead to increased VBW in females relative to males.

4.7. Lumbar lordosis and wedging in the vertebral column while aging

As mentioned previously by using the UNMDID, this project could access detailed demographic information including the age at death of the individuals in the sample. Individuals aged 25 to 50 were selected to see how lordosis and wedging varied by age. As hypothesized, this age range did not reveal a statistically significant correlation with lumbar lordosis in this sample. This aligns with many other studies on lordosis and aging in the vertebral column and refutes the idea that spinal pathologies from aging like disc thinning leads to a straighter lumbar region (Gelb et al. 1995; Vialle; 2005; Damasceno et al. 2006; Been et al. 2010d.; Kalichman et al. 2011; Hansen et al. 2015; Williams et al. 2022). This could change if a wider age span was used (Gelb et al. 1995), but it appears that when studying healthy adults, age does not affect lordotic curvature.

This implies that adult fossils within this age range can be included in lordosis reconstructions. For instance, there are many Neanderthal fossils that are estimated to span this age range, like Kebara 2, estimated at 20-30 years old, Shanidar 3 estimated at 35-50 years old, and the La Chappelle-aux-Saints specimen estimated to be over 40 years of age (Been, Gómez-Olivencia and Kramer, 2012). The lack of variability in lordotic curvature in the human sample based on age coupled with evidence showing curvature forms after the onset of walking (Abitbol, 1987; Martelli, 2019) implies that younger fossil specimens like StS 14 (Broom and Robinson, 1947; Thackeray, Gommery, and Braga et al. 2002) and KNM-WT 15000 (Haeusler, Schiess, and Boeni, 2011) can serve as safe examples of their species in current and future studies on lumbar lordosis reconstruction (Been, Gómez-Olivencia and Kramer, 2012).

4.8. Lordosis in fossil hominins

Another aim of this project was to evaluate some of the current methods used to reconstruct lordosis in hominins based on the morphology of the lumbar vertebrae (See Appendix0b for images of the fossils use in this study). On method used was a comparison of the wedging patterns found in the preserved vertebrae of the fossils with the wedging pattern of modern humans (Been et al. 2010a; Been, Gómez-Olivencia and Kramer, 2012; Williams et al. 2013; Williams et al., 2018; García-Martínez et al. 2020; Williams et al. 2021; 2022) The other method follows Been, Gómez-Olivencia, and Kramer (2012) this study created linear regression formulas to predict lordosis. Both the lumbolumbar angle, and the Cobb angle had three formulas each. The results from this study revealed that the L2 had the strongest correlation with lordosis of any vertebra, so one formula was based on the VBW of the L2 alone. The other two formulas for the Cobb and lumbolumbar angle were likely more accurate. The first predicted each angle from all five of the vertebrae, and the other predicted the angles based on a stepwise linear regression which selected the L2, L3, and L5 for both formulas. This suggests that the L2, L3, and L5 impact the variability found in lordotic curvature the most.

4.9. Lordosis in fossil Homo

Two fossil *H. sapiens* were included in the analysis, Oberkassel 1 and Oberkassel 2. Only the L1 and L2 were adequately preserved for the analysis of this study. Oberkassel 1 is male and Oberkassel 2 is female (Nobis, 1986). As fossil *H. sapiens* these specimens were hypothesised to have VBW that is the very similar to the modern human sample. The L1 of Oberkassel 1 is kyphotic which is the expected condition of the L1 in humans, but the L1 of Oberkassel 2 is very lordotic (Table 25). This presented some issues when analyzing the fossil humans.

Compared to contemporary modern humans, a lordotically wedged L1 is a peculiar condition, which likely cannot be contributed to sexual dimorphism. The VBW of L1 was far more lordotic than any of the females in the modern human sample (Nobis, 1986). In addition, sexual dimorphism in the lumbar vertebrae has only been identified from L3 to L5, but not the L1 (Whitcome, Shapiro and Lieberman, 2007). This might suggest that contemporary humans have more kyphotic wedging on the L1 than fossil *H. sapiens,* but other Fossil *H. sapiens* like La Carihuela (García-Martínez et al. 2020), Cro Magnon 1, and Cro Magnon 2 all have kyphotic wedging on their L1, so it is unlikely this is the case (Been, Gómez-Olivencia and Kramer, 2012). Oberkassel 2 may have a pathological condition because hyper lordosis on vertebra has been linked with conditions like spondylosis, Scheuermann’s kyphosis, and osteoarthritis (Been, Simonovich and Kalichman, 2019).

Oberkassel 1 was excluded from reconstructions because only the L1 was present. Oberkassel 2 only has an L1 and L2, so it could only be reconstructed once. Oberkassel 2 was predicted to have a reconstructed lordosis comparable to the modern human average. In contrast, the reconstructed Cobb angle presented in this study is 62.4° and the reconstructed lumbolumbar angle is 46.79°. Both predicted measurements are higher than the modern human average (Table 26). This may be because the reconstruction is only based on the L2. A reconstruction of Cro-Magnon 3 has a comparable predicted lordosis of '64°' while Cro-Magnon 1 has a predicted lordosis of '46°' (Been, Gómez-Olivencia and Kramer, 2012:71). This is indicative of the variability that is found in contemporary humans and might suggest that fossil humans have a similar range of lordotic curvature that has yet to be depicted from the available fossils.

4.10. Vertebral body wedging in Neanderthals

The lumbar lordosis of Kebara 2 was included in this project, to participate in the debate surrounding the shape of the Neanderthal lumbar region (Been et al. 2010a; Been, Gómez-Olivencia and Kramer, 2012, García-Martínez et al. 2020; Williams et al. 2022). Since Neanderthals are bipeds that share a close evolutionary relationship with humans, Kebara 2 was hypothesised to have a predicted lordosis and VBW that is within the range of modern humans. The results revealed that while Kebara 2 has a wedging pattern that is more kyphotic than the other specimens included in this study, their predicted Cobb angle and lumbolumbar angle is within the range of the contemporary human sample (Table 25). The reconstructed lordosis of Kebara 2 is much higher than the one described in previous literature but is lower than the average within the modern human sample (Been, Gómez-Olivencia and Kramer, 2012) (Table 26). The Cobb angle of Kebara 2 in the current study is estimated to fall between 45.44° and 49.55°, while the lumbolumbar is estimated at 30.88 °and 37.74°.

As predicted, Kebara 2 does fit within the range of individual VBW for the combined modern human sample. The L5 is the only vertebra that is lordotically wedged in Kebara 2, but Kebara 2 still likely has a lordotic curvature that is compatible with bipedalism. This wedging pattern falls in line with the reported wedging pattern of Neanderthals, with kyphotic wedging between the L1 to L4 and a lordotic L5 (Table 26) (Been et al. 2010a; Been, Gómez-Olivencia and Kramer, 2012, García-Martínez et al. 2020; Williams et al. 2022). It has been argued that Neanderthals have a hyper lordotic L5 to compensate for a slight lordosis or a hypolordotic lumbar region (Williams et al. 2022). The issue with the concept of a hyperlordotic L5 amongst Neanderthals is that within this study Kebara 2 does not have an L5 that is hyper lordotically wedged relative to the contemporary sample. It is also unclear how hyperlordosis in the L5 is defined. Another theory suggests that Neanderthals have a wedging pattern comparable to modern humans, but that the wedging they experience is more extreme (García-Martínez et al. 2020). This likely does not explain the wedging for Kebara 2 reported in this study because, the VBW of Kebara 2 fell within the modern human range with only one exception, the L3. The lordosis of Neanderthals may be slightly lower than humans on average, but it does not seem to be enough to impact their locomotion significantly based on the analysis in this study.

As mentioned previously, a straighter back has more stability than a curved back, but can also lead to limitations biomechanically, which has led to a few explanations about why Neanderthals have ahypolordotic lumbar region (Farfan et al. 1995; Been and Bailey, 2019; Plomp, Been and Collard, 2022). One theory suggests that the more robust nature of Neanderthals relative to fossil *H. sapiens* required a straighter and therefore more stable lumbar spine to avoid developing spinal pathologies while walking as a biped (Weber and

Pusch, 2008, Sparrey et al. 2014; Been et al. 2017). Another explanation suggests, the Neanderthal wedging pattern may also be an adaptation to lifting heavier loads because a straighter lumbar region places less stress on the intervertebral discs during heavy lifting (Gómez-Olivencia et al. 2017). A straighter spine while lifting heavy loads also relieves the intervertebral discs from bearing as much compressive forces (Adams and Hutton, 1985). This would suggest that Neanderthals were lifting heavier loads than modern humans and sacrificed the shock absorption beneficial from lordotic wedging for the stability of a straighter back (Gómez-Olivencia et al. 2017).

Another partial explanation for the Neanderthals hypolordotic lumbar region is sexual dimorphism. All Neanderthals with a complete lumbar region have been identified as male which implies that the vertebral body of female Neanderthals may appear quite different (Haeusler et al. 2019). This thesis predicted that Neanderthals would have VBW that was more aligned with the VBW of males within the Modern human sample, than females. This study found that the TVBW of Kebara 2 was closer to the average male from the UNMDID sample (Edgar et al., 2020), than the average female. The similarity between the Neanderthal specimens and human males has been explored previously (Williams et al. 2022) and suggests sexual dimorphism may also influence the Neanderthal's lordotic curvature. These results are difficult to interpret because there are no female Neanderthal remains with a preserved lumbar region for comparison but could provide a partial explanation for the wedging pattern currently found in Neanderthal fossils (Haeusler et al. 2019).

4.11. Lumbar lordosis in Australopithecus africanus

StS 14 was included in this project to study the posture of earlier hominins and is a representative for australopiths evaluated in other studies. As the most distant species evolutionarily, StS 14 was expected to have a predicted lordosis and VBW that was the most different from the contemporary human sample. On the contrary, this study found that StS 14 has a TVBW angle that is very close to the average found in modern humans (Table 25). The Cobb angle reported for StS 14 is estimated somewhere between 52.18° and 53.04°, and the lumbolumbar angle is between 36.56° and 37.51° both are very close to the contemporary human sample (Table 26). The one distinctive aspect of StS 14 is the presence of six lumbar vertebrae instead of five (Haeusler, Martelli, and Boeni, 2002), which if included would make the summed wedging angle much more kyphotic, but still within the modern human range (Table 20).

Previous studies that evaluated the lumbar region of StS 14 compare the VBW from PS1 to PS5 and found that StS 14 had wedging similar to modern humans (Been, Gómez-Olivencia and Kramer, 2012; Williams et al. 2013; Williams et al., 2018; Williams et al., 2021). The previously predicted lordosis of StS-14 is within the range of modern humans albeit, those values are lower than the value reported in this study (Table 26) (Been, Gómez-Olivencia and Kramer, 2012). Other australopith specimens like StW 431 and Sk 3981 all appear to have VBW within the range of modern humans (Been, Gómez-Olivencia and Kramer, 2012; Williams et al. 2013; Williams et al., 2018; Williams et al., 2021). The difference in reconstructions between the analysis from this project and Been et al. (2012) is probably related to the difference in regression formulas used between the two.

Table 25:

A comparison of VBW in fossil hominins between studies. The current study in in red text.

Fossil	Study	PS5	PS4	PS3	PS2	PS1
Kebara 2	Current	-5.73	-7.13	-8.73	-2.23	11.54
	Been, Gómez-Olivencia, and Kramer (2012:67)	-7	-7	-7	-2	9
	García-Martínez et al. (2020:227)	-6.58	-8.56	-10.6	-1.41	11
	Williams et al. 2021:12	N/A	-8.1	-6.9	-4.5	10.6
StS 14	Current	-8.46	-4.17	-2.67	4.53	11.66
	Been, Gómez-Olivencia, and Kramer (2012:67)	-3	-1	0	3	4
	Williams et al. (2021:12)	N/A	-2.3	-1.7	0.9	6.9
	Whitcome, Shapiro, and Lieberman (2007:1077)	-2.0	0.7	0.9	3.7	6
Oberkassel 1	Current	-11.52	3.76	N/A	N/A	N/A
Oberkassel 2	Current	2.28	N/A	N/A	N/A	N/A

Table 26:

A comparison of reconstructed Cobb angle based on VBW in fossil hominins between studies.

Study	Method	Kebara 2 (º)	StS 14(º)
Current	Multiple linear regression model based on VBW in modern humans	45.99	52.18
Been, Gómez-Olivencia, and Kramer (2012:71)	Multiple linear regression model based on IAP of humans	26	44
	Multiple linear regression model based on IAP of primates including humans.	25	38

4.12. Explanations of the wedging patterns found in fossil hominins

The dorsal wedging of the caudal vertebral bodies is a proven functional response to bipedalism that has been detected in experiments on other animals (Nathan et al. 1964; Prueschoft, Hayama, and Hunter, 1998; Yamada et al. 1960; Russo, Marsh, and Forrester, 2020). Modern humans also develop a lordotic curvature as a functional response to walking early in life (Abitbol, 1987; Martelli et al. 2019). This suggests that any individual that engages in bipedality would have some lumbar lordosis and dorsal wedging on the caudal lumbar vertebrae. The different types of VBW patterns found in the hominin vertebral column may relate to the different types of spino-pelvic alignments found in hominins all of which provide an adequate posture to sustain the biomechanical pressures of bipedalism (Been et al. 2017).

Been et al. (2017) has outlined three spino-pelvic alignments typically found in hominins. *Homo* often possesses a 'sinusoidal pelvic alignment' with an evenly developed lumbar lordosis, and thoracic kyphosis (Been et al. 2017: 907). This posture is hypothesised to be the best for shock absorption during locomotion but is less stable than the other alignments referenced below. Neanderthals have been described as having a 'straight spino-pelvic alignment' (Been et al. 2017:907) which provides stability for heavier loads like previous theories on the Neanderthal lumbar region (Weber and Pusch, 2008; Sparrey et al. 2014; Gómez-Olivencia et al. 2017). Australopiths like StS 14 are described with a 'compound spino-pelvic alignment' with a developed lumbar lordosis like sinusoidal alignment, but a less curved thoracic and cervical spine (Been et al. 2017:907). This suggests that *Au. africanus* had mobility in its lumbar region to support an upright walking posture, but a more stable upper body, possibly to increase the stability of the upper body while arboreal (Been et al. 2017). This provides a clear biomechanical explanation for the wedging patterns and lordosis reconstructions reported for the hominins included in the current study.

If this hypothesis on spino-pelvic alignment is accurate, this would suggest that modern humans and fossils would have developed a lordotic curvature that compensates for shortcomings that may exist in other parts of the skeleton (Barry et al. 2013). Been and colleague's (2017) theory coincides with studies that have found a significant correlation between pelvic incidence, cervical lordosis, thoracic kyphosis, and lumbar lordosis (Duval-Beaupère, Schmidt, and Cosson, 1992; Tardieu, Hasegawa, and Haeusler, 2017).

4.13. Success of lordosis reconstructions in fossils and implications for locomotion

This study has reconstructed lordosis based on the vertebral body wedging angles found in fossil hominins. Reconstructions are limited by the fact that vertebral bodies only explain about 32 to 41% of the variability found in lordotic curvature depending on how lordosis is measured. Been et al. (2010d) are the only researchers who have reconstructed lordotic curvature prior to this analysis. They reconstructed lordosis based on IAP and TVBW (Been et al. 2010a; Been, Gómez-Olivencia, and Kramer, 2012). The IAP has been said to explain up to 89% percent of the variability found in lumbar lordosis (Cobb method) based on data from humans and other primates, however when this formula is based on only a human sample this value descends to 62% (Been et al., 2010a; Been, Gómez-Olivencia, and Kramer, 2012). They suggest that the IAP is a better way of calculating the Cobb angle than VBW. This study also finds that VBW explains less variability in the Cobb angle than what is reported for IAP and that the IAP is likely a more accurate method of lordosis reconstruction (Been et al. 2010a; Been, Gómez-Olivencia and Kramer, 2012).

Nevertheless, the accuracy of predictions based on the IAP drops when basing calculations solely on a human sample. This implies that the variability found in primates' locomotion is likely driving the variability found in IAP calculations (Been et al. 2010a; Been, Gómez-Olivencia, and Kramer, 2012). The use of primates in reconstructions in fossil hominins could influence the estimation of lordotic curvature because they are not as close in morphology as modern humans. That is why the reconstructions in this study are based on a sample of modern humans. To increase the accuracy of the relationship between lordosis and vertebral body wedging, this study included reconstructions based on the lumbolumbar angle alongside the Cobb angle. The reason the lumbolumbar angle was selected was because excluding the last intervertebral disc excluded some of the variability that hinders lordosis reconstructions based on the Cobb angle. This could suggest an increase of accuracy in linear regression formulas based on IAP when using modern humans, if they were based on predicting the lumbolumbar angle rather than the Cobb angle (Been et al. 2010a; Been, Gómez-Olivencia and Kramer, 2012).

While reconstructing the lumbar lordosis based on different measurements has revealed interesting results, basing lordosis reconstructions on vertebral morphology, makes large assumptions about intervertebral disc morphology. In hominins (Been, Gómez-Olivencia and Kramer, 2012; Williams et al. 2013; García-Martínez, 2020) and experimental studies on rodents and primates (Yamada et al. 1960, Nathan et al. 1964; Cassidy, 1988; Prueschoft, Hayama, and Hunter, 1998; Russo, Marsh, and Forrester, 2020) trained to walk bipedally, there is a consistent presence of dorsal wedging on the last lumbar vertebrae. This illustrates that dorsal wedging on the caudal lumbar vertebrae is consistent evidence of bipedalism. By attempting to reconstruct lordotic curvature, paleoanthropologists are attempting to understand more complex details about hominin locomotion, like spino-pelvic alignment

(Been et al. 2017), which may be difficult to investigate without the presence of soft tissue. This becomes even more challenging when the negative relationship between IVDW and VBW is considered, because it is impossible to know how VBW and IVDW correlated in fossil specimens. Considering the amount of variable involved and the wide range of lordosis present in modern humans it is hard to suggest that reconstructions on fossils hominins would reflect the true range of curvature and postural habits of whole hominin species.

4.14. Study limitations

This study faced several limitations that could impact the results presented. The first stems from taking the measurements of lordosis from CT scans of individuals who were not scanned for the purpose of this project (Edgar et al. 2020). Often, the vertebral columns were not straight due to the placing of the individual on the table during scanning which made it difficult to get a consistent oblique slice to measure for the Cobb angle that was in the center of both the L1 and last intervertebral disc (Edgar et al. 2020). This led to a discrepancy between the TW angle and the Cobb angle. Further, the CT scans from this study were all recorded in the supine posture, while the standard for lordosis reconstructions uses lateral radiographs in standing posture (Been et al. 2007; Been et al. 2010a; 2010b; 2010d; Been Gómez-Olivencia, and Kramer, 2012). This means that the fossil reconstructions are indictive of lordotic curvature while in the supine posture and could be slightly different when individuals are standing (Meakin et al. 2009; Hansen et al. 2015; Bailey et al. 2016).

Further, some of the results from the contemporary human sample were not applicable to the South African sample because the study was limited by the available information and small sample size (N=27). Without evidence of age, the South African sample was excluded from the age analysis and could have yielded results more like other studies that reported a weak positive correlation between lumbar lordosis and age with larger samples of broader age ranges (Gelb et al. 1995; Vialle; 2005; Damasceno et al. 2006; Been et al. 2010d.; Kalichman et al. 2011; Hansen et al. 2015; Williams et al. 2022). It's also probable that the South African sample would yield a similar result to the UNMDID sample for evaluations on sexual dimorphism, but this cannot be proved without a larger number of individuals.

This study has limited access to fossils with well-preserved spines and lacked a representative of a complete lower back in fossil humans for comparison in this study to others (Been, Gómez-Olivencia and Kramer, 2012; García-Martínez et al. 2020). With access to a more complete human spine, the lordosis calculations of fossil humans would likely have been more comparable to the reconstructions of Cro-Magnon 1 and 3 (Been, Gómez-Olivencia and Kramer, 2012).

5. Conclusion

Ultimately, this study yielded similar results to other studies on variability and function of the vertebral column in modern humans. It introduced the use of CT databases, like the UNMDID (Edgar et al. 2020), to lordosis reconstruction, in hopes of encouraging future analysis using databases that can offer larger sample sizes, and important demographic information on the sample. VBW was found to play a greater role in lordotic curvature's variability than IVDW, but the relationship between VBW, IVDW, and other factors like sex and lifestyle, all play a role in the lordotic curvatures shape of modern humans. Since modern humans have a wide range of lordotic curvatures, it seems likely that vertebral body wedging patterns provide the most concrete information on the posture of fossil hominins, with dorsal wedging on the last lumbar vertebrae being the most consistent evidence of bipedalism found in fossils (Been et al., 2010a; Been, Gómez-Olivencia and Kramer, 2012; Williams et al. 2013; Williams et al., 2018; García-Martínez, 2020; Williams et al., 2021; Williams et al., 2022) and experimental studies (Yamada et al. 1960, Nathan et al. 1964; Cassidy, 1988; Prueschoft, Hayama, and Hunter, 1998; Russo, Marsh, and Forrester, 2020). Lordosis reconstructions based on vertebral morphology may benefit from the use of the lumbolumbar angle over the Cobb angle because it avoids an extra assumption about the angle of the last intervertebral disc (Been et al., 2010a; Been, Gómez-Olivencia and Kramer, 2012). When it comes to the debate on the lordotic curvature of Neanderthals they appear to have a distinctive wedging pattern, possibly due to difference spinopelvic alignments between them and modern humans (Been et al. 2017), but they still have a lordotic curvature characteristic of a habitual biped like contemporary humans.

6. *Works Cited*

Abitbol, M. M. (1987). Evolution of the lumbosacral angle, *American Journal of Biological Anthropology*, 72 (3), 361-372.

Adams, M. A. and Hutton, W.C. (1985). The Effects of Posture on the Lumbar Spine, *The Journal of Bone and Joint Surgery,* 67-b (4), 625-629.

Aiello L. C. and Dean C. (2002). *An introduction to human evolutionary anatomy*. San Diego: Academic Press.

Al Rassy, N., Bakouny, Z., Matta, J., Frenn, F., Maalouf, G., Rizkallah, M., Bachour, F., Sebaaly, A., Hardouin, P., Chauveau, C. and Hage, R. E. (2018). The relationships between bone variables and physical fitness across the BMI spectrum in young adult women. *Journal of Bone and Mineral Metabolism*, 37 (3), 520–528.

Amonoo-Kuofi, U. S. (1992). Changes in the Lumbosacral Angle, Sacral Inclination and the Curvature of the Lumbar Spine during Aging. *Cells Tissues Organs*, 145(4), 373–377.

Arensburg, B., Bar-Yosef, O., Belfer, A., Chech, M., Goldberg, P., Laville, H., Meignen, L. Rak, Y., Tchernov, E., Tillier A-M., Vandermeersch, B. and Weinstein, M. (1983). DÉCOUVERTE D'UN SQUELETTE HUMAIN DANS LES NIVEAUX MOUSTÉRIENS DE LA GROTTE DE KEBARA (ISRAEL), *Paléorient*, 9 (2), 53-54.

Michigan State University (n.d.) “Australopithecus africanus: STS 14,” *Hominid Fossil Repository*, [internet]. Available from: http://projects.leadr.msu.edu/hominidfossils/items/show/39 [accessed 30 August 2022].

Bailey, J. F., Sparrey, C. J., Been, E. and Kramer, P. A. (2016). Morphological and postural sexual dimorphism of the lumbar spine facilitates greater lordosis in females, *Journal of Anatomy*, 229 (1), 82-91.

Bakouny, Z., Assi, A., Massaad, A., Saghbini, E., Lafage, V., Skalli, W., Ghanem, I. and Kreichati, G. (2017). Roussouly’s sagittal spino-pelvic morphotypes as determinants of gait in asymptomatic adult subjects, *Gait Posture*, 54, 27–33.

Barrey, C., Roussouly, P., Le Huec, J-C., D’Acunzi., G. and Perrin., G. (2013). Compensatory mechanisms contributing to keep the sagittal balance of the spine, *European Spine Journal*, 22 (Suppl 6), 834-841.

Been, E. and Bailey, J. F. (2019) The Association Between Spinal Posture and Spinal Biomechanics in Modern Humans: Implications for Extinct Hominins, In: Been, E., Gómez-Olivencia, A., Kramer, P. A . eds. *Spinal Evolution: Morphology, Function, and Pathology of the Spine in Hominid Evolution*. Cham Switzerland: Springer nature, 213-245.

Been, E, Barash, A., Marom, A., Aizenberg, I. and Kramer, P. A. (2010a). A new model for calculating the lumbar lordosis angle in early hominids and in the spine of the neanderthal from Kebara, *The Anatomical Record*, 293 (7), 1140-1145.

Been, E., Barash, A., Marom, A. and Kramer, P.A. (2010b). Vertebral Bodies or Discs: Which Contributes More to Human-Like Lumbar Lordosis, *Clinical Orthopaedics and Related Research*, 468 (7), 1822-1829.

Been, E., Peleg, S., Marom, A. and Barash, A. (2010c). Morphology and function of the lumbar spine of the Kebara 2 Neanderthal, *American Journal of Biological Anthropology*, 142 (4), 549-557.

Been, E., Barash, A., Pessah, H. and Peleg, S. (2010d). A new look at the geometry of the lumbar spine, *Spine*, 35 (20), E1014-E1017.

Been, E., Gómez-Olivencia, A., and Kramer, P. A. (2012). Lumbar lordosis of extinct hominin, *American Journal of Biological Anthropology*, 147 (1), 64-77.

Been, E., Gómez-Olivencia, A. and P. A. Kramer (2014). Brief communication: Lumbar lordosis in extinct hominins: implications of the pelvic incidence, *American Journal of Biological Anthropology*, 154 (2), 307-314.

Been, E., Gómez-Olivencia, A., Shefi, S., Soudack, M., Bastir, M. and Barash, A. (2017). Evolution of Spinopelvic Alignment in Hominins, The Anatomical Record, 300 (5), 900-911.

Been, E., Pessah, H., Been, L., Tawil, A., Peleg, S. (2007). New Method for Predicting the Lumbar Lordosis Angle in Skeletal Material, *The Anatomical Record*, 290 (12), 1568-1573.

Been, E., Simonovich, A. and Kalichman, L. (2019). Spinal Posture and Pathology in Modern Humans, In: Been, E., Gómez-Olivencia, A., Kramer, P. A . eds. *Spinal Evolution: Morphology, Function, and Pathology of the Spine in Hominid Evolution*. Cham Switzerland: Springer Nature, 301-320.

Begun, D. R. (2004). Knuckle-walking and the origin of human bipedalism, In: Meldrum, D. J., Hilto, C. E.. Eds. *From Biped to Strider: The Emergence of Modern Human Walking, Running and resource Transport*. New York: Kluwer Academic/Plenum Publishers, 9-33.

Biau, J. D., Kernéis, S., and Porcher, R. (2008). Statistics in Brief: The Importance of Sample Size in the Planning and Interpretation of Medical Research, *Clinical Orthopaedics Related Research*, 466 (9), 2282-2288.

Broom, R. and Robinson, J. T., (1947). Further Remains of the Sterkfontein ape-man, Plesianthropus, *Nature*, 160 (4065), 430-431.

Cassidy, J. D., Young-Hing, K., Kirkaldy-Willis, W. H. and Wilkinson, A. A. (1988). A study of the effects of bipedalism and upright posture in the lumbosacral spine and paravertebral muscles of the Wister rat, *Spine*, 13 (3), 301-308.

Castillo, E. R. and Lieberman, D. E. (2018) Shock attenuation in the human lumbar spine during walking and running, *Journal of Experimental Biology*. 221 (Pt 9), 1-11.

Cheng, X. G., Sun, Y., Boonen, S., Nicholson, P. H. F, Brys, P., Dequeker, J. and Felsenberg, D. (1998) Measurement of vertebral shape by radiographic morphometry: sex differences and relationship with vertebral level and lumbar lordosis, *Skeletal Radiology*, 27 (7), 380- 384.

Cunningham, D.J., (1886). *The lumbar curve in man and the apes: with an account of the topographical anatomy of the chimpanzee, orang-utan, and gibbon* (No. 11). London: The Academy.

Damasceno, L. H. F., Catarin, S. R. G., Dorival, A. and Defino, H. L. A. (2006). Lumbar lordosis: study of angular values and the participation of vertebral bodies and intervertebral discs, *Brazilian Orthopedist Acta*, 14 (4), 193-198.

DiGiovanni, B.F., Scoles P.V. and Latimer B.M. (1989). Anterior extension of the thoracic vertebral bodies in Scheuermann's kyphosis: An anatomic study, *Spine,* 14 (7): 712–716.

Duval-Beaupère, G., Schmidt, C. and Cosson, P. (1992). A barycentremetric study of the sagittal shape of spine and pelvis: The condition required for an economic standing position, *Annals of Biomedical Engineering*, 20 (4), 451-462.

Edgar, H. J, H., Daneshvari Berry, S., Moes, E., Adolphi, N. L.; Bridges, P., Nolte, K. B. (2020). *New Mexico Decedent Image Database*. Office of the Medical Investigator, University of New Mexico. doi.org/10.25827/5s8c-n515..UNM Data.

Farfan, H. F. (1995). Form and function of the musculoskeletal system as revealed by mathematical analysis of the lumbar spine, *Spine*, 20 (13), 1462-1474.

Fernand, R., and Fox, D. E. (1985). Evaluation of lumbar lordosis A prospective and retrospective Study, *Spine*, 10 (9), 799-803.

Filler, A. G (2007). Emergence and optimization of upright posture among hominiform hominoids and the evolutionary pathophysiology of back pain, *Neurosurgery Focus*, 23 (1), E4.

Freidline, S., Gunz, P., Harvati, K. and Hublin, J-J. (2012). Middle Pleistocene human facial morphology in an evolutionary and developmental context, *Journal of Human Evolution*, 63(5), 723-740.

Gracovetsky, S. (1985). An hypothesis for the role of the spine in human locomotion: A challenge to current thinking, *Journal of Biomedical Engineering*, 7 (3), 205-216.

Gracovetsky, S. (1986). The optimum spine, *Spine*, 11 (6), 543-573.

García-Martínez, D., Martelli, S., Torres-Tomayo, N., Jiménez-Arenas, J. M., González Martín, Campo, M., Cambra-Moo, O., Lois-Zlolniski, S., Nalla, S., Sanchís-Gimeno, J. A. and Bastir, M, (2020). Sexual dimorphism in the vertebral wedging of the human lumbar vertebrae and its importance as a comparative framework for understanding the wedging pattern of Neanderthals, *Quaternary International*, 566-567, 224-232.

Gelb, D. E., Lenke L. G., Bridwell, K. H., Blanket, K. and McEnery, K. W. (1995). An analysis of sagittal spinal alignment in 100 asymptomatic middle and older aged volunteers, *Spine*, 20 (12),1351-1358.

Gómez-Olivencia, A., Arlegi, M., Barash, A., Stock, J. T., Been, E. (2017). The Neanderthal vertebral column 2: The lumbar spine, *Journal of Human Evolution*, 106, 84-101.

Haeusler, M. (2019). Spinal Pathologies in Fossil Hominins, *Spinal Evolution: Morphology, Function, and Pathology of the Spine in Hominid Evolution*. Cham Switzerland: Springer Nature, 213-245.

Haeusler, M., Martelli, S. A., and Boeni, T. (2002). Vertebrae numbers of the early hominid lumbar spine, *Journal of Human Evolution*, 43(5), 621–643.

Haeusler, M., Schiess, R. and Boeni, T. (2011). New vertebral and rib material point to modern bauplan of the Nariokotome *Homo erectus* skeleton, *Journal of Human Evolution*, 61 (5), 575–582.

Haeusler, M., Trinkaus, E., Fornai, C., Müller, J., Bonneau, N., Boeni, T. and Frater, N. (2019). Morphology, pathology, and vertebral posture of the La Chapelle-aux-saints Neanderthal, *Proceedings of the National Academy of Sciences of the United States of America*, 116 (11), 4923-4927.

Hansen, B. B., Bendix, T., Grindsted, J., Bliddal, H, Christensen, R., Hansen, P., Riis, R. and Boesen, M. (2015). Effect of Lumbar Disc Degeneration and Low-Back Pain on the Lumbar Lordosis in Supine and Standing, *Spine*, 40 (21) 1690-1696.

Hay, O., Dar, G., Abbas, J. Stein, D., May, H., Masharawi, Y., Peled, N., Hershkovitz, I. (2015). The Lumbar Lordosis in Males and Females, Revisited, *PLoS ONE*, 10 (8), 1-17.

Humzah, M. D. and Soames, R. W. (1988) Human intervertebral Discs: Structure and Function, *The Anatomical Record*, 220 (4), 337-356.

Hsu, C., Castillo, E. R. and Lieberman, D. E. (2015) The relationship between trunk muscle strength and flexibility, intervertebral discs wedging, and human lumbar lordosis, *Harvard Undergraduate Journal*, 8 (1), 35-41.

Jackson, R. P. and McManus, A. C. (1994). Radiographic analysis of sagittal plane alignment and Balance in standing volunteers and patients with low back pain matched for age, Sex, and Size, *Spine,* 19(14), 1611–1618.

Johanson, D. C. (2004). Lucy, Thirty Years Later: An Expanded View of *Australopithecus afarensis, Journal of Anthropological Research*, 60 (4), 465-486.

Kalichman, L., Li, L., Hunter, D. and Been., E. (2011). Association between CT-evaluated lumbar lordosis and features of spinal degradation evaluated in supine position, *Spine Journal*, 11 (4), 308-315.

Kibii, J. M., Churchill, S. E., Schmid, P., Carlson, K. J. and Reed, N. D. (2011). A partial pelvis of *Australopithecus sediba*. *Science,* 333 (6408), 1407-1411.

Kroemer Elbert, K. E., Kroemer, H. B. and Kroemer Hoffman, A. D. (2018) Bones, Muscles and Strength of the Human Body. In Kroemer Elbert, K. E., Kroemer, H. B. and Kroemer Hoffman, A. D. (Eds). *Ergonomics: How to Design for Ease and efficiency, Third Edition.* Amseterdam, Netherlands: Academic Press Elsevier, 45-88.

Legaye, J., Duval-Beaupère, G., Hecquet, J. and Marty, C. (1998). Pelvic incidence: a fundamental pelvic parameter for three-dimensional regulation of spinal sagittal curves., *European Spine Journal*, 7(2), 99–103.

Lois-Zlonlniski, S., Torres-Tamayo, N., García-Martínez , D., Blanco-Pérez, E., Mata-Escolano, F., Barash, A., Nalla, S., Martelli, S., Sanchís-Gimeno, J. A. and Bastir, M. (2019). 3D geometric morphometric analysis of variation in the human lumbar spine, *American Journal of Biological Anthropology*, 170 (3), 361-72.

Lordkipanidze, D., Jashashvili, T., Vekua, A., Ponce de León, M.S., Zollikofer, C.P., Rightmire, G.P., Pontzer, H., Ferring, R., Oms, O., Tappen, M., Bukhsianidze, M., Agustí, J., Kahlke, R., Kiladze, G., Martínez -Navarro, B., Mouskhelishvili, A., Nioradze, M. and Rook, L. (2007). Postcranial evidence from early Homo from Dmanisi, Georgia. *Nature,* 449 (7160), 305-310 .

Lovejoy CO. (2005). The natural history of human gait and posture. Part 1. Spine and pelvis. *Gait Post* 21 (1), 95–112.

Lovejoy, C.O., Suwa, G., Spurlock, L., Asfaw, B. and White, T. D. (2009). The pelvis and femur of Ardipithecus ramidus: the emergence of upright walking, *Science*, 326 (5949), 71e1-71e6.

Masharawi, Y., Salame, K., Mirovsky, Y., Peleg, S., Dar, G., Dteinberg, N., Hershkovitz, I. (2008). Vertebral body shape variation in the thoracic and lumbar spine: characterization of its asymmetry and wedging, *Clinical Anatomy*, 21 (1), 46–54.

Martelli, S. A. (2005). A Comparative Morphometric Study of the Hominid Lumbar Spine, London: University College London. PhD Thesis.

Martelli, S. A. (2019). The Modern and Fossil Hominin Spinal Ontogeny, *Spinal Evolution: Morphology, Function, and Pathology of the Spine in Hominid Evolution*. Cham Switzerland: Springer Nature, 247-281.

Meakin, J.R., Gregory, J. S., Aspden, R. M., Smith, F. W. and Gilbert, F. J. (2009). The intrinsic shape of the human lumbar spine in the supine, standing and sitting postures: characterization using an active shape model, *Journal of Anatomy*, 215 (2), 206-221.

Meyer, M., R., Williams, S. A., Smith, M. P. and Sawyer, G. J. (2015). Lucy's back: Reassessment of fossils associated with the A. L. 288-1 vertebral column, *Journal of Human Evolution*, 85, 174-180.

Nakatsukasa, M. (2004). Acquisition of bipedalism: the Miocene hominoid record and modern analogues for bipedal protohominids, *Journal of Anatomy*, 204 (5), 385-402.

Nathan, H., Weinberg, H., Robin, G. C. and Aronson, H. B. (1964). A simple method of inducing erect posture in baboons, *American Journal of Biological Anthropology*, 22 (3). 321–327.

Nobis, G. (1986). The wild mammals in the human environment of Oberkassel near Bohn and the domestication problem of wolves in the Upper Paleolithic, *Aufsatz,* 186, 367-376.

.

O'Connell, G. D., Vresilovic, E. J. and Elliot, D.M. (2007). Comparison of animals used in disc research to human lumbar disc geometry, *Spine*, 32 (3), 328-333

Parenteau, C. S., Lau, E. C., Campbell, I.C. and Courtney, A. (2021) Prevalence of spine degeneration diagnosis by type, age, gender, and obesity using Medicare data, *Scientific reports*, 11 (5389), 1-11.

Pilbeam, D. (2004). The anthropoid postcranial axial skeleton: Comments on Development, Variation and Evolution, *Journal of Experimental Zoology Part B Molecular and Developmental Evolution*, 302B (3), 241-267.

Plomp, K. A., Been, E. and Collard., M. (2022). Acquired spinal conditions in humans: the roles of spinal curvature, the shape of the lumbar vertebrae, and evolutionary history.

Palaeopathology and Evolutionary Medicine An Integrated Approach, In: Plomp, K. A., Roberts, C. A., Elton, S. and Bentley, G. R. Eds. Oxford: Oxford University press, 42-61.

Pooni, J. S., Hukins, D. W. L., Harris, P.F. Hilton, R. C. and Davies, K. E. (1986). Comparison of the structure of human intervertebral discs in the cervical, thoracic and lumbar regions of the spine, *Surgical Radiological Anatomy*, 8(3), 175-182.

Prueschoft H. (2004). Mechanism for the acquisition of habitual bipedality: are there biomechanical reasons for the acquisitions of upright bipedal postures, *Journal of Anatomy*, 204 (5), 363-384.

Prueshoft, H., Hayama, S. and Gunter, M. M. (1988). Curvature of the lumbar spine as a consequence of mechanical necessities in Japanese macaques trained for bipedalism, *Folia Primatologica*, 50 (1-2), 42-58 .

Rasband, W.S. (2018). ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, https://imagej.nih.gov/ij/, 1997-2018.

Robinson, J. T. (1972). *Early hominid posture and locomotion*. Chicago:University of Chicago.

Rose, M. D. (1975). Functional proportions of primate vertebrae measures, *Journal of Human Evolution*, 4 (1), 21-38.

Russo, G. A., Marsh, D. and Foster, A. D. (2020). Response of the Axial Skeleton to Bipedal Loading Behaviors in an Experimental Animal Model, *The Anatomical Record*, 303 (1), 150-166.

Sanders, W. J. (1998). Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41, Journal of Human Evolution. 34 (3), 249–302.

Schiess, R., & Haeusler, M. (2013). No skeletal dysplasia in the nariokotome boy KNM-WT 15000 (homo erectus)-A reassessment of congenital pathologies of the vertebral column, *American Journal of Biological Anthropology*, 150 (3), 365–374.

Schultz, A. H. (1950). The Physical Distinctions of Man, *Proceedings of the American Philosophical Society*, 94 (5), 428-449.

Schultz, A. H. (1969). *The Life of Primate*s, New York: Universe Books.

Scoles, P. V., Latimer, B. M., DiGiovanni, B. F. Vargo, E., Bauza, S. and Jellema, L. M. (1991). Vertebral alterations in scheuermann's Kyphosis, *Spine*, 16 (5), 509-515.

Shapiro, L. J. and Kemp, A. D. (2019). Functional and Developmental influences on variation in the Catarrhine vertebrae, *American Journal of Biological Anthropology*, 168 (1), 131-144.

Shymon, S. Hargens, A. R., Minkoff, L. A. and Chang, D. G. (2014). Body posture and backpack loading: an upright magnetic resonance imaging study of the adult lumbar spine, *European Spine Journal*, 23 (7), 1407-1413.

Sparrey, C. J., Bailey, J. F., Safaee, M., Clark, A. J., Lafage, V., Schwab, F., Smith, J. S. and Ames, C. P. (2014). Etiology of lumbar lordosis and its pathophysiology: a review of the evolution of lumbar lordosis, and the mechanics and biology of lumbar degeneration. *Neurosurgery Focus*, 36 (5), 1-16.

Stagnara, P., De Mauroy, J. C., Dean, G., Gonon, G. P., Costanzo, G., Dimnet, J., and Pasquet, A. (1982). Reciprocal angulation of vertebral bodies in a sagittal plane: approach to references for the evaluation of kyphosis and lordosis, *Spine*, 7 (4), 335- 342.

Stokes, I.A. F. and Aronsson, D.,D. (2001). Disc and vertebral wedging in patients with progressive scoliosis, Journal of Spinal Disorders, 14 (4), 317-322.

Tao, Y., Niemeyer, F., Galbusera, F., Jonas, R., Samartzis, D., Vogele, D., Kienle, A. and Wilke, H-J. (2021). Sagittal wedging of intervertebral discs and vertebral bodies in the cervical spine and their associations with age, sex, and cervical lordosis: A large-scale morphological study, Clinical Anatomy, 34 (7), 1111- 1120.

Tardieu, C., Hasegawa, K., Haeusler, M (2017). How Did the Pelvis and Vertebral Column Become A Functional Unit During the Transition from Occasional to Permanent Bipedalism?, *The Anatomical Record*, 300 (5), 912-931.

Taylor, C. R. and Rowntree, V. J. (1973). Running on two or on four legs: which consumes more energy?, *Science*, 179 (4069), 186-187.

Thackery, F. Gommery, D. and Braga, J. (2002). Australopithecine Postcrania (StS 14) from the Sterkfontein Caves, South Africa: the skeleton of 'Mrs Ples'?, *South African Journal of Science*, 98, 211-212.

Toussaint, M. Macho., G. A., Tobias, P. V., Partridge, T. C. and Hughes, A. R. (2003). The third partial skeleton of a late Pliocene hominin (Stw 431) from Sterkfontein, South Africa:research articles, *South African Journal of Science*, 99 (5), 215-223.

Twomey, L. and Taylor, J. (1985). Age changes in lumbar intervertebral discs, *Acta Orthopaedica Scandinavia*, 56 (6), 496-499.

Valladas, H., Joron, J. L., Valladas, G., Arensburg, B., Bar-Yosef, O., Belfer-Cohen, A., Goldberg, P.,, Laville, H., Meignen, L., Rak, Y., Tchernov, T., Tillier, A., M. and Vandermeersch, B. (1987). Thermoluminescence dates for Neanderthal burial sites at Kebara in Israel, *Nature*, 330, 159-160.

Vialle, R., Levassor, N., Rillardon, L., Templier, A., Skalli, W. and Guigui, P. (2005). Radiographic analysis of the sagittal alignment and balance of the spine in asymptomatic subjects, *Journal of Bone and Joint Surgery*, 87(2), 260-7.

Ward, C. V. (2002). Interpreting the posture and locomotion of *Australopithcus afarensis*: Where do we stand?, *American Journal of Biological Anthropology*, 119 (235), 185-215.

Ward, C. V., Rosenman, B. Latimer, B. and Nalla, S. (2020). 'Thoracolumbar vertebrae and ribs' IN Zipfel, B. Richmond, B. G., Ward, C. V. Eds. *Hominin Postcranial Remains from Sterkfontein South Africa. 1936-1995,* Oxford: Oxford scholarship online, 144-186.

Weber, J. and Pusch, C. M. (2008). The lumbar spine in Neanderthals shows natural kyphosis, European Spine Journal, 17 (Suppl 2), 327–330.

Whitcome, K. K., Shapiro, L. J. and Lieberman, D. E. (2007). Fetal load and the evolution of lumbar lordosis in bipedal hominins. *Nature,* 450, 1075–1078.

Williams, S.A., Ostrofsky, K. R., Frater, N., Churchill, S. E., Schmid, P. and Berger, L. R. (2013). The vertebral column of *Australopithecus sediba, Science*, 340 (6129), 1-5.

Williams, S. A., Meyer, M. R., Nalla, S., García-Martínez, D., Nalley, T. K., Eyre, J., Prang, T. C., Bastir, M., Schmid, P., Churchill, S. E. and Berger, L. R. (2018). The Vertebrae, Ribs, and Sternum of *Australopithecus sediba*, *Paleoanthropology*, Special issue: *Australopithecus sediba*, 156-233.

Williams, S. A., and Pilbeam, D. (2021). Homeotic change in segment identity derives the human vertebral formula from a chimpanzee-like one, *American Journal of Biological Anthropology*, 176 (2), 283-294.

Williams, S. A., Prang, T. C., Meyer, M., Nalley, T. K., Van Der Merwe, R., Yelverton, C., García-Martínez , D., Russo, G. A., Ostrofsky, K. R., Spear, J., Grabowski, M., Nalla, S., Bastir, M., Schmid, P. Churchill, S. and Berger, L. R. (2021). New fossils of *Australopithecus sediba* reveal a nearly complete F, *ELife*, 10 (70447), 1-25.

Williams, S. A. (2012) Variation in anthropoid vertebral formulae: Implications for homology and homoplasy in hominoid evolution, *Journal of Experimental Zoology*, 318 (2), 134-147.

Williams, S. A., Zeng, I., Paton, G. J., Yelverton, C., Dunham, C., Ostrofsky, K., Shukman, S., Avilez, M. V., Eyre, J., Loewen, T., Prang, T. C., Meyer, M. R. (2022) Inferring lumbar lordosis in Neanderthals and other Hominins, *Proceedings of the National Academy of Sciences*, 1, 1-10.

Yamada, K., Sakamoto, K., Ushikubo, S.and Sato, Y. (1960). Study of intervertebral disc degeneration in bipedal rats, *Tokyo Journal Experimental Medicine*, 7, 93-103.

7. Appendix-A

Table 27:

The wedging angles of StS 14 from PS1 to PS6. The TVBW is presented like that of the other studies (PS1 to PS5) and the summed wedging angles of PS1-PS6 are referred to as the total wedging for comparison. This demonstrates that the inclusion of PS6 (L1) (Haeusler, Martelli, and Boeni, 2002; Robinson, 1972) decrease the overall lordotic curvature in this specimen.

Measurement type	**Angle (º)**
PS6 (L1)	-5.42
PS5 (L2)	-8.46
PS4 (L3)	-4.17
PS3 (L4)	-2.87
PS2 (L5)	4.53
PS1 (L6)	11.66
TVBW (PS1 to PS5)	0.69
Total Wedging (PS1 to PS6).	-4.73

Table 28:

The summed wedging of StS 14 compared to the modern human average, and one UNMDID specimen that has six instead of 5 lumbar vertebrae.

Specimen (s)	**Modern human Mean ± SD**	**UNMDID Specimen L1-6**	**StS-14**
TVBW (º)	2.66 ± 12.76	42.74	0.69
Total wedging (PS1-6) (º)		36.85	-4.73

Figure 24.

Box-and-whiskers plot of TVBW (PS1 to PS5) of StS 14, the combined modern human sample (N=135) from the original study, and specimens with four (n=4), and six lumbar vertebrae (n=1). The VBW of individuals with four lumbar vertebrae is presented from T13-L4 and is more kyphotic that the modern human average. The TVBW of StS 14 is comparable to the modern human average while and the UNMDID specimen with six lumbar vertebrae has lordotic TVBW that is far outside the range of the Modern human average.

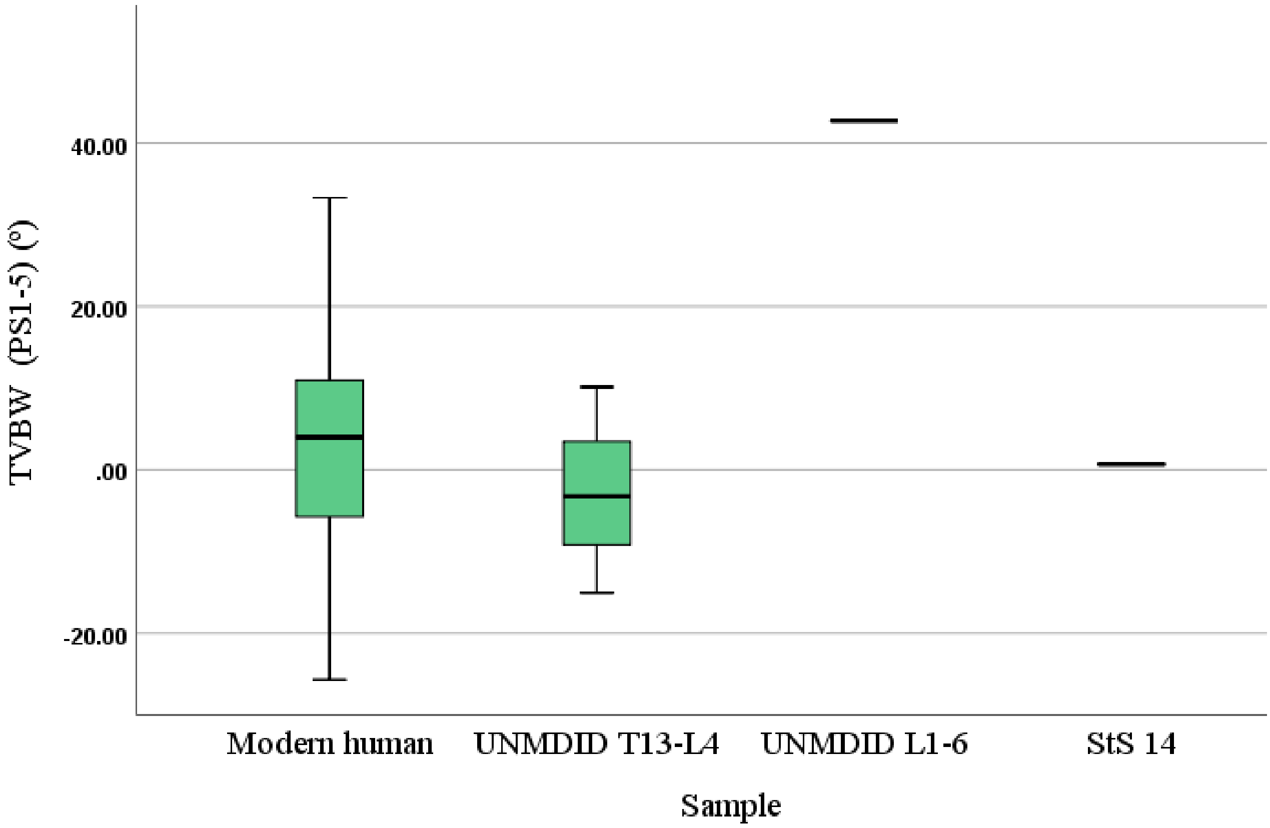
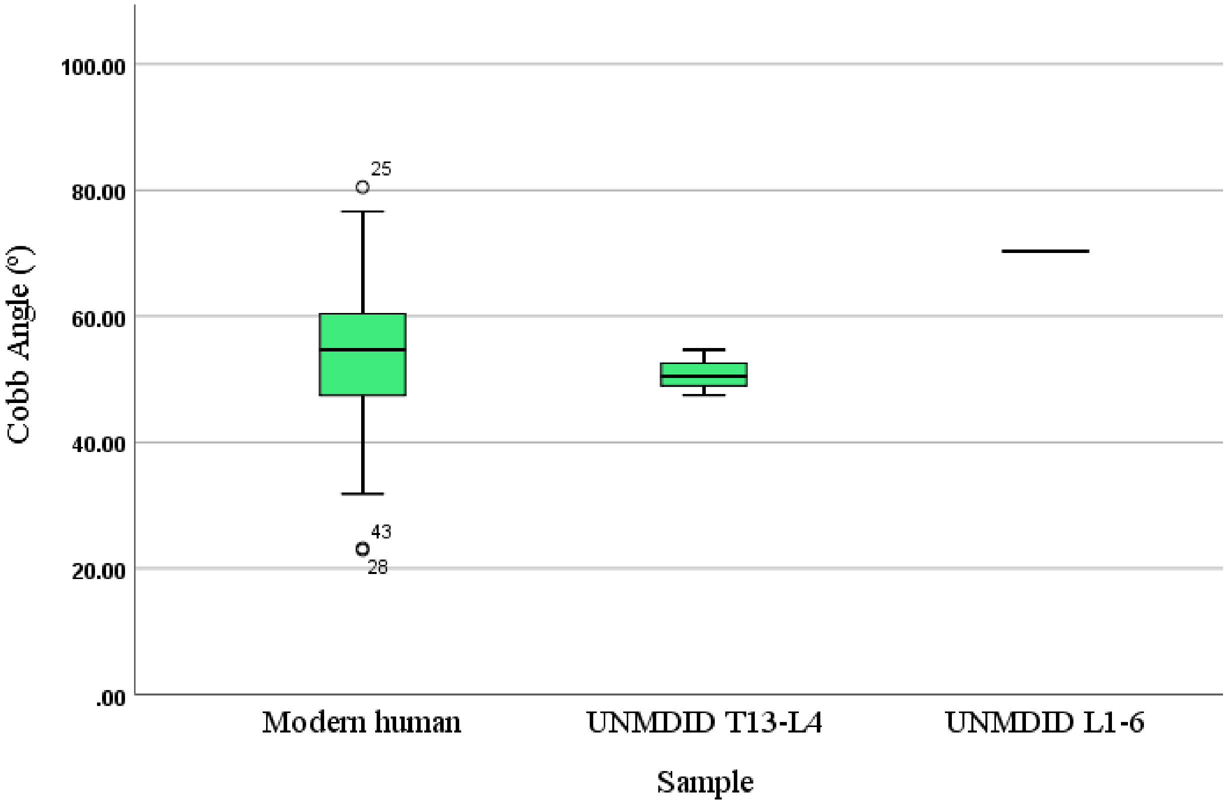


Figure 25.

The Cobb angle in the Modern Human sample comprise of individuals with an L1-5, compared against decedents with four and six vertebrae. Individuals with less lumbar vertebrae appear to have a slightly smaller Cobb angle, while individuals with more lumbar vertebrae have a greater Cobb angle.



8. Appendix-B

Figure 26

The superior and lateral view of the L1 of Oberkassel 1 used in this study.

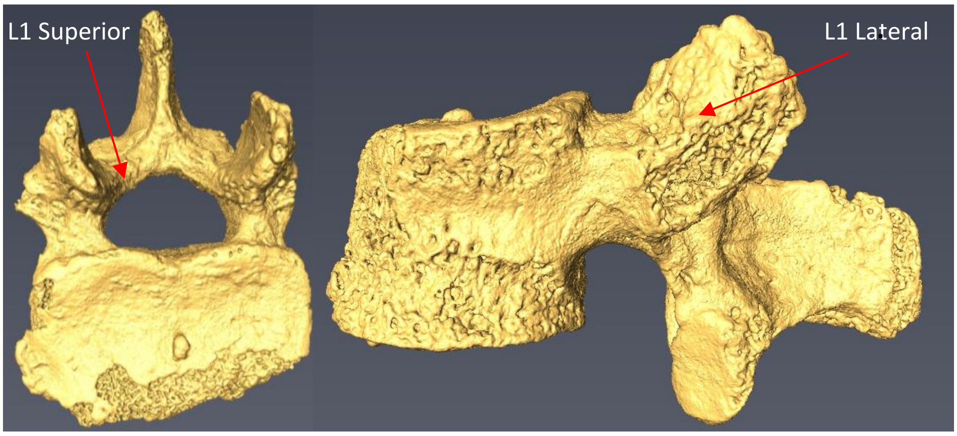


Figure 27

The superior and lateral view of L1 to L2 in Oberkassel 2.

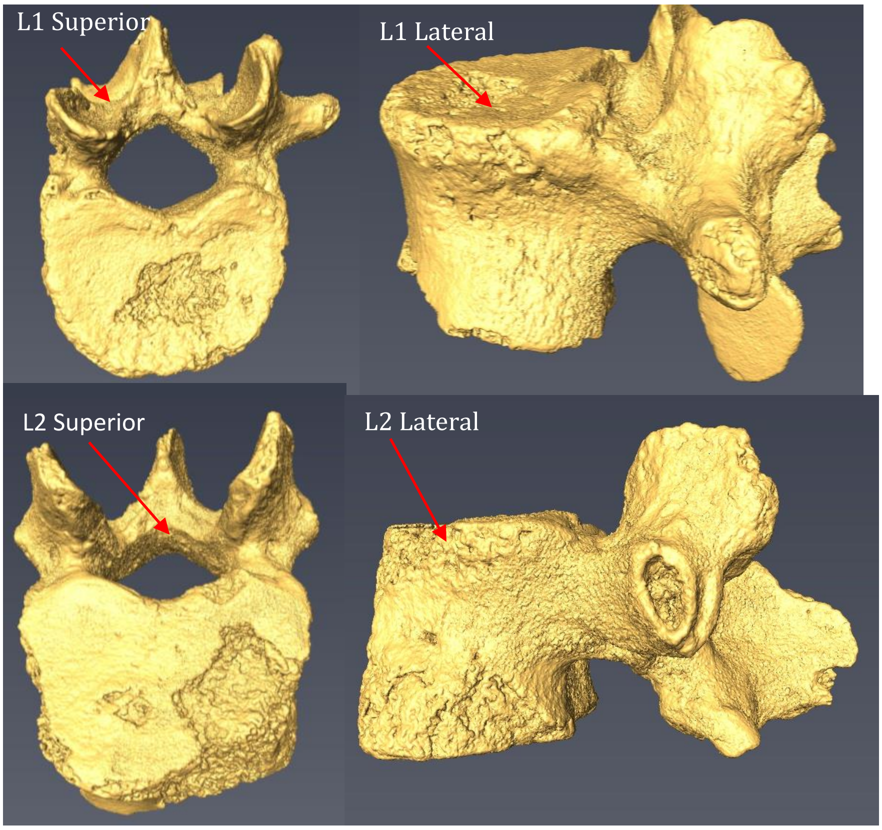


Figure 28. The superior and lateral view of L1 in Kebara 2.

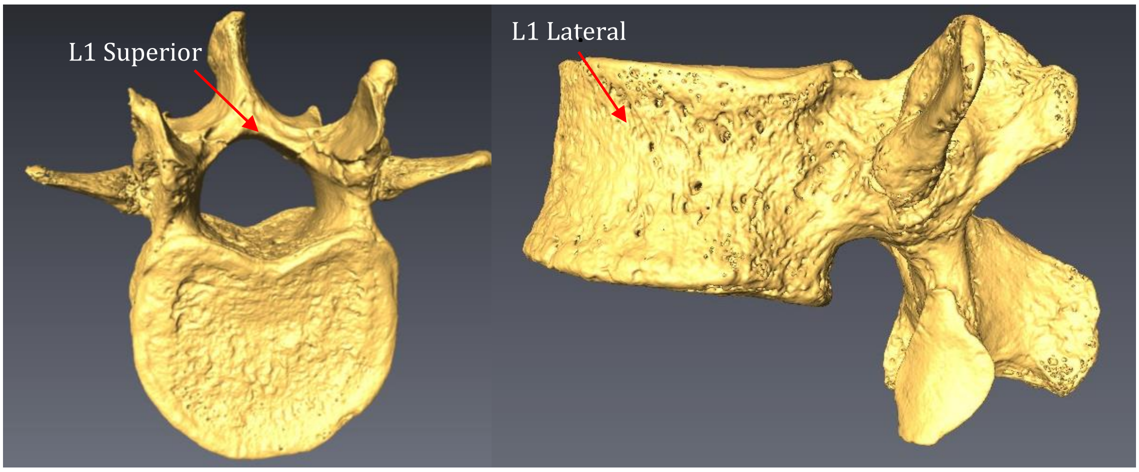


Figure 29. The superior and lateral view of L2 in Kebara 2.

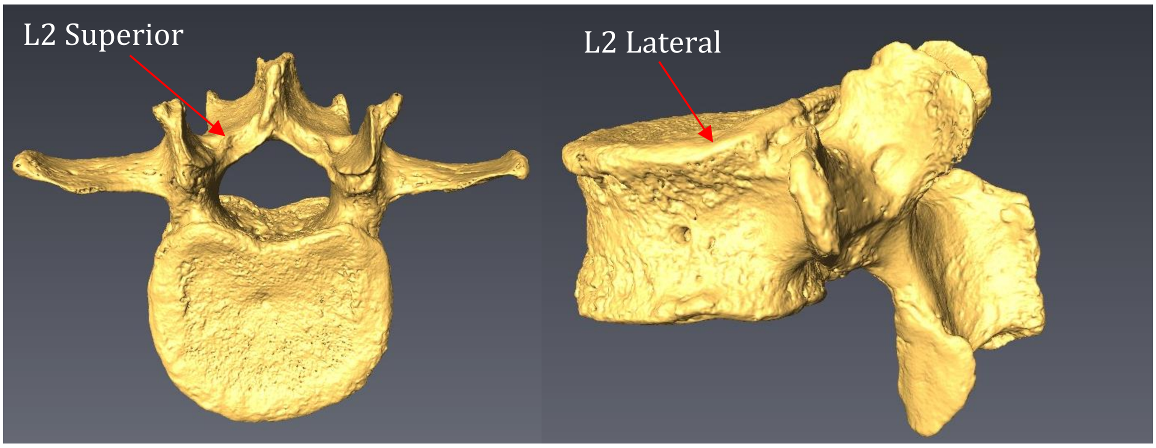


Figure 30. The superior and lateral view of L3 in Kebara 2.

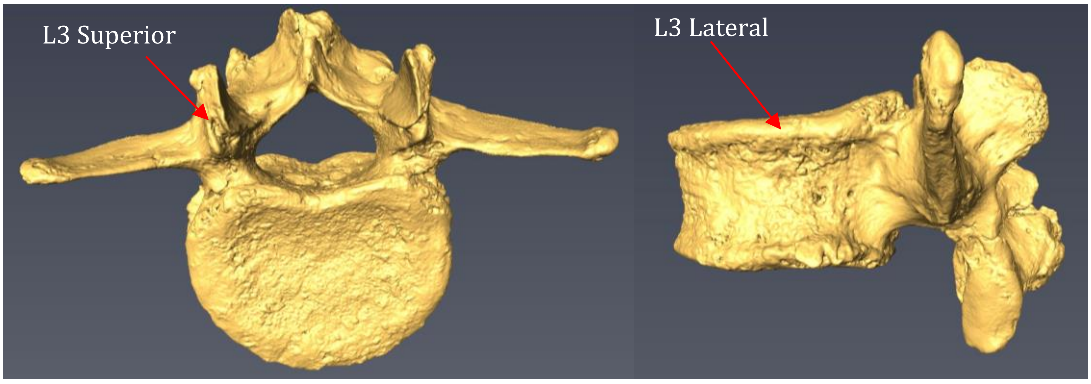


Figure 31. The superior and lateral view of L4 in Kebara 2.

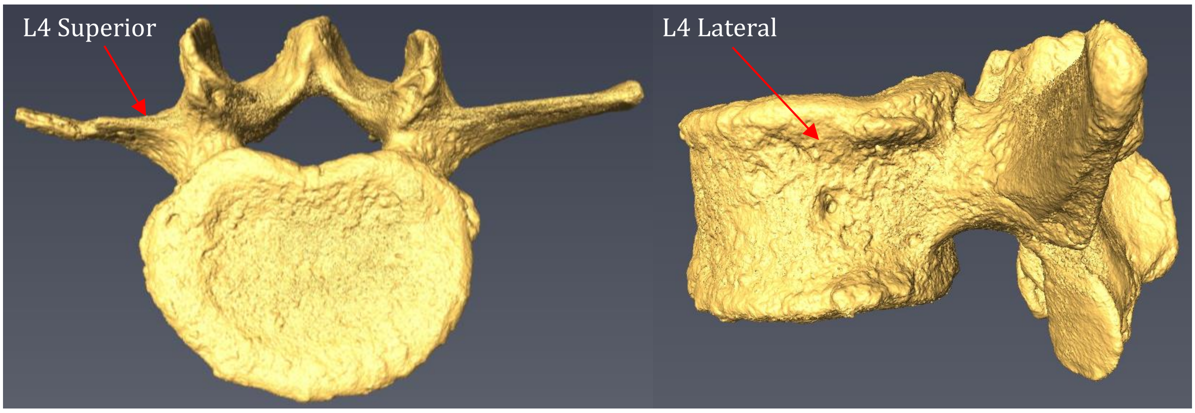


Figure 32. The superior and lateral view of L5 in Kebara 2.

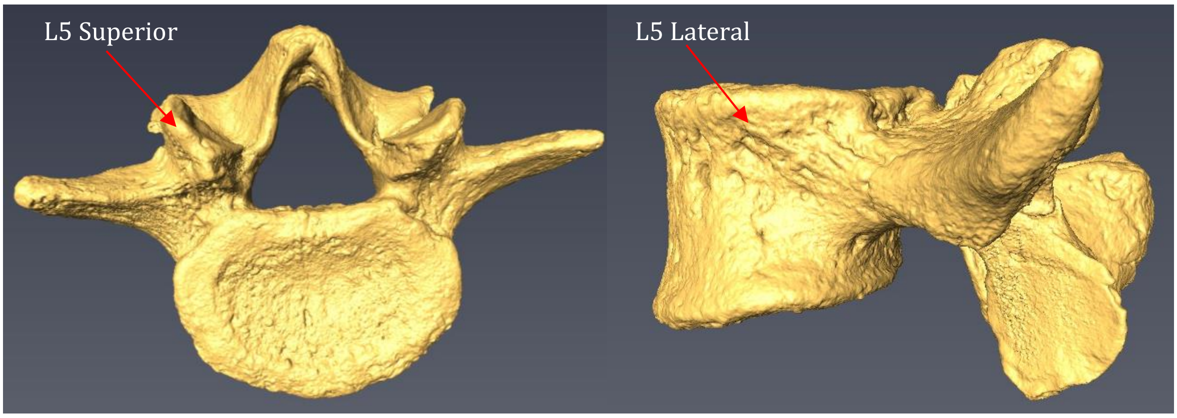


Figure 33. The superior and lateral view of the L1 of Sts 14.

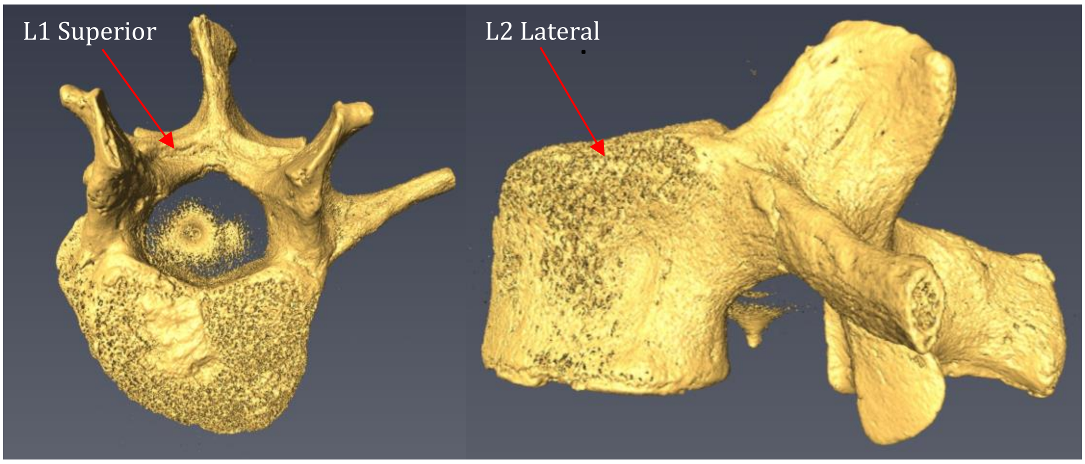


Figure 34. The superior and lateral view of the L2 of Sts 14.

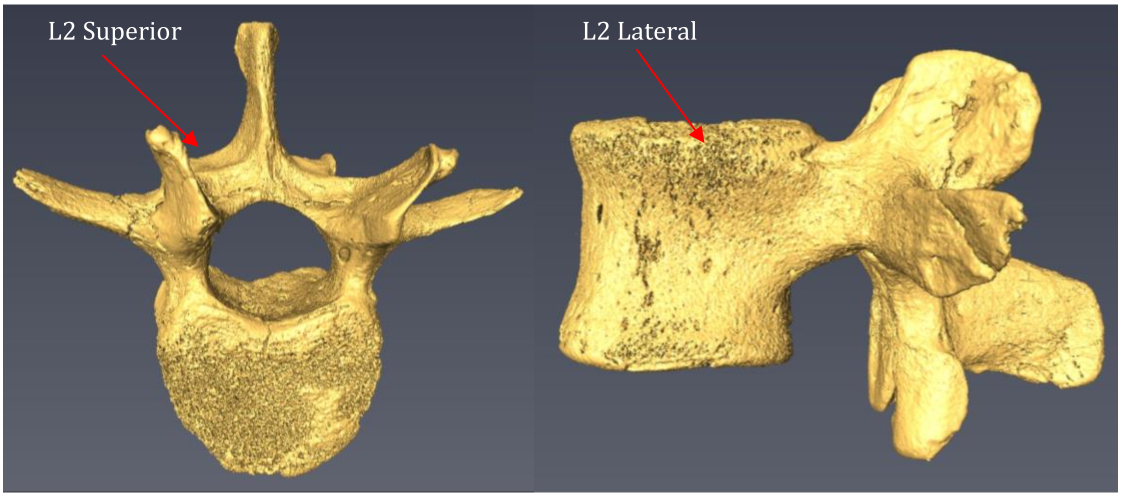


Figure 35. The superior and lateral view of the L3 of Sts 14.

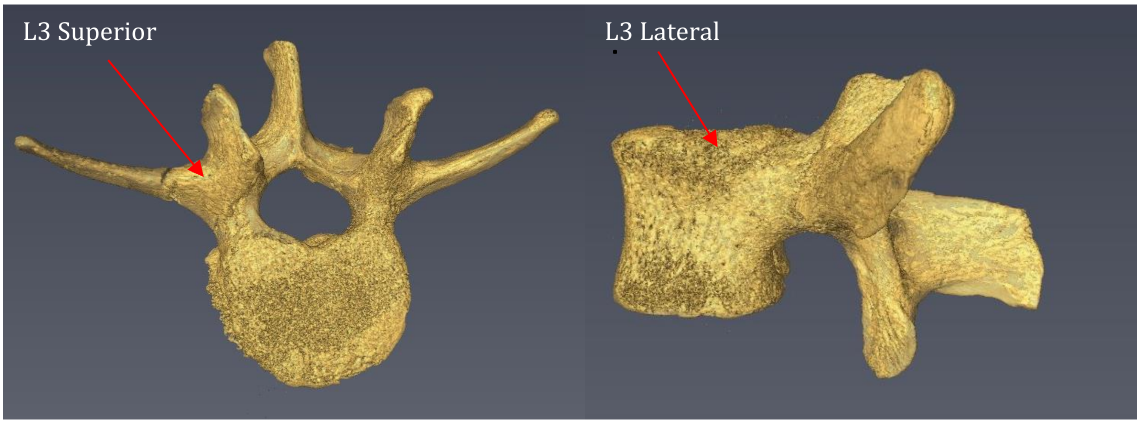


Figure 36. The superior and lateral view of the L4 of Sts 14.

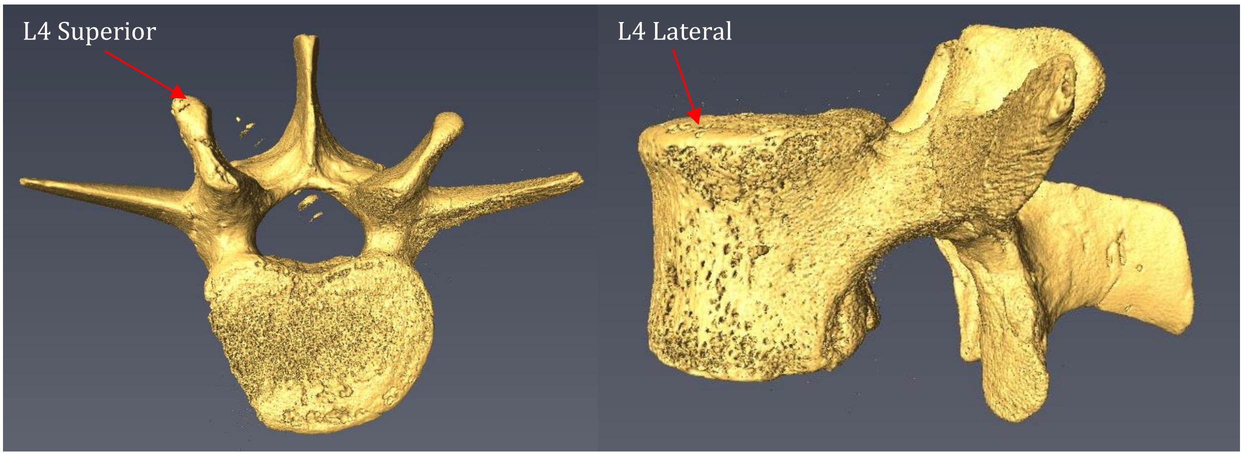


Figure 37. The superior and lateral view of the L5 of Sts 14**.**

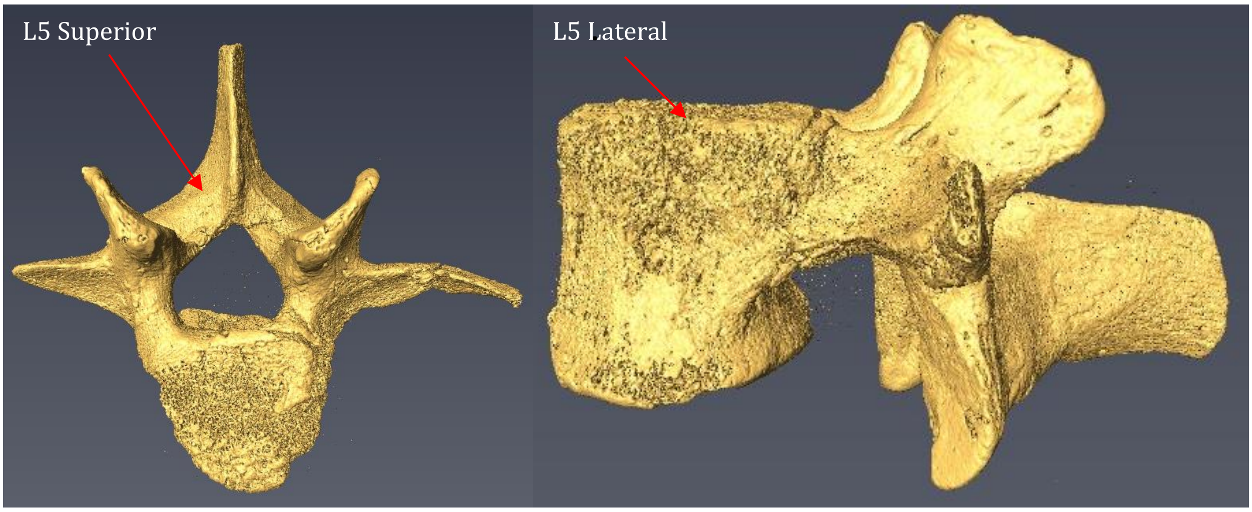


Figure 38. The superior and lateral view of the L6 of Sts 14.