Comparison of bone density patterns of the subaxial spine between chimpanzees and gorillas – a case study

Niina Korpinen[1]

[1]Department of Archaeology, Faculty of Humanities, University of Oulu, Finland

Correspondence to: Niina Korpinen Department of Archaeology, University of Oulu P.O. Box 1000, 90014 Oulu, Finland. E-mail: niina.korpinen@student.oulu.fi

Orcid ID 0000-0003-0979-4890

Funding statement

The research has received grants from the Finnish Cultural Foundation and the Finnish Academy of Science and Letters.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Competing interests

The author declares no competing interests.

Abstract

Abstract: Case study on the bone density pattern of subaxial vertebral column in African apes.

Introduction: African apes have been noted to experience fewer back ailments than humans and to have higher vertebral bone density. Yet, research on the subject is quite limited and has usually included only one or few vertebrae. However, to understand vertebral column as whole and how posture and locomotion might have affected it, we need to know how bone density varies between adjacent vertebrae.

Materials and methods: Bone density in the vertebral body was measured for all subaxial vertebrae of five specimens including two *Pan troglodytes* (1 male and 1 female) and three *Gorilla gorilla* (2 males and 1 female) using peripheral quantitative computed tomography (pQCT)

Results: The results tentatively indicated differences between species, especially in the trabecular density of the cervical segment and support the need for further studies on this subject.

Keywords: Bone density, African apes, Vertebrae, subaxial spine

Introduction

Compared to humans, African apes, have been shown to suffer less from vertebral degenerative diseases (Jurmain, 2000). They also do not seem to suffer greatly from vertebral fractures and especially from non-traumatic vertebral fractures (Carter et al., 2008; Jurmain, 1997; Schultz, 1939) which in humans are growing health concern especially in the ageing populations (Riggs and Melton, 1995). As the non-traumatic vertebral fractures are usually considered osteoporotic fractures, it is not unimaginable to think that part of the reason for the differences between species could lie in the lower vertebral density found in humans (Cotter et al., 2009; Hernandez et al., 2009). However, it is good to note that this lower bone density has been detected quite broadly in the axial skeleton (Addison and Lieberman, 2020; Chirchir, 2019; Russo, 2019; Ryan and Shaw, 2015; Scherf et al., 2013; Tsegai et al., 2018). Yet the vertebral density could play especially important part when it comes to the non-traumatic vertebral fractures, which in humans are usually associated with lower bone density and seen as the hallmark of osteoporosis (Fujiwara et al., 2003; Marshall et al., 1996; O'Neill and The European Prospective Osteoporosis Study (EPOS) Group, 2002; Van Der Klift et al., 2002). Interestingly, apes might also experience less age-related bone loss (Ohman et al., 1997; Ruff et al., 2020), although finding old individuals with bone density below human osteoporosis levels are not unheard-of (Gunji et al., 2003).

In addition to the bone density differences, several studies have also observed differences between humans and other primate species in bone microstructure (Russo, 2019; Ryan and Shaw, 2012; Tsegai et al., 2018, 2013) and in the concentration of bone minerals inside individual bones (Patel & Carlson, 2007; Sukhdeo et al., 2020; Zeininger et al., 2011). Indicating that bone density itself may not be the only impacting factor in the non-traumatic fractures. Instead, microstructure and how the bone material is concentrated in the bone could influence its durability. Although vertebral column consists of numerous individual bones they do function in more or less as one element (Aiello and Dean, 1990; Kent and Miller, 1996; Putz and Müller-Gerbl, 1996; Rockwell et al., 1938). Hence, the bone density pattern in whole column could showcase differences between species that are related to mechanical workings of the spine: posture, locomotion etc.

Most of the previous research on bone density in African apes or other hominoids has concentrated in different parts of the axial skeleton and only few has focused on the vertebral bone density or included vertebrae in the study (Cotter et al., 2009; Hernandez et al., 2009; Ruff et al., 2020; Russo, 2019; Tsegai et al., 2018) and those that have, either concentrated only on one vertebra or only one vertebra was included in the data. More numerous studies have been conducted with other primates, usually with monkeys (e.g. Cerroni et al., 2003, 2000; Havill et al., 2003; Hiyaoka et al., 1996; Nuckley et al., 2004; Pomchote, 2015), which have also often concentrated only on one vertebra. This author has not come across any research that would have reported bone densities for the whole spine or even more than one segment in apes or monkeys. However, to understand the vertebral column as whole, we also need to know how bone density varies between the adjacent vertebrae. This could help us to understand if the bone density pattern is conservative feature among hominoids or if it is influenced by the gait and locomotion.

Yet, even in humans, it is difficult to find studies reporting density for the whole spine. There are some studies that have reported bone density for one or two vertebral column segments (Curylo et al., 1996; Hayashi et al., 2011; Salzmann et al., 2020; Yoganandan et al., 2006a, 2006b), which have given us tentative idea how the density pattern for the whole spine might look in humans. However, most of this research has been concentrated on just trabecular density.

To determine how the density pattern of vertebral column in African apes might look, a case study was conducted using 2 *Pan troglodytes* (1 male and 1 female) and 3 *Gorilla gorilla* (2 males and 1 female). One scan from all their subaxial vertebra was taken from the middle of the vertebral body using peripheral quantitative computed tomography (pQCT). The aim was to examine the need for a larger study by observing if there were any clear differences in the density pattern of the vertebral column between the ape species or if their patterns seem to differ from the ones observed in humans (Curylo et al., 1996; Hayashi et al., 2011; Salzmann et al., 2020; Yoganandan et al., 2006a, 2006b).

Materials and methods

The present sample included two (1 male and 1 female) wild shot central chimpanzee (*Pan troglodytes troglodytes*) and three (2 males and 1 female) wild shot western lowland gorilla (*Gorilla gorilla gorilla*) specimens from the Powell-Cotton Museum collection. Only specimens, that were labeled as an adult or an old adult and had fully fused vertebral endplates, were included.

Quantitative computed tomography scanning

All samples of this study were scanned at the Powell-Cotton Museum using the Norland Stratec XCT Research SA pQCT scanner (Stratec Medizintechnik GmbH, Pforzheim, Germany). See figure 1. for examples of the taken scans. Scans were taken as a frontal scan and performed using the slice thickness of 1.0mm and the voxel size of 0.1mm. A hydroxyapatite phantom was employed with daily quality assurance (measurement error < 1%). The scans were processed using the manufacturer's software version 6.20 with built-in algorithms to convert the CT scan into quantitative bone density measures and all the vertebral densities (mg/cm^3) were acquired directly from the output of pQCT software. For more detailed description of the program and the scanner see Augat et al. (1998), Ferretti (1999) and Chichir et al. (2015; 2019).

The scanner indicates the exact scanning location by a laser light. All the specimens were placed in the scanner so that the scanning site was at the anterior-posterior mid-section of the vertebral corpus. Specific information about the exact scanning location is demonstrated in figure 2. For each scan, the region of interest (ROI) was selected to include the whole corpus.

Results

The results for the five specimens (1 chimpanzee male, 1 chimpanzee female, 2 gorilla males and 1 gorilla female), show that the total density and the cortical density are mainly higher in cervical vertebrae compared to thoracic and lumbar segments for both species. Both sexes in chimpanzees show greatly higher total and cortical density in cervical segment. In gorillas, total density is somewhat higher in the C3-C4 vertebrae in one of the male gorillas and the female gorilla. The other male does not show noticeably higher densities in the cervical vertebrae than what is observed in the mid-thoracic segment (see figs. 3A-B and 4A-B). The total density is also lower in the females for both species from the C7 onwards (see fig. 3A-B).

In both species, total and cortical densities experience drop at the end of the cervical spine and beginning of the thoracic segment. Total density increases in gorillas from T2 until around T10 after which it decreases once again, till having a small increase again around L3/L4 (see fig. 3B). In chimpanzees, total density stays quite stable between T2 and T11 after which it decreases slightly towards the caudal end of the lumbar segment. In the last lumbar vertebrae male experiences new increase in density (see fig. 3A). Cortical density stays also quite stable in chimpanzees from T3 to T13/L1 after which it shows slight increase (see fig. 4A). In gorillas, cortical density seems to slightly increase from T3 onwards (see fig. 4B).

Trabecular density in the cervical vertebrae is noticeably lower for gorillas compared to chimpanzees. It is also clearly lower in cervical vertebrae than in thoracic vertebrae (see fig. 5A-B). From C7 onwards the clear density difference between the species seems to disappear. There is quite a lot of fluctuation between the adjacent vertebrae in the thoracic segment overall in both species, but main pattern seems to stay stable in chimpanzees (see fig. 5A). Gorillas on the other hand, show pattern of increasing density from T2 onwards until mid-thoracic after which the density decreases slightly (see fig. 5B). From around T11/T12 onwards both species show clear decrease in density. However, most of the specimens experience a new increase in the end of the lumbar segment, except for chimpanzee female whose density stays stable for the last three vertebrae.

Discussion

The results suggests that there are possible differences in the vertebral bone density patterns of the subaxial vertebral column between African apes. The preliminary results from the five specimens showed that in the total density and the cortical density chimpanzees and gorillas follow mainly a similar pattern. Both densities tend to be highest in the cervical vertebrae and experience especially sharp drop around the C7 and the T1. From there onwards they remain fairly stable. There is also noticeable sex difference in the thoracic and the lumbar segments, interestingly though it is not as clear in the cervical segment. Unfortunately, no studies on humans have reported total or cortical densities for even one vertebral segment so it is not possible to comment if this pattern is similar in humans.

The pattern in the trabecular density instead is quite surprising, especially in the cervical vertebrae. There is clearly noticeable difference between the species from C3 to C6. In chimpanzees, the density is mostly higher in the cervical vertebrae than in the thoracic more so for the female than the male. In gorillas, the density from C3 to C6 is noticeable lower than in the thoracic vertebrae. Interestingly, in humans, it has been reported that the mineral density (g/cm^2) and the trabecular density (mg/cm^3) peak usually around the C4 and C5 (Anderst et al., 2017; Curylo et al., 1996; Kandziora et al.; Salzmann et al., 2020; Yoganandan et al., 2006a, 2006b; Zhang et al., 2016) which is similar to what is observed here for chimpanzees but completely opposite to gorillas to whom these showed the lowest trabecular values.

This is also not the first time that research has pointed to differences in the cervical segment between the African apes. The results are consistent with previous ones that have noted differences in allometric pattern of the subaxial cervical spine between chimpanzees and gorillas (Arlegi et al., 2018, 2017). Curiously, gorillas´ spinous processes are at their largest in the same C4-C5 vertebrae that shows the lowest density in here, whereas in chimpanzees similarly to humans, largest spinous process is in C7 (Arlegi et al., 2017). The spinous processes of gorillas are overall considerable longer than chimpanzees´ (or other hominoids´) which has been thought to limit the flexion-extensions movement of gorilla´s neck (Arlegi et al., 2018). The species have also been shown to differ about 25 degrees in the inclination of the neck (Strait and Ross, 1999).

In the thoracic vertebrae, the results show less difference between the species and quite a lot of fluctuation of the density between the adjacent vertebrae inside the specimens. Despite this fluctuation, gorillas seem to experience the highest density around middle of the thoracic segment, especially the males. Whereas in chimpanzees, the density fluctuation is quite significant which makes it hard to note clear drop in overall density pattern until in the caudal end of the segment. In human thoracic vertebrae, trabecular density has been observed mainly to decrease slowly from cranial to caudal direction (Hayashi et al., 2011) which does not seem to be similar to either of the apes.

In lumbar segment, the volumetric density in humans has been documented to continue the decrease from thoracic until L3 after which it starts to slightly increase (Hayashi et al., 2011; Yoganandan et al., 2006a, 2006b). Both ape species seem to follow similar pattern, with decrease of density until around L2 after which some of them experienced slight increase in the last one or two lumbar vertebrae.

Unfortunately, we did not have human values for direct comparison with these results. The comparative studies on bone density between humans and other primates have indicated that humans seem to clearly differ from other primates with their lower bone density, which is not limited only to spine, but seems to be the overall pattern for the whole axial skeleton (Hernandez et al., 2009; Russo 2019; Tsegai et al, 2018; Chirchir et al., 2019; Scherf et al, 2013; Ryan & Shaw, 2015; Addison & Liberman, 2020). Quite numerous studies have also concentrated on the bone microstructure and the pattern of the bone density inside individual bones (Patel and Carlson, 2007; Russo, 2019; Sukhdeo et al., 2020; Tsegai et al., 2018, 2013; Zeininger et al., 2011). These studies have indicated variability between the species potentially related to differences in locomotion. Comparing the preliminary results reported here with the ones reported for humans (Curylo et al., 1996; Hayashi et al., 2011; Yoganandan et al., 2006b, 2006a) indicate possible differences in the overall bone density pattern of vertebral column between humans and apes. This seems to line up with the previous results, especially on the bone mineral concentration that have indicated differences between humans and other apes (Griffin et al., 2010; Tsegai et al., 2013). These results also support the notion that there are differences in bone density and microstructure of the vertebrae between humans and other hominoids.

These microstructures of the bone such as the orientation of the trabeculae and cortical thickness, can have large effect on the mechanical strength of the bone (Roux et al., 2010; Sornay-Rendu et al., 2009a, 2009b) and have been demonstrated to be influenced by the mechanical loading of the bone (Armbrecht et al., 2011; Baker et al., 2013; Barak et al., 2017; Roux et al., 2010; Smit et al., 1997; Warner et al., 2006). Animal trials have shown that trabecular orientation can adopt to this loading and therefore it´s microstructure can reflect the usage of the bone (Christen et al., 2012; Ryan and Ketcham, 2005) which has also been noted in hominoids (Barak et al., 2017). Cortical thickness also seems to have positive relationship with physical activity and be thicker in the muscle attachment sites (Niinimäki et al., 2013). Therefore, one influencing factor on the differences between species found in this study could be the species-specific characteristics of the muscle morphology. Although very few research has directly compared the chimpanzee´s and gorilla´s muscle morphology, there are indications of differences between species. Some of the muscles have been documented to be larger in gorillas compared to chimpanzees, one example being M rhomboideus which has also been documented to attach on to the cervical spine in gorillas (Macalister, 1870). The significantly larger spinous processes in cervical segment (Arlegi et al., 2017) could also indicate larger muscle´s for gorillas in a neck area. As research on humans has indicated that the trabecular density is lower in the center of the vertebral body, which also seems to experience less loading compared to other areas of the vertebral body (Smit et al., 1997), maybe the larger muscles in gorilla´s neck could lessen the axial loading on the cervical bodies, decreasing the trabecular density. However, very little is yet known about the microstructure of the great ape vertebrae or even the muscle morphology differences between species. Hence in the future, larger and more comprehensive studies on both bone density and structure but also the muscle morphology are recommended to confirm not only our preliminary findings on the bone density patterns in the vertebral column of African apes but also to consider the causes of the species-specific differences.

The main limitation of this case study is the small sample size. However, the results are not meant to provide any large conclusions of the differences between species. Rather these are meant to be preliminary result to show us if there is possible need for larger study on the subject. The clear difference between the species on the trabecular density, especially in the cervical segment, despite the sex differences does support the possibility that there could be difference in cervical segment between the ape species. Second possible limitation is the use of dry bones that were scanned in air. This is likely to affect the values, but as method here is to compare the data mainly against itself and study the overall pattern of the bone densities in the spine and not to use them as absolute values to compare any other data, hopefully this limits the effect of possible measuring error.

The strength of the study is the well-preserved bone material that all have been conserved and stored similarly, limiting the effect of different taphonomic processes on the bones. The second strength is the use of pQCT to study the bone density. There are previous studies that that have utilized this method on dry bones with promising results (Chirchir et al, 2015; 2017; 2019; Ruff et al., 2020). There are also no previous studies on the subject that the author is aware of and hence this study is useful in shedding some light on the subject and helping future studies to plan what they might like to concentrate on.

In conclusion, the results of this study tentatively indicate that there seem to be differences in the bone density pattern of the subaxial spine between the African apes. These findings may be also applied on humans. As such this study have shown that there is a need for further larger study on the subject. Hopefully with larger sample size species-specific patterns for the densities could be made clearer.

Acknowledgements

I would like to thank the Powell-Cotton Museum, Birchington, UK, for the access to their Large Primate Collection. I would also like to thank my supervisors Juho-Antti Junno and Markku Niskanen for their support in this project.

This work was financially supported by the Finnish Cultural Foundation and Finnish Academy of Science and Letters, who had no involvement in the study design, execution, or reporting.

Bibliography

Addison BJ, Lieberman DE. Assessing patterns of variation in BV/TV in the calcaneus and C2 vertebra of Gorilla gorilla, Pan troglodytes, and populations of Homo sapiens from the Pleistocene and Holocene that differ in physical activity levels. Am. J. Phys. Anthropol. 2020; 173:337–349. https://doi.org/10.1002/ajpa.24064

Aiello L, Dean C. The Hominoid Thorax and Vertebral column. In: Introduction to Human Evolutionary Anatomy 1990; San Diego, USA: Academic Press, p. 275–308.

Anderst WJ, West T, Donaldson III WF, Lee JY. Cervical spine bone density in young healthy adults as a function of sex, vertebral level and anatomic location. Eur. Spine J. 2017; 26:2281–2289. https://doi.org/10.1007/s00586-017-5119-2

Arlegi M, Gómez-Olivencia A, Albessard L, Martínez I, Balzeau A, Arsuaga JL, Been E. The role of allometry and posture in the evolution of the hominin subaxial cervical spine. J. Hum. Evol. 2017; 104:80–99. https://doi.org/10.1016/j.jhevol.2017.01.002

Arlegi M, Gomez-Robles A, Gomez-Olivencia A. Morphological integration in the gorilla, chimpanzee, and human neck. Am. J. Phys. Anthropol. 2018; 166:408–416.

Armbrecht G, Belavý DL, Backström M, Beller G, Alexandre C, Rizzoli R, Felsenberg D. Trabecular and cortical bone density and architecture in women after 60 days of bed rest using high-resolution pQCT: WISE 2005. J. Bone Miner. Res. 2011; 26:2399–2410. https://doi.org/10.1002/jbmr.482

Augat P, Gordon CL, Lang T, Iida H, Genant HK. Accuracy of cortical and trabecular bone measurements with peripheral quantitative computed tomography (pQCT). *Phys Med Biol.* 1998; 43:2873-2883. doi: 10.1088/0031-9155/43/10/015

Baker JF, Davis M, Alexander R, Zemel BS, Mostoufi-Moab S, Shults J, Sulik M, Schiferl DJ, Leonard MB. Associations between body composition and bone density and structure in men and women across the adult age spectrum. Bone 2013; 53:34–41. https://doi.org/10.1016/j.bone.2012.11.035

Barak MM, Sherratt E, Lieberman DE. Using principal trabecular orientation to differentiate joint loading orientation in the 3rd metacarpal heads of humans and chimpanzees. J. Hum. Evol. 2017; 113:173–182. https://doi.org/10.1016/j.jhevol.2017.08.018

Carter ML, Pontzer H, Wrangham RW, Peterhans JK. Skeletal pathology in Pan troglodytes schweinfurthii in Kibale National Park, Uganda. Am. J. Phys. Anthropol. 2008; 135:389–403. https://doi.org/10.1002/ajpa.20758

Cerroni AM, Tomlinson GA, Turnquist JE, Grynpas MD. Effect of parity on bone mineral density in female rhesus macaques from Cayo Santiago. Am. J. Phys. Anthropol. 2003; 121:252–269. https://doi.org/10.1002/ajpa.10238

Cerroni AM, Tomlinson GA, Turnquist JE, Grynpas MD. Bone Mineral Density, Osteopenia, and Osteoporosis in the Rhesus Macaques of Cayo Santiago. Am. J. Phys. Anthropol. 2000; 113:389–410. https://doi.org/10.1002/1096-8644(200011)113:3<389::AID-AJPA9>3.0.CO;2-I

Chirchir H, Kivell T, Ruff C, Hublin J, Carlson K, Zipfel B, Richmond B. Recent origin of low trabecular bone density in modern humans. PNAS – Proc Natl Acad Sci USA. 2015; 112:366-371. doi: 10.1073/pnas.1411696112

Chirchir H, Ruff C, Junno J, Potts R. Low trabecular bone density in recent sedentary modern humans. Am J Phys Anthropol. 2017; 162:550-560. doi: 10.1002/ajpa.23138

Chirchir H. Trabecular Bone Fraction Variation in Modern Humans, Fossil Hominins and Other Primates. Anat. Rec. 2019; 302:288–305. https://doi.org/10.1002/ar.23967

Christen P, Van Rietbergen B, Lambers FM, Müller R, Ito K. Bone morphology allows estimation of loading history in a murine model of bone adaptation. Biomech. Model. Mechanobiol. 2012; 11:483–492. https://doi.org/10.1007/s10237-011-0327-x

Cotter MM, Simpson SW, Latimer BM, Hernandez CJ. Trabecular microarchitecture of hominoid thoracic vertebrae. Anat. Rec. 2009; 292:1098–1106. https://doi.org/10.1002/ar.20932

Curylo L, Lindsey RW, Doherty BJ, LeBlanc A. Segmental variations of bone mineral density in the cervical spine. Spine (Phila. Pa. 1976). 1996; 21:319–322. https://doi.org/10.1002/1096-8644(200011)113:3<389::AID-AJPA9>3.0.CO;2-I

Ferretti JL. Peripheral quantitative computed tomography for evaluating structural and mechanical properties of small bone. *Mechanical testing of bone and the bone-implant interface.* CRC Press; 1999: 409-430.

Fujiwara S, Kasagi F, Masunari N, Naito K, Suzuki G, Fukunaga M. Fracture Prediction From Bone Mineral Density in Japanese Men and Women. J Bone Min. Res 2003; 18:1547–1553. https://doi.org//10.1359/jbmr.2003.18.8.1547

Griffin NL, D'Août K, Ryan TM, Richmond BG, Ketcham RA, Postnov A. Comparative forefoot trabecular bone architecture in extant hominids. J. Hum. Evol. 2010; 59:202–213. https://doi.org/10.1016/j.jhevol.2010.06.006

Gunji H, Hosaka K, Huffman MA, Kawanaka K, Matsumoto-Oda A, Hamada Y, Nishida T. Extraordinarily low bone mineral density in an old female chimpanzee (Pan troglodytes schweinfurthii) from the Mahale Mountains National Park. Primates 2003; 44:145–149. https://doi.org/10.1007/s10329-002-0030-8

Havill LM, Mahaney MC, Czerwinski SA, Carey KD, Rice K, Rogers J. Bone mineral density reference standards in adult baboons (Papio hamadryas) by sex and age. Bone 2003; 33:877–888. https://doi.org/10.1016/S8756-3282(03)00231-X

Hayashi T, Chen H, Miyamoto K, Zhou X, Hara T, Yokoyama R, Kanematsu M, Hoshi H, Fujita H. Analysis of bone mineral density distribution at trabecular bones in thoracic and lumbar vertebrae using X-ray CT images. J. Bone Miner. Metab. 2011; 29:174–185. https://doi.org/10.1007/s00774-010-0204-1

Hernandez CJ, Loomis DA, Cotter MM, Schifle AL, Anderson LC, Elsmore L, Kunos C, Latimer B. Biomechanical allometry in hominoid thoracic vertebrae. J. Hum. Evol. 2009; 56:462–470. https://doi.org/10.1016/j.jhevol.2008.12.007

Hiyaoka A, Yoshida T, Cho F, Yoshikawa. Changes in bone mineral density of lumbar vertebrae after parturition in African Green Monkeys. 1996;

https://doi.org/10.1538/expanim.45.257

Jurmain R. Degenerative joint disease in African great apes: An evolutionary perspective. J. Hum. Evol. 2000; 39:185–203. https://doi.org/10.1006/jhev.2000.0413

Jurmain R. Skeletal Evidence of Trauma in African Apes, with Special Reference to the Gombe Chimpanzees. Primates 1997; 38:1–14. https://doi.org/10.1007/BF02385918

Kandziora F, Pflugmacher R, Scholz M, Schnake K, Lucke M, Schröder R, Mittlmeier T. Comparison Between Sheep and Human Cervical Spines An Anatomic, Radiographic, Bone Mineral Density, and Biomechanical Study., SPINE.

Kent GC, Miller L. Vertebrae, Ribs, and Sterna. In: Kemp M. Ed. Comparative Anatomy of the Vertebrates 1996; Dubuque, USA: Wm. C. Brown Publishers, p. 135–154.

Macalister A. The Muscular Anatomy of the Gorilla. Proc. R. Irish Acad. 1870; 1:506–513.

Marshall D, Johnell O, Wedel H, Bmj S, Medical B, May N, Marshall D, Johnell O, Wedel H. Meta-Analysis Of How Well Measures Of Bone Mineral Density Predict Occurrence Of Osteoporotic Fractures. Br. Med. J. 1996; 312:1254–1259.

Niinimäki S, Söderling S, Junno JA, Finnilä M, Niskanen M. Cortical bone thickness can adapt locally to muscular loading while changing with age. HOMO- J. Comp. Hum. Biol. 2013; 64:474–490. https://doi.org/10.1016/j.jchb.2013.07.004

Nuckley DJ, Eck MP, Carter JW, Ching RP. Spinal maturation affects vertebral compressive mechanics and vBMD with sex dependence. Bone 2004; 35:720–728. https://doi.org/10.1016/j.bone.2004.04.015

O'Neill TW, The European Prospective Osteoporosis Study (EPOS) Group. The Relationship Between Bone Density and Incident Vertebral Fracture in Men and Women. J. Bone Miner. Res. 2002; 17:2214–2221. https://doi.org/10.1359/jbmr.2002.17.12.2214

Ohman JC, Mensforth RP, Latimer B. Age-related osteopenia in Gorilla gorilla and Pan troglodytes. Am. J. Phys. Anthropol. 1997; 24:181.

Patel BA, Carlson KJ. Bone density spatial patterns in the distal radius reflect habitual hand postures adopted by quadrupedal primates. 2007; 52:130–141. https://doi.org/10.1016/j.jhevol.2006.08.007

Pomchote P. Age-related changes in osteometry, bone mineral density and osteophytosis of the lumbar vertebrae in Japanese macaques. Primates 2015; 56:55–70. https://doi.org/10.1007/s10329-014-0448-9

Putz RL V., Müller-Gerbl M. The Vertebral Column-A Phylogenetic Failure? A Theory Explaining the Function and Vulnerability of the Human Spine. Clin. Anat. 1996; 9:205–212. https://doi.org/10.1002/(SICI)1098-2353(1996)9:3<205::AID-CA12>3.0.CO;2-V

Riggs L, Melton L. The worldwide problem of osteoporosis: Insights Afforded by Epidemiology. Bone 1995; 17:2–3.

Rockwell H, Evans FG, Pheasant HC. The comparative morphology of the vertebrate spinal column. Its form as related to function. J. Morphol. 1938; 63:87–117. https://doi.org/10.1002/jmor.1050630105

Roux JP, Wegrzyn J, Arlot ME, Guyen O, Delmas PD, Chapurlat R, Bouxsein ML. Contribution of trabecular and cortical components to biomechanical behavior of human vertebrae: An ex vivo study. J. Bone Miner. Res. 2010; 25:356–361. https://doi.org/10.1359/jbmr.090803

Ruff CB, Junno J-A, Eckardt W, Gilardi K, Mudakikwa A, McFarlin SC. Skeletal ageing in Virunga mountain gorillas. Philos. Trans. R. Soc. B Biol. Sci. 2020; 375:20190606. https://doi.org/10.1098/rstb.2019.0606

Russo GA. Trabecular Bone Structural Variation in the Proximal Sacrum Among Primates. Anat. Rec. 2019; 302:1354–1371. https://doi.org/10.1002/ar.23978

Ryan TM, Ketcham RA. Angular orientation of trabecular bone in the femoral head and its relationship to hip joint loads in leaping primates. J. Morphol. 2005; 265:249–263.

https://doi.org/10.1002/jmor.10315

Ryan TM, Shaw CN. Gracility of the modern Homo sapiens skeleton is the result of decreased biomechanical loading. Proc. Natl. Acad. Sci. U. S. A. 2015; 112:372–377. https://doi.org/10.1073/pnas.1418646112

Ryan TM, Shaw CN. Unique suites of trabecular bone features characterize locomotor behavior in human and non-human anthropoid primates. PLoS One 2012; 7. https://doi.org/10.1371/journal.pone.0041037

Salzmann SN, Okano I, Ortiz Miller C, Chiapparelli E, Reisener MJ, Winter F, Shue J, Carrino JA, Sama AA, Cammisa FP, Girardi FP, Hughes AP. Regional bone mineral density differences measured by quantitative computed tomography in patients undergoing anterior cervical spine surgery. Spine J. 2020; 20:1056–1064. https://doi.org/10.1016/j.spinee.2020.02.011

Scherf H, Harvati K, Hublin JJ. A comparison of proximal humeral cancellous bone of great apes and humans. J. Hum. Evol. 2013; 65:29–38. https://doi.org/10.1016/j.jhevol.2013.03.008

Schultz AH. Notes of diseases and healed fractures of wild apes. Bull. Hist. Med. 1939; 7:571–582.

Smit T, Odgaard A, Schneider E. Structure and Function of Vertebral Trabecular Bone. Spine (Phila. Pa. 1976). 1997; 22:2823–2833.

Sornay-Rendu E, Boutroy S, Munoz F, Bouxsein ML. Cortical and trabecular architecture are altered in postmenopausal women with fractures. Osteoporos. Int. 2009a; 20:1291–1297. https://doi.org/10.1007/s00198-009-1008-9

Sornay-Rendu E, Cabrera-Bravo JL, Boutroy S, Munoz F, Delmas PD. Severity of vertebral fractures is associated with alterations of cortical architecture in postmenopausal women. J. Bone Miner. Res. 2009b; 24:737–743. https://doi.org/10.1359/jbmr.081223

Strait DS, Ross CF. Kinematic Data on Primate Head and Neck Posture: Implications for the Evolution of Basicranial Flexion and an Evaluation of Registration Planes Used in Paleoanthropology. Am J Phys Anthr. 1999; 108:205–222. https://doi.org/10.1002/(SICI)1096-8644(199902)108:2<205::AID-AJPA6>3.0.CO;2-F

Sukhdeo S, Parsons J, Niu XM, Ryan TM. Trabecular Bone Structure in the Distal Femur of Humans, Apes, and Baboons. Anat. Rec. 2020; 303:129–149. https://doi.org/10.1002/ar.24050

Tsegai ZJ, Kivell TL, Gross T, Nguyen NH, Pahr DH, Smaers JB, Skinner MM. Trabecular bone structure correlates with hand posture and use in hominoids. PLoS One 2013; 8:e78781. https://doi.org/10.1371/journal.pone.0078781

Tsegai ZJ, Skinner MM, Pahr DH, Hublin JJ, Kivell TL. Systemic patterns of trabecular bone across the human and chimpanzee skeleton. J. Anat. 2018; 232:641–656. https://doi.org/10.1111/joa.12776

Van Der Klift M, De Laet CEDH, Mccloskey E V, Hofman A, Pols HAP. The Incidence of Vertebral Fractures in Men and Women: The Rotterdam Study. J. Bone Miner. Res. 2002; 17:1051–1056. https://doi.org/10.1359/jbmr.2002.17.6.1051

Warner SE, Shea JE, Miller SC, Shaw JM. Adaptations in cortical and trabecular bone in response to mechanical loading with and without weight bearing. Calcif. Tissue Int. 2006; 79:395–403. https://doi.org/10.1007/s00223-005-0293-3

Yoganandan N, Pintar FA, Stemper BD, Baisden JL, Aktay R, Shender BS, Paskoff G, Laud P. Trabecular bone density of male human cervical and lumbar vertebrae. Bone 2006a; 39:336–344. https://doi.org/10.1016/j.bone.2006.01.160

Yoganandan N, Pintar FA, Stremper B, Baisden JL, Aktay R, Shender BS, Paskoff G. Bone mineral density of human female cervical and lumbar spines from quantitative computed tomography. Spine (Phila. Pa. 1976). 2006b; 31:73–76.

Zeininger A, Richmond BG, Hartman G. Metacarpal head biomechanics: A comparative backscattered electron image analysis of trabecular bone mineral density in Pan troglodytes, Pongo pygmaeus, and Homo sapiens. J. Hum. Evol. 2011; 60:703–710. https://doi.org/10.1016/j.jhevol.2011.01.002

Zhang Y, Zhou Z, Wu C, Zhao D, Wang C, Cheng X, Cai W, Wang L, Duanmu Y, Zhang C, Tian W. Population-stratified analysis of bone mineral density distribution in cervical and lumbar vertebrae of Chinese from quantitative computed tomography. Korean J. Radiol. 2016; 17:581–589. https://doi.org/10.3348/kjr.2016.17.5.581

Figure 1. Images of the pQCT scans for the chimpanzee male and one male gorilla from three different vertebrae.

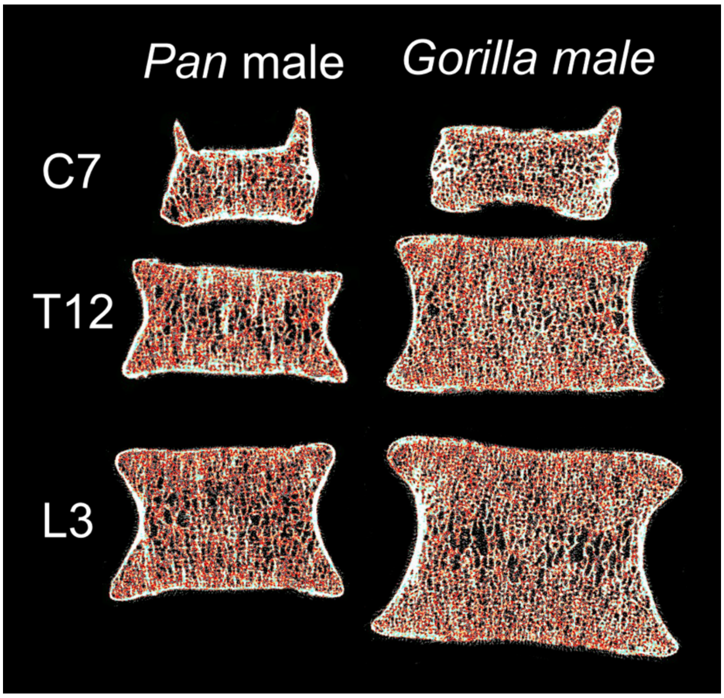


Figure 2. Illustrates the specific site where the pQCT scans were taken.

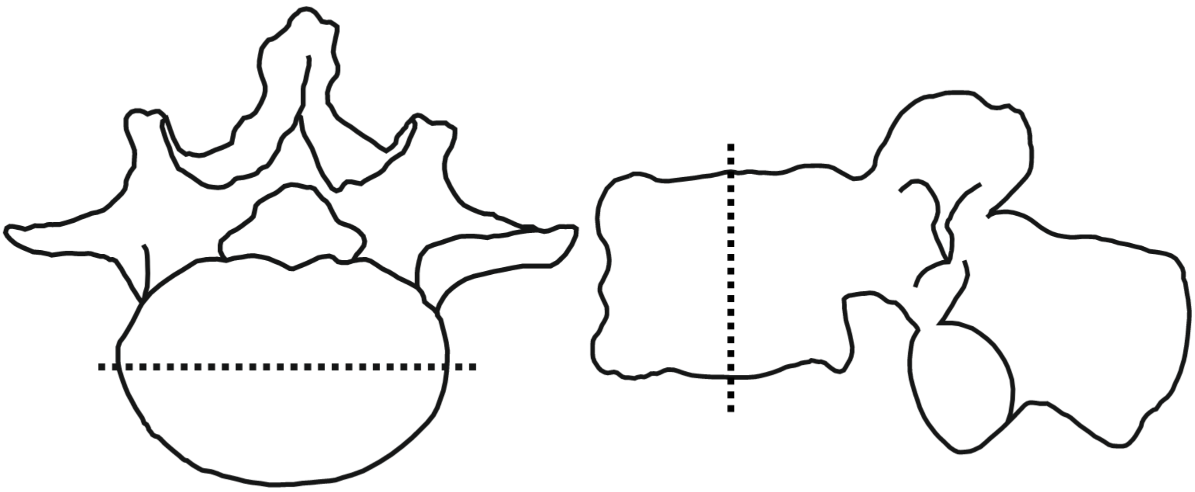
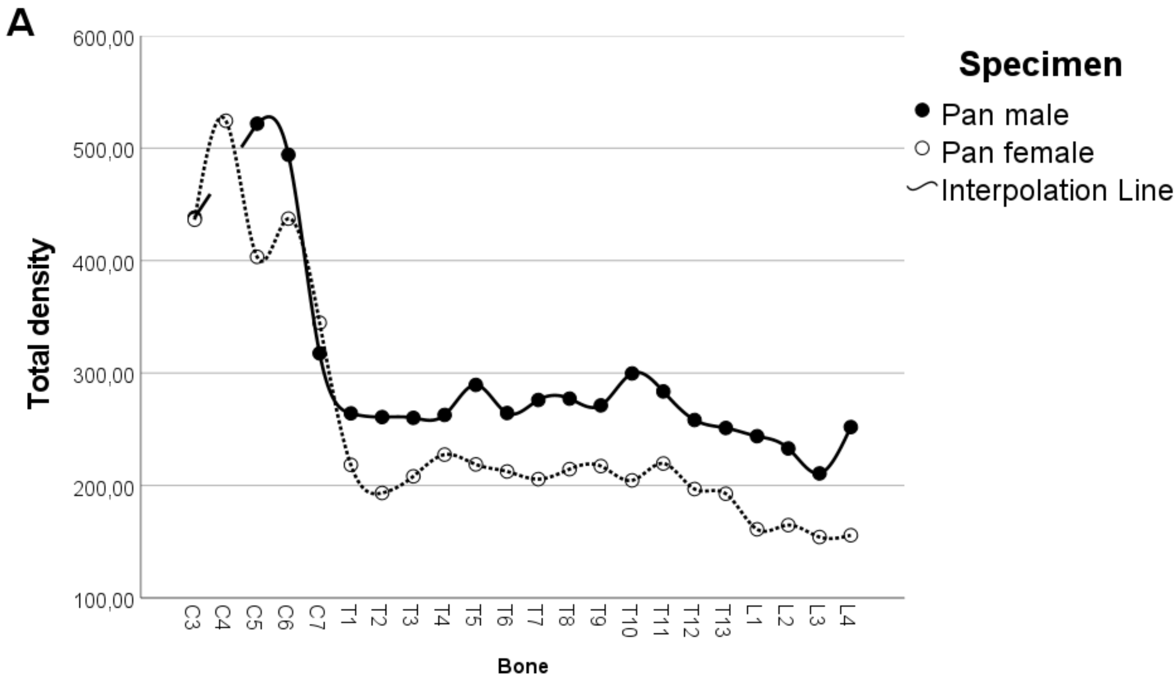


Figure 3. Presents the total density in all subaxial vertebrae for chimpanzees (A) and gorillas (B).



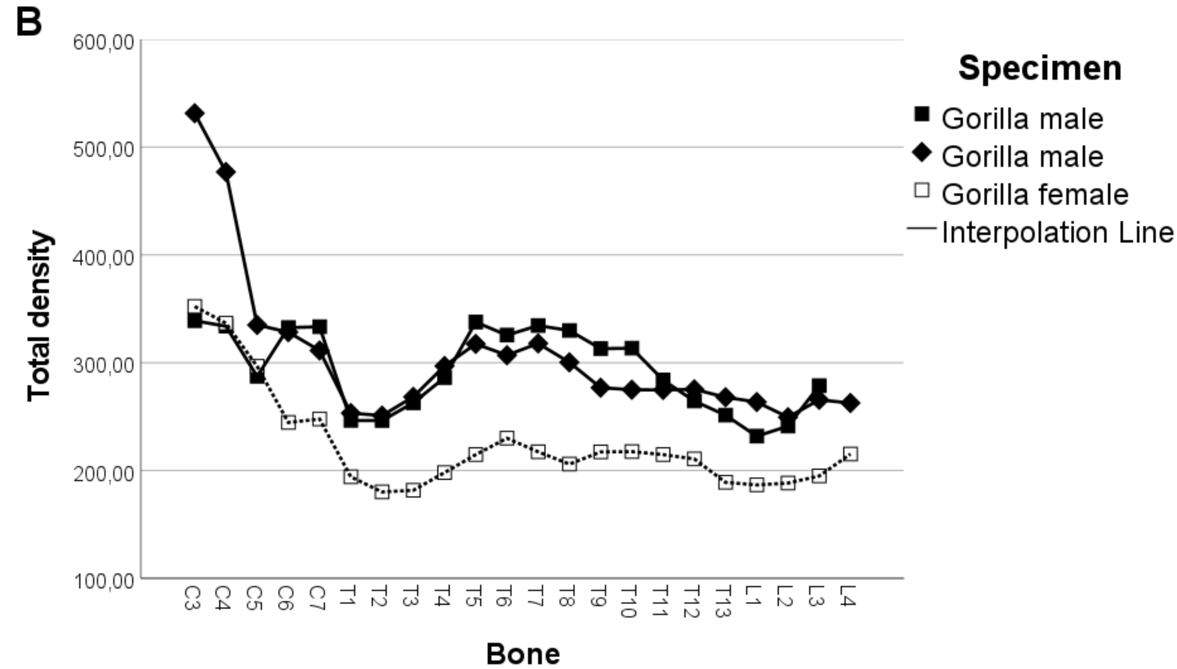


Figure 4. resents the cortical density in all subaxial vertebrae for chimpanzees (A) and gorillas (B).

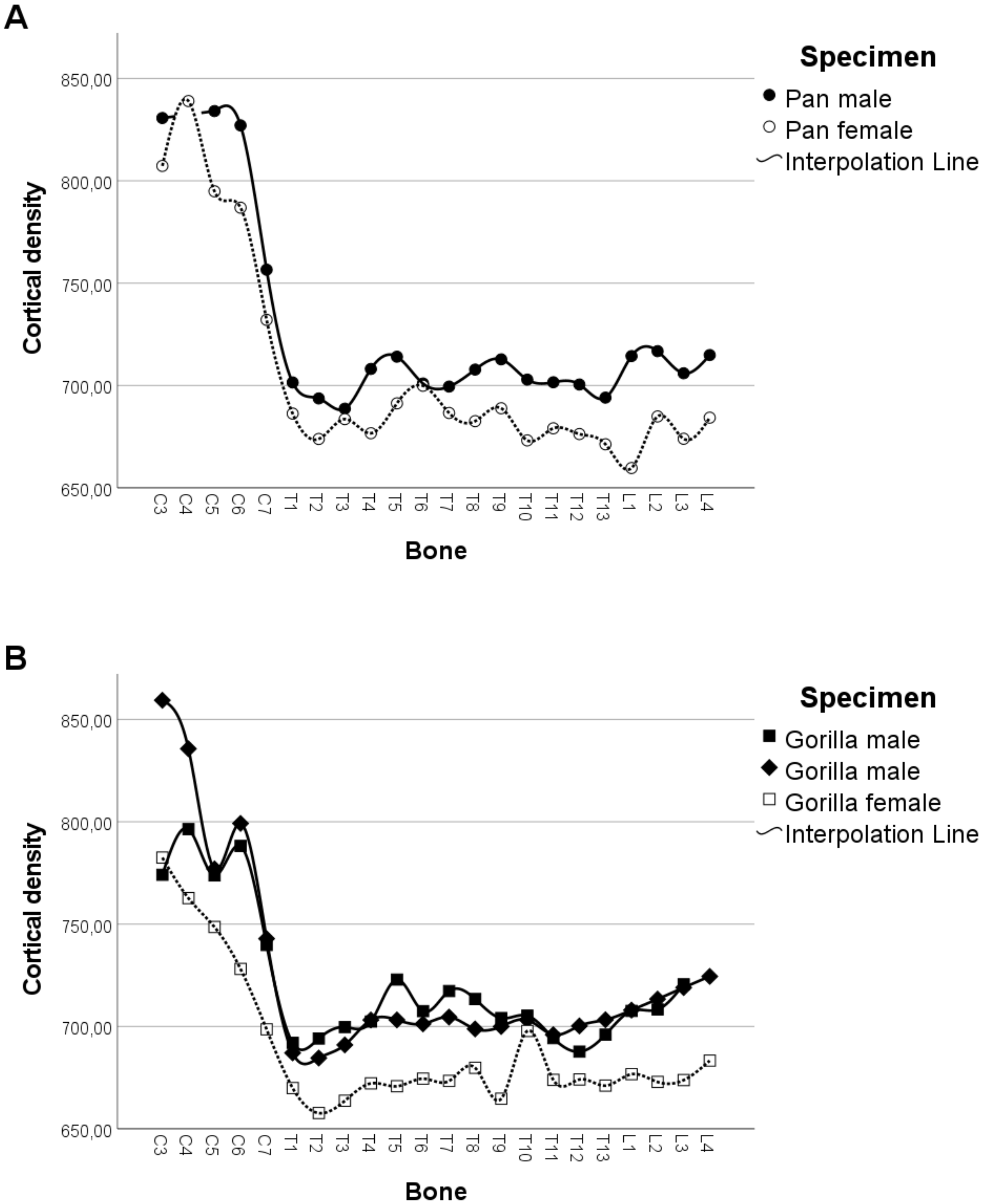


Figure 5. Presents the trabecular density in all subaxial vertebrae for chimpanzees (A) and gorillas (B).