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Niina Korpinen

EVOLUTIONARY DEVELOPMENT OF THE SPINE. THE BACKGROUND OF MODERN BACK PROBLEMS?

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Abstract

Bipedalism and upright posture are some of the defining characteristics of humans. However, adapting to these changes has required numerous anatomical changes, especially in the back, which has not been easy, as 84% of all people are estimated to suffer from back pain at some point in their lives. Since the Great Apes do not appear to showcase numerous spinal lesions compared to humans, this has led to the suggestion that the roots of the problems might lie in upright posture and bipedalism. As such, it is important to investigate how posture and locomotion have affected the vertebral column and vertebrae. This can help us understand how the vertebrae have evolved to accommodate the new posture and locomotion. However, human lifestyle has also gone through dramatic changes in recent history, and we now live the most sedentary lifestyle of our history, which has brought a completely new set of requirements for the back. Hence, it is also important to understand the changes that have taken place in contemporary humans compared to past populations and what impact these changes could have on our spinal health.

To study this, linear measurements of vertebral bodies of archaeological and anatomical skeletal specimens, African apes and fossil hominoids were compared using statistical analyses. Bone density was also studied from one of the anatomical skeletal samples and the ape sample. The focus was on the lower back, as it is most vulnerable to pain. Comparison of the measurements of all samples indicated that the shape of the vertebral body has not experienced significant changes during human evolution. However, there appears to be a shift in contemporary humans towards a rounder shape, which could influence both vertebral strength and intervertebral disc health. On the other hand, the bone density pattern in the whole subaxial spine seems to be relatively similar between humans and chimpanzees; but the differences found between the ape species might indicate less influence of locomotion on this feature. It was also observed that females in the past experienced less age-related bone loss compared to contemporary females. It was suspected that the large changes in the physical activity levels and sedentary lifestyle of contemporary humans could have influenced the vertebral bodies in a short time span.

Keywords: African apes, bone density, evolution, humans, morphology, spine, vertebra, vertebral column

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Tiivistelmä

Pystykävely ja pystyasento ovat tärkeimpiä ihmistä luonnehtivia piirteitä. Niihin sopeutuminen sen sijaan on vaatinut lukuisia anatomisia muutoksia varsinkin selässä. Nämä muutokset eivät ole olleet helppoja sillä on arvioitu, että 84 % ihmisistä tulee elämänsä aikana kärsimään jonkinlaisesta selkäkivusta. Sen sijaan selkävaivat vaikuttavat olevan harvinaisempia muilla ihmisapinoilla. Onkin epäilty, että syyt ihmisten lukuisiin selkävaivoihin saattaisivat osaksi juontaa juurensa pystyasennosta. Tästä syystä on tärkeää tutkia, miten selkäranka ja nikamat ovat kehittyneet evoluutiomme aikana ja millainen merkitys pystyasennolla ja kahdella jalalla kävelyllä on ollut niihin. Tämä auttaa meitä ymmärtämään miten selkä on aikoinaan sopeutunut uuteen ryhtiin ja liikkumistapaan. Ihmisten elämäntapa on myös kokenut radikaaleja muutoksia lähihistorian aikana, ja elämmekin tällä hetkellä koko historiamme vähiten liikkumista sisältävää elämäntapaa. Tämä on tuonut mukanaan aivan uusia haasteita selälle. Näin ollen on tärkeää ymmärtää myös mitä muutoksia nikamat ovat kokeneet nykyihmisillä ja mikä vaikutus näillä saattaa olla selän terveyteen.

Muutoksia tutkittiin käyttäen nikamansolmun lineaarisia mittoja nykyihmisiltä ja arkeologisilta ja anatomisilta ihmisaineistoista. Käytössä oli myös nykyisten ja fossiilisten ihmisapinoiden aineistoja. Lisäksi tutkittiin luuntiheysmittoja yhdessä ihmisaineistossa ja apinoilla. Lineaarisia mittoja ja luuntiheysarvoja tutkittiin käyttäen tilastollisia menetelmiä. Työssä keskityttiin pääasiassa alaselkään, sillä se on yleisin selkäkivun ongelma alue. Tulokset viittasivat siihen, ettei nikamansolmun muodossa ole evoluution aikana tapahtunut suuria muutoksia. Sen sijaan nikamansolmun muoto näyttäisi tämän päivän ihmisellä muuttuneen pyöreämmäksi, millä saattaa olla vaikutus nikaman kestävyyteen ja välilevyjen terveyteen. Luun tiheyden vaihtelu koko selässä vaikutti olevan samanlainen ihmisten ja simpanssien välillä. Apinoiden välillä sen sijaan löytyi eroja luun tiheydessä, jotka viittasivat liikkumistavan vähäiseen vaikutukseen tässä ominaisuudessa. Ikääntymisestä johtuva luukato sen sijaan oli erilainen historiallisen ajan populaatiolla, kun mitä on havainnoitu tänä päivänä. Varsinkin naisten luukato nikamassa vaikutti olleen pienempi menneisyydessä. Syynä lyhyen aikavälin muutoksiin epäiltiin olevan laskeneen fyysisen liikunnan määrä.

Asiasanat: evolutiivinen kehitys, ihmiset, isoapinat, luun tiheys, nikamat, nikamien morfologia, selkäongelmat, selkäranka, selkäsairaudet

To my mother

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1.10.2023 Niina Korpinen

Abbreviations and symbols

AP	anterior posterior
C	cervical vertebra
CC	craniocaudal
CSA	cross-sectional area
e.g.	exempli gratia
etc.	et cetera
FHtotD	femoral head total density
FHtraD	femoral head trabecular density
FNcrtD	femoral neck cortical density
FcrtD	femoral saft cortical density
i.e.	id est
L	lumbar vertebra
SNs	Schmorl's nodes
ML	mediolateral
T	thoracic vertebra
VtotD	vertebral total density
VtraD	vertebral trabecular density

List of original publications

This thesis is based on the following publications:

I Korpinen, N. Shape differences in all lumbar vertebrae between humans and African apes. Manuscript.

II Korpinen, N. (2023) Comparison of bone density patterns of subaxial apine between chimpanzees and gorillas – a case study. *Journal of Medical Primatology, 52*(2), 85-91. https://doi.org/10.1111/jmp.12627

III Korpinen, N. Differences in vertebral bone density between African apes. Manuscript.

IV Korpinen, N., Oura P., Väre T., Niskanen, M. Niinimäki, J., Karppinen, J. & Junno, J.-A. (2020) Temporal trends in vertebral dimensions – a case study from Finland. *Scientific Reports* 10(1). https://doi.org/10.1038/s41598-020-58340-9

V Korpinen, N., Oura, P. & Junno J-A. (2023) Sex- and site-specific, age-related changes in bone density – a Terry collection study. *HOMO Journal of Comparative Human Biology, 74*(1), 17-32. https://doi.org/10.1127/homo/2023/1662

Contributions

In article IV, the author wrote the main body of the text and was also partly responsible for collecting part of the used data. In article V, the author wrote the main text and did the analysis.

Contents

1 Introduction

A person with the strength of character and courage to do things that need to be done is often referred to as having a backbone. It illustrates to us the metaphorical strength that the backbone represents and the cultural importance of a “straight back”. This is fitting as our backbone does showcase quite a deal of strength, as it is not only required to carry the weight of the whole upper body but also facilitates an extensive range of movement. The axial loading is also both amplified and altered by the movements of the body. Yet, as strong as our backbone might seem, it can be surprisingly vulnerable to ailments.

Although hominins are not the only creature, or even the only mammal, to have adopted an upright position, the curvatures of our spine that have abled our posture and the bipedal locomotion are unique to us. Turning the bauplan that was originally designed for horizontal posture into a completely vertical one has required numerous anatomical changes and adaptations. Although the spine is not the only structure in the body that has gone through changes, it has required some of the most extensive adaptations. Considering the numerous back ailments of modern humans, it is safe to say these changes have not been easy on the spine. It has been estimated that as many as 84% of people end up experiencing some sort of back pain at some point in their lives (Airaksinen et al., 2006), and with the increasing elderly population, back ailments, such as osteoporotic fractures and intervertebral disc generation, are growing health concerns. Reasons for back pain and ailments can be very diverse and are often influenced by muscles and other soft tissues. The source of the pain can be the intervertebral discs or facet joints (Truumees, 2011), but non-spinal causes can also be the source of the pain (Ellenberg & Ellenberg, 2011). Unfortunately, the cause of the pain often remains a mystery (Balagué et al., 2012; Maher et al., 2017). However, the focus of this research was on the bone elements, as those are also often available for study in the fossil records and archaeological contexts.

Numerous studies on the different aspects of the spine and vertebral column have been conducted in the medical field (e.g., Ballane et al., 2017; Brinjikji et al., 2015; Bruno et al., 2014; Curry et al., 2016; Duan, Seeman et al., 2001; Harrington Jr. et al., 2001; Homminga et al., 2004; Läubli et al., 2021; Pouriesa et al., 2013; Ritzel et al., 1997; Ruyssen-Witrand et al., 2007; Schroeder et al., 2016; Takahashi et al., 2020). These have provided important understanding in both the biomechanics of the spine and on the aetiology of spinal disorders. However, as good as it is to study the current situation, it is sometimes also good to look back at where we have come from. It has taken millions of years for our spine to evolve to what it is today. Studies on fossil hominins have shown morphological differences in single vertebrae but also in the curvature of the spine (Been et al., 2012, 2017; Haeusler et al., 2011; Nalley et al., 2019; Sanders, 1998; Sanders & Bodenbender, 1994), indicating that the changes have not followed a one-way street. In addition, back disorders are not a new phenomenon; instead, signs of them have already been found in some of the oldest hominins, Australopithecines (Haeusler, 2019). Hence, understanding the changes that have occurred due to our upright posture and bipedal locomotion, and also in the course of hominin evolution, may help us to better understand the spine as it is today. This would not only be beneficial concerning spinal health, but also an important part of understanding our own evolution, as our back is a huge facilitator of our way of life. The upright position and bipedal locomotion are, after all, features that have preceded some of the most important human characteristics, such as brain size expansion, lithic tools and infant nursing (Vaughan, 2003; Ward, 2002).

Understanding the evolutionary background of our spine can help us discover the optimal conditions for the back and its health. In this way, we can evaluate the possible effects of the modern lifestyle on spinal health. We know, for example, that exercising and physical activity are better for the spine's bone density and intervertebral disc health than a sedentary lifestyle (Belavý et al., 2016, 2017; Bowden et al., 2018; Fredericson et al., 2007; Langsetmo et al., 2012; Raichlen et al., 2020; Strope et al., 2015), not a surprise given that past human populations are usually considered to have been more active. Our lifestyles have experienced rapid changes not only in the last few thousand years, which has seen the shift from hunter-gathering to agriculture, but even as recently as a couple hundred years, as we have shifted to an industrialised and then post-industrialised society. This time is relatively short compared to the time it took us to evolve from our common ancestor with the apes to *Homo sapiens* (around 8 to 5 million years) (B. Wood & Richmond, 2000). This means less time for any large evolutionary adaptations (Gingerich, 2001), especially considering that all this time our lifestyles have been in constant change. As such, it is possible that our spine is not well adapted to the new conditions it has been faced with and has not had enough time to properly adjust to them. On the other hand, bones are surprisingly good at adapting to changed biomechanical demands. An example of this could be the strengthening of the humerus and radius in long-term tennis players (especially if playing is started in prepuberty) (Ducher et al., 2005, 2009; Haapasalo et al., 1996) or the loss of bone density experienced by astronauts (Sibonga et al., 2015, 2019). As such, we need to consider both of the following: what kind of conditions and needs have moulded our spine originally throughout a long time span, and how the short-term adaptations to the changed physical activity levels might have influenced it in a short time span. Then, we need to consider how the divergence between the original and modern conditions might influence the current spinal health problems, while also taking into consideration the changes that have occurred in the vertebrae and spine in the most recent past.

As such, in this research, both evolutionary and short-term changes are studied, and the focus is mainly on the lower back. The first reason for concentrating on the lower back is that lower back pain is the most typical back ailment experienced by humans (Buchbinder et al., 2018; S. Chen et al., 2022). This relates to the second reason, which is that the lower back carries the most weight compared to the rest of the spinal elements. Finally, from an archaeological point of view, the vertebrae in the lower back are usually some of the most well-preserved vertebrae in archaeological material due to their larger size. Hence, they are both more numerous and in sufficient condition to be measured and studied.

The majority of the axial loading is carried by vertebral bodies, approximately 80% of compression forces versus the 20% carried by the neural arch and facets (Ghezelbash et al., 2020; Mobbs et al., 2013; Pollintine et al., 2004). Although, the posterior element facets have a significant contribution on the load-bearing, especially in extension and during shear forces, when they can support over 60% of the loads (Ghezelbash et al., 2020). Also, the degeneration and narrowing of the intervertebral disc increases the load-bearing of the facets and neural arch, which can end up resisting even 90% of the compressive loading (Pollintine et al., 2004). Yet as vertebral bodies and intervertebral discs are the main supporter of the compressive forces (Cramer, 2014; R. J. Leonard, 1995; Vipula & Atula, 2018), changes in the vertebral body's morphology or bone density could have significant effects on vertebral biomechanics. Ailments of the intervertebral discs can also be related to the vertebral bodies; for example, a fracture in the vertebral endplate can end up displacing the disc content into the vertebral body (Adams et al., 1993, 2000). The shape of the vertebral body and intervertebral disc can also impact the biomechanics of the discs and predispose them for disc herniation (Harrington Jr. et al., 2001; Hong-sheng et al., 2010; Pouriesa et al., 2013; Yates et al., 2010). Again, from an archaeological perspective, the vertebral bodies are often found to be a relatively well-preserved part and can, therefore, be very informative. For these reasons, the focus here was on the vertebral bodies of the lower back.

As the aim of this study was to research both the evolutionary and short-term changes, the logical start was to observe what types of morphological and bone density changes the vertebral bodies have experienced during evolutionary development. In the case of vertebral bodies, since they carry a significant part of the weight in all primates, they are influenced by the changed locomotion and weight distribution. Although previous studies have looked at some of the dimensional and relative size differences between humans and other primates (Cotter, 2011; Rose, 1975; Sanders, 1998; Sanders & Bodenbender, 1994; Schultz, 1961; Shapiro & Kemp, 2018), fewer have looked at the shape of the vertebral body (Plomp, Dobney et al., 2019; Plomp, Viðarsdóttir et al., 2015, 2019). As such, my first research question was how the vertebral body shape differs between extant hominoids and how it has changed over the course of human evolution. In addition to morphology, our bone density also adapts to new demands. Although humans have overall lower bone density than other primates (Chirchir, 2019; Cotter, 2011; Hernandez et al., 2009; Tsegai et al., 2018), the bone density and the inner structure of the bones have been demonstrated to be influenced by the locomotion and use of limbs (Patel & Carlson, 2007; Russo, 2019; Ryan & Shaw, 2012; Scherf et al., 2013; Sukhdeo et al., 2020; Tsegai et al., 2013). Although the spine works mainly as one element (Cramer, 2014; Glaser & Qureshi, 2017; Kent & Miller, 1996; Putz & Müller-Gerbl, 1996; Rockwell et al., 1938), the different functional segments of the spine are faced with different biomechanical conditions. Therefore, there could be differences in the pattern of bone density in the vertebral columns between species related to the different biomechanical demands due to locomotion and postural differences. Hence, my second research question is the following: does locomotion influence the vertebral bone density and its pattern in the subaxial vertebral column?

The second part of the research concentrates on the short-term changes. The aim was to study how past populations differed in vertebral body dimensions and age-related bone loss from contemporary populations. As already mentioned, bones can adapt to biomechanical demands during our lifetime. Although these changes are not hereditary and are influenced by individual lifestyles, hormones, the intake of calcium, etc. (e.g., Alghadir et al., 2015; Devine et al., 2004; Di Daniele et al., 2004; Goolsby & Boniquit, 2017; Helge & Kanstrup, 2002; Kelly et al., 1990; Modarress-Sadeghi et al., 2019; Narla & Ott, 2018; Oura, Auvinen, et al., 2019; Oura, Junno, et al., 2019; Oura, Niinimäki, et al., 2019; Prince et al., 1995), they can also demonstrate the influence of large-scale changes in societal lifestyles.

Hence, the following is my third research question: are there short-term changes in the vertebral dimensions?

Bone density, as already mentioned, is influenced by physical strain and can be impacted by the amount of physical activity. Earlier studies have already shown a decrease in bone density in the more modern sedentary populations (Chirchir et al., 2015, 2017). Research into more short-term changes has also demonstrated that age-related bone loss, which is a normal occurrence in contemporary humans, could have varied in the past populations (Agarwal, 2012; Agarwal & Grynpas, 2009; Lees et al., 1993; Mays et al., 2006). Since age-related bone loss and osteoporosis are such important concerns for the growing elderly population, my fourth research question was the following: have the considerable lifestyle changes in recent history impacted age-related bone loss?

Since aspects from both the evolutionary and short-term changes influence spinal health, my final research question was as follows: what are the implications of these evolutionary and short-term changes for spinal health?

In a way, our backbone really is our strength. It carries us through our lives and has abled our upright posture and bipedal locomotion that has led to our modern way of life. As such an important part of our past and present, we really should learn more about it and how to successfully manage it. After all, there are very few people who are unaware of the uncomfortable and crippling nature of back pain.

1.1 Vertebral column

The vertebral column´s main functions are to support the trunk and upper extremities, protect the spinal cord and spinal nerve roots, and to allow the movement of the trunk and head. It is composed of 34 vertebrae in humans. These consist of cervical vertebrae (7 vertebrae), thoracic vertebrae (12 vertebrae), lumbar vertebrae (5 vertebrae), sacral vertebrae (5 vertebrae) and coccygeal vertebrae (3–5 vertebrae) (Fig. 1). There is some variation in humans in the number of thoracic, lumbar or sacral vertebrae, although these anomalies are rarer. There might be 11 thoracic vertebrae or 6 or 4 lumbar vertebrae. The number of sacral vertebrae can also vary (Cramer, 2014; Devereaux, 2007; Huynh et al., 2012; Leppäluoto et al., 2008; Schultz, 1932, 1961).

In African apes, the typical number of thoracic vertebrae is 13 but they can also have 12 or 14 thoracic vertebrae, although similarly to humans, this is rarer. The lumbar segment consists of 3–4 vertebrae and does not usually vary from this. The sacrum consists mainly of 5–6 vertebrae. The cervical number of 7 vertebrae is very conservative across the mammals (Galis, 1999; Narita & Kuratani, 2005), which is also the case in hominoids (Schultz, 1961).

The vertebrae are composed of two parts: the vertebral body and arch. The vertebral bodies are the cylindrical, main weight-bearing parts that are connected through the intervertebral discs, which represent about 25% of the height of the spine (Cramer, 2014; Devereaux, 2007; R. J. Leonard, 1995; Leppäluoto et al., 2008; Vipula & Atula, 2018). The arch is a u-shaped element attached to the body. It consists of two laterally placed, cylindrical pedicles that are united posteriorly (R. J. Leonard, 1995). It has several unique structures, including the superior and inferior articular processes (Fig. 2 and 3) that form synovial joints on the posterior side (see Fig. 1 for an illustration of the directional terms). The spinal canal that is located between the body and the arch is formed by the posterior wall of the vertebral body and the arch (Mathis et al., 2004).

The different vertebrae are commonly referred to in the abbreviated form of C, T, L and S, followed by the running number of the segment from a cranial direction, e.g., C1, which is the first cervical vertebrae from the cranium or T1, which is the first thoracic vertebrae after the cervical vertebrae (Aiello & Dean, 1990a:285).

In humans, the vertebral column is not straight; instead, each of the segments is slightly curved. In the cervical and lumbar segments, the curve is convex forward and called lordosis. In the thoracic segment and sacrum, the curves are concaved forward and called kyphosis (Fig. 1) (Aiello & Dean, 1990a:285; Viranta-Kovanen, 2019). The concave forward curvatures in the thoracic segment and the sacrum are primary curvatures that are present already in prenatal life, making the back appear "C-shaped". The convex forward curvatures in the cervical and lumbar segments are secondary and appear in early childhood, changing the appearance of the spine to "S-shaped". The cervical lordosis starts to appear around three months of age, as the infant starts to hold their head upright and the lumbar lordosis, around 1.5 years of age, when the child learns to walk. This s-shape is the main feature that enables humans to balance their weight efficiently over the feet in bipedal locomotion (Aiello & Dean, 1990b:429–441; Bagnall et al., 1977; Cramer, 2014; Rajalakshmi & Legesse, 1940).

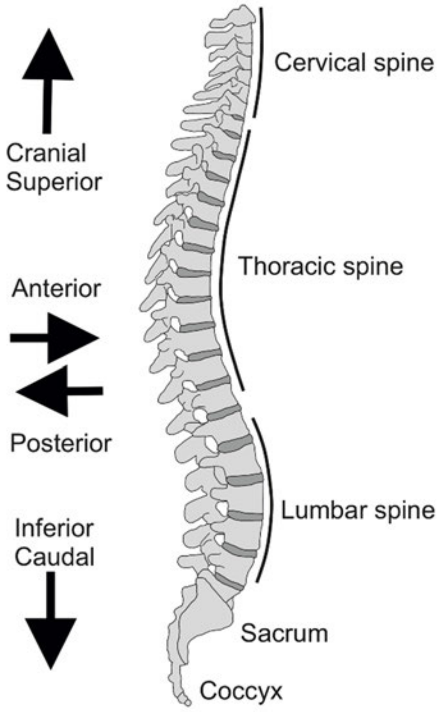

Fig. 1. Illustration of the spine and its segments. Also illustrates the directional terms.

In apes, the vertebral column lacks extreme curvatures, and has an overall slight C-curvature (Aiello & Dean, 1990a:285; Torres-Tamayo et al., 2020). A slight cervical curvature evolves when they are able to carry the head independently. The thoracic kyphosis is already present from birth, and a very slight lumbar lordosis is established postnatally (Martelli, 2019:269–270). The lumbar region is short and relatively straight. The final lumbar vertebra is often flanked from both sides by the high iliac blades that almost reach the lowest ribs, which also limits the flexibility of the lower back in apes (Aiello & Dean, 1990a:285, 1990b:429; Shapiro & Russo, 2019; Torres-Tamayo et al., 2020).

One of the main functions of the vertebral column is to facilitate the movement of the body. Together the vertebrae, the intervertebral discs, facet joints and the associated ligaments form a semiflexible rod that allows flexion, extensions, lateral flexion (or side bending), rotation and circumduction. The relative thickness of the individual intervertebral disc determines the amount of possible motion between adjacent vertebrae. The total movement of the vertebral column is the sum of the motion of the individual intervertebral discs (Cramer, 2014; Mathis et al., 2004; Vipula & Atula, 2018). The facet joints also allow motion to occur but are perhaps more important in their ability to determine the direction and limitation of the movement that can occur between vertebrae (Cramer, 2014).

The vertebrae are formed during development from three primary centres that surround the developing neural tube. One primary centre is located in the anterior part of the future vertebrae and forms the vertebral body. The other two primary ossification centres are located on each side of the portion of the vertebra that surrounds the neural tube. These regions form the vertebral arch (Cramer, 2014).

1.1.1 Types of vertebrae

In the cervical vertebral column, the first two vertebrae (C1 and C2) are untypical, as they differ in morphology from other vertebrae and are called the atlas and axis. The atlas is ring-shaped and has no vertebral body or spinous process. It has a large vertebral foramen, and its superior facets are concaved and elongated to articulate with the occipital condyles at the bottom of the skull. The movement of nodding the head relies mostly on this joint. The axis also lacks the vertebral body but has the dens, a small peg of bone that protrudes upwards behind the anterior arch of the atlas. This enables the horizontal rotation of the head (Aiello & Dean, 1990a:275–285; White & Folkens, 2005:163–169).

The C3 to C6 are typical cervical vertebrae with small vertebral bodies that interlock with their saddle-shaped superior and inferior surfaces. At the root of the vertebral arch and to both sides of the vertebral body are transverse foramina, holes through which the vertebral arteries pass. Their spinous processes are small and bifid at the end and tend to project somewhat horizontally behind the vertebral body. The transverse processes are very small. The articular facets (superior and inferior) that articulate with those from the neighbouring vertebrae are cup-shaped or planar (Aiello & Dean, 1990a:275–285; White & Folkens, 2005:163–169).

The C7 is also an untypical cervical vertebra, as it is transitional between typical cervical and typical thoracic vertebrae. It has the largest vertebral body of the cervical vertebrae, and its inferior surface is flat. The spinous process is relatively long, and the transverse processes are well-formed. But unlike thoracic vertebrae, it has the transverse foramina next to the vertebral body, and it lacks the articular facets for the ribs (Aiello & Dean, 1990a:275–285; Forseen & Borden, 2016a:70–76; Hervonen, 1994; White & Folkens, 2005:163–169).

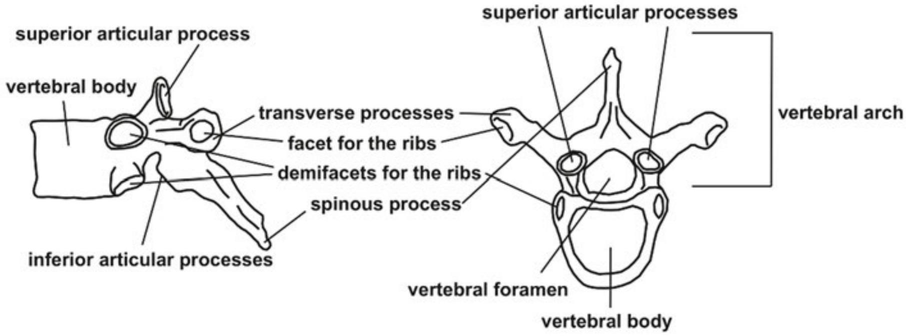

Fig. 2. Illustration of the structure of a typical thoracic vertebra.

Thoracic vertebrae T1–T10 (Fig. 2) can be recognised from their articular demifacets for the ribs on the lateral sides of the vertebral body and “whole” facets in the transverse processes. T11 and T12 only have superiorly placed facets on each side of the vertebral bodies. All thoracic vertebrae have prominent, laterally oriented transverse processes. Their spinous processes are elongated, straight and narrow, and are oriented downwards. The articular facet joints for the neighbouring vertebrae are vertically aligned, making a larger rotation movement possible compared to lumbar vertebrae (Aiello & Dean, 1990a:275–285; Forseen & Borden, 2016b:136–144; White & Folkens, 2005:180–176).

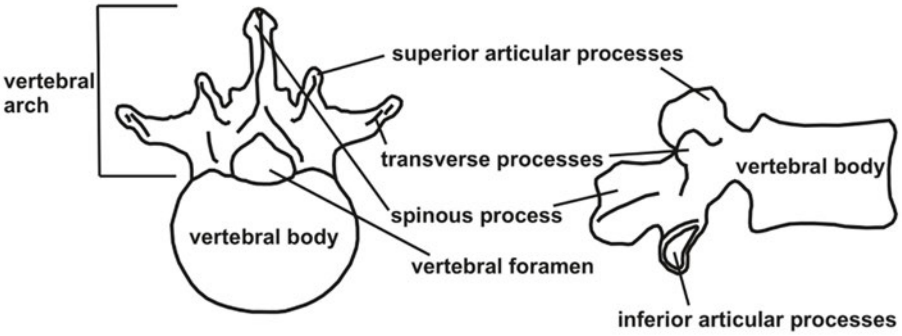

Fig. 3. Illustration of the structure of typical lumbar vertebra.

Lumbar vertebrae L1–L5 (Fig. 3) are the largest vertebrae in the whole column. Vertebral bodies have larger transverse dimensions than anterior-posterior dimensions. In the axial plane, vertebral bodies of L1 to L4 have anterior concavity, which causes them look kidney shaped. The L5 vertebral body instead has a convex anterior margin, making it ellipse shaped. Vertebral bodies also increase in size from L1 to L5. Lumbar lordosis is more pronounced than the cervical lordosis and begins at L1–L2, increasing towards the sacrum. Hence the vertebral bodies, especially the lower vertebrae, are wedged, with their anterior height being greater than posterior height (Aiello & Dean, 1990a:275–285; Devlin & Bergey, 2011:26–27; Forseen & Borden, 2016c:188–193; White & Folkens, 2005:176–180).

Lumbar vertebrae lack both the transverse foramina and the facets for the ribs. The vertebral arch is relatively small compared to the size of the vertebral body. The spinous processes are hatchet-shaped, large and blunt. They are more horizontally oriented than in the thoracic vertebrae. The transverse processes are also relatively smaller and thinner than in thoracic vertebrae but increase in size towards the sacrum. They have concave superior and convex inferior articular facets, which limits their movement with each other (Aiello & Dean, 1990a:275–285; Devlin & Bergey, 2011:26–27; White & Folkens, 2005:176–180).

1.2 Biomechanics of the vertebrae

Biomechanics is the application of mechanical principles on a living organism (Innocenti, 2017). In the case of the bone, this refers to the relationship between forces, or loads, applied to the bone and the deformations that result from these applied forces. This includes external forces, such as a ground reaction force during walking or an impact force due to a fall, internal forces created by ligament tension or muscle contractions, and internal bone-on-bone contact forces (Castillo & Lieberman, 2018; K. Kim et al., 2010; Morgan & Bouxsein, 2008; Myers & Wilson, 1997; Rohlmann et al., 2006; Shirazi-Adl et al., 2005; Snijders et al., 1991). These usually create compression and shear forces on the vertebrae, where compression acts in the crania-caudal direction and shear in the anterior-posterior direction. The loading on the vertebrae is influenced by posture or activity, falls, an individual's height and weight, muscle forces, spinal curvature, disc degeneration and neuromuscular control (Cai et al., 2020; Castillo & Lieberman, 2018; Christiansen & Bouxsein, 2010; Frei et al., 2002; Han et al., 2013; K. Kim et al., 2010; Myers & Wilson, 1997; Prakash et al., 2007; Rohlmann et al., 2006; Shirazi-Adl et al., 2005; Snijders et al., 1991). Forces have been demonstrated to be up to eight-fold higher during bending and lifting (depending on the weight of the lifted object) than experienced during upright standing (Bouxsein et al., 2006). About three-quarters of the axial loading is carried by the anterior column (i.e., the vertebral bodies and intervertebral discs) (Ferguson & Steffen, 2003). Vertebral body strength is influenced by the vertebral size and shape, bone density and microarchitecture, and bone tissue properties (Christiansen & Bouxsein, 2010).

From an engineering point of view, a vertebral fracture represents a structural failure of the bone. This happens when forces applied to the bone exceed its load-bearing capacity (Morgan & Bouxsein, 2008). Research on vertebral fractures has shown that both the larger size of the vertebral body and higher bone density increase the strength of the bone (Christiansen & Bouxsein, 2010). Women have demonstrated to have about 25% smaller vertebral bodies than men, even if matched for age, weight, bone density (mg/cm^3) and vertebral body height (Gilsanz et al., 1994). Due to the larger size of the vertebral bodies, men have higher vertebral strength at all ages (Bouxsein et al., 2006). There is also some research that indicates that the shape of the vertebral body could have a connection to vertebral fractures (Ross et al., 1995; Vega et al., 1998), but this is still a relatively scarcely studied subject. However, vertebral shape has been found to have a possible connection on intervertebral disc herniation (Harrington Jr. et al., 2001; Hong-sheng et al., 2010) and Schmorl’s nodes (which are caused by disc herniation into vertebral body) (Plomp, Dobney et al., 2019; Plomp et al., 2012; Plomp, Roberts et al., 2015; Plomp, Viðarsdóttir et al., 2015).

Most often, the vertebral fractures are connected to bone density and the microarchitecture. Vertebral bodies consist mainly of the spongy trabecular bone (Genant et al., 2007; Legrand et al., 2000; Myers & Wilson, 1997; Nevitt et al., 1999).The cortical bone, which is often described as condensed trabeculae in vertebrae, forms the thin shell of the vertebral body (Eswaran et al., 2005). Most of the compressive forces are carried by trabecular bone (Myers & Wilson, 1997). Roux et al. (2010) suggested that the cortical shell could influence the flexibility and energy absorption of the vertebral body, whereas trabecular bone might affect the load-bearing capacity. Although, it might be that the contribution of the cortical shell on the load-bearing capacity increases during ageing due to age-related trabecular bone loss (Christiansen et al., 2011). Age-related bone density loss is a normal occurrence in both men and women during ageing. It is caused by bone turnover, which becomes unbalanced with age, meaning that more bone is being resorbed than is deposited (Robey & Bianco, 1999). In women, menopause has been documented to increase bone loss (Bouxsein & Karasik, 2006; Hayashi et al., 2011; Oppenheimer-Velez et al., 2018; Riggs et al., 2004). This is related to oestrogen, which normally inhibits bone turnover and limits resorption. After menopause, the loss of oestrogen increases bone remodelling, which especially increases resorption compared to bone formation (Brickley et al., 2008).

This remodelling of the bone material affects the microstructure of the trabecular bone and compromises its strength. Studies have been conducted on how the microarchitecture of the trabecular bone changes during ageing. For example, it has been shown that the number of trabeculae decreases, which increases the trabeculae separation. Some studies have also reported the thinning of the trabeculae during ageing. These changes make the bone more porous and fragile (H. Chen et al., 2013; Stauber & Müller, 2006).

According to bone microarchitecture, it seems that vertebrae and vertebral bodies are well adapted on axial compression (Smit et al., 1997). However, they must also be able to withstand additional forces from contraction of the axial and proximal limb muscles (Cramer, 2014). Especially from the biomechanical point of view, spinal loads are an important factor, and as muscle forces stabilise the spine, they have a great influence on spinal loading (Rohlmann et al., 2006). Studies on spinal loads have also demonstrated that movements cause changes in spine loading, and movements like flexion and extension tend to increase the compressive forces in parts of the spine (e.g., Arshad et al., 2018; Bayoglu et al., 2019; Bruno et al., 2017; Ignasiak et al., 2018; Rohlmann et al., 2006).

1.3 Back ailments as a current health concern

Back ailments and back pain are increasing health concerns across the world. Systematic reviews of studies on lower back pain have indicated that a one-year prevalence of lower back pain ranges between 22–65% and a lifetime prevalence between 11–84% (Airaksinen et al., 2006). According to the Global Burden of Diseases, Injuries, and Risk Factors Study in 2017 (IHME, 2023), lower back pain was the leading cause of years lived with disability (YLDs) globally. The increase in YLDs from 1990 to 2017 had been 52.7% (Wu et al., 2020).

In Finland alone, the lifetime cumulative occurrence of back pain has been reported to be 76.7% for men and 75.8% for women in the Health 2000 study. The prevalence of back pain in the previous month (prior to the survey) was 28.2% for men and 33.1% for women. Eleven per cent of the participants (both sexes) had received chronic low-back syndrome diagnoses. Even in the youngest age group, from 18 to 24 years old, nearly two-thirds were reported to have suffered from back pain sometime during their lives (Publications of the National Public Health Institute, 2007).

Musculoskeletal system diseases were the second largest category to receive KELA's (the Social Insurance Institution of Finland) sickness allowances and partial sickness allowance in 2021 after mental health problems. For back pain alone, 32 068 people received sickness allowance costing 83 213 000 euros, which was 9.7% of sickness allowances paid in the year 2021. Partial sickness allowances for back pain was received by 3 149 people, costing 6 265 000 euros, which was 10.4% of the partial allowances (Kela, 2022). The paid allowances appear to have decreased since the 2011 statistics (Kela, 2012), but whether this was caused by an improvement in people´s health or tightening of the allowance terms is unknown. Private healthcare provider Terveystalo estimated in 2013 that back-problem-related sick leaves had cost society and businesses around 120 million euros in the previous year. They also pointed out that the actual number is likely larger, as their estimation did not include the sick leaves that did not require doctor visits, which are often related to back pain (Lapintie, 2013). In 2016, Terveystalo also reported that back pain was the largest cause of sick leaves in the preceding year (Simonen, 2016). As a large provider of occupational healthcare, their statistics can reflect the health of the entire working population.

A large portion of back ailments, unfortunately, do not get a proper clinical diagnosis (Airaksinen et al., 2006; Ellenberg & Ellenberg, 2011; Kirnaz et al., 2022; Maher et al., 2017). The reason for this is that the causes of back pain can be very diverse, and sometimes other conditions and diseases around the body can be the origin (Airaksinen et al., 2006; Ellenberg & Ellenberg, 2011; Maher et al., 2017). Yet a number of spinal disorders are related to the bones themselves, which can be very painful. Some of the most common ones are vertebral fractures, vertebral disc herniation, osteoarthritis and vertebral disc degeneration (Adams & Roughley, 2006; Borenstein, 2004; Huang et al., 1996; Kendler et al., 2016; Kirnaz et al., 2022; Luoma et al., 2000; Matthis et al., 1998; Ross, 1997; Truumees, 2011; Yeung et al., 2012). As already mentioned, the focus of this research is on the bony structure of the spine (i.e., the vertebrae), and specifically the morphology and bone density of the vertebral body. Hence, this research mainly discusses disc herniation, osteoporosis and vertebral fractures.

1.3.1 Osteoporosis and vertebral fractures

Osteoporosis is a chronic metabolic bone disease, that leads to the detrition of bone mass and microarchitecture, affecting the strength of the bone (Holroyd et al., 2008; Mika et al., 2005; Rachner et al., 2011). It increases the fragility of the bone and, as a consequence, increases the susceptibility to fractures. The definition of osteoporosis is typically based on bone mineral density (BMD). In women of European ancestry, this means a fall of more than 2.5 standard deviation (SD) below the young mean (Holroyd et al., 2008). As men tend to suffer less from this condition, there is not a clear consensus in the definition for men compared to women. However, some research has suggested that the same cut-off point might work for men too (Kaufman & Goemaere, 2008). In addition to primary osteoporosis, bone density loss can also be caused by some general illnesses, medications and cancerous metastatic tumours in the skeleton.

For females, the prevalence of osteoporosis in industrialised countries is estimated to range between 9 to 38% based on hip and vertebral BMD. In men, the prevalence ranged from 1 to 8% (Wade et al., 2014). Hence, it is not surprising that women tend to have a two-to-three-fold greater incidence of vertebral fractures than men (Cummings & Melton III, 2002; O'Neill & The European Prospective Study Group, 2002). Research has indicated that as young adults, men and women do not seem to differ significantly in bone density. (Bouxsein & Karasik, 2006; Ebbesen et al., 1999; Oppenheimer-Velez et al., 2018; Riggs et al., 2004). Osteoporosis is, however, aggravated by age-related bone loss, which especially increases in women after menopause (Bouxsein & Karasik, 2006; Hayashi et al., 2011; Oppenheimer-Velez et al., 2018; Riggs et al., 2004). Although some research has suggested that instead of losing a greater amount of bone material, the difference in bone density might be caused by women's reduced periosteal bone formation. In other words, as bone resorption occurs during ageing, causing the decrease of both cortical and trabecular bone density, a new bone is laid down on the outer (periosteal) surface of the bone, reducing the net loss of bone. As women experience less formation of new bone, this would increase bone loss compared to men (Duan, Turner et al., 2001). Bone loss is also influenced by the intake of calcium and vitamin D. The received vitamin D levels can be affected by the geographical location and especially affect people in northern latitudes, where sunlight is scarce for a large part of the year.

Vertebral fractures are seen as the hallmark of osteoporosis. Non-traumatic or low-impact vertebral fractures are typically very rare unless the strength of the vertebral body has been compromised by low bone density. It is estimated that less than half of vertebral fractures end up being clinically diagnosed (Lindsay et al., 2001) due to them often being asymptomatic (N. Kim et al., 2004). However, both symptomatic and asymptomatic fractures are associated with increased morbidity (Lems, 2007; Ross et al., 1995) and mortality (Ensrud et al., 2000; Kado et al., 1999, 2003). If they remain untreated, they can cause height loss, increased kyphosis, chronic back pain and spinal-related functional disability (Burger et al., 1997; Fink et al., 2003, 2017; Lyles et al., 1993). Studies have also shown that vertebral fractures are associated with decreased quality of life (Al-Sari et al., 2016; Lips et al., 1999; Nuti et al., 2014; van Schoor et al., 2005). The clinical diagnosis of the vertebral fractures would also be important, as one fracture significantly increases the risk of a subsequent fracture in both men and women (Hasserius et al., 2003; Ismail et al., 2000; Lindsay et al., 2001; Lunt et al., 2003).

1.3.2 Intervertebral disc degeneration, Schmorl's nodes and disc herniation

The intervertebral discs separate the consecutive vertebrae and facilitate movement of the back. The facilitated movement of a single disc is only minimal, but as a whole they enable great flexibility of the spine. The discs also have an important role in providing support and dissipating energy during activities (Adams et al., 2006, 2013:11–13; Hussien et al., 2009; Kirnaz et al., 2022). For this reason, the discs need to be pliable, but at the same time strong and stiff, to sustain the compression loads between the vertebral bodies. They have mainly three components: the annulus fibrosus, which consists of 10–20 sheets of collagen, which are tightly packed together in a circumferential fashion; the nucleus pulposus, a hydrated gel that is located in the centre of the disc; and superior and inferior vertebral endplates, consisting of hyaline cartilage that covers the superior and inferior side of the disc and binds the discs to the vertebral bodies (Adams et al., 2013:11–13; Devlin & Bergey, 2011; Kirnaz et al., 2022; Martin et al., 2002). The overall content of the disc collagen decreases with age. The nucleus also becomes dry, fibrous and physically stiff with age (Adams et al., 2006, 2013:95-96; Newell et al., 2017; Urban et al., 2000). However, old but non-degenerated discs do not normally narrow with age (Adams et al., 2013:96). An interesting observation is that mammals seem to be the only vertebrates with nucleus pulposus (Bruggeman et al., 2012). It also seems that not all mammals experience similar ageing of the nucleus pulposus as humans. In these animals (e.g., rodents and cats), notochordal cells that disappear in humans by four years old persist throughout adulthood, keeping the disc translucent and semi-liquid (Urban et al., 2000).

Disc degeneration is not the same as ageing of the disc, but it does occur more often in older discs. It is also often difficult to separate ageing from degeneration. Although degeneration can involve the same changes as seen in ageing discs, it is also associated with gross structural changes, which tend to appear after the age of 20 (Adams et al., 2006, 2013:196–199; Kirnaz et al., 2022; Martin et al., 2002; Peng et al., 2006). The structural failures are also naturally progressive, e.g., damage in one part of a disc increases the load bearing of adjacent tissues, hence spreading the damage (Adams et al., 2000, 2013:196–199). For this reason, the frequency and severity of the condition increase with age. The original damage is usually caused by different combinations of compression, bending and torsion loads, which can be produced by injury or wear-and-tear ‘fatigue’ loading (Adams, 2004; Adams et al., 2013:196–199). However, the most important factor of human disc degeneration might be the various processes that weaken the disc prior to the damage, or hinder its healing process (Adams, 2004; Adams et al., 2013:196–199; Battié & Videman, 2006; Chan et al., 2006). This is supported by results that have indicated a strong genetic influence on disc degeneration (Adams et al., 2013:196–199; Ala-Kokko, 2002; Battié et al., 2004; Feng et al., 2016).

One of the tears that can occur in disc degeneration is radial fissures, which progress outwards from the nucleus. These fissures can cause disc radial bulging, which can create osteophytic growth in the outer margin of the vertebral body; and/or nucleus degeneration, which can lead to disc herniation. Disc herniation occurs when the nucleus pulposus is displaced through the annulus through these fissures to the periphery of the disc (Adams et al., 2013:200–201; Adams & Dolan, 2012; Vialle et al., 2010). Depending on the extent of the displacement, this can cause either protrusion, where the annulus bulges clearly, but is not ruptured; extrusion, where the annulus is ruptured, but the expelled nucleus is still attached to the disc; or complete prolapse, where the disc tissue is expelled from the disc and is no longer attached to it (Adams et al., 2006, 2013:200–201; Devlin, 2011).

In the case of endplate fractures, it is often followed by vertical herniation of the nucleus pulposus tissue into the vertebral body. A calcified shell is created around the displaced tissue. This shell is detectable in radiographs and referred to as Schmorl’s node (SNs). It is also easily observable in dry bones. They are most common near the thoracolumbar junction and can often be found also in asymptotic individuals (Adams et al., 2013:206–207; Kyere et al., 2012; F. M. K. Williams, et al., 2007). They are, however, strongly connected to degenerative disc disease that is known to cause pain. Research has shown that both SNs and degenerative disc disease have a strong relationship with genetics (Adams et al., 2013: 206–207; Mattei & Rehman, 2014). Also, the increased size of the SNs can increase the risk of vertebral fractures due to the disruption of the integrity of the vertebral body (Mattei & Rehman, 2014).

1.4 Evolutionary background of back ailments

Although back ailments seem to be on the rise in contemporary populations, due to the increase in average life expectancy and an increasingly larger elderly population, they are not a new problem. Numerous archaeological studies have documented occurrences of spinal pathologies in past populations, typically looking for signs of osteoarthritis, SNs, osteophytosis and fractures (e.g., Hussien et al., 2009; Jiménez-Brobeil et al., 2012; Novak & Šlaus, 2011; Richardson, 2018; Saluja et al., 1986; Üstündağ, 2009). Degenerative lesions (e.g., osteoarthritis and vertebral osteophytosis) are typically caused by degenerative changes in the vertebral disc with secondary changes in the adjacent vertebrae, which can then be observed in the bones. These lesions are often found on the vertebral body and the superior and inferior articular facets (Hussien et al., 2009). They are typically found in over half of the mature (approximately +45 years old) population and are usually slightly more common in males. SNs are an easily observable pathology in archaeological vertebrae, and although much rarer than the degenerative lesions, they are similarly slightly more common in males. The frequency or severity of SNs do not increase with age, and they tend to be more common in thoracic than lumbar vertebrae (Jiménez-Brobeil et al., 2012; Novak & Šlaus, 2011; Saluja et al., 1986; Üstündağ, 2009).

However, the roots of the ailments seem to be even further in the past, as even the fossil hominins reportedly show signs of spinal pathologies. For example, some of the older fossil hominins (*A. afarensis*, *A. africanus*, *P. robustus*) and a few *H. neanderthalensis* seem to have suffered from Scheuermann's disease, also known as juvenile kyphosis. It causes an abnormal increase in thoracic kyphosis, which is then also compensated in the lumbar by increased lordosis. This condition is one of the most common spinal deformities in humans and has been connected to upright bipedalism. The surprisingly high prevalence of the disease found in fossil hominins is contrasted by their lack of idiopathic scoliosis, the prevalence of which in modern humans is about the same as Scheumann's disease. Also, many specimens, from the earliest hominins to the Neanderthals, have shown signs of degenerative osteoarthritis changes in the facet joints, although these seem to become more widespread in the Neanderthals. Scheumann's disease usually indicates problems in the growth phase of the spine, whereas osteoarthritis is more typical in older individuals (Haeusler, 2019).

Instead, our closest extant relatives, the Great Apes, seem to show fewer signs of spinal pathologies, as Jurmain (2000) reported that African apes exhibited less vertebral osteophytes (bony projections that form along joint edges) and spinal osteoarthritis than humans. Vertebral fractures, both traumatic and low-energy, are also relatively rare (Carter et al., 2008; Jurmain, 2000; Schultz, 1939). This could suggest that issues with the back seem to have risen after the postural change and adaptation to bipedal locomotion. Interestingly, Plomp, Viðarsdóttir et al. (2015) studied the connection between vertebral morphology and SNs in two vertebrae in humans, chimpanzees (*Pan troglodytes*) and orangutans. They found that humans with SNs and chimpanzees tended to fall between healthy humans and orangutans. Humans with SNs and chimpanzees did show more similarities in morphology than the two human groups. They suggested that this could mean that humans who are closer to the ancestral end of the range of shape variation in *Homo* might not be as well adapted for bipedalism and hence be more affected by disc herniations. They later continued the study by including different extinct hominins, and similarly, the results indicated more similarity between the pathological humans and the extinct hominins than healthy humans (Plomp, Dobney et al., 2019).

Humans also appear to have lower bone density in the vertebrae compared to other hominoids (Cotter, 2011; Hernandez et al., 2009), although this pattern seems to be typical in the whole axial skeleton (Chirchir, 2019; Tsegai et al., 2018). Lower bone density in the vertebrae is suspected to increase human susceptibility to spinal disorders, such as osteoporosis (Cotter et al., 2011; Hernandez et al., 2009). The results have also indicated that African apes might not experience as much age-related bone loss as humans (Ruff et al., 2020), which could partly explain the differences in back ailments between humans and other hominoids.

The research on fossil hominin vertebrae and vertebral column features has implied that the vertebral column can adapt to accommodate different needs. Been et al. (2017) studied the spinopelvic alignment (i.e., the interaction between pelvic orientation, spinal curvatures and the line of gravity) in four different hominin groups (*H. sapiens*, *H. neanderthalensis*, *H. erectus* and *Australopithecus*) by measuring the pelvic incidence, lumbar lordosis, thoracic kyphosis and cervical lordosis. They found that *H. sapiens* and *H. erectus* had moderate to high spinal curvature and pelvic incidence. Neanderthals instead had small spinal curvatures and pelvic incidence. Australopithecines, on the other hand, had compound alignment with moderate pelvic incidence and lumbar lordosis but an almost straight cervical segment. Been et al. (2017) suggested that different configurations of the curvatures could have offered different advantages and disadvantages for different hominin species. For example, Neanderthals had straighter curvatures, which made their backs more stable and was an advantage for carrying heavy loads.

On the other hand, the configuration was not as good at absorbing ground reaction forces and likely meant lower walking velocity on flat terrain. The straighter neck in compound alignment found in Australopithecines was similarly suspected to produce a more stable neck and was often associated with larger spinous processes, indicating larger muscle attachments in the neck. The smaller cervical lordosis was also associated with larger mandibles, likely giving them more room to move. A stable neck would have also provided a good basis for upper limb muscle attachments, which might have been needed given that at least some of the species are known to have relatively large upper limbs (Been et al., 2017).

1.5 Aims of the research

The aim of my research was to study the evolutionary and short-term changes that have occurred in the morphology and bone density of the vertebral body, mainly focusing on the lumbar segment. Can some kind of overall temporal trend be observed, and how have these changes possibly contributed to some of the most common back ailments found in modern humans?

The lumbar shape comparison of humans and African apes (article I) was to give us perspective on how the locomotion differences have affected the shape of the vertebrae. Previous research has already shown that humans have relatively larger and mediolaterally (ML) wide vertebral bodies (Hernandez et al., 2009; Cotter, 2011; Rose, 1975; Schultz, 1961). Only a few studies have focused on the shape of the cranial surface of the vertebral body (Plomp, Dobney et al., 2019; Plomp, Viðarsdóttir et al., 2015), but there are indicators that vertebral shape might actually play a part in some of the most common vertebral ailments (Harrington Jr. et al., 2001; Hong-sheng et al., 2010; Plomp et al., 2012; Plomp, Roberts et al., 2015; Plomp, Viðarsdóttir et al., 2015; Ross et al., 1995; Vega et al., 1998). Hence, to determine if the shape of the vertebral body is influenced by locomotion, four hominoid species (*H. sapiens*, *P. troglodytes*, *G. gorilla* and *G. beringei*) were compared in all lumbar levels to see if they differed from each other. They were then also compared by using the second to last lumbar vertebrae, as it represents anatomically corresponding vertebrae. To give us even a wider perspective, fossil hominins (Late Pleistocene *H. sapiens*, *H. neanderthalensis*, *A. seliba*, *A. africanus*, *A. afarensis*, *P. robustus* and *H. erectus*) and a few fossil hominoids (*P. nyanzea*, UMP67-28 and StW656) were also added to indicate if the shape of the vertebral body has already been similar from the beginning of the bipedal locomotion or if it is a derived trait that has evolved after bipedalism. It is also interesting to see if there is an evolutionary trend towards a certain shape.

The bone density and cortical thickness of the apes and their pattern was studied (articles II and III) to see if the variation of the bone parameters between the vertebrae in the whole subaxial vertebral column or between the functional segments are different, not only compared to humans but also between the ape species themselves. It is shown that humans tend to have lower bone density compared to other primates and apes (Chirchir, 2019; Chirchir et al., 2015; Cotter, 2011; Hernandez et al., 2009; Tsegai et al., 2018). Studies have also been conducted on how bone density or its microarchitecture varies in different bones (Russo, 2019; Ryan & Shaw, 2012; Scherf et al., 2013) or inside of single bones (Patel & Carlson, 2007; Sukhdeo et al., 2020; Tsegai et al., 2013) between different species of primates in relation to the locomotion, posture or use of the limbs. They have indicated that differences in bone density, or its microarchitecture, can be observed between different locomotion and posture groups, showcasing the adaptability of the bone to mechanical demands. However, there is no research that would have studied the variation of bone density between adjacent vertebrae of the whole vertebral column or between the functional segments in apes or other primates. Although this is not widely studied in humans either, at least multiple vertebral segments have been studied, which give us an idea of the variation of bone density in the whole vertebral column (Curylo et al., 1996; Hayashi et al., 2011; Salzmann et al., 2020; Yoganandan, Pintar, Stemper, Baisden, Aktay, Shender, & Paskoff, 2006; Yoganandan, Pintar, Stemper, Baisden, Aktay, Shender, Paskoff et al., 2006). The vertebral column, although consisting of individual vertebrae does function as more or less a single unit (Kent & Miller, 1996; Putz & Müller-Gerbl, 1996; Rockwell et al., 1938); hence, the hypothesis was that, as such, it could display a different pattern of bone density related to locomotion or posture, similarly to what is found in single bones. On the other hand, the different spinal functional segments are also confronted by different biomechanical conditions, due to their differences in mobility and loading. Therefore, it is likely that there are differences in the bone parameters between the functional segments. Due to differences in locomotion and posture, comparison of the observations of the apes to contemporary humans is expected to show variation in both the pattern of bone parameters in the whole spine but also between the functional segments. As the ape species also represents a great deal of size variation, and in the case of gorillas, sexual dimorphism, the difference between the ape species and sexes was also studied. This was done to see if the apes themselves showcased differences despite having very similar locomotion and posture and if the pattern between sexes was similar between species.

In the second part of this study, to observe the short-term changes in vertebral morphology, a sample of Finnish archaeological individuals was compared to a contemporary Northern Finnish population, to determine if there have been changes in the size, shape or dimensions of the vertebral body (article IV). A previous study comparing contemporary and medieval populations found that contemporary humans may have less mediolaterally wide but craniocaudally taller vertebral bodies (Junno et al., 2009). As the size and shape of the vertebral body have been indicated to influence the vulnerability to vertebral fractures and disc herniation (e.g., Harrington Jr. et al., 2001; Hong-sheng et al., 2010; Ross et al., 1995; Ruyssen-Witrand et al., 2007; Vega et al., 1998), these sorts of changes could affect the spinal health of contemporary populations. On the other hand, since large lifestyle changes have occurred in the Finnish population in the last couple of hundred years, the observed changes could also illuminate the adaptations that the spine and vertebrae exhibit in relation to the decreased physical activity. This could also give us a better idea of what might happen in the future, given the increasingly sedentary lifestyle of the post-industrialised society. The influence of the increased stature of contemporary humans was also taken into consideration as the parameters were also analysed adjusted for the height.

In addition to the short-term changes in vertebral morphology, changes in age-related bone loss were also studied (article V). Age-related bone loss is a normal occurrence in contemporary humans, however, sometimes this bone loss is so great that it leads to osteoporosis. Previous studies on archaeological populations have indicated that the pattern of bone loss might not have always been the same as that observed in contemporary post-industrialised populations (Agarwal, 2012; Agarwal et al., 2004; Agarwal & Grynpas, 2009; Beauchesne & Agarwal, 2017; Ekenman et al., 1995; Lees et al., 1993; Mays, 1996, 2000, 2001, 2006; Mays et al., 2006). For example, a difference was observed between past rural and urban populations. In medieval rural settings, both men and women tended to lose density already at a younger age but not in older ages. In medieval urban settings, the pattern was more like the one found in contemporary populations, with women also losing more bone than men (Agarwal, 2012). It has also been reported that, whereas medieval and industrialised women tended to experience cortical bone loss, only industrialised men showed signs of bone loss (Mays, 1996, 2000, 2001, 2006). As osteoporosis and fractures related to it are especially an increasing health concern given the growing elderly population, understanding the influence of lifestyle and the increased urbanisation on age-related bone loss can yield its own view on the discussion.

As for the final part of my research, the aim was to consider all the results together and answer the fifth and final research question: what do all of these observations tell us about the adaptation of the vertebrae, and what might be the implications for spinal health? As this discussion is based on the results from the other four research questions, this question is covered at the end of the discussion section.

1.5.1 Research questions and hypothesis

Here I present my five research questions:

1. How does the vertebral body shape differ in extant hominoids, and how has it changed during human evolution?
2. Does locomotion influence the vertebral bone density and its pattern in the subaxial vertebral column?
3. Are there short-term changes in the vertebral morphology?
4. Have the significant lifestyle changes in recent history affected age-related bone density loss?
5. What do these observations tell us about the adaptation of the vertebrae, and what might the implications be for spinal health?

The hypotheses of this research were the following: I expected to find a difference between humans and the African apes in both the shape of the vertebral body but also in the pattern of bone density. Considering previous results, I would expect to find that humans had relatively wide vertebral bodies, which could also mean a more oval shape. Apes, on the other hand, would likely have rounder-shaped vertebral bodies. In bone density, I would expect to find apes having relatively high bone density, in which the pattern, I would assume, would differ from humans considering their difference in locomotion. As the African apes have very few differences in their locomotion, the assumption was that they should appear very similar compared to humans.

In the case of the short-term changes in humans, the expectation was that there are likely some differences in both vertebral body morphology and age-related bone density loss. The assumption related to the morphology was that contemporary humans would have taller and narrower vertebral bodies than archaeological humans. For the age-related bone density loss it was expected as the Terry collection individuals come from an industrialised society, they might show features from both contemporary and past medieval conditions.

As for the final research question, the assumption was that there would be both observable evolutionary changes but also short-term adaptation to current lifestyles. The expectation was that there could be an evolutionarily trend towards certain features, such as less round vertebral bodies; as already mentioned, humans have been observed to have relatively wide vertebral bodies. The aim was to consider all the observations from the earlier questions together and to determine how these might affect the biomechanics and health of the spine.

2 Material and methods

2.1 Data

The data in this research has been collected from contemporary humans, anatomical skeletal human collections, archaeological individuals and African ape skeletal collections.

2.1.1 Fossil hominins and hominoids (article I)

Linear measurements of fossil hominin and hominoid vertebrae (mainly L3 or L4) were collected from the literature. Overall measurements for 17 specimens were found in the literature. (The list of the specimens and the sources can be found in Supplement 1.) This included two *H. neanderthalensis* (Kebara 2 and Sh3), four late Pleistocene *H. sapiens* (CM2, CM3, Sk. 4, CC), one *A. sediba* (MH2), three *A. africanus* (Sts-14, sts-73, Stw-H8), two *A. afarensis* (A.L. 288, A.L 33-73), one or two *P. robustus* (SK 3981, SK 853 – might be from same individuals), one *H. erectus* (KNM-WT 15000), one *P. nyanzea* (KNM-MW13142) and two fossil hominoids (UMP67-28, StW656). These were collected from the following articles: Sanders and Bodenbender (1994), Sanders (1998), Been et al. (2010), Pickering et al. (2019), and Williams at al. (2021).

2.1.2 The archaeological sample (article IV)

The archaeological sample of 42 individuals was comprised of individuals from three different archaeological sites in Finland. This included 15 individuals (11 males and 4 females) from the cemetery of the Church of St Jacobs, located in Renko in inland southern Finland; 12 individuals (8 males and 4 females) from the burial ground of the Porvoo Cathedral, located in the town of Porvoo on the southern coast of Finland; and 15 individuals (5 males and 10 females) from the churchyard of the Holy Trinity Church in Rauma on the southwest coast of Finland.

The cemetery of the Church of St Jacobs dates between the 16th and 19th centuries and is a rural site (Salo, 2008). The site in the burial ground of the Porvoo Cathedral dates between the 14th and 18th centuries, but as the majority of the individuals were buried in coffins, the excavators suspected that they were probably buried in the 17th and 18th centuries (Salo, 2007).

Fig. 4. All lumbar vertebrae from one archaeological individual.

Porvoo is one of the oldest towns in Finland, founded already in the 14th century. It was also one of the largest towns in Finland in the mid-18th century. Rauma is also one of the oldest towns in Finland, established in the 15th century. It is a port town and has a long tradition of shipbuilding. The church yard of the Holy Trinity Church has been estimated to date between the 18th and 19th centuries (Helamaa & Uotila, 2015; Uotila & Lehto, 2016). This sample was utilised in article IV. Figures 4 and 5 show examples of the lumbar vertebrae from the archaeological samples.

Fig. 5. Lumbar vertebrae from the archaeological sample.

2.1.3 The African ape sample (articles I, II, and III)

The great ape sample included 50 (20 males and 30 females) central chimpanzees (*Pan troglodytes*) and 41 (21 males and 20 females) western lowland gorillas (*Gorilla gorilla*) that have been shot in the wild, from the primate collection of the Powell-Cotton Museum, Quex House and Gardens, Birchington, Kent, United Kingdom. All specimens were classified as adults. From this sample, the dimensions of the vertebral bodies were measured. The bone density of the vertebral bodies was collected from a subsample of 32 *Pan* (15 males and 17 females) and 26 *Gorilla* (11 males and 15 females).

Additionally, vertebral dimensions were measured from six specimens of *Gorilla beringei* (three males and three females), one specimen of *Gorilla gorilla* (male), and three specimens *Pan troglodytes* (all females) from the collection of The Swedish Museum of Natural History. Figure 6. shows an example of three gorilla’s lumbar vertebrae. The ape samples were used in articles I, II and III.

Fig. 6. Gorilla's lumbar vertebrae from the Swedish Museum of Natural History.

2.1.4 The Robert J. Terry Collection (articles I and V)

Part of the historical human sample from the 20th century came from the Robert J. Terry Anatomical Skeletal Collection that is curated by the Physical Anthropology Division at the Smithsonian National Museum of Natural History in Washington, D.C., United States. Collected between 1898 and 1976, it is comprised of 1 728 individuals, whose ages at death range from 14 to 102 years, with the majority being between 20 and 80 years. The collection derives from the lower socioeconomic classes from St. Louis and Missouri, that were obtained from local St. Louis hospitals and morgues when the bodies were not claimed by relatives or family members (Hunt & Albanese, 2005).

I was able to utilise a subsample of 119 individuals from this collection that had their L4 vertebral dimension collected. This included 59 males and 60 females of European ancestry, who were born between 1852 and 1933. Their ages ranged from 27 to 75 years (mean age of 48) for males and from 24 to 77 years (mean age of 50) for females. They did not show any visible spine pathologies (Junno et al., 2015). These data were used in article I.

Bone density was also measured from the same individuals for the L4 and femur. The bone density data of 114 individuals, including 55 males and 59 females, were utilised in article V. Five individuals were excluded from the original 119 individuals' sample, as they were missing at least one of the bone measurements. The age range was from 28 to 75 years (mean age 48) for males and from 24 to 75 years (mean age 50) for females. The bone dimensions and bone density values were measured by Juho-Antti Junno.

2.1.5 Hamann-Todd human osteological collection (article I)

The Hamann-Todd collection has also been collected in the 20th century, between 1912 and 1938. It consists of more than 3 000 human skeletons that were collected and documented by Carl A. Hamann and T. Wingate Todd in the Anatomical Laboratory of Western Reserve University. It is housed at the Cleveland Museum of Natural History in Cleveland, Ohio, United States. Almost the entire collection consists of people of European ancestry and African Americans, with a majority of the individuals being men (Cleveland Museum of Natural History). The individuals were born between 1825 and 1910. The collection includes the ages, sexes, ethnicity and causes of death of the individuals (The Hamann-Todd Osteological Collection (1893–1938)). Similarly, to the Terry collection, the individuals in this collection were obtained from unclaimed bodies from local hospitals, morgues and workhouses. Unsurprisingly, this meant that the majority of the skeletons represent low-income individuals that lived in the city of Cleveland. They also tended to exhibit higher rates of diseases and illnesses (Miller, 2020). A birthplace is known for 55.6% of the individuals. Out of these individuals, 60% of the whites are European born. Native whites, on the other hand, came from 21 states, with the majority born in three: Ohio, New York and Pennsylvania (Cobb, 1935).

A subsample of 82 individuals was collected by the author, which included 43 males of European ancestry and 39 females of European ancestry. Their ages ranged between 21 and 78 years (mean age of 46) for males and between 23 and 82 years (mean age of 45) for females. This sample did include individuals with different spinal pathologies (mainly Schmorl's nodes and osteoarthritis), unlike the Terry collection sample. This was not considered to be an issue, since the sample was compared to the ape sample, which also included some pathological individuals. The sample was used in article I.

2.1.6 Northern Finland Birth Cohorts (article IV)

The contemporary human sample consists of two population-based birth cohorts (NFBC1966 and NFBC1986), that were comprised of individuals born in 1966 and 1986, respectively, in the Northern Finnish provinces of Oulu and Lapland. Both cohorts have had follow-ups at regular intervals to collect new data during ageing.

The cohorts are administrated by the NFBC Project Center (http://www.oulu.fi/nfbc/). The collection of the cohorts was conducted in accordance with the Declaration of Helsinki and approved by the Ethical Committee of the Northern Ostrobothnia Hospital District in Oulu, Finland. Written informed consent was collected from all cohort members. All personal identity information is encrypted and replaced with identification codes, providing full anonymity for the whole cohort study population.

In this study, three subsamples of MRI-scanned individuals from the cohorts were utilised. The NFBC1986 population had lumbar MRI scans, available from ages 20 and 30 (n=375 individuals), and NFBC1966 had scans from the age of 46 (n=1 363 individuals). These individuals did not exhibit vertebral pathologies. Data on sex and stature were available via additional cohort data collections. Data about the sex were available for all individuals, but stature data were available only for the 20- and 46-year-old samples. The measurements from this sample were collected by Petteri Oura. This sample was used in article IV.

2.2 Methods

2.2.1 Osteological measurements

Four measurements from the vertebral body were collected of individuals from the archaeological sample, Terry collection, Hamann-Todd collection, the Primate collection and The Swedish Museum of Natural History. From the Terry collection, measured by Juho-Antti Junno, only one vertebra was measured (L4). For the Haman-Todd, the Powell-cotton Primate collection, and the apes from The Swedish Museum of Natural History, all the lumbar vertebrae and T11/T12 and C7 vertebrae were measured (Fig. 7). However, the height measurements of the lumbar vertebrae were only collected for the second to last lumbar in the Powell-Cotton ape sample. The archaeological sample was collected, together with Tiina Väre, and it also included measurements for all the lumbar vertebrae and T11 and C7 vertebrae. The measurements were taken with a standard digital osteometric caliper and standard osteometric caliper and included the following: maximum mediolateral width, maximum anterior-posterior depth, anterior height and posterior height (Fig. 8).

Fig. 7. Illustrates the locations of vertebrae C7, T11 and L4 on the spine.

For the NFBC1966 and NFBC1986 samples, the vertebral dimensions were collected only for the L4 from the MRI images. Vertebral height dimensions (anterior height, posterior height) were measured using the sagittal view and the most medial slice that was available. The maximum mediolateral width was measured using the appropriate axial MRI slices, which varied among participants. The depth was measured using the axial slice of the most superior slice just before the intervertebral disc (Oura, Paananen, Ojaniemi et al., 2017).

All measurements were recorded to either the nearest 0.1 mm when using a digital caliper or the nearest 0.5 mm when using a standard caliper. From the vertebral measurements, three size indicators were calculated: the mean height, which was the mean of anterior and posterior heights; the vertebral cross-section area (CSA), which was calculated with the following formula: $\pi \cdot a \cdot b$, where ′a′ is the vertebral mediolateral width/2 and ′b′ is the vertebral anterior-posterior depth/2. These measurements were utilised in articles I, IV, and V.

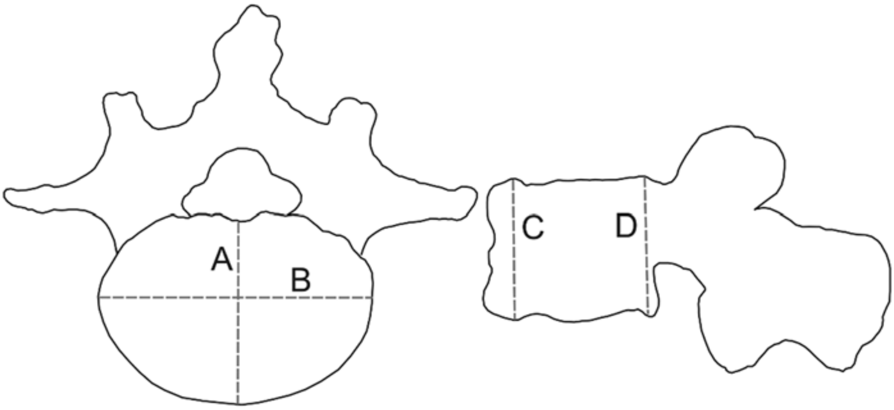

Fig. 8. Illustrates the measurement taken from the vertebral bodies. (A) anterior-posterior depth, (B) mediolateral width, (C) anterior height and (D) posterior height. Taken from article IV: Korpinen et al., 2020.

In addition, to evaluate the shape and robusticity of the vertebral bodies, the following three values were calculated. The ratio between the width and depth was calculated to observe the overall shape of the vertebral body. The width index was calculated as width/mean height and the depth index as depth/mean height. These were used to observe the robusticity of the vertebral body. These were used in article I.

2.2.2 Peripheral quantitative computed tomography

The bone density of the corpus of the L4 vertebra and the head, neck and shaft of the femur was measured by Juho-Antti Junno for 114 (59 females and 55 males) individuals from the Terry collection. The density of the C7, T12 and L3/L2 vertebrae were measured for 32 (15 males and 17 females) chimpanzees and 26 (11 males and 15 females) gorillas from the Powell-Cotton Museum. Also, the densities for all subaxial vertebrae (C3-L3/L4) were measured for two chimpanzees (one male and one female) and three gorillas (two males and one female). The bone density was measured using the Norland Stratec XCT Research SA scanner (Stratec Medizintechnik GmbH, Pforzheim, Germany) (Fig. 9). Slice thickness of 1.0 mm, with a voxel size of 0.1 mm, was used. The pQCT scanner employs an x-ray source that is collimated to a narrow fan beam with a width of about 2.5 mm. It reports bone mineral density based on the attenuation of X-rays, and the raw data represents linear attenuation coefficients. Scans were then analysed using the manufacturer's software version 6.20, with built-in algorithms that use hydroxyapatite phantom to convert the CT scan into quantitative bone density measures. This program has an external contour threshold of 267 mg/cm^3 for defining the total bone area. To acquire the trabecular region of interest inside the total bone area, the program erodes the external contour until 45% of the total area remains. The cortical area is defined by using global thresholding of 464 mg/cm^3 for the total bone area (Augat et al., 1998; Chirchir, 2019; Chirchir et al., 2015). For the apes, bone densities were taken directly from the values provided, by the program. However, as the densities for humans calculated by the program were so low, we obtained the densities using the method described by Chirchir et al. (2017).

Fig. 9. The pQCT scanner at the Powell-Cotton Museum.

The scanner has a laser that indicates the location of the scanning. All the specimens were placed in the scanner so that the laser was in the position of the anterior-posterior middle of the body, and a frontal scan was taken from the middle of the body. Figure 10 shows examples of the scans. Specific information about the exact site of the scans is demonstrated in Figure 11. For the vertebrae, the frontal scan was chosen, as it was able to include the whole vertebral body from the middle of the corpus. Because of the size limitation of the scanner, taking a scan from the sagittal plane would have excluded the samples from male gorillas. Also, taking the scan from the anterior-posterior middle of the body made it easy to repeat the scan from the same location for all the vertebrae. For each scan, the region of interest (ROI) was then cropped to include the whole corpus.

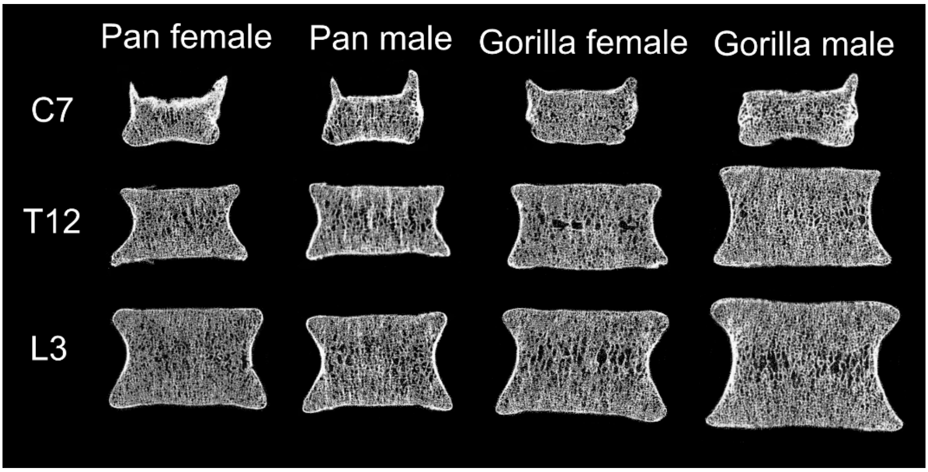

Fig. 10. Examples of the scans of the three separated vertebrae for each species and sex. The figure is taken from article III.

The ape bone density measurements were used in articles II and III. The Terry collection densities were utilised in article V. Article V also had density measurements from the femur. These were taken from three locations of the femur: the middle part of the femoral shaft, the femoral neck and the femoral head. The locations are illustrated in Figure 12.

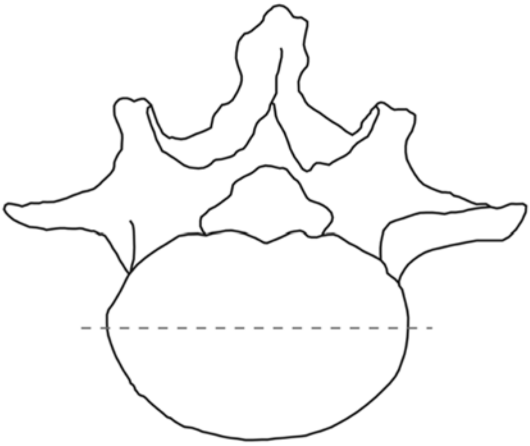

Fig. 11. Illustrates the specific site on the vertebrae where the pQCT scan was taken. The figure is taken from article V: Korpinen et al., 2023.

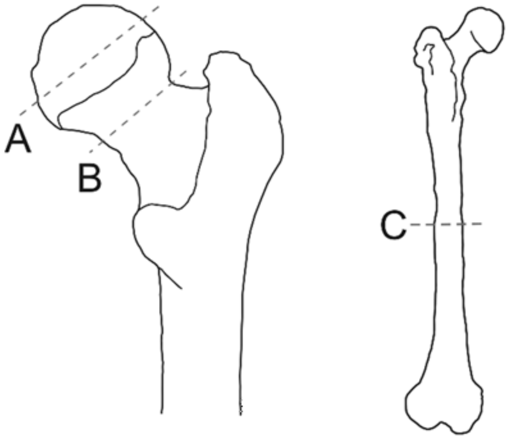

Fig. 12. Demonstrates the specific sites on the femur where the pQCT scans were taken. (A) the head, (B) the neck and (C) the shaft. The figure is taken from article V: Korpinen et al., 2023.

2.2.3 Statistical analysis

All the statistical analyses were performed using IBM SPSS Statistics (versions 25 – 27). A p-value of < 0.05 was considered statistically significant. In article I, III and V, for comparison of more than two groups, the homogeneity of variance was tested using Levene’s test, and normality was tested with Shapiro-Wilks. Given that in both cases not all groups fulfilled the required assumptions, the subsequent analyses were conducted using non-parametric Kruskal-Wallis’s test with Dunn-Bonferroni pairwise comparison in articles I and V. In article I, this was used to assess the differences in the parameters between the species but also between vertebrae. For article V, the analysis was used to study changes in bone density between three age groups for both sexes. In article III, a non-parametric Wilcoxon signed-rank test was used to assess the differences in the bone parameters between the three individual vertebrae in pooled, species-specific, and sex and species-specific samples. To study the species and sex differences in bone densities in article III a non-parametric Mann-Whitney U test was used.

A general linear model was utilised in article IV to compare the archaeological and contemporary human samples. Vertebral dimensions were used as the main outcome variables. The sample variable (i.e., archaeological, contemporary 20 years/ contemporary 30 years/ contemporary 46 years) acted as an explanatory variable. The archaeological sample was used as a reference category to which the contemporary samples were compared. The analyses were also re-run, including the stature in the model as a continuous covariate. This was done, as stature has been demonstrated to have a strong connection to the vertebral dimensions (Oura, Nurkkala et al., 2019). Stature has also significantly increased in humans overall (NCD Risk Factor Collaboration (NCD-RisC), 2016), and the increase was also clear between our study populations.

For article V, in addition to the Dunn-Bonferroni pairwise comparison, a Linear Regression analysis was used to study differences in the bone densities between the two age groups (< 50 years and ≥ 50 years). The bone densities were compared across the groups in terms of six outcome variables: (1) vertebral total density (VtotD), (2) vertebral trabecular density (VtraD), (3) femoral head total density (FHtotD), (4) femoral head trabecular density (FHtraD), (5) femoral neck cortical density (FNcrtD) and (6) femoral shaft cortical density (FcrtD). The cut-off was set at 50 years, since it seems to be an important point after which the deterioration of bone quality markedly increases (Bergström et al., 2008; Compston et al., 2009; Eastell & Lambert, 2002; Felsenberg et al., 2002). Also, the non-parametric Mann-Whitney U test was used to study the differences between sexes in pooled, young and old samples.

Pearson’s bivariate correlation analysis was used in articles III and V. For article III, it was used to study the relationship between vertebral bone parameters and vertebral body height, CSA and Volume. In article V, the relationship between bone densities and age and age groups was studied.

3 Results

3.1 Research question 1 – How does the vertebral body shape differ in extant hominoids, and how has it changed during human evolution?

In article I, the comparison of the four hominoid species (*H. sapiens, P. troglodytes, G. gorilla*, and *G. beringei*) in terms of CSA showed that size-wise *P. troglodytes* had the smallest vertebral bodies; whereas, the largest are found in *G. beringei*. *H. sapiens* and *G. gorilla,* on the other hand, had very similarly sized vertebral bodies. Statistically, *P. troglodytes* was different from the other groups in all vertebral levels (Table 1). On the other hand, no statistically significant difference was found between *H. sapiens*, *G. gorilla* and *G. beringei* at any lumbar levels.

Table 1. Kruskal-Wallis with Dunn-Bonferroni pairwise test results for the differences in CSA in different lumbar levels between the species.

Pairing	L1		L2		L3		L4	
	Mean	p-value	Mean	p-value	Mean	p-value	Mean	p-value
Homo – Pan	10.48	< 0.001	11.44	< 0.001	12.24	< 0.001	12.95	< 0.001
	6.56		7.44		7.76		7.94	
Homo – G. gorilla	10.48	1.000	11.44	1.000	12.24	1.000	12.95	0.173
	11.21		12.09		12.49		11.80	
Homo – G. beringei	10.48	0.646	11.44	0.638	12.24	1.000		
	13.52		14.96		15.08			
Pan – G. gorilla	6.56	< 0.001	7.44	< 0.001	7.76	< 0.001	7.94	< 0.001
	11.21		12.09		12.49		11.80	
Pan – G. beringei	6.56	< 0.001	7.44	< 0.001	7.76	< 0.001		
	13.52		14.96		15.08			
G. gorilla – G. beringei	11.21	1.000	12.09	1.000	12.49	1.000		
	13.52		14.96		15,08			

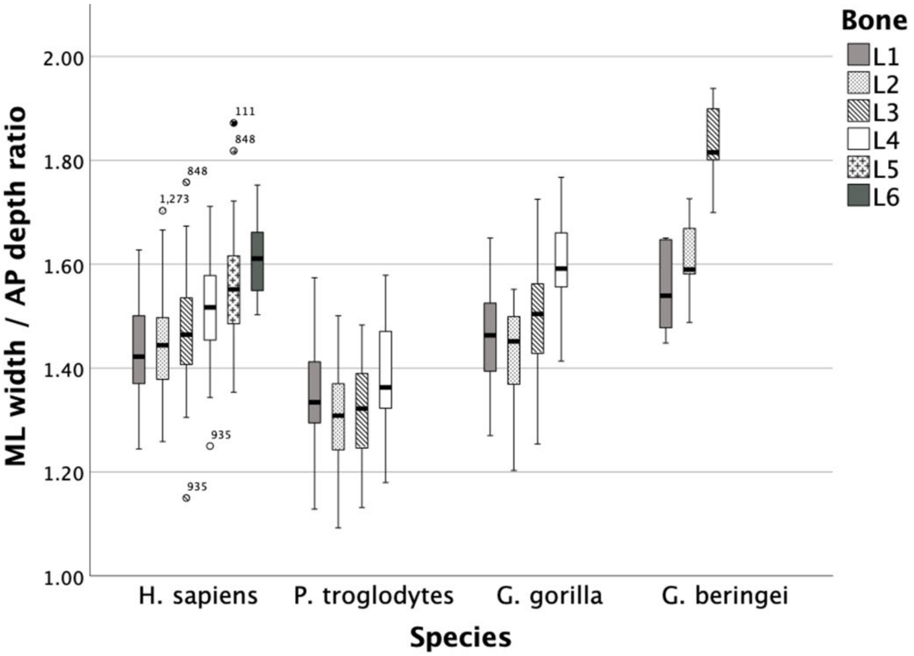

Fig. 13. Boxplot illustration of the variation in the ML width / AP depth ratio at different lumbar levels in different species.

When observing the shape of the vertebral bodies, it seems that the pattern is very similar to the CSA. *P. troglodytes* has the most round-shaped (less difference between width and depth) vertebral bodies; whereas, *G. beringei* is once again in the opposite end with the largest difference between the ML width and AP depth of the vertebral body (Fig. 13). The difference between *G. beringei* and other groups is at its largest in L3, although it is good to note that none of the *G. beringei* had four lumbar vertebrae. Likewise, *G. gorilla* also showed a relatively large increase in the ratio in L4, indicating a change in the shape of the last lumbar in *Gorilla* species. The Kruskal-Wallis with Dunn-Bonferroni pairwise comparison showed that *H. sapiens* and *G. gorilla* were again very similar to one other, with only a statistically significant difference between them found in L4 ($p = 0.004$, Table 2). No statistically significant difference was found between *G. gorilla* and *G. beringei* in L1 ($p = 0.555$), but L2 and L3 did show a difference ($p < 0.05$). Similarly, *G. beringei* had no statistically significant difference with *H. sapiens* in L1 ($p = 0.076$) but was different in L2 and L3. *P. troglodytes* was statistically significantly different from all other groups in all vertebrae.

When observing the ML width / AP depth ratio changes between lumbar levels, *H. sapiens* and maybe *G. beringei* appear to have a tendency of increasing ML width relation to AP depth in the caudal direction (Fig. 13). This change is more gradual in *H. sapiens* (Fig. 13 and Table 3), likely due to the larger number of vertebrae. *P. troglodytes* and *G. gorilla,* on the other hand, seem to exhibit, first, a decrease of the ML width / AP depth ratio in L2 and L3 in the case of *P. troglodytes*. After this, the ratio increases in the remaining vertebrae. This can also be observed with the Kruskal-Wallis with Dunn-Bonferroni pairwise comparison presented in Table 3.

Table 2. Kruskal-Wallis with Dunn-Bonferroni pairwise test results for the differences in ML width / AP depth ratio in different lumbar levels between the species.

Pairing	L1		L2		L3		L4	
	Mean	p-value	Mean	p-value	Mean	p-value	Mean	p-value
Homo – Pan	1.43	< 0.001	1.44	< 0.001	1.47	< 0.001	1.52	< 0.001
	1.35		1.31		1.32		1.39	
Homo – G. gorilla	1.43	0.571	1.44	1.000	1.47	1.000	1.52	0.004
	1.46		1.43		1.50		1.59	
Homo – G. beringei	1.43	0.076	1.44	0.033	1.47	0.004		
	1.55		1.61		1.83			
Pan – G. gorilla	1.35	< 0.001	1.31	< 0.001	1.32	< 0.001	1.39	< 0.001
	1.46		1.43		1.50		1.59	
Pan – G. beringei	1.35	< 0.001	1.31	< 0.001	1.32	< 0.001		
	1.55		1.61		1.83			
G. gorilla – G. beringei	1.46	0.555	1.43	0.024	1.50	0.037		
	1.55		1.61		1.83			

The species were also compared using only the second to last lumbar. This was done because, as the second most caudal vertebrae, it serves a similar function in all the species, and it is also the second most loaded vertebrae after the most caudal vertebrae but presents less variation in morphology (Apazidis et al., 2011; Paik et al., 2013). Comparing the species using this combination of the second to last lumbar indicated no statistically significant difference in AP depth, ML width or CSA between *H. sapiens*, *G. gorilla* and *G. beringei* ($p > 0.050$, Table 4). *Gorilla* species were similar in all values ($p > 0.050$). *P. troglodytes,* on the other hand, differed from all the other species. The mean height of the vertebra seems to differ most between the groups, except between the *Gorilla* species ($p = 0.913$).

Table 3. Kruskal-Wallis with Dunn-Bonferroni pairwise test results for the differences in ML width / AP depth between the lumbar levels in all four species.

Pairing	Homo		Pan		G. gorilla		G. beringei	
	Mean	p-value	Mean	p-value	Mean	p-value	Mean	p-value
L1-L2	1.43	1.000	1.35	0.166	1.46	0.889	1.55	1.000
	1.44		1.31		1.43		1.61	
L1-L3	1.43	0.141	1.35	1.000	1.46	0.656	1.55	0.003
	1.47		1.32		1.50		1.83	
L1-L4	1.43	< 0.001	1.35	0.371	1.46	< 0.001		
	1.52		1.39		1.59			
L1-L5	1.43	< 0.001						
	1.56							
L1-L6	1.43	0.001						
	1.61							
L2-L3	1.44	0.883	1.31	1.000	1.43	0.014	1.61	0.052
	1.47		1.32		1.50		1.83	
L2-L4	1.44	< 0.001	1.31	< 0.001	1.43	< 0.001		
	1.52		1.39		1.59			
L2-L5	1.44	< 0.001						
	1.56							
L2-L6	1.44	0.004						
	1.61							
L3-L4	1.47	0.087	1.32	0.011	1.50	0.005		
	1.52		1.39		1.59			
L3-L5	1.47	< 0.001						
	1.56							
L3-L6	1.47	0.044						
	1.61							
L4-L5	1.52	0.373						
	1.56							
L4-L6	1.52	0.762						
	1.61							
L5-L6	1.56	1.000						
	1.61							

Table 4. Kruskal-Wallis with Dunn-Bonferroni pairwise test results for the differences in the second to last lumbar vertebra's AP depth, ML width, Mean height and CSA between the species.

Pairing	AP depth		ML width		Mean height		CSA	
	Mean	p-value	Mean	p-value	Mean	p-value	Mean	p-value
Homo – Pan	32.9	< 0.001	49.9	< 0.001	26.6	< 0.001	12.9	< 0.001
	27.3		35.8		23.1		7.7	
Homo – G. gorilla	32.9	1.000	49.9	0.975	26.6	0.032	12.9	1.000
	32.6		47.7		28.9		12.4	
Homo – G. beringei	32.9	1.000	49.9	1.000	26.6	0.035	12.9	1.000
	34.2		54.9		30.9		15.0	
Pan – G. gorilla	27.3	< 0.001	35.8	< 0.001	23.1	< 0.001	7.7	< 0.001
	32.6		47.7		28.9		12.4	
Pan – G. beringei	27.3	0.002	35.8	< 0.001	23.1	< 0.001	7.7	< 0.001
	34.2		54.9		30.9		15.0	
G. gorilla – G. beringei	32.6	1.000	47.7	0.543	28.9	0.913	12.4	1.000
	34.2		54.9		30.9		15.0	

The width/depth ratio of the second to last lumbar did not demonstrate a difference between *H. sapiens* and *G. gorilla* (p = 0.075) or *G. beringei* (p = 0.685, Table 5). There was also no statistically significant difference between the *Gorilla* species. In the width index, *H. sapiens* showed no statistically significant difference with *G. beringei* (p = 1.000). Also, no differences between the ape species were detected (p > 0.050). Depth index was also mainly similar between the ape groups (p > 0.050), but in addition, no statistically significant difference was found between *G. beringei* and *H. sapiens* (p = 0.055). The means and standard deviations of the ML width and AP depth ratio, CSA and width and depth indexes for the species are presented in Supplement 2. Observing the values of the sex level shows that *H. sapiens* males tend to have the most robust vertebral bodies of all the other groups (see Supplement 3).

Table 5. Kruskal-Wallis with Dunn-Bonferroni pairwise test results for the differences in the second to last lumbar vertebra's ML width / AP depth ratio, Width index, and Depth index between the species.

Pairing	ML width / AP depth		Width index		Depth index	
	Mean	p-value	Mean	p-value	Mean	p-value
Homo – Pan	1.52	< 0.001	1.88	< 0.001	1.24	0.042
	1.31		1.56		1.19	
Homo – G. gorilla	1.52	0.075	1.88	< 0.001	1.24	< 0.001
	1.46		1.65		1.13	
Homo – G. beringei	1.52	0.685	1.88	1.000	1.24	0.055
	1.61		1.77		1.10	
Pan – G. gorilla	1.31	< 0.001	1.56	0.196	1.19	0.201
	1.46		1.65		1.13	
Pan – G. beringei	1.31	< 0.001	1.56	0.061	1.19	0.919
	1.61		1.77		1.10	
G. gorilla – G. beringei	1.46	0.053	1.56	0.803	1.13	1.000
	1.61		1.77		1.10	

3.1.1 Comparison to fossil hominins

Comparing the L3/L4 vertebrae of the fossil hominoids and the combination of the second to last lumbar vertebrae of the extant hominoids (which also included the Terry collection data), the ML width and AP depth ratio does not seem to indicate large differences between groups, although some outliers do exist (Figs. 14 and 15). *P. robustus* seems to especially have a relatively large ML width and AP depth ratio, as does one of the specimens of *A. afarensis*. But curiously it would seem that *Pan* might be the clearest outlier of the whole group, showing the smallest ML width and AP depth ratios.

The width index also indicates a smaller width in *Pan* relative to the height of the vertebral body (Fig. 16). This also seems to be the case for most of the earlier hominins (*A. seliba*, *A. africanus*, *A. afarensis*). *G. gorilla* also shows a relatively higher vertebral body compared to its width. In the depth index (Fig. 17), the earlier hominins including *P. robustus* seem to have relatively high vertebral bodies compared to the depth. This is also the case in *G. beringei*. The size of the vertebral body was also significantly lower in earlier hominoids than in *Homo* species (Supplement 1). The means of the ML width and AP depth ratio, CSA and width and depth indexes for the fossil hominoids are shown in Supplement 1. These results would seem to indicate that the size and shape of the vertebral body are similar between *H. sapiens* and *Gorilla* species, probably indicating the relationship to the axial loading rather than locomotion. Compared to fossil hominoids, the shape of the vertebral body (ML width / AP depth ratio) appears to have stayed relatively similar throughout human evolution. It also seems that the height of the vertebral body has decreased in *Homo* species compared to earlier extinct hominoids or extant hominoids.

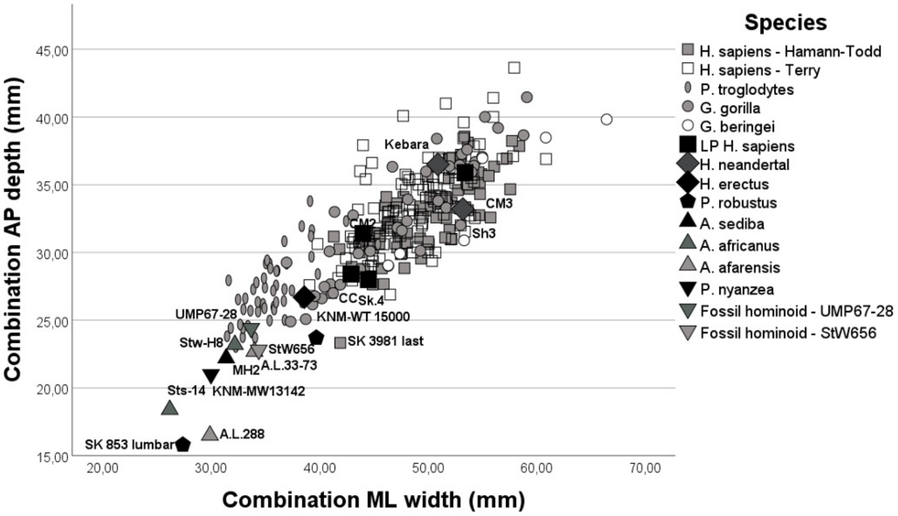

Fig. 14. Scatterplot illustration of the relationship between combination AP depth and ML width in both extant and extinct hominoids. The figure is taken from article I.

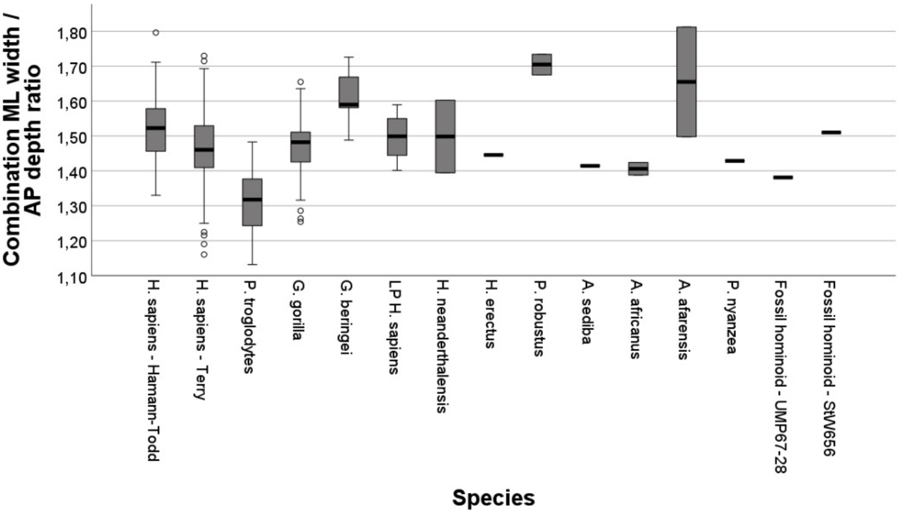

Fig. 15. Boxplot illustration of the variation in combination ML width / AP depth ratio in different extant and extinct hominoid species. The figure is taken from article I.

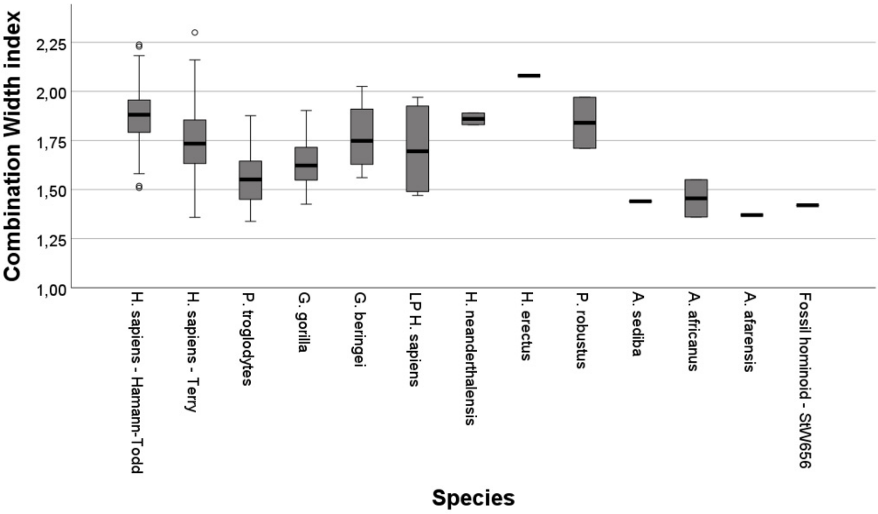

Fig. 16. Boxplot illustration of the variation in combination width index in different extant and extinct hominoid species. The figure is taken from article I.

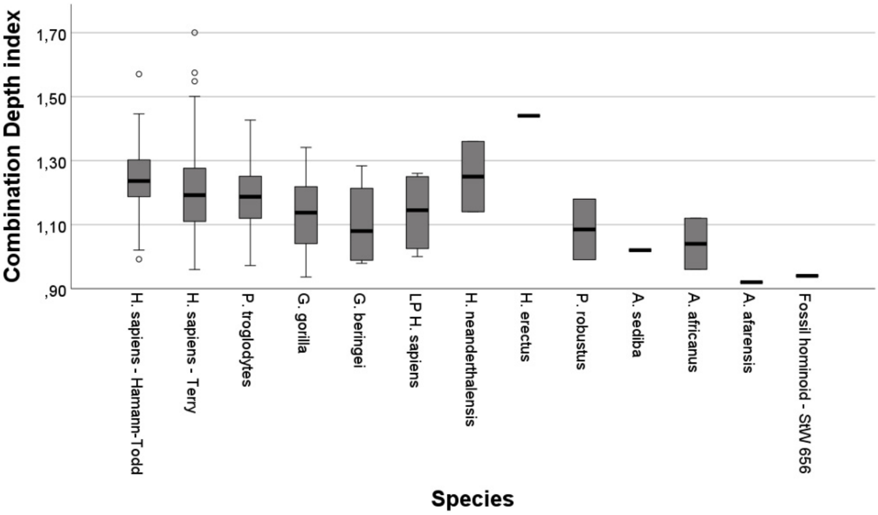

Fig. 17. Boxplot illustration of the variation in combination depth index in different extant and extinct hominoid species. The figure is taken from article I.

3.2 Research question 2 – Does locomotion influence the vertebral bone density and its pattern in the subaxial vertebral column?

Since *Pan* and *Gorilla* are known to have very similar knuckle-walking locomotion and showcase relatively similar positional behaviour (Doran, 1996; Finestone et al., 2018), I studied if they exhibit any differences in vertebral bone density or cortical thickness or their pattern in the whole subaxial column. As presented in article II, comparing the patterns of bone densities in the whole subaxial vertebral column of two *P. troglodytes* and three *G. gorilla* (shown in Figures 18–21) indicated differences between the species. The differences are especially noticeable in the trabecular density and particularly in the cervical segment (Fig. 18). In the cervical vertebrae, *Gorilla* has observably lower trabecular density compared to the thoracic segment than *Pan*. The density is at its lowest in the C5 region but increases sharply in C7. For *Pan*, trabecular density is mainly highest in the cervical segment compared to other spinal segments and peaks around C5 and C6. In the thoracic segment, *Gorilla* seems to experience an increase in trabecular density from T1 or T3 until around mid-thoracic T6. The density then starts to decrease from T9 or T10 onwards. This decrease continues until around L1 or L2, after which it increases again. *Pan* did not exhibit any clear pattern of increase or decrease in the density of the thoracic segment, as there was a great deal fluctuation in the density between adjacent vertebrae. However, the *Pan* male does experience a clear increase in T10, after which the density decreases. In the lumbar segment, density continues to decrease in *Pan* male until L4, in which it shows a clear increase. For the female, there is a clear decrease in density in L1, but after that, the density remains stable.

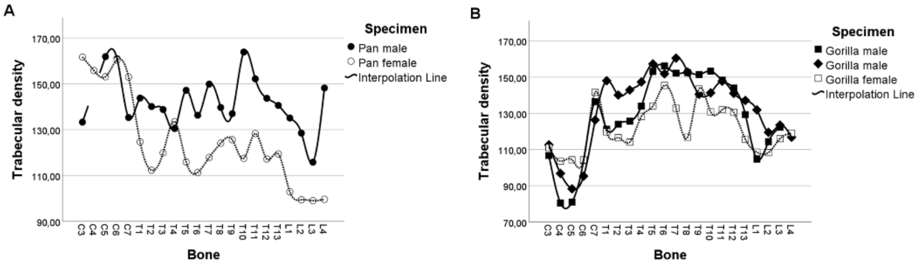

Fig. 18. Presents the trabecular density in the subaxial vertebrae for *P. troglodytes* (A) and *G. gorilla* (B). Taken from article II: Korpinen, 2022.

The cortical density pattern between the species is very similar as can be seen in Figure 19. Density is highest in the cervical segment, after which it drops and stays relatively stable in the thoracic column. It does increase slightly in the lumbar segment towards the sacrum. For cortical thickness, the pattern is quite different (Fig. 20). Apart from one of the *Gorilla* males, the others showed higher cortical thickness in the cervical segment compared to the lower thoracic or lumbar segment. *Pan* does not show any clear change in the cortical thickness after the initial decrease at the beginning of the thoracic segment. *Gorilla*, on the other hand, presented a pattern of steadily increasing cortical thickness following the initial decrease after the cervical segment. Therefore, the cortical thickness in the lumbar segment is almost the same as in the cervical segment.

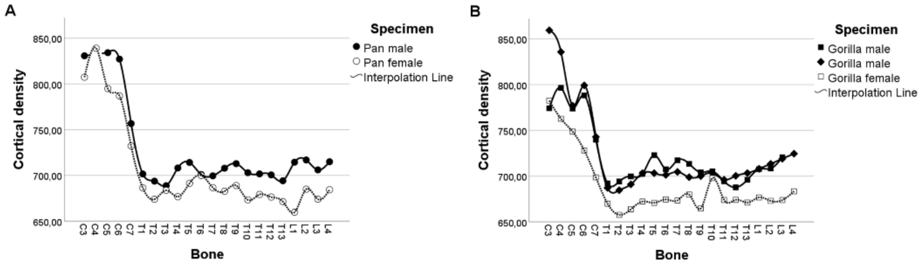

Fig. 19. Presents the cortical density in the subaxial vertebrae for *P. troglodytes* (A) and *G. gorilla* (B). Taken from article II: Korpinen, 2022.

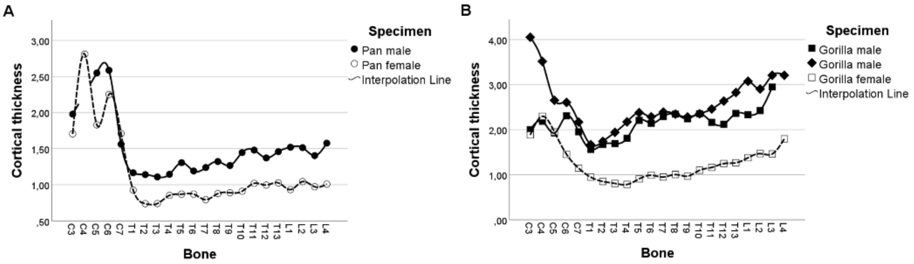

Fig. 20. Presents the cortical thickness in the subaxial vertebrae for *P. troglodyt*es (A) and *G. gorilla* (B).

Some differences in total density of the cervical and thoracic segments can be detected (Fig. 21). In the cervical segment, *Pan* seems to exhibit more typically high densities, whereas only one of the *Gorilla* showcases a similar, clearly higher density. In the thoracic segment, the *Gorilla* males especially show a density increase in the mid-segment, which is not present in *Pan*. Considering the similarities in locomotion and positional behaviour observed between the species, these differences could indicate that locomotion and posture may not be the only factors influencing the bone density pattern of the vertebral column. These differences could indicate differences in the loading of the vertebrae, either related to size and muscularity differences between these species or differences in positional behaviour that is yet to be observed.

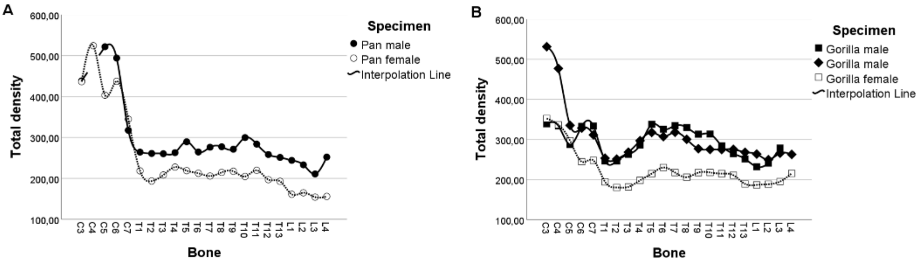

Fig. 21. Presents the total density in the subaxial vertebrae for *P. troglodytes* (A) and *G. gorill*a (B). Taken from article II: Korpinen, 2022.

3.2.1 Differences in bone density of three vertebrae between African apes

All the means, standard deviations, minimum, maximum and median values for the bone densities and the cortical thickness in the vertebrae C7, T12 and L3 are presented in supplements 3–5. Results for the three individual vertebrae (C7, T12 and L3) indicated that the trend for the total densities is to decrease in a caudal direction (Fig. 22 A), which was also supported by the Wilcoxon signed rank test showing a statistically significant difference in the total density between all three vertebrae ($p < 0.001$, Table 6). As for the trabecular density (article III), *Pan* was observed to have no statistically significant difference between C7 and T12 ($p = 0.808$) but displayed a statistically significant decrease between T12 and L3 ($p < 0.001$, Table 6 and Fig. 22 C). *Gorilla*, on the other hand, experienced a slight increase in trabecular density between C7 and T12 ($p = 0.003$), although this was only statistically significant in females ($p = 0.015$). In cortical density, both species experience decreases in density from C7 to T12 ($p < 0.001$). Between T12 and L3 no statistically significant change in density was detected for *Pan* ($p = 0.563$). *Gorilla*, instead, showed a slight increase in density (Fig. 22 B), although the change was not statistically significant for females ($p = 0.495$). Cortical thickness mainly increased towards the sacrum in *Gorilla,* although the change was only statistically significant between T12 and L3 ($p < 0.050$). For *Pan*, cortical thickness decreased between C7 and T12 ($p < 0.001$) and did not increase significantly between T12 and L3 ($p = 0.068$, Table 6 and Fig. 22 D). There was also no statistically significant difference in cortical thickness between C7 and L3 for *Pan* females ($p = 0.124$).

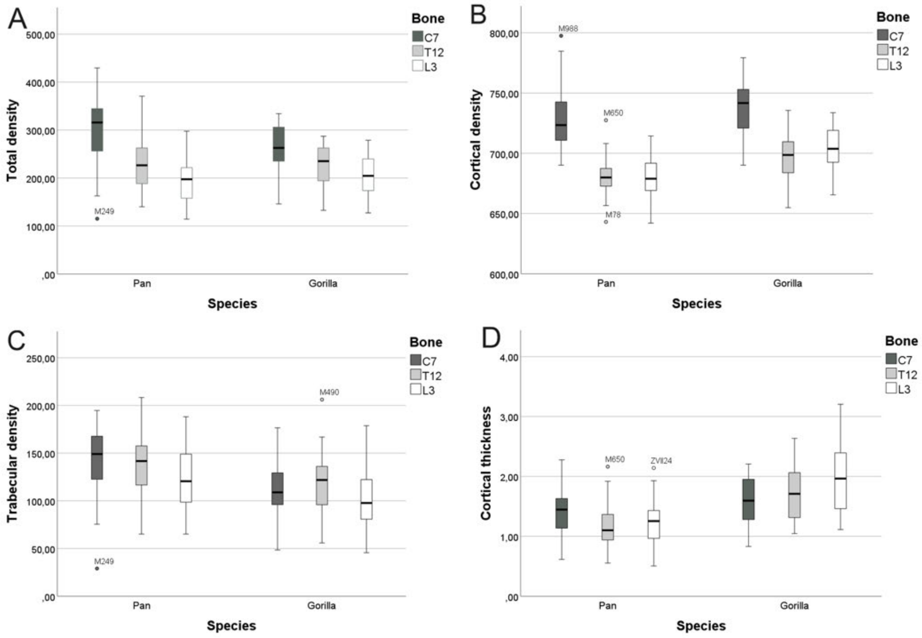

Fig. 22. Bloxplot illustrations of the density variations in different species for all three vertebrae: (A) the total density, (B) the cortical density, (C) the trabecular density and (D) the cortical thickness. Partly taken from article III.

Species and sex differences

The results from the Mann-Whitney U test are presented in Tables 7–9. They showed no statistically significant difference between the species in T12 and L3 total density and in C7 cortical density and cortical thickness. Trabecular density was constantly lower in *Gorilla*. On the other hand, cortical density and thickness in T12 and L3 were lower for *Pan* (Table 7). Testing between the sexes found that *Pan* females had a statistically significantly lower cortical thickness of C7 and T12, total density of T12 and L3, and trabecular density of T12 than the males. *Gorilla,* instead, presented statistically significantly lower cortical thickness for females in all three vertebrae, and in the cortical density of C7 and L3 (Table 8).

Table 6. Wilcoxon signed-rank test of differences between the bones in different densities and cortical thickness in pooled, species-specific, and sex- and species-specific samples.

Bone and density pairing	Pooled	*Pan*	*Gorilla*	*Pan* male	*Pan* female	*Gorilla* male	*Gorilla* female
C7 total density – T12 total density	< 0.001	< 0.001	< 0.001	< 0.001	0.001	0.004	0.001
C7 trabecular density – T12 trabecular density	0.129	0.808	0.003	0.691	0.653	0.075	0.015
C7 cortical density – T12 cortical density	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.003	< 0.001
C7 cortical thickness – T12 cortical thickness	0.067	<0.001	0.118	0.027	0.009	0.722	0.053
C7 total density – L3 total density	< 0.001	<0.001	< 0.001	< 0.001	< 0.001	0.003	< 0.001
C7 trabecular density – L3 trabecular density	< 0.001	<0.001	< 0.001	< 0.001	< 0.001	0.003	< 0.001
C7 cortical density – L3 cortical density	< 0.001	<0.001	< 0.001	< 0.001	< 0.001	0.003	< 0.001
C7 cortical thickness – L3 cortical thickness	0.196	0.007	< 0.001	0.017	0.124	0.026	< 0.001
T12 total density – L3 total density	< 0.001	<0.001	< 0.001	< 0.001	< 0.001	0.010	< 0.001
T12 trabecular density – L3 trabecular density	< 0.001	< 0.001	< 0.001	0.001	0.001	0.003	< 0.001
T12 cortical density – L3 cortical density	0.060	0.563	0.032	0.615	0.758	0.028	0.495
T12 cortical thickness – L3 cortical thickness	<0.001	0.068	< 0.001	0.362	0.068	0.003	< 0.001

Testing the differences between species separately in males and females revealed that males tended to demonstrate more differences than females (Table 9). For males, only total density of T12 and L3 ($p = 0.330$; $p = 0.683$) showed no statistically significant difference. For females, on the other hand, only statistically significant differences were found in cortical thickness of T12 and L3 ($p = 0.001$; $p < 0.001$) and cortical density of L3 ($p = 0.027$).

Table 7. Mann-Whitney U test of differences in densities between the species.

Bone and density	Species	Mean density	p-value
C7 total density	*Pan*	304.1	0.003
	Gorilla	262.6	
C7 trabecular density	*Pan*	142.0	<0.001
	Gorilla	108.4	
C7 cortical density	*Pan*	729.1	0.144
	Gorilla	736.1	
C7 cortical thickness	*Pan*	1.42	0.125
	Gorilla	1.60	
T12 total density	*Pan*	231.4	0.988
	Gorilla	225.3	
T12 trabecular density	*Pan*	140.6	0.024
	Gorilla	117.5	
T12 cortical density	*Pan*	680.8	< 0.001
	Gorilla	697.9	
T12 cortical thickness	*Pan*	1.18	<0.001
	Gorilla	1.69	
L3 total density	*Pan*	196.8	0.491
	Gorilla	203.9	
L3 trabecular density	*Pan*	122.2	0.012
	Gorilla	98.6	
L3 cortical density	*Pan*	680.1	< 0.001
	Gorilla	703.6	
L3 cortical thickness	*Pan*	1.25	< 0.001
	Gorilla	2.00	

Table 8. Mann-Whitney U test of differences in densities between sexes in species-level.

Bone and density	Sex	*Pan*		*Gorilla*	
		Mean density	p-value	Mean density	p-value
C7 total density	male	329.5	0.097	278.8	0.121
	female	281.7		250.7	
C7 trabecular density	male	153.3	0.153	100.8	0.384
	female	131.9		113.9	
C7 cortical density	male	736.1	0.132	753.5	0.001
	female	722.9		723.4	
C7 cortical thickness	male	1.58	0.0.44	1.94	< 0.001
	female	1.28		1.35	
T12 total density	male	249.4	0.027	225.2	0.959
	female	215.5		225.4	
T12 trabecular density	male	153.2	0.049	109.1	0.305
	female	129.5		123.7	
T12 cortical density	male	679.4	0.882	703.0	0.198
	female	682.0		694.2	
T12 cortical thickness	male	1.31	0.018	1.98	0.003
	female	1.07		1.47	
L3 total density	male	213.5	0.033	206.1	0.878
	female	182.2		202.3	
L3 trabecular density	male	131.9	0.114	89.3	0.330
	female	113.6		105.5	
L3 cortical density	male	679.1	0.655	714.2	0.009
	female	681.0		695.8	
L3 cortical thickness	male	1.36	0.069	2.38	0.002
	female	1.15		1.71	

Correlations between bone densities and vertebral size indicators

In order to observe any connection between bone densities and the size of the vertebrae (including mean height, CSA and volume), a bivariate correlation analysis was used (Table 10). The strongest correlations were found for the pooled sample in T12 and L3. Cortical thickness especially showed a moderately strong negative correlation with all three size indicators (r = 0.598–0.734). Additionally, cortical density displayed a moderately strong correlation with all size indicators in L3 (r = 0.484–0.514) and somewhat less strong correlation in T12 (r = 0.355–0.356). Trabecular density showed some negative correlation with the size indicators in all three vertebrae.

Table 9. Mann-Whitney U test of differences in densities between species on a sex level.

Bone and density	Species	Males		Females	
		Mean density	p-value	Mean density	p-value
C7 total density	*Pan*	329.5	0.027	281.7	0.123
	Gorilla	278.8		250.7	
C7 trabecular density	*Pan*	153.3	0.001	131.9	0.123
	Gorilla	100.8		113.9	
C7 cortical density	*Pan*	736.1	0.020	722.9	0.655
	Gorilla	753.5		723.4	
C7 cortical thickness	*Pan*	1.58	0.011	1.28	0.682
	Gorilla	1.94		1.35	
T12 total density	*Pan*	249.4	0.330	215.5	0.295
	Gorilla	225.2		225.4	
T12 trabecular density	*Pan*	153.2	0.003	129.5	0.852
	Gorilla	109.1		123.7	
T12 cortical density	*Pan*	679.4	< 0.001	682.0	0.114
	Gorilla	703.0		694.2	
T12 cortical thickness	*Pan*	1.31	< 0.001	1.07	0.001
	Gorilla	1.98		1.47	
L3 total density	*Pan*	213.5	0.683	182.2	0.165
	Gorilla	206.1		202.3	
L3 trabecular density	*Pan*	131.9	0.003	113.6	0.628
	Gorilla	89.3		105.5	
L3 cortical density	*Pan*	679.1	< 0.001	681.0	0.027
	Gorilla	714.2		695.8	
L3 cortical thickness	*Pan*	1.36	< 0.001	1.15	< 0.001
	Gorilla	2.38		1.71	

However, on a species level, only a few slightly stronger correlations can be seen. In *Pan*, this is found in C7, where total and trabecular density and cortical thickness show some correlation with the mean vertebral height. *Gorilla* on the other hand showed moderate correlation between all size indicators and cortical thickness in all three vertebrae. Cortical density also showed moderate correlations in L3 and C7.

The results from the three individual vertebrae support the observation from the whole subaxial column in the differences between species in the cervical and thoracic segments, which, as already mentioned, is surprising considering the similarity in locomotion and positional behaviour between the species. Additionally, it was observed that larger vertebrae seem to have lower trabecular density, but higher cortical density and thickness, which also might explain many of the differences between species at the vertebral level. This also indicates a possibly stronger connection of bone density to axial loading than locomotion. It may even partly explain the significantly lower bone density found in humans compared to other hominoids (Chirchir, 2019; Chirchir et al., 2015; Hernandez et al., 2009). Overall, the differences between species are not as clear at the single vertebral level as they are at the vertebral column level.

Table 10. Pearson's bivariate correlations between vertebral densities and vertebral body height, CSA and volume.

Vertebral dimensions	N	C7				T12				L3			
		Total density	Trabecular density	Cortical density	Cortical thickness	Total density	Trabecular density	Cortical density	Cortical thickness	Total density	Trabecular density	Cortical density	Cortical thickness
Pooled													
Vertebral body height	56	-0.110	-0.299*	0.359*	0.511**	-0.051	-0.295*	0.355**	0.625**	0.102	-0.275*	0.514**	0.734**
Vertebral body CSA	56	-0.186	-0.334*	0.200	0.405**	-0.103	-0.323*	0.356**	0.598**	0.012	-0.344**	0.484**	0.676**
Vertebral body volume	56	-0.162	-0.335*	0.278*	0.456**	-0.084	-0.315*	0.356**	0.623**	0.051	-0.314*	0.506**	0.714*
Pan													
Vertebral body height	30	0.413*	0.480*	0.008	0.505**	-0.101	-0.057	-0.097	-0.036	-0.025	0.054	-0.147	-0.008
Vertebral body CSA	30	-0.181	-0.028	-0.342	-0.029	-0.096	-0.033	-0.057	-0.040	-0.005	0.095	-0.354	0.096
Vertebral body volume	30	-0.005	0.161	-0.299	0.149	-0.109	-0.041	-0.083	-0.048	-0.007	0.109	-0.364*	0.090
Gorilla													
Vertebral body height	26	0.213	-0.142	0.596**	0.653**	0.094	-0.124	0.125	0.670**	0.128	-0.134	0.401*	0.693**
Vertebral body CSA	26	0.334	0.046	0.295	0.607**	-0.095	-0.220	0.105	0.529**	-0.094	-0.330	0.421*	0.542**
Vertebral body volume	26	0.300	-0.030	0.439*	0.669**	-0.046	-0.198	0.110	0.585**	-0.003	-0.241	0.417*	0.614**

**Correlation is significant at the 0.01 level

*Correlation is significant at the 0.05 level

3.3 Research question 3 - Are there short-term changes in the vertebral morphology?

The short-term changes in vertebral dimensions in the Finnish population were studied in article IV. The general linear model comparison of the raw, unadjusted vertebral dimensions between the Finnish archaeological and contemporary 46-year-old samples indicated an increase in CC height and AP depth in contemporary humans. Women also showed an increase in CSA; but in men, no statistically significant difference was found in CSA between the temporal groups (Tables 11 and 12). Additionally, ML width did not show a significant change in women; but in males, there was a statistically significant decrease in this dimension. The dimensions of the contemporary 20-year-olds were either smaller or similar to the archaeological individuals. Only the CC height in men showed an increase value compared to the archaeological men.

The vertebral dimensions of the 46-year-old contemporary males showed an average increase of 16.5 mm^2 in CSA, 2.9 mm in CC height, and 2.2 mm in AP depth in comparison to their archaeological counterparts. The 46-year-old contemporary females exhibited an average increase of 101.9 mm^2 in CSA, 1.6 mm in CC height, and 3.1 mm in AP depth. In contrast, ML width showed an average decrease of 2.5 mm among the males, although stayed almost the same in females, with only a 0.3 mm decrease.

Since stature was greater in both contemporary samples (20-year-olds and 46-years-olds) compared to the stature estimations of the archaeological individuals (Tables 11 and 12), the dimensions were adjusted for the stature in the general linear model. The results from these stature-adjusted models showed that both the older and younger contemporary males had a smaller ML width and CSA, but the CC height was greater than the archaeological samples. Although the raw value of CSA in the older sample was larger than in the archaeological males, the stature-adjusted value was smaller. AP depth, on the other hand, was smaller in younger contemporary individuals than their archaeological counterparts; whereas, the older contemporary individuals were the same size as the archaeological ones.

Table 11. Stature and vertebral dimensions in archaeological and contemporary male samples, with crude and stature adjusted.

Variable and sample	Mean values ± standard deviation	Crude comparison		Stature-adjusted comparison	
		p-value	n	p-value	n
Stature (cm)					
Archaeological	166.9 ± 5.8	Ref.	24	-	-
Contemporary 20y	175.3 ± 7.2	< 0.001	143	-	-
Contemporary 30y	-	-		-	-
Contemporary 46y	178.7 ± 6.2	< 0.001	616	-	-
Vertebral CSA (mm^2)					
Archaeological	1496.4 ± 241.3	Ref.	22	Ref.	22
Contemporary 20y	1330.7 ± 185.5	< 0.001	143	< 0.001	143
Contemporary 30y	1443.9 ± 188.6	0.268	144	-	-
Contemporary 46y	1512.9 ± 214.0	0.713	616	< 0.001*	616
Vertebral CC height (mm)					
Archaeological	26.5 ± 1.8	Ref.	24	Ref.	24
Contemporary 20y	29.0 ± 1.8	< 0.001	143	< 0.001	143
Contemporary 30y	29.7 ± 1.8	< 0.001	144	-	-
Contemporary 46y	29.4 ± 1.6	< 0.001	616	< 0.001	616
Vertebral ML width (mm)					
Archaeological	53.8 ± 4.5	Ref.	23	Ref.	23
Contemporary 20y	49.4 ± 4.1	< 0.001	143	< 0.001	143
Contemporary 30y	51.1 ± 3.9	0.004	144	-	-
Contemporary 46y	51.3 ± 4.1	0.004	616	< 0.001	616
Vertebral AP depth (mm)					
Archaeological	35.2 ± 3.3	Ref.	23	Ref.	23
Contemporary 20y	34.2 ± 2.4	0.107	143	< 0.001	143
Contemporary 30y	35.8 ± 2.4	0.271	144	-	-
Contemporary 46y	37.4 ± 2.8	< 0.001	616	0.990	616
Vertebral ML width / AP depth ratio					
Archaeological	1.52 ± 0.11	Ref.	22	Ref.	22
Contemporary 20y	1.45 ± 0.11	0.001	143	0.001	143
Contemporary 30y	1.43 ± 0.10	< 0.001	144	-	-
Contemporary 46y	1.38 ± 0.09	< 0.001	616	< 0.001	616

*After height adjustment, dimension was smaller among the contemporary humans than the archaeological individuals.

The stature-adjusted models showed that both younger and older contemporary females had a smaller ML width than the archaeological specimens (Tables 11 and 12). Also, no significant differences in CC height were found compared to the archaeological sample. The CSA was larger in archaeological individuals, but only in comparison to the younger contemporary sample. AP depth was larger in the older sample than in the archaeological one. In younger females, although the raw value was slightly larger than the archaeological ones', the stature-adjusted value was, on the other hand, smaller. CSA in younger contemporary females was smaller than the archaeological one, but there was no difference between the older contemporary females and their archaeological counterparts.

Table 12. Stature and vertebral dimensions in archaeological and contemporary female samples, with crude and stature adjusted.

Variable and sample	Mean values ± standard deviation	Crude comparison		Stature-adjusted comparison	
		p-value	n	p-value	n
Stature (cm)					
Archaeological	155.7 ± 5.0	Ref.	18	-	-
Contemporary 20y	163.9 ± 6.0	< 0.001	217	-	-
Contemporary 30y	-	-	-	-	-
Contemporary 46y	164.8 ± 5.8	< 0.001	742	-	-
Vertebral CSA (mm^2)					
Archaeological	1108.3 ± 198.1	Ref.	18	Ref.	18
Contemporary 20y	1061.3 ± 125.9	0.199	217	< 0.001	217
Contemporary 30y	1152.0 ± 130.9	0.232	227	-	-
Contemporary 46y	1210.2 ± 158.8	0.004	742	0.742	742
Vertebral CC height (mm)					
Archaeological	26.1 ± 1.4	Ref.	18	Ref.	18
Contemporary 20y	26.7 ± 1.5	0.125	217	0.289	217
Contemporary 30y	27.3 ± 1.5	0.001	227	-	-
Contemporary 46y	27.7 ± 1.6	< 0.001	742	0.098	742
Vertebral ML width (mm)					
Archaeological	46.4 ± 3.8	Ref.	18	Ref.	18
Contemporary 20y	44.1 ± 3.0	0.004	217	< 0.001	217
Contemporary 30y	45.9 ± 2.9	0.489	227	-	-
Contemporary 46y	46.1 ± 3.4	0.627	742	0.001	742

Variable and sample	Mean values ± standard deviation	Crude comparison		Stature-adjusted comparison	
		p-value	n	p-value	n
Vertebral AP depth (mm)					
Archaeological	30.2 ± 3.4	Ref.	18	Ref.	18
Contemporary 20y	30.5 ± 2.1	0.518	217	0.039*	217
Contemporary 30y	31.9 ± 2.1	0.003	227	-	-
Contemporary 46y	33.3 ± 2.4	< 0.001	742	0.003	742
Vertebral ML width / AP depth ratio					
Archaeological	1.55 ± 0.11	Ref.	18	Ref.	18
Contemporary 20y	1.45 ± 0.09	< 0.001	217	< 0.001	217
Contemporary 30y	1.44 ± 0.09	< 0.001	227	-	-
Contemporary 46y	1.38 ± 0.09	< 0.001	742	< 0.001	742

*After height adjustment, dimension was smaller among the contemporary humans than the archaeological individuals.

To see if there have been temporal changes in the shape of the vertebral body, the ratio of the ML width and AP depth was compared between the contemporary and the archaeological samples. The unadjusted ratio was greater in the archaeological sample compared to any of the contemporary samples (Tables 11 and 12). Stature adjustment did not change the results. This would seem to indicate that the ratio between ML width and AP depth in the contemporary population has decreased. As such, it seems that contemporary people have smaller and slightly rounder-shaped vertebral bodies than the archaeological individuals, which suggests a temporal change in vertebral body size and shape.

3.4 Research question 4 – Have the significant lifestyle changes in recent history affected age-related bone density loss?

As reported in article V, age-related bone loss was detected in the sample of 114 individuals from the Terry Collection. The density means of the sex and age groups, and the differences between them, are presented in Table 13. All the measurement sites indicated a slight to moderate decrease in bone density between the two age groups (< 50 years and ≥ 50 years). In the pooled sample, the greatest decrease in the older age group was seen in the VtraD (-17%). In males, the largest decrease was also detected in VtraD (-20 %) and after that in VtotD (-15 %). The femoral densities showed a very minimal change between the age groups (between -2 %

and -5 %). As for the females, the greatest decrease was observed in FHtotD (-20 %) and FHtraD (-20 %). The rest of the vertebral and femoral densities exhibited moderate decreases between the age groups (between -11 % and -14 %). The differences in vertebral densities between the sexes were very small in the younger age group and only got smaller in the older age group. As for the femur, the largest differences between sexes could be detected in the head and the shaft. In both cases, the density loss was greater in females, which increased the differences between sexes in the older age group.

Table 13. Presents the mean (± standard deviation) bone densities in different categories (sex, age and age/sex-specific groups) and shows the changes in bone densities between age and sex groups.

	Pooled Young	Pooled Old	Change between age groups	Males Young	Males Old	Change between age groups	Females Young	Females Old	Change between age groups	Difference between sexes (female to male) Young	Difference between sexes (female to male) Old	Pooled ages Males	Pooled ages Females	Difference between sex (females to males)
N	59	55		28	27		30	39				55	59	
Density	Mean	Mean	%	Mean	Mean	%	Mean	Mean	%	%	%	Mean	Mean	%
VtotD¶ (mg/cm^3)	360.1 ± 61.3	311.7 ± 67.9	-13 %	371.7 ± 64.1	317.4 ± 62.7	-15 %	349.5 ± 58.7	307.9 ± 72.6	-12 %	-6 %	-3 %	345.0 ± 68.6	329.0 ± 68.6	-5 %
VtraD† (mg/cm^3)	271.1 ± 55.5	225.5 ± 40.0	-17 %	278.7 ± 61.1	223.2 ± 40.8	-20 %	264.5 ± 50.6	228.7 ± 39.5	-14 %	-5 %	+2 %	251.4 ± 58.8	246.9 ± 48.6	-2 %
FHtotD‡ (mg/cm^3)	525.3 ± 99.9	461.1 ± 118.0	-12 %	538.6 ± 104.8	527.9 ± 121.7	-2 %	508.3 ± 92.8	406.0 ± 84.4	-20 %	-6 %	-30 %	533.3 ± 112.5	458.0 ± 102.0	-16 %
FHtraD✦ (mg/cm^3)	796.6 ± 154.7	695.4 ± 184.5	-13 %	817.1 ± 164.1	795.0 ± 192.7	-3 %	770.3 ± 141.8	613.6 ± 135.1	-20 %	-6 %	-30 %	806.2 ± 177.4	693.3 ± 158.4	-16 %
FNcrtD✢ (mg/cm^3)	415.7 ± 70.4	381.3 ± 66.6	-8 %	397.2 ± 69.7	379.1 ± 73.6	-5 %	432.1 ± 68.9	385.5 ± 60.4	-11 %	+8 %	+2 %	388.3 ± 71.5	409.2 ± 68.5	+5 %
FcrtD❖ (mg/cm^3)	1057.3 ± 64.7	980.4 ± 99.0	-7 %	1075.5 ± 53.5	1048.0 ± 41.9	-3 %	1042.6 ± 70.6	917.7 ± 93.7	-12 %	-3 %	-14 %	1062.0 ± 49.7	981.2 ± 103.4	-8 %

¶ Vertebral total density

† Vertebral trabecular density

‡ Femoral head total density

✦ Femoral head trabecular density

✢ Femoral neck cortical density

❖ Femoral shaft cortical density

✷ Calculated as change percentage

✯ Calculated as reference percentage

The Pearson bivariate correlations were done using both the age as a continuous variant and the two age groups (Table 14). In the pooled sample, a statistically significant negative correlation between the age and all the densities was observed. Males exhibited a slightly stronger negative correlation between age and VtraD and VtotD than females. However, only the females showed statistically significant negative correlations between age and femoral densities.

Linear regression analysis (Table 15) showed that there was a statistically significant change between the age groups in the pooled sample for all densities, with the older group having a lower density. Similarly, for females, all the vertebral and femoral densities exhibited a statically significant decline. As for the males, only the VtraD and VtotD were lower in the older age group.

Table 14. Presents Pearson´s bivariate correlations between age or age group and stature, weight, vertebral densities, and femoral densities.

Density	Pooled		Males		Females	
	Age	Age group	Age	Ages group	Age	Age group
VtotD (mg/cm^3)	-0.391**	-0.353**	-0.410**	-0.405**	-0.364**	-0.306*
VtraD (mg/cm^3)	-0.432**	-0.427**	-0.442**	-0.479**	-0.419**	-0.372**
FHtotD (mg/cm^3)	-0.343**	-0.285**	-0.150	-0.091	-0.548**	-0.506**
FHtraD (mg/cm^3)	-0.355**	-0.288**	-0.172	-0.105	-0.552**	-0.499**
FNcrtD (mg/cm^3)	-0.241*	-0.245**	-0.209	-0.157	-0.303**	-0.343**
FcrtD (mg/cm^3)	-0.462**	-0.423**	-0.219	-0.225	-0.656**	-0.609**

**Correlation is significant at the 0.01 level

*Correlation is significant at the 0.05 level

In the independent samples Mann-Whitney U test, the differences between sexes were studied in pooled, young age and old age samples (Table 16). Only FHtotD, FHtraD and FcrtD showed a statistically significant difference between the sexes in pooled and old age samples. At a young age, no difference in bone densities was found between sexes. Additionally, the sample was divided into three age categories (< 40, 40-50, > 50) and studied with Kruskal-Wallis's test with Dunn-Bonferroni pairwise comparison (Table 17) to see if the bone loss could be detected already in the earlier age. Males tended to lose bone density in vertebrae at a more even pace than females. A statistically significant change between age groups was observed between groups 1 and 3 in males. For females, the change was observable already between groups 1 and 2. In the femur, men showed no statistically significant difference between the groups; whereas, females mainly showed a difference between groups 2 and 3. Only in the FNcrtD was there a change between groups 1 and 3 for females.

Table 15. Presents the linear regression results for all densities in the pooled sample that was adjusted for age group and sex. The table also shows the results for the separate samples of men and women that are adjusted only for the age group.

Density	Pooled		Males		Females	
	Lower among older^2	P for age difference	Lower among older^2	P for age difference	Lower among older^2	P for age difference
VtotD (mg/cm^3)	-48.1 (-24.2; -72.1)	<0.001	-55.2 (-20.9; -89.4)	0.002	-41.6 (-7.2; -76.0)	0.019
VtraD (mg/cm^3)	-45.5 (-27.3; -63.6)	<0.001	-55.8 (-27.6; -84.1)	<0.001	-35.8 (-12.1; -59.5)	0.004
FHtotD (mg/cm^3)	-62.8 (-24.6; -101.0)	0.001	-20.2 (41.0; -81.5)	0.511	-102.4 (-56.1; -148.6)	<0.001
FHtraD (mg/cm^3)	-99.1 (-39.3; -158.8)	0.001	-37.1 (59.3; -133.6)	0.444	-156.6 (-84.4; -228.9)	<0.001
FNcrtD (mg/cm^3)	-34.8 (-9.6; -60.1)	0.007	-22.2 (16.4; -60.9)	0.253	-46.6 (-12.7; -80.4)	0.008
FcrtD (mg/cm^3)	-75.4 (-48.3; -102.5)	<0.001	-22.2 (4.3; -48.6)	0.099	-124.9 (-81.7; -168.1)	<0.001

Table 16. Presents the differences between sexes according to the independent-samples Mann-Whitney U test.

Density	Pooled	Young	Old
	p-value	p-value	p-value
VtotD (mg/cm^3)	0.228	0.172	0.601
VtraD (mg/cm^3)	0.614	0.252	0.522
FHtotD (mg/cm^3)	< 0.001	0.203	< 0.001
FHtraD (mg/cm^3)	< 0.001	0.187	< 0.001
FNcrtD (mg/cm^3)	0.136	0.087	0.572
FcrtD (mg/cm^3)	< 0.001	0.097	< 0.001

Table 17. Differences between three age groups for both sexes according to Kruskal-Wallis with Dunn-Bonferroni pairwise comparison.

Sex	Group	Age group (years)	N	VtotD	VtraD	FHtotD	FHtraD	FNcrtD	FcrtD
				Mean density	Mean density	Mean density	Mean density	Mean density	Mean density
Males	1	< 40	28	367.7	276.4	541.0	820.7	396.8	1071.0
	2	40–50	6	368.7	250.8	564.4	855.1	409.2	1054.4
	3	> 50	21	308.0	218.3	514.1	773.0	371.1	1047.0
p < 0.005 between age group means				1 vs. 3	1 vs. 3	NA	NA	NA	NA
Females	1	< 40	15	373.2	282.0	514.4	782.1	449.4	1051.6
	2	40–50	20	318.7	240.1	480.6	727.5	410.2	1019.1
	3	> 50	24	310.0	230.7	404.0	609.2	383.3	905.6
p < 0.005 between age group means				1 vs. 2	1 vs. 2	2 vs. 3	2 vs. 3	1 vs. 3	2 vs. 3

Occupation

Occupational information was available for 77 individuals (40 males and 37 females). The division of the occupation by categories is presented in Figure 23. The clear majority of males were laborers or day laborers; whereas, almost three-quarters of the females were either housewives or had housework listed as their occupation. The next category for both sexes was service and crafts work. Very few had some type of office work or factory work as their occupation, and only a couple of the males were listed as farmers. There was a clear difference in jobs done by the males and the females.

The results here indicate a difference in age-related bone loss compared to contemporary humans. First of all, there was a similarity between the sexes in vertebral bone loss that was even slightly higher in males; this is in contrast to the contemporary condition where females tend to lose more bone than men (Hayashi et al., 2011; Oppenheimer-Velez et al., 2018; Riggs et al., 2004). Surprisingly, females also tended to lose bone relatively early (between 40–50 years); whereas, in the males, the loss was more gradual. Femoral bone loss was significantly greater in females, except in the neck, where they lost less density than males. The distribution of the occupation does indicate a clear divide in male and female occupations, while indicating relatively physically active jobs for both that could have influenced the age-related bone density loss, especially considering that retiring was uncommon at the time (Ransom & Sutch, 1986), and average life expectancy was lower (Bastian et al., 2020).

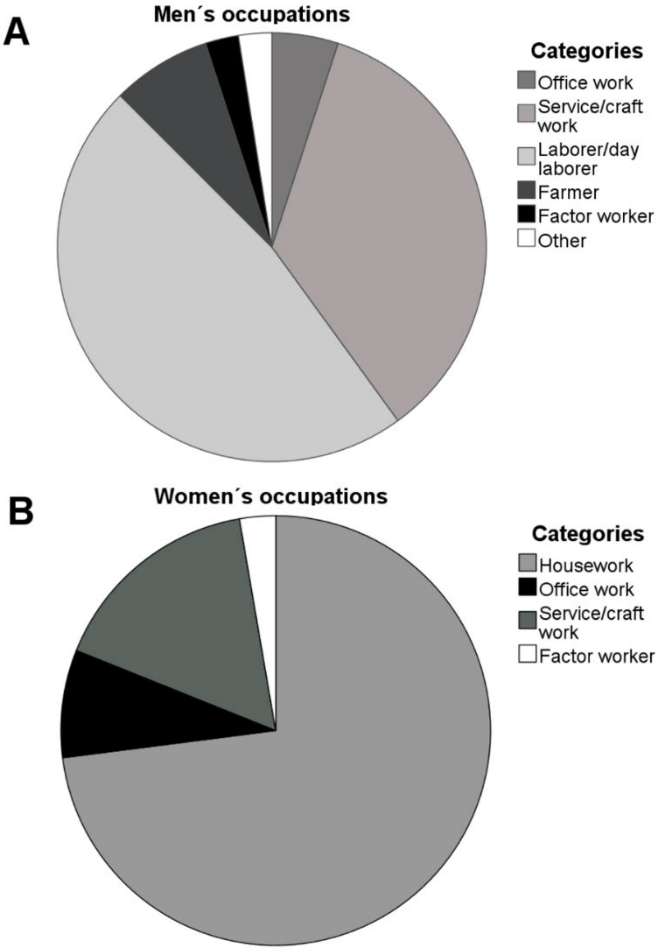

Fig. 23. Pie charts presenting the division of occupations in (A) males and (B) females. Taken from article V: Korpinen et al., 2023.

4 Discussion

4.1 Research question 1 - Morphological differences in hominoids

H. sapiens and *Gorilla* species seem to have approximately similar-sized vertebral bodies, which is not surprising, as both are heavier than *P. troglodytes*. However, there is also a large weight difference between these species to consider. The average weight for the Dutch, who are statistically the tallest people in the world, and in the 70s did not yet display obesity, was 71.4 kg for males (177.7 cm) and 60 kg for females (166.3 cm) (Eveleth & Tanner, 1976: Appendix Tables 5a, b). For Bunia Pygmies, who on the other hand represent the smallest humans, the male average weight is 40 kg (145 cm) and females 37 kg (138 cm) (Eveleth & Tanner, 1976: Appendix Tables 44 and 45). Male gorillas, on the other hand, weigh an average of 169.5 kg, and the female average is around 77.5–80.3 kg (Leigh & Shea, 1996). Therefore, to simply assume that larger vertebral bodies are likely to result from an increase in size would be an oversimplification. Previous research has indicated that humans have relatively large vertebral body sizes compared to other hominoids (Cotter, 2011; Schultz, 1961) so this is not a new observation. The relative increase in the vertebral size is likely related to the growth of the biomechanical loading towards the vertebral bodies. In *Gorilla*, this is caused by the increased body weight. In humans, it is likely a consequence of a combination of an increase in body mass and a change in weight distribution due to bipedal locomotion. Habitual bipedal locomotion has shifted the axial loading pass through the lower vertebrae to the sacrum and the lower legs. Both weight and bipedal locomotion have been shown to influence vertebral size (M. B. Leonard et al., 2004; Oura, Nurkkala, et al., 2019; Russo et al., 2020).

Regarding the shape of the vertebral body, the ratio between the ML width and AP depth seem to indicate that *P. troglodytes* has a slightly rounder vertebral corpus than *H. sapiens* but also compared to the gorillas. This would seem to line up with the results reported by Plomp, Viarsdóttir et al. (2015) who found that *Pan* (together with humans with SNs) had rounder-shaped vertebral bodies although this difference was mainly at the posterior part of the thoracic vertebral body. As my research used a very simplified method to study the overall difference in the shape, it is not possible to pinpoint exactly where this difference might lie. Interestingly, there were also some clear differences between the *Gorilla* species and *P. troglodytes*. On the other hand, there was also a difference between the *Gorilla* species in L2 and L3, as *G. beringei* seems to have wider vertebral bodies than *G. gorilla* in the last two lumbar vertebrae. *G. gorilla* and *H. sapiens* instead seem to have similarly shaped vertebral bodies in L1-L3. Similarly to *G. gorilla*, *H. sapiens* and *G. beringei* are statistically significantly different in L2 and L3. This could indicate that the shape of the vertebral body is not at least solely determined by posture and locomotion. The relative similarity between *H. sapiens* and the *Gorilla* species does, however, suggest that the shape of the vertebral body might also have a connection to the loading of the vertebral body.

Unfortunately, fewer studies have focused on the shape of the vertebral body or the cranial endplate than their size. Sanders & Bodendender (1994) did include the shape in their study and used the analysis of 28 Fourier harmonic coefficients for the shape differences. The first principal component in Figure 6A appears to indicate a more heart-shaped vertebral body in *Pan* versus a more kidney-shaped vertebral body in *Gorilla. H. sapiens* fell in the middle range here. The second principal component in Figure 6B suggested more of a divide between *H. sapiens* and apes by indicating more ovoid-shaped vertebral bodies in *H. sapiens* than the slightly more kidney-shaped found in apes (Figure 6 in Sanders & Bodenbender, 1994).

Plomp, Viarsdóttir et al. (2015), Plomp, Dobney et al. (2019), Plomp, Viarsdóttir et al. (2019) and Plomp et al. (2020) studied both thoracic and lumbar vertebra and suspected that the rounder shape of the vertebral body could be closer to the ancestral shape of *H. sapiens* and *Pan* and when found in humans could increase the vulnerability to Schmorl's nodes and sponylosis due to poorer adaptation to bipedality. My analysis did not unfortunately include thoracic vertebrae, but the results from the lumbar do not necessarily support this hypothesis. On the other hand, it does not automatically dispute it either. Considering that humans and gorillas had similarly shaped vertebrae compared to chimpanzees, one could suggest that the shape of the vertebral bodies is related to the increased biomechanical loading experienced by both species rather than strictly related to locomotion. It is possible that the species have experienced convergent evolution, where they have evolved less round vertebral bodies due to increased loading. This would leave the possibility that more round vertebral bodies could be less beneficial in bipedal locomotion, where biomechanical loading is increased compared to chimpanzees. Yet, the vertebral shape of the fossil hominoids and hominins does not appear to have been significantly rounder than modern humans or gorillas. Instead, in the whole group, it is the chimpanzees that seem to appear as the odd one.

The increased ML width would, as a consequence, increase the CSA and size of the vertebral body, but it would also increase in AP depth. The question, therefore, would be the following: is the less round vertebral body somehow more beneficial to bear the increased loading? Since *Pan* and *G. gorilla* have been shown to have very similar gait and locomotion (Finestone et al., 2018), the difference in vertebral shape should not be caused by this. Although, previous research (Isler, 2002; Neufuss et al., 2018) has observed that there are some differences in their climbing styles likely to accommodate their size differences. It is also good to consider that despite sharing very similar locomotion, both ape species have gone through their own evolutions, as gorillas split from the lineage leading to humans and chimpanzees already 6–7 million years ago, or maybe even earlier, 8-19 million years, as suggested by Langergraber et al. (2012).

A big question in bioanthropology and hominoid evolution has also long been whether chimpanzees and gorillas inherited the knuckle-walking locomotion from a common ancestor, or has it independently evolved in each species (Begun & Kivell, 2011; Crompton et al., 2008; Dainton & Macho, 1999; S. A. Williams et al., 2023). The question is directly related to human evolution: did our bipedal locomotion evolve from knuckle walking or from a more generalised arboreal, climbing-oriented locomotion. This has prompted numerous studies into the origin of the bipedality and whether apes differ in their knuckle walking (Arias-Martorell et al., 2021; Begun & Kivell, 2011; Finestone et al., 2018; Inouye & Shea, 2004; Lovejoy & McCollum, 2010; Lovejoy et al., 2009; Marchi, 2005; Matarazzo, 2008, 2013; Richmond et al., 2001; Richmond & Strait, 2000; Simpson et al., 2018; Syeda et al., 2023; Tarrega-Saunders et al., 2021; Thompson et al., 2018; S. A. Williams, 2010). Finestone et al. (2018) found no significant differences in walking kinematics between the ape species. The species have, however, been shown to have ontogenetic and postural differences in knuckle-walking behaviour (Inouye, 1994). Also, in the wrist posture, chimpanzees have been shown to use a more extended wrist than gorillas (Inouye, 1994; Kivell & Schmitt, 2009). Their wrists and hands show anatomical differences that have been suggested to be indicative of the different origin of their knuckle walking (Crompton et al., 2008; Dainton & Macho, 1999; Kivell & Schmitt, 2009). A manual pressure distribution study has also shown a difference in their use of hand position and touch-of-digit, which was suggested to relate to their positional behaviour differences (Matarazzo, 2013). Others have suggested that we should expect some differences between *Pan* and *Gorilla* considering their different ecologies, body sizes and millions of years of independent evolution (S. A. Williams et al., 2023). It has also been pointed out that the apes share numerous morphological and behavioural synapomorphies, which also include features retained in hominins; for example, African apes and humans share foot posture that is peculiar among primates (S. A. Williams et al., 2023). This is likely related to heel-strike plantigrady shared by the species (Gebo, 1996). Other similarities, like short stiff lower spine, forelimb elongation, hindlimb shortening, etc., are thought to be adaptive responses to favour suspension and vertical climbing in African apes (Simpson et al., 2018).

Hence, if the shape of the vertebral is not relate to the locomotion but rather influenced by the loading, what would be the benefit of less round vertebral body? Unfortunately, the shape of the cranial surface of the vertebral body is not often considered in the research on spinal disorders. However, few studies have found a connection between the rounder shape of the vertebral body or endplate and spinal pathologies (Harrington Jr. et al., 2001; Plomp et al., 2012; Plomp, Roberts et al., 2015). For example, Harrington Jr. et al. (2001) noted that the circular shape of the vertebral endplate had a stronger association with disc herniation than the overall size. They suggested that the longer anterior-posterior radius of the round-shaped vertebral body could create greater posterior annular tension according to the LaPlace law, which states that wall tension in any sector of an oval tube is proportional to the radius of curvature. This might then lead more frequently to posterior annular failure. As the stress towards the vertebral column is higher in bending and increases especially when lifting heavier loads (Bouxsein et al., 2006), increased body mass could, in theory, also lead to relatively higher stress in bending as the weight of the upper body becomes heavier. Despite the higher loading in both flexion and extension (forward and backward bending), the stress is surprisingly well distributed across the whole intervertebral disc (Adams et al., 2013:177–179) but can also create some increase in stress in the posterior and anterior parts of the disc (Adams et al., 2013:177–179; Costi et al., 2007). In this case, the decreased anterior-posterior radius might help to reduce wall tension in bending.

To limit the possible influence of the different number of lumbar vertebrae found between the species, the comparison was also done using only the second to last lumbar. As the second most caudal vertebrae, it serves a similar function in all the species and is the second most loaded vertebrae after the most caudal vertebrae but showcases less variation in morphology (Apazidis et al., 2011; Paik et al., 2013). Interestingly, this comparison seemed to decrease the difference in ML width / AP depth ratio of *G. beringei* with *G. gorilla* and *H. sapiens*, as neither was statistically significantly different from *G. beringei. Pan,* on the other hand, was still different from other species. This would seem to indicate that the number of lumbar vertebrae, and hence its corresponding position in the vertebral column relative to other vertebrae, can influence the vertebral body shape. As such, it is not surprising that all three heavier species showed similarity in shape when compared to the vertebrae from the same anatomical position. Cotter (2011) also noted that her estimated body mass did not correlate well with the transverse diameter index in the cervical and thoracic segments, unlike in the lumbar segment, suspecting that loading could influence the transverse width of the vertebral body. Her results also indicated that *H. sapiens* had relatively wide vertebral bodies in the entire column. The width index used here also indicated relatively mediolaterally wide vertebral bodies in *H. sapiens* relative to the mean height of the body. However, no statistically significant difference was found between *H. sapiens* and *G. beringei.* Schultz (1961) also demonstrated that *H. sapiens* had relatively wide vertebral bodies compared to the trunk length. Rose (1975), on the other hand, found that *Pan* would have the largest transverse diameter index, followed closely by *H. sapiens*. However, it is good to note that he measured all but the last lumbar vertebrae and compared all these vertebrae together, which could partly explain the differences in the results presented here. Yet, the difference does seem surprisingly significant considering that, in my study, *Pan* had the smallest width index compared to other species. Unfortunately, I could not calculate the width index to the other lumbar vertebrae (as I had the height measurements only for the second to last lumbar) to rule out the possibility of the difference lying in the upper vertebrae. However, Cotter's (2011) transverse diameter index results for the other lumbar did not indicate that *Pan* would have had a larger index in the upper lumbar vertebrae.

Similarly to the width index, the results from my study agree with Cotter (2011) in that *H. sapiens* had anterior-posteriorly deeper vertebral bodies than other hominoids. However, unlike in her results, where she found *Pan* having the lowest sagittal diameter index of the three species (*H. sapiens*, *Pan* and *G. gorilla*), here it was demonstrated that the *G. gorilla* had the lowest depth index followed by *G. beringei*. This is not surprising, as both species had a higher difference between ML width and AP depth than *Pan*. *H. sapiens,* on the other hand, demonstrated lower vertebral height than the gorillas. Actually, both indexes appeared to indicate that *H. sapiens* has a relatively wider and deeper vertebral body compared to its height. As seen in the transverse diameter index, Rose (1975) again found *Pan* having the largest sagittal diameter index, followed by *H. sapiens,* which differs from my observations.

However, my results are not directly comparable to Cotter (2011) or Rose (1975), as they used anterior height in their index, whereas I used the mean of the anterior and posterior height. Yet, my results do agree with Cotter's (2011) in that *H. sapiens* had the most robust vertebral bodies. On the sex level, the greatest differences could be observed in *H. sapiens* and *G. beringei*. Males from both species also had significantly higher indexes than any other group, even the male *G. gorilla*.

4.1.1 Shape in the fossil hominoids

The comparison of the extant species and the fossils hominoids was done using the second to last lumbar vertebrae of the extant species and preferably either the L3 or L4 vertebrae of the fossil specimens. The shape of the vertebral body does not seem to have changed greatly from the earlier hominins to modern humans. The ML width / AP depth ratio was slightly lower in some of the earlier hominins, but on the other hand, some showed an even higher ratio. The clearest outlier of the group instead seemed to be *P. troglodytes,* which had a significantly lower mean difference between ML width and AP depth than the other extant species. The mean ratio was also lower than any of the fossil values, although the individual variation of *Pan* would have included most of the earlier fossils.

I suggested that the reason for the shape in the extant species could be related to the greater axial loading of the vertebral bodies due to either increased body mass (gorillas) or changed weight distribution (humans). The relatively similar shape found in the earlier fossils that are thought to have been bipedal could support this. It could mean that the shape of the vertebral body might have shifted to a more ovoid-shaped when the axial loading has increased as a consequence of adapting to bipedality. On the other hand, the shape appears to have already been the same in *P. nyanzea,* whose locomotion has been described as non-specialised arboreal quadruped (Nakatsukasa, 2004) and the two other fossil hominoids. This could, therefore, also indicate that the more ovoid-shaped of the vertebral body is a more ancestral trait rather than necessarily related to locomotion and size. If this is the case, it would suggest that *P. troglodytes* is the one that has diverted from this condition. Since most of the fossil hominoids have been similar to the size of *P. troglodytes* (Pickering et al., 2019; Sanders & Bodenbender, 1994), the difference should not be related simply to size.

Research on the fossil hominins has suggested that earlier hominins (such as *A. afarensis, A. africanus, A. sediba*), and even *H. erectus,* had relatively small vertebral bodies compared to humans (Schiess & Haeusler, 2013; S. A. Williams et al., 2021; S. A. Williams & Russo, 2015), which was observed here too. It has also been reported that their vertebral body shape is almost intermediate between humans and apes (Meyer, 2005; Sanders, 1998; S. A. Williams et al., 2021). The Australopithecines vertebrae were reported to have been relatively craniocaudally tall compared to the ML width than that of the extant hominoids (Sanders, 1998). My results from the width index appear to agree with this, since especially the Australopithecines and the fossil hominoid had a clearly lower width index than the extant species or fossil *Homo* species. However, Sanders (1998) reported that the regressions of the vertebral body dimensions against body weight seemed to indicate that *H. erectus* and *A. afarensis* had relatively wide vertebral bodies, whereas the *A. africanus* vertebral body was narrow. The vertebral bodies of *H. erectus* were also less deep compared to the extant species. My results indicated that in the ratio between ML width and AP depth, *H. erectus* was similar to the Australopithecines, but it had relatively short vertebral bodies relative to the width and depth. It had one of the highest width and depth indexes compared to even the extant species. However, it is good to note that KNM-WT 15000 is a juvenile individual, which might affect especially the height of the vertebral body, as the ring apophyses are not yet fused (Haeusler, 2019). My results also lined up with Sanders (1998) in the observation that *A. afarensis* had relatively wide vertebral bodies, at least compared to AP depth. In the width index, it did not differ from other earlier hominins. The vertebral body of *A. africanus* was also narrower than *A. afarensis*, which was also comparable to what was reported earlier (Sanders, 1998).

P. robustus, on the other hand, appears as a strange outlier of the group, with very wide vertebral bodies both compared to AP depth and CC height. Although its massive masticatory apparatus might at first glance suggest massive body mass to match it, it has been estimated to have weighed around the same as small modern humans or chimpanzees (around 40 to 50 kg, McHenry, 1991). This would not suggest the need for such wide vertebral bodies if considered from a weight point of view. It has been suggested that an increase in the dietary breadth of the hominins could have antedated the first members of Paranthropus (Sponheimer et al., 2006). This could have also meant a change in the foraging habits that could have affected the vertebrae.

Not surprisingly, the later hominins of the *Homo* genus showed almost the same values in all three parameters as modern humans which is what one might expect from hominins closer to us in evolution. Overall, it seems that fossils fall mainly into two groups: the earlier Australopithecines and later *Homo* species, which might indicate the effect of the increased size. On the other hand, the difference appears to be clearer in the width and depth indexes and, therefore, seems to relate to the relatively taller vertebral bodies of the earlier species. In the ML width and AP depth ratio, the fossils do not clearly differ from *H. sapiens* or *G. gorilla*. This is similar to what was found by Sanders (1998) who reported relatively similar centrum shape indices for *H. sapiens*, *P. troglodytes*, *G. gorilla*, *A. africanus* and *A. afarensis* (Table 4 in Sanders, 1998). However, he did not find a clear difference in *P. troglodytes* compared to *H. sapiens* and *G. gorilla*. This difference to my results could be related to either methodological differences or population differences. Plomp, Viarsdóttir et al. (2019) also found that *H. neanderthalensis*, *H. naledi*, and *A. africanus* were more similar in vertebral shape with *H. sapiens* with SN's than healthy humans. As they found that *H. sapiens* with SN's were closer to *P. troglodytes* vertebral shape than healthy humans this would suggest that the fossil hominins are also closer to vertebral shape of *P. troglodytes*. They unfortunately did not compare the fossil hominins to each other or *P. troglodytes*, making it hard to consider how the vertebral shape might have changed from one species to other. My results did not indicate significant difference between fossil hominins and *H. sapiens* or *G. gorilla*, although most of the earlier hominins are on the lower range of *H. sapiens* and upper range of *P. troglodytes*. The difference in the results likely lies in the very different methodology as Plomp, Dobney et al. (2019) used 3D analysis whereas in my study only very basic ratio of width-to-depth was used. Therefore, according to my results it does not appear that the shape of the vertebral body would have changed greatly from the beginning of human evolution.

4.2 Research question 2 - Bone density in African apes and differences between species

Studying the overall bone density and cortical thickness patterns in the whole subaxial vertebral column of *P. troglodytes* and *G. gorilla* in article II was to get a rough idea of how the density and cortical thickness varies between adjacent vertebrae in the whole subaxial spine. The aim was also to help place the results from the three individual vertebrae (C7, T12 and L3) studied in article III in the context of the vertebral column. As the densities and cortical thickness for all the subaxial vertebrae were measured only for five specimens, these results are mainly preliminary and directive.

The results from the five specimens (article II) did indicate some differences in the bone density and cortical thickness patterns between African apes but also showed some similarities. Especially for total density and cortical density, the pattern between species did not greatly differ. In *Pan*, both densities were highest in the cervical segment and density tended to decrease in C7 and T1, after which they remained relatively stable. There may be a slight increase in the last few lumbar vertebrae, especially in cortical density. In *Gorilla*, the pattern of cortical density is quite similar to *Pan*'s; but in total density, there is some increase in density in the middle of the thoracic segment, which is more noticeable in the males than in the female. Unfortunately, there are not many studies on the vertebral densities in the whole vertebral column in *H. sapiens*, apes or monkeys. Also, most of the comparative studies have concentrated mainly on trabecular density, making it hard to compare the total or cortical densities between species. The three individual vertebrae (C7, T12 and L3) from article III showed a similar variation in total density, where it was highest in the cervical segment but decreased towards the lumbar. The cortical density showed no significant change between T12 and L3, especially in *Pan* but also in *Gorilla* females.

The measurements of trabecular density, on the other hand, showed the greatest differences between species in article II. The first and most noticeable difference was the significantly lower density in the cervical segment of *Gorilla* compared to *Pan*. In P*an*, especially the female showed the highest trabecular densities between C3–C6. The male also showed some of the highest densities in C5–C6, although these were about the same as those found in T10–T11. In *Gorilla*, both sexes showed the lowest densities of the whole subaxial column in vertebrae C3–C6. This difference is interesting especially since in humans the highest mineral density (mg/cm^2) and trabecular density (mg/cm^3) have been observed in the cervical segment, peaking usually around C4 and C5 (Anderst et al., 2017; Curylo et al., 1996; Kandziora et al., 2001; Salzmann et al., 2020; Yoganandan, Pintar, Stemper, Baisden, Aktay, Shender & Paskoff, 2006; Yoganandan, Pintar, Stemper, Baisden, Aktay, Shender, Paskoff et al., 2006; Zhang et al., 2016). This human pattern is similar to that observed here for *Pan,* although the male did not show this as clearly as the female. *Gorilla,* on the other hand, showed a completely opposite pattern, with the C4 and C5 having the lowest densities. The results from article III indicated no statistically significant difference in the density between C7 and T12 for *Pan* and *Gorilla* males. But as shown by the density pattern of the cervical spine (article II), C7 seems to be the vertebrae that experiences the clearest change from the rest of the cervical vertebrae. Similarly to *Pan,* in humans, C7 has the lowest trabecular density of the cervical segment (Anderst et al., 2011, 2017; Kandziora et al., 2001; Yoganandan, Pintar, Stemper, Baisden, Aktay, Shender & Paskoff, 2006; Yoganandan, Pintar, Stemper, Baisden, Aktay, Shender, Paskoff et al., 2006).

The thoracic segment density does not greatly differ between species (article III), although the pattern was once again somewhat different (article II and article III). In *Pan*, there was quite a lot of fluctuation between adjacent vertebrae, and despite the male showing the highest density in T10, it did not appear that either sex would show any clear pattern of increase or decrease in density at this segment. For *Gorilla*, on the other hand, there seemed to be a pattern of increasing density from the beginning of the segment until it started to decrease from around T10. Similar results can be observed in article III, where the density did not decrease between C7 and T12 for *Pan* and actually increased in T12 for *Gorilla* females. The density was also slightly higher in *Gorilla* males, although no statistically significant differences were found. In humans, trabecular density has been observed to decrease slowly towards the caudal end in the thoracic column (Hayashi et al., 2011), which does not seem similar to either of the ape species here.

In the lumbar segment of humans, the volumetric density has been documented to continue to decrease from L1 to L3, after which it experiences a slight increase in the remaining vertebrae (Hayashi et al., 2011; Yoganandan, Pintar, Stemper, Baisden, Aktay, Shender & Paskoff, 2006; Yoganandan, Pintar, Stemper, Baisden, Aktay, Shender, Paskoff et al., 2006). This seems to be similar to what was observed here for the African apes (article II). Both species showcased some level of decrease in density from the lower thoracic segment to the upper lumbar vertebrae (article II and article III) and then experienced an increase in density in the last one or two lumbar vertebrae. Only the *Pan* female did not show any increase in density at the end of the lumbar segment (article II). In L3 (article III), trabecular density was observably lower than T12 for all groups, which lines up with the overall pattern (article II), where the T12 did have a higher density than the highest lumbar density (except for the *Pan* male).

In addition to trabecular density, cortical thickness also showed some differences between species. In *Pan*, the thickness was clearly highest in the cervical segment. After the initial decrease in C7–T3, the thickness did slightly increase in the caudal direction. Similarly in *Gorilla*, cortical thickness tended to start high at the beginning of the cervical segment but decreased almost straight afterward; although, one of the males had a lower thickness in the cervical vertebrae that did not decrease until T1. In *Gorilla* males, the thickness then started to increase again from T2 onwards quite steadily and was approximately at the same level in the lumbar segment as in the cervical vertebrae. Similarly, the female's cortical thickness increased from T5 onwards until it was at about the same level on the lumbar vertebrae as in the cervical vertebrae. Interestingly though, the cortical thickness increase did stagnate in the mid-thoracic, between T5–T10 in the males and T6–T9 in the female. The results from the three individual vertebrae (article III) mainly supported these observations: as in *Gorilla,* the cortical thickness clearly increased from C7 to L3. In *Pan*, cortical thickness was lower in T12 than in C7, which was also the case in the whole pattern, as C7 still had higher cortical thickness than the beginning of the thoracic segment or T12. Although, in the *Pan* male the cortical thickness in the lumbar was approximately the same as in C7, likely explaining the lack of difference found between T12 and L3; this was not the case in the female.

My results indicated that the largest difference between the species seems to lie in the trabecular density of the cervical and thoracic segments and overall cortical thickness. Considering the difference in the neck, this is not the first time that research has indicated differences between the ape species in this area. The results reported here do seem to line up with the earlier ones that have reported differences in the allometric pattern of the subaxial cervical spine between the *Pan* and *Gorilla* species (Arlegi et al., 2017, 2018). The species have also been shown to differ by about 25 degrees in the inclination of the neck (Strait & Ross, 1999). Although the cervical segment is the least loaded segment of the three, it is typically the most mobile (Aiello & Dean, 1990a:284–285). Studies on intradiscal pressures in humans have shown that pressure on the intervertebral discs is usually increased by the flexion of the spine (Bayoglu et al., 2019; Dmitriev et al., 2005; Ghezelbash et al., 2016). These small vertebrae also seem to rely significantly on surrounding ligaments to withstand the bending stresses (Adams et al., 2013:168–169). Hence, the mobility could be the reason the cervical vertebrae in humans and *Pan* show high trabecular density and cortical thickness. Curiously, the spinous processes of *Gorilla* are at their largest in C4–C5 vertebrae, which had the lowest bone densities. In humans and *Pan*, the largest spinous process in the cervical segment is typically found in C7 (Arlegi et al., 2017). The spinous processes of gorillas are overall considerably longer than in chimpanzees (or other hominoids), which may limit the flexion-extensions movement of the gorilla's neck (Arlegi et al., 2018) and, therefore, decrease the forces created by these movements. The large spinous processes also indicate greater muscularity in the gorilla's neck, which could shield the vertebrae from some of the axial loading. This may decrease the trabecular density as it has been observed to be lower in parts of the vertebrae that experience less loading (Smit et al., 1997).

In addition to the cervical column, differences between the species in the trabecular density of the thoracic segment were also observed. Both articles (II and III) seem to indicate some kind of rise in trabecular and total density at the mid-thoracic segment in *Gorilla*. Curiously, for *Gorilla,* the T12 was the only vertebrae where the sexes did not differ in cortical density; whereas for *Pan,* T12 is the only vertebrae that shows no difference in trabecular density between the sexes (article III). There was also no clear pattern of increase or decrease in trabecular density in the whole segment for *Pan* (article II). These could indicate some sort of difference in loading at this segment between the species. Considering the similarity in locomotion and walking kinematics between the African apes (Finestone et al., 2018), this finding is not surprising. It could be related to allometric differences found in the thorax between the species, as there are indications that larger species of hominoids have relatively wider and flatter ribcages (Bastir et al., 2017). Since it has been hypothesised that the thorax and the pelvis are integrated in primates (Schultz, 1961), this could impact the muscle morphology of the area and affect the biomechanical loading of the vertebrae, which then could influence bone density. The ribcage has been also estimated to have a significant impact on the predicted compressive forces, intervertebral disc pressure, and muscle activation patterns of the trunk (Anderson et al., 2018; Ignasiak et al., 2016). It also limits the range of movement of the thoracic segment (Mannen et al., 2018). Hence, any differences in the dimensions and size of the trunk could impact the forces applied to the vertebral segment. Also, the cortical shell is thought to determine the flexibility and energy absorption of the vertebrae, whereas trabecular bone is influenced more by the load-bearing (Roux et al., 2010). This could suggest that any difference in compressive or shear forces could induce a different response from either bone and may explain the different variation in the two types of bone in the thoracic segment.

In article III, the sex and interspecific differences in the three individual vertebrae were also analysed. The results of the interspecific differences appear to line up with previous studies (Addison & Lieberman, 2020; Cotter et al., 2009). All the density parameters, apart from the cortical density, were higher in *Pan* than *Gorilla*. Cortical thickness was also higher in *Gorilla* for the T12 and L3. However, comparing the species at the sex level implied that the majority of the interspecific differences lie mostly with *Gorilla* males. As my results from the correlations indicated that larger vertebrae tended to have lower trabecular density, but higher cortical density and cortical thickness, it could partly explain the similarity between

Gorilla and *Pan* females, as they are more similar in size compared to the males. Considering the possible effect that the size of the vertebrae might have on the density, one might wonder if the lower bone density found in humans (Cotter et al., 2009; Hernandez et al., 2009), compared to other hominoids, could be related to the relatively large size of the human vertebrae (Cotter, 2011; Schultz, 1961). Maybe larger vertebrae can distribute the loading and stress more widely. It has been demonstrated that in humans, larger vertebral bodies experience smaller load per unit area (stress) (Duan, Seeman et al., 2001), and as already mentioned, the possible lower trabecular density in the areas of the vertebral body that experiences lower loading (Smit et al., 1997). This could technically decrease the density of the vertebral body in the larger vertebrae. It is also possible that the thicker cortical shell in larger apes could contribute to the shielding of the trabecular bone from some of the loading. However, this might not be the case in humans, as they tend to have relatively thin cortical shells (Cotter et al., 2011; Ritzel et al., 1997; Thomas Edwards et al., 2001).

Regarding the sex-related differences in the species, for *Gorilla*, the clearest differences seemed to lie in the higher cortical density and cortical thickness of C7 and L3 found in males. Cortical thickness was also higher in males for T12. It did seem that the males tended to exhibit higher cortical density and thickness, whereas females presented higher trabecular density (although the trabecular density difference was not statistically significant). For *Pan*, males had a higher total density of T12 and L3 and cortical thickness of C7 and T12. The trabecular density of T12 was also higher in males. Unfortunately, the sex-specific differences in the bone density of apes or monkeys are scarcely studied. One of the few, Gunji et al. (2003), reported bone mineral densities (g/cm^2) for *P. troglodytes schweinfurthii* that included only a handful of individuals, and only one was a male. They noted that this old male´s bone density was close to the young females' densities and suspected that the young male´s density would likely have been higher, a notion that is supported by the very low bone density found in the older female. This would seem to agree with my results, as *Pan* males tended to show higher densities than females. In *Cercopithecidae*, males have also been reported to have higher bone density than females (Cerroni et al., 2000; Havill et al., 2003), although it is good to note that these are usually bone mineral density results, which can be influenced by the bone size, and both species are known to exhibit sexual dimorphism (Ankel-Simons, 2007). In humans, males and females are not usually found to have a significant difference in vertebral density at a younger age (Ebbesen et al., 1999; Riggs et al., 2004); however, females tend to have a lower density in older age due to increased bone loss after menopause (Hayashi et al., 2011; Oppenheimer-Velez et al., 2018; Riggs et al., 2004). Yet almost all the research in humans has focused on trabecular density. In my study, the only statistically significant difference between sexes in trabecular density was observed in T12 for *Pan*. Although the trabecular density was lower for *Gorilla* males, no statistically significant difference between the sexes was observed. Also, in the whole subaxial column, only *Pan* females had clearly lower trabecular density in the thoracic and lumbar segments compared to the male, indicating that there might be less trabecular density difference between sexes in *Gorilla* than *Pan*. Interestingly, Ruff et al. (2020) also did not observe differences in age-related bone density loss between the sexes in *G. beringei*.

Considering the results here, it does seem that if comparing only specific or individual vertebrae, there does not appear to be large differences between the African apes. This is likely why, in comparison to other hominoids, humans included, they tend to appear very similar. However, when we look at the pattern of bone density across the whole subaxial vertebral column, or between the functional segments, it becomes clearer that the assumption of similarity between species might not hold up. Vertebral bone density is at currently very scarcely studied in apes, and most comprehensive studies have mainly focused on thoracic vertebrae (Cotter et al., 2011; Cotter et al., 2009; Hernandez et al., 2009). More research, especially on the overall pattern of the apes' and humans' vertebral column density, is needed to shed light on how different locomotion techniques and body size can affect bone density.

4.3 Research question 3 - The morphological changes in the Finnish population

In the case of short-term changes between contemporary and archaeological Finns, it was found that in addition to the increased CC height in contemporary males, their ML width had decreased. The decrease in ML width likely contributed to them having relatively smaller vertebral CSA than the archaeological males. In contrast, contemporary females did not show a decrease in ML width but did instead demonstrate an increase in AP depth, which likely contributed to a relatively similar CSA as the archaeological females. Similar observations were made by Junno et al. (2009), who also reported that contemporary males had smaller ML width and CSA compared to two archaeological samples. However, they noted the same pattern in females, whereas in our research, females seem to experience different changes than males.

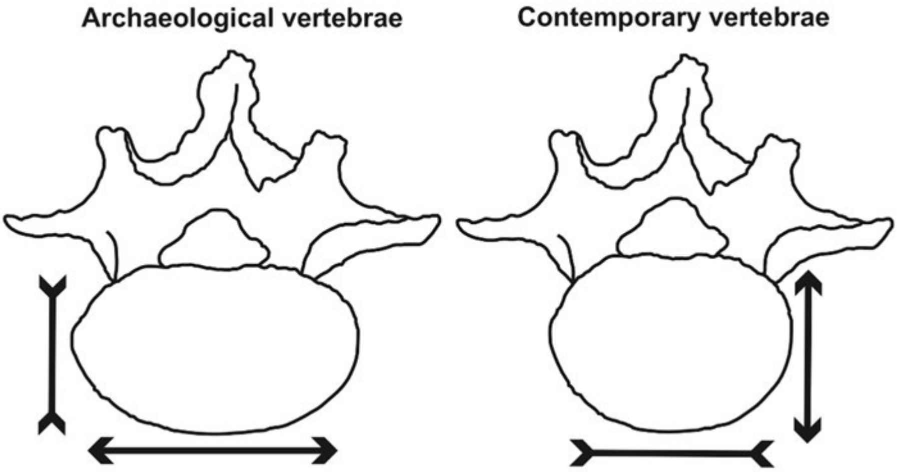

Fig. 24. The change in the shape of the vertebral body. Modified version of figure from article IV.

These changes seem to have caused the ML width and AP depth ratio to decrease in contemporary males and females compared to the archaeological population (Fig. 24). The ratio was already statistically smaller in the contemporary population, even without the height adjustment, indicating a clear change in the shape of the vertebral body. This could be perceived as slightly worrying, as some research has indicated a possible connection between the "rounder" shape of the vertebral cranial surface and intervertebral disc herniations. Harrington Jr. et al. (2001) found that the shape of the endplate had a stronger association with disc herniation than the larger size of it, especially among men. Plomp et al. (2012), Plomp, Roberts et al. (2015) and Plomp, Viarsdóttir et al. (2015) also found a connection between a rounder posterior part of the vertebral cranial surface, larger vertebral body size and Schmorl's nodes. All three studies suspected that this might have something to do with the Laplace law of wall tension if the intervertebral discs are considered as fluid-filled tubes. Harrington Jr. et al. (2001) proposed that the tension of fluid-filled tube is related to the radius and, in theory, in the case of elliptical shape to the radius of the curvature. Hence, in an ovoid tube, this could lead to the failure of the surface in lateral sectors, which in the case of the vertebra, could help to protect the nerve root from herniated discs. Plomp et al. (2012) and Plomp, Roberts et al. (2015), on the other hand, suggested that an increased radius of rounder and larger intervertebral discs could lower the resistance to wall tension.

In our research, only the females showed an increase in CSA together with an increased AP depth, although the change in CSA was not statistically significant when adjusted to the height; yet in absolute terms, their vertebral body had increased. This could, therefore, increase their vulnerability to disc herniations. If, in theory, the smaller radius of ovoid-shaped tube would decrease the wall tension in the anterior and posterior parts of the intervertebral disc, this would likely mean that the decreased ML width/AP depth ratio might also increase the risk for disc herniation in the anterior or posterior side of the vertebral body. Interestingly, lateral disc herniations are mainly found in the lower lumbar levels, which have the longest mediolateral radius (Epstein, 2002). This could support the idea of a negative effect of a longer radius on disc herniations. Also, forward bending is a very typical movement in humans, often coupled with lifting some sort of weight, which causes an increase of stress on the intervertebral discs (Adams et al., 2013:177; Ignasiak et al., 2016; Iyer et al., 2010). Decreased anterior-posterior radius might, therefore, reduce the wall tension in anterior and posterior sides and direct pressure in lateral sides that have a longer radius.

Curiously, Pouriesa et al. (2013) also reported that a disproportion of AP depth of the neighbouring endplates could have a connection to disc herniations. They found that on levels L4-L5 and L5-S1, there was a significant difference in AP depth between herniated and normal intervertebral disc study groups. Each 1 mm increase of difference between the following endplates was associated with over 50% elevation in disc herniation risk in corresponding levels.

The rounder shape might also increase the risk of vertebral fractures, as Ross et al. (1995) reported that females with greater AP depth and lower bone density had a higher risk of vertebral fractures. Vega et al. (1998) also found that males with vertebral fractures tended to have smaller ML width, however, this could be related to the size of the vertebrae. Considered together, both would have the same effect on the ML width/AP depth ratio and, therefore, would indicate a rounder vertebral shape. Since this rounder shape does not seem to have many positive outcomes, what might drive the temporal trend toward it?

Junno et al. (2009) speculated that the decreased activity levels since medieval times could partly explain the decreased ML width. Interestingly though, research on contemporary humans did not find any clear indications of the effects of higher physical activity on vertebral dimensions (Junno et al., 2011, 2013). On the other hand, these studies have focused mainly on leisure time activities. In the 18th and 19th centuries, from where the archaeological populations originate, it was not unusual to start working from a very young age, even under 10 years old. The working days were long and physically hard. The peasants particularly had to work from early morning until evening all year around to make ends meet (Häkkinen, 2007; Kauranen, 2007; Satokangas, 2007). This continuous, strenuous physical activity could have had a greater effect on the vertebral dimension throughout the lifespan than what we can observe in current populations. A good indication of this may be the observations of the strengthening of the humerus in long-term tennis players, especially when playing has been started before puberty (Ducher et al., 2005; Haapasalo et al., 1996). Hence, it is not possible to rule out physical activity as a contributing factor.

Apart from the change in physical activity, there is also another very clear change between the populations: that is the almost 10 cm increase in stature in contemporary people. This height increase is likely connected to the improvement in diet (Norgan, 2002; Perkins et al., 2016), as prior to the mid-19th century, Finland experienced multiple famines, and the diversity and quality of the food were rather poor, especially in the lower economic classes (Alto, 2006; Häkkinen, 2007). This meant that many people suffered from some level of malnourishment and nutrient deficiency (Häkkinen, 2007) that almost certainly influenced their growth. As diet has improved in the last 100 years, so has the average stature of the Finnish population increased (NCD Risk Factor Collaboration (NCD-RisC), 2016). Although most of the height increase in humans has been documented to have occurred in the legs (Bogin et al., 2002; Malina et al., 2004), there are also indications that sitting height has increased (Malina et al., 2004). In our study, it was observed that both males and females in the contemporary sample had increased CC height compared to archaeological individuals. This is most likely related to the stature increase, as the connection was already demonstrated by Junno et al. (2009). The fact that CC height change in our study was not significant in females when adjusted to stature also supports this connection. It is, however, unclear how the CC height increase might have affected the other vertebral dimensions or their proportion. What seems to be clear is that other dimensions have not increased similarly in the isometric scale, as ML width in males had decreased and in females stayed the same. Although AP depth did show an increase in both males and females in older age, the CSA in males did not show an increase compared to the archaeological males. This could indicate that contemporary males have more gracile vertebrae than their archaeological counterparts. The contemporary females, on the other hand, seem to have been able to keep up with the height increase with their overall vertebral size, mainly due to the increased AP depth.

As seen in our research, which has also been demonstrated in an earlier study (Autio et al., 2019), the vertebral dimensions tended to grow during ageing, likely due to periosteal apposition. Although both sexes experienced an increase in all the dimensions, there seems to be larger growth in the males for CSA and AP depth than in the females (Autio et al., 2019). As the study sample is the same as used in our study, it is interesting to note that the growing disparity between ML width and AP depth seem to change the vertebral shape during ageing, making them rounder in older age. As the archaeological sample was small, and their age estimation can be very broad, it was not possible to study if they would have shown a similar pattern in the age-related changes. Junno et al. (2015) did find a moderate age-related increase in vertebral CSA in 19th-century Americans, which was mainly due to an increase in ML width. Although it is good to point out that unlike the study on contemporary humans, which was longitudinal (Autio et al., 2019), the latter was a cross sectional study, which could affect the results, as the change is not observed between the same individuals. However, it is curious that a population that would have been exposed more to physical activity in the early industrialised society seems to experience growth of ML width rather than AP depth, which seems to increase more in the post-industrialised sedentary population. Whether this could be directly related to physical activity levels is still open to debate and does require further consideration. It also raises the question of what the biomechanical driving forces would be to increase certain dimensions but not others. This would be an interesting aspect to consider, but unfortunately it lies outside of the scope of this research. However, it is also important to mention that there is a possibility of different genetic influences between the temporal groups in this study, as they are not technically from the same population.

4.4 Research question 4 – Age-related changes in bone density of 19th-century Americans

Age-related changes were observed in the vertebra and femur of 19th-century Americans in article V. Both sexes lost bone density in L4 vertebrae and no statistically significant difference between the sexes was found in either age category. The bone loss was even slightly higher in males, which is an interesting observation, since in studies on contemporary populations, females tend to lose more density than males (Hayashi et al., 2011; Oppenheimer-Velez et al., 2018; Riggs et al., 2004). The differences between the sexes are not usually observable in younger age groups in volumetric trabecular density (Bouxsein & Karasik, 2006; Ebbesen et al., 1999; Oppenheimer-Velez et al., 2018; Riggs et al., 2004) but tend to emerge in later years, especially after menopause in women (Hayashi et al., 2011; Oppenheimer-Velez et al., 2018; Riggs et al., 2004). A similar pattern of bone loss has also been noted in an archaeological medieval urban population (Agarwal, 2012). On the other hand, in a rural medieval archaeological context, both males and females have been observed to lose density before the age of 50 but experience less density loss later in life (Agarwal, 2012; Agarwal et al., 2004; Agarwal & Grynpas, 2009). Additionally, not all studies on contemporary populations have reported the same results. For example, Ebbesen et al. (1999) did not detect differences between the sexes in age-related trabecular or total density loss in the L3 vertebra. Similarly, Eckstein et al. (2007) found no sex-related differences in the bone microstructure of the lumbar vertebrae in older individuals.

Although our study was mainly conducted using two age categories, to see if differences in the timing of the bone loss between sexes could be detected, three categories were also tested. The results indicated that the males tended to lose density more evenly, whereas females experienced a significant decrease already in their 40s but not as much afterwards. Interestingly, this would indicate that females in this industrialised population might have lost bone density at an earlier age, similar to the medieval rural population (Agarwal, 2012), indicating that something seems to compensate for the bone loss in later years. Also, the density loss between the two age categories appears to be significantly smaller than what is usually observed in contemporary humans (Hayashi et al., 2011; Oppenheimer-Velez et al., 2018; Riggs et al., 2004). Oppenheimer-Velez (2018) reported a 25% loss in females and 15% in males in only 6 years (baseline age over 60 for both sexes). Our sample showed a similar change between the under 50 year olds and over 50 year olds, indicating possibly a smaller density loss. However, as the sample here comes from the dry bones from a skeletal collection, and the comparison was not done between the same individuals at different age points, this could affect the results. Even so, the change between age categories does seem rather small.

Compared to the vertebra, the femoral bone loss was completely different. Males did not experience any noticeable density loss in any of the three sites. Females, on the other hand, lost the most density in the femoral head and somewhat less in the neck and shaft. It is useful to point out though that density loss in the cortical bone has been reported to be overall less than the trabecular bone in contemporary humans (Beck et al., 2000; Meta et al., 2006), most likely explaining the lower density loss in the cortical sites. The femoral neck was the only site that did not show differences between the sexes in either age group. Although females did lose double the amount of bone density compared to men at this site, the slightly higher density in a younger age caused the difference not to be significant even in an older age. In contemporary humans, the femoral neck density has also been observed to be similar between the sexes or just slightly higher in younger females (Duan et al., 2003; Saeed et al., 2009). Yet, females tend to lose more density than men during ageing (Marshall et al., 2006; Meta et al., 2006; Sigurdsson et al., 2006; Tsai et al., 1997), which was also the case in this study and has been observed in archaeological populations (Lees et al., 1993; Mays, 2006; Poulsen et al., 2001), indicating that this characteristic has not changed despite lifestyle changes.

The femoral head showed the largest decrease in density for females, even larger than the vertebra, which is opposite to the males. In contemporary populations, the femoral head has been demonstrated to lose density (Greenwood et al., 2018; Whitmarsh et al., 2019) but differences between the sexes do not appear to be as great compared to those observed here (Greenwood et al., 2018). The density loss, however, seems to occur more significantly later in life (Whitmarsh et al., 2019), which is similar to what was observed in our study. However, the studied age groups in the contemporary populations would have been included in the oldest age group in our study (> 50 years old). Hence, the exact comparison is difficult, but considering the increased life span of contemporary humans, the observation is interesting.

The density loss in males was lowest at the femoral shaft's cortical density. This lines up with results from the contemporary populations (Marshall et al., 2006). Although results from bone mineral density (mg/cm^2) studies have reported a larger bone loss in females (Hannan et al., 1992; Tsai et al., 1997), volumetric cortical bone density has been reported to show a relatively small decrease in both sexes (Marshall et al., 2006; Meta et al., 2006; Sigurdsson et al., 2006). Hence, it is interesting that females in our study showed clearly higher density loss than males.

Both bones, therefore, seemed to suggest some differences in bone density loss patterns compared to contemporary populations. As already hinted at by the results from the archaeological populations, which indicated possible differences between rural and urban populations (Agarwal, 2012), these changes could also be related to lifestyle changes that have happened in the last hundred years. One of the most obvious changes is the decreased level of physical activity, as contemporary post-industrialised societies are likely the most sedentary in human history. In the 19th century, and even in the early 20th century, the majority of people would have worked in occupations that required at least some amount of physical labour, especially in the lower economic levels. Weekly working hours were also higher than today (Floud et al., 2011). Increased urbanisation also meant changes not only in lifestyle but also in types of occupations.

In this sample, most males were recorded as laborers or day laborers. As this category could have included a variety of different jobs, it is not possible to downright label them as physically demanding, although most of them likely required some level of physical activity. The next most common occupations were service and crafts work. Very few were recorded to have been farmers, factory workers or office workers. Among females, almost three-quarters were listed as housewives or had housework listed as their occupation. Apart from that, the next most common occupation category was service and crafts work. A couple of women were recorded as office workers, and only one individual was a factory worker. Although less is known about female employment and retirement from the period, working days were likely long and strenuous for both sexes.

Retirement was also not very common in the 19th century, and over half of the men aged 60 and above were reported to still be working in the second half of the 19th century, and this did not seem to drop much before the 1930s (Ransom & Sutch, 1986). Considering that the average life expectancy in the USA prior to 1930 was under 60 years (Bastian et al., 2020), this meant working almost to the grave. In other words, most people likely never properly retired. As for the housework, especially if it is one’s own house, it is not really something you can retire from. Hence, housewives likely worked as long as they could until it was not physically possible for them anymore.

Physical activity has been shown to have a mostly positive effect on bone health and hinders bone density loss (Chastin et al., 2014; Johansson et al., 2015; Langsetmo et al., 2012; Strope et al., 2015). Although the results are quite varied, some of them have suggested that the male femur might benefit more from physical activity than the female femur (Chastin et al., 2014; Johansson et al., 2015; Nguyen et al., 2010; Vuillemin et al., 2001). It also seems that the cortical bone is especially affected by high-impact sports, whereas trabecular bone is affected by the overall levels of exercise (Saers et al., 2021). Therefore, the males who likely worked late in life in physically demanding jobs, which could have included physical activity similar to impact sports, may have benefited from them, especially in their lower limbs. Females, on the other hand, do not seem to benefit from physical activity as much and especially in their lower limbs (Chastin et al., 2014; Gába et al., 2012; Gerdhem, Åkesson et al., 2003; Gerdhem, Ringsberg et al., 2003; Puntila et al., 2001; Silman et al., 1997). Instead, there are indications that they may benefit from lighter activities and standing jobs, especially regarding their vertebrae (Douchi et al., 2000; Ebrahim et al., 1997; Puntila et al., 2001; Silman et al., 1997). This could mean that the household chores might have been more beneficial for their spine than lower limbs.

It is, however, good to note that, although regarded here as "lighter" work compared to what males might have been doing, housework in the 19th and 20th centuries would have been quite different from what it is today. It was typically a whole day job that included long days on your feet doing physically laborious chores. Also, unlike a male's day that mostly ended when they came home, a female's day would have lasted from the moment they woke up until they went to bed. Even the emergence of electronic devices did not originally shorten female workdays, as the time that was saved on one chore was often transferred to another (Davidson, 1982; Simonton, 1998). Sometimes, housewives might also add to the family's income by either helping with their husband's occupation or practicing boarding or innkeeping (Goldin, 1993). So, although it might first seem like females could have had it easier at home, this most likely was not the case.

Of course, in addition to the changes in physical activity levels, other lifestyle changes have happened in the last hundred years that could have affected age-related bone density loss. One change could be the improvements in diet and nutritional conditions. Throughout the 19th century, and in the early 20th century, the weights of males seem to decrease in the US, likely due to an increased demand for food in the growing urban centres that witnessed an influx of immigrants (Carson, 2015; Floud et al., 2011). Nutritional deficiencies, and especially lower levels of calcium, could affect the bones. Calcium, together with physical activity, has a positive influence on bone density in contemporary humans (Dawson-Hughes et al., 1997; Devine et al., 2004; Di Daniele et al., 2004). Food production was heavily reliant on crops, which did experience a great increase in production in the early 19th century, although even this was not quite enough to keep up with the growing population. Dairy products, on the other hand, suffered from the same problem as meat products, which was spoilage, but they did represent about 9% of the caloric intake during the 19th century. It is not surprising though that the adoption of refrigeration increased dairy consumption by 1.7% and overall protein intake by 1.25% annually after the 1890s. Overall, America became better nourished over the course of the late 19th century (Floud et al., 2011). Although it does seem that the intake of calcium might have not been at the same level as it is today, it is still difficult to estimate how large an effect this might have had on bone density and especially in the age-related loss in the frame of our study.

It must also be mentioned that, in regard to bone loss in females, it might be useful to consider possible changes in the hormonal balance that could affect the bone loss, such as the age of menarche, the number of years of menstruation, the number of children and time used in nursing. They all reportedly have some kind of effect on bone density (Chevalley et al., 2008; Crandall et al., 2017; Fehily et al., 1992; Fox et al., 1993; Galuska & Sowers, 1999; Ho & Kung, 2005; Ito et al., 1995; Kritz-Silverstein & Barrett-Connor, 1993; Lee, 2019; Seo et al., 2021; Streeten et al., 2005; Vico et al., 1992). For example, a younger age at menarche, older age at menopause, and longer period of menstruation have all been shown to have positive effects on bone density (Chevalley et al., 2008; Fox et al., 1993; Galuska & Sowers, 1999; Ito et al., 1995; Kritz-Silverstein & Barrett-Connor, 1993; Sioka et al., 2010), which could be seen as a positive sign for contemporary females, since temporal trends seem to favour these (Gottschalk et al., 2020). In the frame of our study, it was not unfortunately possible to consider in detail the influence of these on bone density or age-related bone loss.

Considering our study, the strength here was the large sample from the well-kept Terry Collection that included documented ages and occupations. Yet as Terry's skeletal collection consists of individuals mainly from the latter half of the 19th century and early 20th century, when reaching the age of 60 years likely meant you were healthier and more robust than your average peer. This could mean that we are comparing weaker individuals (those who died at a younger age) to stronger individuals (those who lived until an old age). Hence, the bone densities in the younger group could have been lower than average or higher than average in the older group. This should mean that the bias could decrease the age differences observed here, maybe partly explaining the relatively small density loss compared to contemporary humans. As such, it needs to be acknowledged that the observed age-related bone loss in our sample could be less than in a hypothetical longitudinal study.

4.5 Research question 5 – Evolutionary and short-term changes

Previous research has already concluded that humans tend to have relatively larger and mediolaterally wider vertebral bodies compared to other hominoids (e.g., Cotter, 2011; Rose, 1975; Schultz, 1961). The results here support the notion of relatively larger vertebral bodies in humans, as despite having smaller weight, they have approximately the same size vertebral bodies as both *Gorilla* species. Answering the first research question about the differences in the shape of the vertebral body between extant hominoids, the comparison of ML width to CC height indicated that humans have relatively wider vertebral bodies than the apes, although the difference between humans and *G. beringei* was not statistically significant. Similarly, the ratio between ML width and AP depth did not differ between humans and the *G. beringei* but was mostly similar between the apes (article I). This could indicate that humans have relatively shorter vertebral bodies rather than just relatively wide vertebral bodies. In terms of the ML width/AP depth ratio, especially humans and *G. gorilla* seem to share a similar shape of the vertebral body. *G. beringei* instead appears to have even more ovoid-shaped vertebral bodies than the other species (article I). Chimpanzees instead have the roundest-shaped vertebral bodies compared to humans and gorillas, which lines up with earlier results reported by Plomp, Viarsdóttir et al. (2015).

As for the second part of the first research question, regarding how the shape of the vertebral body has changed during human evolution, comparing the extant species to fossil hominoids seemed to indicate that no large changes have taken place in the ML width and AP depth across the evolutionary development. There are few outliers that indicate larger differences between the dimensions to those observed in extant species, e.g., *P. robustus* and one of the *A. afarensis* (A.L.288). *P. robustus* also had a high width index, but not a very high depth index, indicating a relatively wide vertebral body compared to the extant species. The *A. afarensis* (A.L. 233) showed the largest ratio observed between the ML width/AP depth in all species. Interestingly though, the other specimen of *A. afarensis* (A.L.33-37) did not show such a large ratio, rather the ratio was more in the line with humans, which could illustrate either sex-related differences inside the *A. afarensis* species or individual variation. The width and depth indexes of A.L.33-37 indicated that it had a rather tall vertebral body, which if it is also the case for the A.L.233, would mean that it had relatively wide vertebral bodies (article I).

The width and depth indexes overall were relatively low in earlier fossil hominins (*A. afarensis, A. africanus* and *A. sediba*) and in the fossil hominoid StW656, indicating that they had relatively tall vertebral bodies (article I), which has also been noted by earlier research (Sanders, 1998). Despite this, the shape of the vertebral cranial surface was similar to the extant hominoids. Comparing the extant groups and the fossils in terms of ML width/AP depth ratio, it seems that the chimpanzees were the outlier of the group (article I). Hence, considering the locomotion types used by these species, it does not appear that a vertebral shape would be related to locomotion or necessarily even posture. Maybe the shape is driven by the size increase of the vertebral bodies alone. Considering that the vertebral bodies of fossil hominins have been documented to be smaller than modern humans, often similar to the size of chimpanzees (Sanders, 1998; Sanders & Bodenbender, 1994; S. A. Williams et al., 2018), but already display less round shape than chimpanzees, it does not seem to support this idea either. Instead, one could contemplate if this has more to do with the biomechanical loading of the vertebral body; as in humans it has been demonstrated that larger vertebral bodies decrease the load per unit area (Duan, Seeman et al., 2001) and it could be argued that increasing ML width would have also increased the overall size of the vertebral body. For example, Sanders (1998) proposed that humans have relatively wider vertebral bodies, as they need to support the weight of their upper body vertically on their vertebral column. But why ML width? If this is only related to the overall size increase, this could be achieved by increasing both ML width or AP depth. What benefit does an increase of ML width have in supporting a greater body weight?

On the other hand, it has also been suggested that the vertebrae of quadrupedal animals may actually experience larger axial loading than vertebrae of the bipeds (Smit, 2002), indicating that the change to an upright position might not have had as large an effect on axial loading as one would first think. Also, vertebrae are well adapted to compressive forces, already from the beginning of mammalian evolution (Adams et al., 2013:10; Viranta-Kovanen, 2019). Yet, considering the size difference between the chimpanzees and *G. beringei,* that represented the opposite ends of the ratio, one cannot help but wonder if there might be a connection between the ratio of ML width and AP depth and the loading of the vertebral body. Considering that Smit (2002) studied the effect of the loading in terms of bone density rather than shape, it could be that bone density and shape are influenced differently by the stresses experienced by the bone.

When studying the bone density of African apes (articles II and III), the question was, does locomotion influence the bone density of the subaxial vertebrae? Considering that African apes have been shown to have very similar walking kinematics (Finestone et al., 2018) and positional behaviour (Doran, 1996), they seem to exhibit surprisingly different patterns of bone density between adjacent vertebrae. This could indicate either differences in loading patterns unrelated to locomotion or that there are differences in their locomotion that are yet to be documented. The pattern of bone density for the chimpanzees was slightly more similar to those observed in contemporary humans (Anderst et al., 2017; Curylo et al., 1996; Hayashi et al., 2011; Kandziora et al., 2001; Salzmann et al., 2020; Yoganandan, Pintar, Stemper, Baisden, Aktay, Shender & Paskoff, 2006; Yoganandan, Pintar, Stemper, Baisden, Aktay, Shender, Paskoff et al., 2006; Zhang et al., 2016) than that observed in gorillas. This could suggest that this feature may be slow to adapt to locomotion or postural changes.

It was also observed that larger vertebral bodies overall appeared to have lower trabecular density, but higher cortical density and thickness. Although the cortical density did not appear to increase significantly towards the sacrum in either species, the cortical thickness did increase in *Gorilla*. Both sexes showed an increase in cortical thickness (article III), and the thickness seemed to sometimes be even higher in the last lumbar vertebrae than in the cervical vertebrae. This is very similar to what has been reported for humans (Ritzel et al., 1997), which could indicate a relationship with the growing loading experienced by the vertebrae when moving toward the sacrum. Human studies have shown that the cortical shell does have a significant biomechanical role in sustaining compressive forces (Eswaran et al., 2005). The growing cortical thickness could increase the vertebral shell's strength to carry the loading and hence shield the trabecular bone from it. As the density of the bone has been documented to be lower in areas that experience less axial loading (Smit et al., 1997), this could be why the larger vertebrae have lower trabecular density overall in apes.

Although the cortical thickness was not significantly higher in the cervical segment for gorillas compared to the lumbar, it was still relatively high. Combined with the lower axial loading in the neck, and possibly limited movement due to longer spinous processes, high shoulders, larger jaws and enlarged air sacks in the neck (Aiello & Dean, 1990a: 284–285; Arlegi et al., 2017), this may end up shielding the trabecular bone from loading enough to decrease the density in the area. In the case of *Pan*, the cortical thickness was clearly highest in the cervical segment, but interestingly so was the trabecular density. Similarly to *Pan*, in humans, the cervical segment has been observed to have the highest trabecular density (Salzmann et al., 2020; Yoganandan, Pintar, Stemper, Baisden, Aktay, Shender & Paskoff, 2006; Yoganandan, Pintar, Stemper, Baisden, Aktay, Shender, Paskoff et al., 2006; Zhang et al., 2016), but the cortical thickness was not significantly higher in the cervical vertebrae compared to lumbar or even thoracic vertebrae (Ritzel et al., 1997). The cervical segment is the most mobile spinal segment in humans, and the small vertebrae rely heavily on the ligaments to cope with the resistance to bending (Aiello & Dean, 1990a:284; Adams et al., 2013:168–

169). This might have influenced the need to increase the durability of the vertebrae via denser bones. However, since the cortical shell of the vertebral body has been thought to influence the flexibility and energy absorption of the vertebra versus the load-bearing function of the trabecular bone (Roux et al., 2010), it is curious that the cortical thickness is not higher in humans.

While humans have been documented to have lower bone density (mainly trabecular density), their cortical thickness (Thomas Edwards et al., 2001) appears also to be lower compared to the apes (Cotter et al., 2011). Hence, the thickness of cortical bone likely does not explain the lower bone density in humans, despite the large size of the vertebral body. Additionally, humans and gorillas have been observed to differ in vertebral trabecular density (Cotter et al., 2009) but have similar-sized vertebral bodies (article I); hence, the lower bone density in humans is likely not caused by the same factor as in apes. Instead, studies on earlier human populations have indicated that the decreased bone density of contemporary humans might be a very recent phenomenon and be related to a sedentary lifestyle (Chirchir et al., 2015, 2017). As such, the bone density's connection to biomechanical loading might not be simple, but rather it is influenced by different aspects, from bone structure to locomotion. This would also not exclude the possibility of the shape of the vertebral body being influenced by the increased biomechanical loading, due to either increased body size or changes in weight distribution.

The ML width/AP depth ratio seemed to indicate shape differences in the vertebral body mainly between *Pan* and the other groups (both extant species and fossil hominoids), but surprisingly also *Gorilla* species seem to show some differences from one another. The CSA of the vertebral bodies did indicate that *G. beringei* specimens appear to be somewhat larger than the average *G. gorilla* specimens, which could partly explain the differences found between these species. This would also support the hypothesis about the axial loading affecting the shape of the vertebral body, since the species with the largest vertebral bodies and likely the highest body mass appears to also have the most ovoid-shaped vertebral bodies.

If we hypothesise that the shape of the vertebral body or the cranial surface was related to the axial loading, the results showing a temporal trend for decreasing ML width/AP depth ratio in humans in the last couple hundred years (article IV) are rather interesting. Answering the question as to whether there have been short-term changes in vertebral bodies, it was observed that there was a secular trend towards rounder vertebral body shape in the Finnish population. Especially in males the ML width had clearly decreased in the contemporary population. Similar results were also observed in an earlier study (Junno et al., 2009). It was also interesting that during ageing, the vertebral bodies kept getting rounder, as the AP depth increased more than the ML width. This contrasts the observation in industrialised 19th century American females that showcased more increase in ML width than AP depth between age groups. However, males did not show a significant increase in either dimension (Junno et al., 2015).

Vertebral body size also had not increased in a similar manner with the increased stature, and contemporary males were observed to have relatively smaller vertebral bodies than their archaeological counterparts. It was suspected that the declined level of physical activity could have affected the bone dimensions. As physical activity increases the dynamic loading of the vertebrae, which has been documented to be beneficial both in terms of bone density but also intervertebral disc health (Belavý et al., 2017; Bowden et al., 2018; Fredericson et al., 2007), it would make sense that decreased axial loading following the reduction of physical activity could also impact the shape of the vertebral body, leading to a less ovoid-shape. For example, running has positive effects on the intervertebral discs. There seems to be an optimal loading magnitude window concerning intervertebral disc health, and walking and running seem to fall into this (Belavý et al., 2017). Interestingly, although we humans are very poor sprinters, we excel in endurance running, which is quite unique to us compared to other primates or even among most mammals (Bramble & Lieberman, 2004). This could partly explain why running may be beneficial to intervertebral disc health. It has already been demonstrated that decreased physical activity seems to have both lowered bone density (Chirchir et al., 2015, 2017) and declined diaphyseal robusticity (Ruff, 2006; Ruff et al., 2015) in modern humans, which may be caused by the decreased biomechanical loading (Ryan & Shaw, 2015). Since we are now living the most sedentary life in our history, although this change has also been quite fast, it is not surprising to see even short-term changes in response to the changing lifestyles. The observed differences in age-related changes in ML width between contemporary humans (article IV) and 19th-century humans (Junno et al., 2015) could also support this, since even such a short period of time has seen a significant drop in physical activity levels. Interestingly, the changes in contemporary human vertebral bodies seem to steer us back towards the more “ancestral” shape with taller and slightly less wide vertebral bodies that could be observed in the Australopithecines (article I).

However, unlike the positive effect of exercising and physical activity on vertebral bone density and intervertebral disc health shown in contemporary humans, physical activity levels did not appear to have any notable effect on the vertebral dimensions, especially in males (Junno et al., 2011; Oura, Paananen, Niinimäki, Auvinen et al., 2017; Oura, Paananen, Niinimäki, Tammelin et al., 2017). This suggests that maybe the amount of physical activity that we can fit in our modern way of life is not enough to compensate for the change. Studies on the effects of occupational physical activity on the bones have not yielded any concrete results either, as some research has found a possible connection between the two (Biver et al., 2016), but others have not (Coupland et al., 2000; Oura, Paananen, Niinimäki, Auvinen et al., 2017). However, the overall consensus seems to be that sitting for long periods of time is not good for our health (Chau et al., 2013; Eanes, 2018; van Uffelen et al., 2010). On the other hand, as mentioned before, the optimum loading window for the intervertebral discs included running and walking, which might have been very typical activities in hunter-gatherer societies. However, how much of that is included in contemporary occupations? Could there be a disparity between the types of activities we do and what might be beneficial to our vertebrae?

Age-related bone loss was studied in a population of 19th-century Americans (Terry collection) to observe if the large lifestyle changes of recent history have changed them compared to contemporary humans (Article V). Earlier studies on archaeological populations have indicated that the timing of age-related bone loss would have changed as people moved to urban centres (Agarwal, 2012). Although the population used here comprises mainly of urban dwellers, there were still differences in age-related bone loss compared to what has been observed in contemporary human studies. This was speculated to be related mostly to the different physical activity levels of the period. The vertebral density loss seemed to be similar in both sexes (article V), which is not typical in the case of contemporary humans (Hayashi et al., 2011; Oppenheimer-Velez et al., 2018; Riggs et al., 2004). On the contrary, the sex-related differences were obvious in the femoral sites. We suggested that there is the possibility of different sexes benefiting from different activities and in different bones (Chastin et al., 2014; Douchi et al., 2000; Ebrahim et al., 1997; Gába et al., 2012; Gerdhem, Åkesson et al., 2003; Gerdhem, Ringsberg et al., 2003; Puntila et al., 2001; Silman et al., 1997). Maybe these differences could reflect some ancestral differences between sexes in labour or food acquisition. One good example is that in both chimpanzees and humans, males are usually habitual hunters, whereas females tend to stick with foraging and gathering (Hawkes et al., 1997; Hurtado et al., 1985; Silverman et al., 2007). Although hunting and foraging strategies are highly influenced by the territory, environment and cultural practices in humans, sexual division does usually exist and is related to females' reproductive and nursing activities that typically exclude females from certain tasks (W. Wood & Eagly, 2012). However, it has been argued that the sexual division of labour might have emerged relatively late in human evolutionary history (Kuhn & Stiner, 2006), which could indicate that there might not have been enough time for this division to affect the bone's adaptation to physical strain and maybe this difference is only down to biological differences between males and females.

Overall, it appears that vertebral bodies may have features that have a long history, such as the shape of the cranial surface and in extension vertebral bodies, but which might be experiencing changes in recent history thanks to the major changes in lifestyle and physical activity. Similarly, bone density appears to have been influenced by the sedentary lifestyle of contemporary humans, both in an overall decrease in bone density but also as changes in age-related bone loss. The pattern of the bone density in the subaxial vertebral column, on the other hand, might be slower to adapt to the changes, or the changes are not mainly driven by locomotion and size differences. These suggest that as we consider the evolutionary history of our spine and the health implications, we need to take into consideration not only the original demands that have shaped our vertebrae but also how the needs of the new lifestyles are shaping them. What is the disparity between the old and new requirements of the spine, and what is the spine's ability to adapt to these?

4.6 Research question 5 - The implications on current back health and the future?

Back problems are not a new phenomenon in humans (Donat et al., 2019; Knüsel et al., 1997; Lieverse et al., 2007; Novak & Šlaus, 2011; Ward et al., 2009) or even in our ancestors. The fossil hominins have even suffered from back ailments. Considering the overall limited number of fossils that have been found and the number of spinal issues found in them, it has been estimated that these were likely a relatively common occurrence (Haeusler, 2019). On the contrary, back issues have been noted to be rarer in other extant hominoids (Jurmain, 2000), indicating that the current health concerns of the back are probably somewhat related to the upright posture and bipedal locomotion. The comparison of extant and extinct species here seemed to indicate a relative increase in overall vertebral size and a decrease in CC height of the vertebral body compared to ML width and AP depth. From the point of view of human spinal health, larger vertebral bodies may decrease the risk of fractures (Duan, Seeman et al., 2001; Ruyssen-Witrand et al., 2007; Vega et al., 1998), but on the other hand, it seems that they might be more vulnerable to intervertebral disc herniations (Harrington Jr. et al., 2001; Plomp et al., 2012; Plomp, Roberts et al., 2015). Additionally, research on the degeneration of the intervertebral discs has indicated that a larger axial area might be related to the severity of the disc degeneration (Fazzalari et al., 2001; Peloquin et al., 2014). On the other hand, both Harrington Jr. et al. (2001) and Hong-sheng et al. (2010) found that the shape of the vertebral endplate also has a strong connection to disc herniation. It seemed that the more round-shape vertebral endplates increased the vulnerability to disc herniation. Interestingly, Peloquin et al. (2014), in addition to the larger size, also found the depth of the disc was slightly more strongly correlated with the degenerative grade than the width of the disc. Schmorl's nodes have also been connected to the rounder shape of the vertebral body (Plomp et al., 2012; Plomp, Roberts et al., 2015; Plomp, Viðarsdóttir et al., 2015). The more round-shaped vertebral body might also have a negative effect when it comes to vertebral fractures, as research has found that larger vertebral depth may increase the risk of vertebral fractures (Ross et al., 1995) and that people with fractures have less wide vertebral bodies than those without fractures (Vega et al., 1998). As such, the observation of a temporal trend towards less mediolaterally wide and rounder vertebral bodies might be considered worrying.

As the larger and more ovoid-shaped vertebral bodies seemed to be more typical to humans and gorillas, this could be directly related to the heavier loading of the vertebrae, which might be influenced by the decreased physical activity in contemporary populations. However, the possible change to the rounder shape is more curios, considering that across human evolution, ovoid-shaped vertebral bodies seem to have been common. It may indicate how much the current lifestyle has changed the biomechanical demands of the vertebrae. As a simple resolution, one could, therefore, suggest that we just need to increase our physical activity levels to solve the problem. However, although women seem to benefit from life-long high physical activity levels or high-impact physical activity in vertebral dimensions, this trend was not observed in men (Oura et al., 2016; Oura, Paananen, Niinimäki, Auvinen et al., 2017; Oura, Paananen, Niinimäki, Tammelin et al., 2017) This could indicate that either the amount physical activity that we can pack into our leisure time is not enough to replace the amount of physical activity in the past, or the vertebral shape is influenced also by something else than just physical activity. Maybe the vertebrae require certain kinds of physical activity to influence the vertebral dimensions and the shape, which is not typical in modern sports or physically active occupations.

Bone density has also been observed to be lower in contemporary sedentary populations compared to both other primates and past populations (Chirchir, 2019; Chirchir et al., 2015, 2017). The results here indicated that, in the past, the age-related vertebral density loss might have been relatively lower in women compared to contemporary women. Men, on the other hand, seem to lose less density in the femur. Considering both the clear occupational division between the sexes, and that both sexes had long working hours and physically hard days, these have likely influenced bone loss in the past. We also suggested that males and females benefit from different physical activities differently, which could also impact the density loss.

Supporting the importance of physical activity for the health of the spine and back is the fact that back pain seems to be less common in low-income countries and more so in the countryside (Volinn, 1997). This could indicate that people from wealthier countries are less exposed to physical activity, and it is not good for their backs. It has already been noted before that a lack of physical activity and long hours spent sitting down are not good for the human body overall (Eanes, 2018; Raichlen et al., 2017, 2020; van Uffelen et al., 2010). Interestingly, captive monkeys reportedly have a similar occurrence of degenerative changes in the spine as humans (Kramer et al., 2002; Nuckley et al., 2008). This could obviously be related to the longer life span of the captive animals, but research has also shown that the captive macaques populations tended to spend more time sitting than their wild counterparts (Kramer et al., 2002; Nuckley et al., 2008).

The lack of physical activity could both affect our vertebral shape and bone density, as bones are known to be quite good at adapting to changes in physical conditions. This adaptation is not always for the better, as demonstrated by the decreased bone density in astronauts (Sibonga et al., 2015, 2019) or patients on bed rest (Armbrecht et al., 2011; LeBlanc et al., 1995). These changes in vertebral shape and microstructure could end up weakening the vertebrae's biomechanical durability. Additionally, the lack of physical activity could weaken the back muscles offering less support to the spine. Together the weakened biomechanical durability and decreased muscle support could create conditions that, already from the start, predispose us to different back ailments, but these conditions could then be aggravated during ageing, as the normal age-related loss of bone density and muscle mass/strength starts to influence the back.

4.7 Limitations and future research

Considering the very wide subject area, spinal health and the evolution of the spine, it goes without saying that this research can only consider a fraction of both topics. Back pain and back disorders can also be caused by numerous other reasons that are not related to the bony parts of the back. By concentrating only on the bone elements, this research is relevant only to a small portion of the spinal disorders that can be related to the vertebrae themselves.

Also, by concentrating mainly only on one or a few vertebrae, although important in view of the biomechanics of the vertebrae, it was not possible to consider the back as a whole. As the back does function mainly as one element, more research is needed to understand the function of the entire back as one. On the other hand, the functional segments are also met by very different biomechanical conditions, and these should also be considered both separately and also in the context of the whole spine. The preliminary results here for the pattern of bone density in the apes' subaxial vertebral column suggest that by concentrating only on individual vertebrae, we might miss the differences in the bigger picture.

The choice to use very simplistic indicators for the shape of the vertebral body or the cranial surface is also a limitation, in the sense that it is not able to detect the detailed shape of the vertebral body. Hence, it likely misses details of the shape differences that could also be important when considering the biomechanics of the vertebral bodies. But I considered that it would be able to give us an overall idea of the shape of the vertebral body. The results indicated both lack of great change in this feature on the evolutionary scale and a more significant change in recent history. These would suggest that the vertebral shape would require further examination in the future.

The small sample size of the *G. beringei* (in article I) might mean that they do not represent the average of the species. All specimens seemed relatively large in size compared to the *G. gorilla*. As the two species of *Gorilla* do not typically differ greatly in weight, there is a possibility that they are just larger individuals, which might also be the reason they have ended up in the museum collection. Additionally, a small sample was also used in the study of the pattern of bone density in the subaxial vertebral column, which likely limits the accuracy of the results. As such, it may represent more individual variation rather than a species average difference. The results were mainly taken as reference a point when considering the three individual vertebras' densities and as preliminary results to observe if there might be a need for a broader study on the topic. However, the very clear divide between the species, especially in the cervical segment, does seem to indicate that differences in the bone density pattern may exist between the species, and hence further studies on the overall pattern of bone density in the vertebral column are needed, both in the apes and in humans.

The inability to compare the ape bone densities and cortical thickness directly to those of the humans was also a clear limitation of the study. Although there are some studies on humans and how their bone density varies between adjacent vertebrae, making the comparison between species possible on an overall level, the direct comparison would have likely been more precise. As such, future research should consider including humans in the data when comparing the species on the whole vertebral column level.

The use of a cross-sectional study in article V meant that we were not able to study the age-related changes in the same individuals, rather it was a comparison of average changes between those who died young and those who were able to live to an older age. Considering that the average life expectancy in the period was much lower, those who were able to live longer likely have been more robust individuals with possibly higher bone density. Since bone density is influenced by multiple factors during a lifetime, such as nutrition and hormones, this could create a bias in the results towards decreasing the differences between the age groups.

It also needs to be acknowledged that since not all the vertebral dimension measurements were collected by the author, this could have caused a slight possibility of bias in the results. However, the osteological measurements have well-stablished standards that are followed in the academic research; meaning that the collected measurements usually are equivalent to the each other's. We also tested the interobserver error in article IV and found it to be very small. As such, this should have only a minor influence on the results.

Future studies should concentrate especially on the vertebral shape, as it is relatively less studied than other vertebral dimensions when it comes to vertebral biomechanics, intervertebral disc health or comparative studies among primates. The observations here regarding the temporal change that might have occurred in the shape of the vertebral body also highlight the need to understand the significance of this feature in terms of spinal health. The second area that would also require more extensive examination is the bone density pattern in the whole vertebral column. The results here do indicate that the pattern of the bone density is not necessarily the same between the ape species and likely is also different compared to humans. The differences could also help shed light on the biomechanical demands created by different size, locomotion and muscularity, things that have also been important in the development of the human spine.

5 Conclusions

My research only scratches the surface of this topic, which would require broader and more comprehensive studying. However, some suggestions do rise from the results presented here. The shape of the vertebral body (the cranial surface) seems to have been relatively similar during most of the human evolution. Instead, the greatest outlier of the group, including both extant and fossil hominoid species, appears to be the chimpanzees. This could indicate that the shape of the vertebral body is influenced by the weight or axial loading directed at it. Although the fossil hominoids have often been estimated to be approximately the same weight as the chimpanzees, and tend to have small vertebrae, the less round shape of the vertebral body could indicate increased axial loading due to upright posture and bipedal locomotion. It is interesting that in contemporary humans, the vertebral shape seems to be moving towards a rounder shape, despite the increase in stature and, therefore, in body weight. Also, the relative size of the vertebral body appears to have slightly decreased, although mainly in males. As the less ovoid shape might increase vulnerability for both vertebral fractures and intervertebral disc herniation, this change might not be good in terms of spinal health. The cause for this change was suggested to be the significant drop in the physical activity levels that have followed the rapid changes in lifestyle on a societal level. Although studies on contemporary humans have not found a clear connection between the levels of physical activity and vertebral body dimensions, the decreased bone density levels in recent sedentary populations compared to the past's more physically active populations do indicate a clear influence that the physical activity levels might have on the bones. The problem may be that we are not able to include enough physical activity in our modern way of life or the activities are not the same as those which have originally shaped our spine and hence are less beneficial.

This increasingly sedentary lifestyle could have also influenced age-related bone density loss. In contemporary humans, females tend to lose more bone in the vertebrae than males; however, in the 19th-century population, it appears that both sexes lost approximately a similar amount of density. The less severe bone loss for females in the past might be related to the greater physical activity levels required by housework of the period. Physical activity is known to slow down age-related bone loss, together with calcium and vitamin D in contemporary humans, but what might not show up in these studies is the type or the scale of the physical activity that might be needed, not only to maintain bone density but maybe even increase it.

Human lifestyle has experienced great changes since the start of farming. As fast as the changes have seemed in the past, the pace of these changes is constantly increasing. On an evolutionary scale, even the 10 000 years that it has taken us to move from early farming to a post-industrialised society is a relatively short time, not including the changes that have occurred in lifestyles in only the last couple of centuries. The backbone, that has taken millions of years to evolve to what it is today, is put under increasing pressure to support us through a completely different life compared to what it was originally adapted to. As such, it is no wonder that issues have been rising. What we need to do is to learn to understand the history of the back, so we can better understand it today and in the future.

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Supplements

Supplement 1	Table presenting the used fossil species, specimens and source of the data. It also shows the ML width / AP depth ratio, Width index, Depth index and CSA for each fossil specimen.
Supplement 2	Table presenting the average ML width / AP depth ratio, CSA, Width index and Depth index for the combination of the second to last lumbar for all species.
Supplement 3	Table presenting the average ML width / AP depth ratio, CSA, Width index and Depth index for the combination of the second to last lumbar in sex and species level.
Supplement 4	Table presenting the mean, standard deviation, minimum, maximum and median of the cortical thickness and total, trabecular and cortical bone densities in C7 for all species and sexes.
Supplement 5	Table presenting the mean, standard deviation, minimum, maximum and median of the cortical thickness and total, trabecular and cortical bone densities in T12 for all species and sexes.
Supplement 6	Table presenting the mean, standard deviation, minimum, maximum, and median of the cortical thickness and total, trabecular, and cortical bone densities in L3 for all species and sexes.

First supplement

Table presenting the used fossil species, specimens and source of the data. It also shows the ML width / AP depth ratio, Width index, Depth index and CSA for each fossil specimen.

Species	Specimen	Source	ML width /AP depth ratio	Width index	Depth index	CSA
LP *H. sapiens*	CC (L4)	Been et al. 2010	1.51	1.51	1.00	9.57
LP *H. sapiens*	CM 2 (L4)	Been et al. 2010	1.40	1.47	1.05	10.85
LP *H. sapiens*	CM 3 (L4)	Been et al. 2010	1.49	1.88	1.26	15.06
LP *H. sapiens*	Sk. 4 (L4)	Been et al. 2010	1.59	1.97	1.24	9.79
H. neanderthalensis	Kebara (L4)	Been et al. 2010	1.39	1.89	1.36	14.59
H. neanderthalensis	Sh3 (L4)	Been et al. 2010	1.60	1.83	1.14	13.87
A. sediba	U.W.88 (L4)	Williams et al. 2021	1.41	1.44	1.02	5.47
A. africanus	Sts-14 (L4)	Sanders 1998	1.42	1.36	0.96	3.79
A. africanus	Stw-H8 (L4)	Sanders 1998	1.58			5.80
A. afarensis	AL.33-37 (L3?)	Sanders 1998	1.50	1.37	0.92	6.06
A. afarensis	A.L.288 (L2/L3)	Sanders 1998	1.81			3.87
P. robustus	SK3981b (last lumbar)	Sanders 1998	1.68	1.97	1.18	7.39
P. robustus	SK853 (lumbar)	Sanders 1998	1.73	1.71	0.99	3.40
H. erectus	KNM-WT 15 000 (L5)	Sanders 1998	1.45			8.09
P. nyanzea	KNM-WT13142 (L4)	Sanders & Bodenbender, 1994	1.43			4.95
Fossil hominoid	UMP67-28 (L4)	Sanders & Bodenbender, 1994	1.38			6.46
Fossil hominoid	StW656 (second last lumbar)	Pickering et al., 2019	1.51	1.91	1.13	7.51

Second supplement

Table presenting the mean (± standard deviation) of the ML width / AP depth ratio, CSA, Width index and Depth index for the combination of the second to last lumbar for all extant species.

Species	N	CSA	ML width /AP depth ratio	N	Width index	Depth index
H. sapiens	82	12.97 (±2.1)	1.52 (±0.09)	82	1.88 (±0.14)	1.24 (±0.10)
P. troglodytes	50	7.72 (±1.2)	1.31 (±0.09)	50	1.56 (±0.13)	1.19 (±0.10)
G. gorilla	41	12.42 (±3.2)	1.46 (±0.09)	40	1.65 (±0.13)	1.13 (±0.10)
G. beringei	6	14.96 (±4.1)	1.61 (±0.08)	6	1.77 (±0.17)	1.10 (±0.13)

Third supplement

Table presenting the mean (± standard deviation) of the ML width / AP depth ratio, CSA, Width index and Depth index for the combination of the second to last lumbar for the extant species in sex and species level.

Species and sex	N	CSA	ML width /AP depth ratio	N	Width index	Depth index
H. sapiens male	43	14.25 (±1.5)	1.54 (±0.07)	43	1.93 (±0.11)	1.26 (±0.08)
H. sapiens female	39	11.55 (±1.6)	1.51 (±0.11)	39	1.82 (±0.16)	1.22 (±0.12)
P. troglodytes male	20	8.34 (±1.5)	1.30 (±0.08)	20	1.59 (±0.12)	1.23 (±0.11)
P. troglodytes female	31	7.32 (±0.7)	1.32 (±0.09)	30	1.53 (±0.14)	1.16 (±0.10)
G. gorilla male	21	14.92 (±2.1)	1.46 (±0.10)	20	1.68 (±0.11)	1.16 (±0.10)
G. gorilla female	20	9.78 (±1.8)	1.47 (±0.09)	20	1.62 (±0.15)	1.10 (±0.11)
G. beringei male	3	18.38 (±2.4)	1.58 (± 0.09)	3	1.91 (±0.12)	1.21 (±0.08)
G. beringei female	3	11.55 (±1.2)	1.64 (±0.08)	3	1.63 (±0.07)	1.00 (±0.03)

Fourth supplement

Table presenting the mean, standard deviation, minimum, maximum and median of the cortical thickness and total, trabecular and cortical bone densities in C7 for all species and sexes.

Species and sex	Description	Total bone density	Trabecular bone density	Cortical bone density	Cortical thickness
Pan	N	32	32	32	32
	Mean	304.1	142.0	729.1	1.42
	Std. Deviation	69.2	38.9	26.7	0.40
	Min	115.1	29.0	690.1	0.61
	Max	429.4	194.8	797.5	2.28
	Median	317.6	149.1	723.4	1.45
Gorilla	N	26	26	26	26
	Mean	262.6	108.4	736.1	1.60
	Std. Deviation	47.8	31.7	23.7	1.40
	Min	145.9	48.4	690.1	0.83
	Max	334.2	176.6	779.3	2.21
	Median	262.8	108.9	741.7	1.60
Pan males	N	15	15	15	15
	Mean	329.5	153.3	736.1	1.58
	Std. Deviation	48.9	27.7	27.5	0.32
	Min	225.1	84.6	692.9	1.12
	Max	429.4	194.8	797.5	2.28
	Median	326.6	155.0	729.6	1.56
Pan females	N	17	17	17	17
	Mean	281.7	131.9	722.9	1.28
	Std. Deviation	77.8	45.0	25.1	0.41
	Min	115.1	29.00	690.1	0.61
	Max	392.7	193.2	773.9	1.97
	Median	295.2	132.5	715.5	1.34
Gorilla males	N	11	11	11	11
	Mean	278.8	100.8	753.5	1.94
	Std. Deviation	52.7	37.6	14.2	0.28
	Min	181.6	48.4	728.4	1.31
	Max	334.2	173.6	779.3	2.21
	Median	290.6	105.2	753.0	2.00

Species and sex	Description	Total bone density	Trabecular bone density	Cortical bone density	Cortical thickness
Gorilla females	N	15	15	15	15
	Mean	250.7	113.9	723.4	1.35
	Std. Deviation	41.7	26.6	21.1	0.26
	Min	145.9	59.0	690.1	0.83
	Max	312.0	176.6	759.0	1.71
	Median	251.9	112.8	721.2	1.33

Fifth supplement

Table presenting the mean, standard deviation, minimum, maximum and median of the cortical thickness and total, trabecular and cortical bone densities in T12 for all species and sexes.

Species and sex	Description	Total bone density	Trabecular bone density	Cortical bone density	Cortical thickness
Pan	N	32	32	32	32
	Mean	231.4	140.6	680.8	1.18
	Std. Deviation	53.7	35.9	16.8	0.36
	Min	140.0	65.2	643.0	0.55
	Max	370.6	208.4	727.4	2.16
	Median	226.5	141.7	679.9	1.10
Gorilla	N	26	26	26	26
	Mean	225.3	117.5	697.9	1.69
	Std. Deviation	43.0	33.8	18.7	0.44
	Min	132.6	55.8	654.8	1.05
	Max	287.0	206.2	735.6	2.64
	Median	235.3	121.9	698.6	1.71
Pan males	N	15	15	15	15
	Mean	249.4	153.2	679.4	1.31
	Std. Deviation	41.3	27.7	14.0	0.29
	Min	185.5	108.5	656.6	0.93
	Max	331.3	207.2	700.5	1.92
	Median	246.2	150.7	679.7	1.28
Pan females	N	17	17	17	17
	Mean	215.5	129.5	682.0	1.07

Species and sex	Description	Total bone density	Trabecular bone density	Cortical bone density	Cortical thickness
	Std. Deviation	59.3	39.3	19.2	0.39
	Min	140.0	65.2	643.0	0.55
	Max	370.6	208.4	727.4	2.16
	Median	196.9	124.7	680.0	0.98
Gorilla males	N	11	11	11	11
	Mean	225.2	109.1	703.0	1.98
	Std. Deviation	44.4	34.6	12.6	0.37
	Min	143.7	55.8	685.6	1.35
	Max	275.4	166.9	724.8	2.64
	Median	240.5	117.9	708.6	2.06
Gorilla females	N	15	15	15	15
	Mean	225.4	123.7	694.2	1.47
	Std. Deviation	43.6	33.0	21.8	0.36
	Min	132.6	55.9	654.8	1.05
	Max	287.0	206.2	735.6	2.26
	Median	223.1	124.6	693.0	1.43

Sixth supplement

Table presenting the mean, standard deviation, minimum, maximum and median of the cortical thickness and total, trabecular and cortical bone densities in L3 for all species and sexes.

Species and sex	Description	Total bone density	Trabecular bone density	Cortical bone density	Cortical thickness
Pan	N	32	32	32	32
	Mean	196.8	122.2	680.1	1.25
	Std. Deviation	47.9	33.6	17.9	0.36
	Min	114.3	65.2	642.0	0.50
	Max	297.6	188.2	714.3	2.14
	Median	197.4	120.6	678.9	1.25
Gorilla	N	26	26	26	26
	Mean	203.9	98.6	703.6	2.00
	Std. Deviation	42.4	31.8	18.5	0.55

Species and sex	Description	Total bone density	Trabecular bone density	Cortical bone density	Cortical thickness
	Min	127.2	45.6	665.5	1.11
	Max	278.7	178.8	733.6	3.21
	Median	204.5	97.7	703.7	1.96
Pan males	N	15	15	15	15
	Mean	213.5	131.9	679.1	1.36
	Std. Deviation	37.0	26.2	19.8	0.32
	Min	150.8	79.0	642.0	0.80
	Max	297.6	171.8	714.0	2.14
	Median	210.8	130.0	675.2	1.34
Pan females	N	17	17	17	17
	Mean	182.2	113.6	681.0	1.15
	Std. Deviation	52.6	37.6	16.5	0.37
	Min	114.3	65.2	644.50	0.50
	Max	285.6	188.2	714.3	1.93
	Median	186.00	110.2	680.7	1.01
Gorilla males	N	11	11	11	11
	Mean	206.1	89.3	714.2	2.38
	Std. Deviation	46.6	33.1	13.8	0.50
	Min	129.2	45.6	692.5	1.42
	Max	278.7	142.1	733.6	3.21
	Median	202.3	94.3	719.0	2.39
Gorilla females	N	15	15	15	15
	Mean	202.3	105.5	695.8	1.71
	Std. Deviation	40.6	30.2	18.0	0.39
	Min	127.2	49.6	665.5	1.11
	Max	259.4	178.8	729.7	2.56
	Median	206.6	99.5	699.7	1.64

List of original publications

I Korpinen, N. Shape differences in all lumbar vertebrae between humans and African apes. Manuscript

II Korpinen, N. (2022) Comparison of bone density patterns of subaxial apine between chimpanzees and gorillas – a case study. Journal of Medical Primatology. https://doi.org/10.1111/jmp.12627

III Korpinen, N. Differences in vertebral bone density between African apes. Manuscript.

IV Korpinen, N., Oura P., Väre T., Niskanen, M. Niinimäki, J., Karppinen, J. & Junno, J.-A. (2020) Temporal trends in vertebral dimensions – a case study from Finland. Scientific Reports 10(1). https://doi.org/10.1038/s41598-020-58340-9

V Korpinen, N., Oura, P. & Junno J-A. (2023) Sex- and site-specific, age-related changes in bone density – a Terry collection study. HOMO Journal of Comparative Human Biology. https://doi.org/10.1127/homo/2023/1662

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