MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

Association of pelvic shape, body height, and head circumference in Khoisans

verfasst von / submitted by

Julia Andrea März, BSc

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien, 2016 / Vienna, 2016

Studienkennzahl lt. Studienblatt / degree programme code as it appears on the student record sheet:	A 066 827
Studienrichtung lt. Studienblatt / degree programme as it appears on the student record sheet:	Masterstudium Anthropologie
Betreut von / Supervisor:	Ass.-Prof. Mag. Dr. Philipp Mitteröcker

Inhaltsverzeichnis

Acknowledgements

I would like to thank some people who were directly or indirectly involved in writing this thesis. First, I want to thank my supervisor Ass.-Prof. Mag. Dr. Philipp Mitteröcker who gave me the opportunity to work on this project. Especially his patient and extensive feedback and supervision at each step of my master project were supportively. A special thanks also to Mag. Dr. Barbara Fischer for her helpful input and debating on my results. Her help while programming the software Mathematica 10.0 (Wolfram Research, Inc.) was more than welcome. I also thank Mag. Martin Dockner for his assistance with formatting my master thesis in LaTeX.

Further thanks go to my family and friends who offered me all kinds of help during my studies. I'm thankful for each coffee, each tea, each nice word, each walk, and each postcard, every time I was bogged down.

Zusammenfassung

Die Geburt ist ein riskantes Ereignis im menschlichen Leben und ist relativ häufig mit Komplikationen verbunden, die manchmal auch den Tod der Mutter oder des Neugeborenen zur Folge haben. Die meisten Komplikationen sind auf die Diskrepanz zwischen den mütterlichen Beckendimensionen und der Größe des Neugeborenen zurückzuführen. Das weibliche Becken muss bei Menschen einen Kompromiss finden, zwischen einem schmallen Becken, um eine bipede Fortbewegung zu ermöglichen, und einem breiten Becken, um ein relativ großes Neugeborenes zu gebären. Diese sich widersprechenden Anforderungen werden auch "obstetric dilemma" genannt. Besonderem Risiko sind hierbei kleine Frauen und Frauen mit einem großen Kopfumfang ausgesetzt.

Fischer und Mitteröcker fanden in einer kaukasischen Stichprobe eine Assoziation zwischen Kopfgröße, Körperhöhe und Beckenform. Kann dieser Zusammenhang nur bei kaukasischen Populationen gefunden werden oder auch in Populationen, die sich bezüglich ihrer Körpergröße und ihres Sexualdimorphismus von kaukasischen Populationen unterscheiden?

Von der sogenannten S Sammlung an dem Department der Anthropologie der Universität Wien habe ich die Skelette von 72 erwachsenen Individuen der Khoisan untersucht. An den Hüftknochen habe ich die Koordinaten von 41 Landmarks und 209 Semilandmarks erfasst. Der Femur und der Schädel wurden vermessen und gemeinsam mit der Geschlechterbestimmung und der Größenberechnung von Pacher aus 1962 verwendet, um die Assoziation zwischen diesen Eigenschaften und der Beckenform zu untersuchen.

Ich fand eine signifikante Assoziation zwischen Körperhöhe und Kopfumfang mit der Beckenform in Frauen und Männern, sowie eine signifikante Assoziation zwischen Femurlänge und Kopfumfang mit der Beckenform in Männern. Kleinere Frauen haben im Durchschnitt einen runderen Beckeneingang und ein stärker nach hinten geneigtes Sakrum. Diese Gestaltveränderungen vergrößern den Geburtskanal und senken somit die Wahrscheinlichkeit von Geburtskomplikationen bei Frauen mit besonders hohem Risiko. Frauen mit einem größeren Kopfumfang haben im Durchschnitt ebenfalls einen rund geformten Beckeneingang, jedoch ein weiter nach vorne geneigtes Sakrum. Ei-

ne Übereinstimmung zwischen der kaukasischen und der Khoisan Stichprobe konnte hauptsächlich im unteren Becken, vor allem im Beckeneingang, gefunden werden.

Die Resultate deuten darauf hin, dass der Selektionsdruck aufgrund des Geburtsvorganges einen besonders starken Einfluss auf das untere Becken von Frauen hat. Da der Beckeneingang in verschiedenen Populationen eine Assoziation mit der Körperhöhe aufweist, scheint vor allem der Beckeneingang eng mit dem "obstetrical dilemma" verbunden zu sein. Die Gestaltveränderungen des Beckeneingangs sind daher, assoziiert mit der Körpergröße, vermutlich auch zwischen verschiedenen Populationen stärker konserviert.

Abstract

Human childbirth is often accompanied by obstructed labor, which can sometimes lead to the death of the mother or the newborn. Most of the complications are associated with the mismatch of the maternal pelvic dimensions and the size of the newborn. The female pelvis needs to find a balance between having a narrow shape to enable bipedal locomotion and being as broad as possible to give birth to relatively large newborns. The conflicting demands are known as the “obstetric dilemma”. On special risk are shorter females and females with a large head circumference, who may give birth to relatively larger newborns.

Associations between head circumference, body height, and pelvic shape were found in a recent study by Fischer and Mitteröcker in a Caucasian sample. Are these results only represented in Caucasian populations or can they also be found in populations that differ in stature and sexual dimorphism from Caucasian populations?

I investigated the skeletons of 72 Khoisan individuals out of the S collection held by the Department of Anthropology of the University in Vienna. On the pelvic bones I collected 41 landmark coordinates and 209 semilandmark coordinates. Measurements of the femur and the cranium, along with the sex determination and height estimation by Pacher in 1962, were utilized to investigate the association between these body traits and pelvic shape.

Using geometric morphometrics, I found significant associations of body height and head circumference with pelvic shape in males and in females. Shorter females, who are on higher risk for obstructed labor, had, on average, a round pelvic inlet and a more backwards bent sacrum. Both shape patterns increase the birth canal and therefore decrease the likelihood of obstructed labor. Whereas, females with a larger head circumference had, on average, a round-shaped pelvic inlet and a forwards bent sacrum. The consensus between the Caucasian and the Khoisan sample was mostly seen in the lower part of the pelvis and especially in the pelvic inlet.

I suggest that obstetric selection has an impact especially on the lower part of the female pelvis, whereby the pelvic inlet has a high impact on the probability of obstructed labor. Therefore, the shape patterns of the pelvic inlet associated with body height may be more conserved between different populations.

1 Introduction

Two important steps in human evolution have been the change to an upright walk and the encephalisation, which had an impact on survival and reproductive success. Therefore, the pressure of natural selection on these two features had to be massive (Gruss and Schmitt, 2015; Rosenberg, 1992).

1.1 Bipedalism

Approximately 4 to 7 million years ago, the bipedal mode of locomotion evolved in humans. Some mammalian species walk occasionally upright, and also a few primates adopt an upright pose for short times, whereas the bipedalism as locomotion in humans is unique in the mammal world (Lovejoy, 2005; Trevathan, 2015; Wittman and Wall, 2007). As a result of the new type of obligate locomotion in humans, the skeleton adapted to meet the biomechanical requirements. The skeleton was modified to maintain balance while walking upright and to make bipedal walking more energetically efficient by a minimal risk of possible injuries (Gruss and Schmitt, 2015). Due to these requirements, the iliac blades became shorter and broader and changed their orientation, the sacrum became broader and moved caudal, the sacral width increased, the ischial spine became more prominent and moved medially. The acetabulum became larger and also the anterior inferior iliac spine became more pronounced (Harcourt-Smith, 2007; Wittman and Wall, 2007). The selection on bipedal locomotion favoured a narrow pelvis to minimize the energetic and the biomechanical requirements (Correia, Balseiro, and Areia, 2005).

1.2 Encephalisation

In human evolution, brain size started to increase around 2.4 million years ago, beginning with a modest increase for the initial one million years. About 150.000 to one million years ago, brain size increased massively (Ruff, Trinkaus, and Holliday, 1997; Wittman and Wall, 2007). Human brains are significantly larger than estimated for an animal with this body size (Wittman and Wall, 2007). To enable the massive increase in human brain size, two modifications happened: pelvic shape and, thus, the mechanism of birth altered. Also, infants were born with a smaller percentage of adult brain size, experiencing brain growth postnatal (Martin, 1983). The newborns are thus extremely helpless and depending on other individuals (Rosenberg and Trevathan, 2002).

The change to bipedalism has happened before the encephalisation took place. Females now have to give birth to neonates with an increased head size through a pelvis which already has been adopted to bipedal locomotion.

Both modifications – bipedal locomotion and encephalisation – led to the obstetric dilemma in females (Rosenberg, 1992; Wells, 2015). The adaptation of the pelvis to bipedal walking has caused a skeletal structure, which has, compared to a fetal head, relatively small dimensions. By increasing the brain size of newborns, the likelihood of obstructed labor also increased. The delivery of larger newborns became therefore a risky process.

1.3 Thermoregulation

Humans regulate their body temperature. Important is the ratio of the surface area to the mass or volume, because the volume increases as the cube of body size whereas the surface increases as the square. Therefore, if a body becomes larger, the ratio of surface area to volume gets smaller. The size of the pelvis defines overall body proportions and, hence, also the ratio of surface area to volume. The heat production is proportional to body volume and the heat loss is proportional to the exposed body surface. Considering the surface-to-volume ratio, a larger individual has, compared to a smaller individual, a higher ratio of heat production to heat loss (Gruss and Schmitt, 2015; Ruff, 1994). The heat loss through the surface of the body is thereby also influenced by the pelvis. Different climate conditions would therefore impose different selective pressure on body shape and, therefore, also on pelvic shape.

1.4 Consequences of the different steps of human evolution

1.4.1 Sexual dimorphism

To increase the population's mean fitness a birth process without hurting the mother or the newborn is necessary. From a selective standpoint, the pelvic shape is here central to surviving. The effects of a successful delivery on reproductive success are far reaching and, hence, its selective force is massive (Gruss and Schmitt, 2015; Lovejoy, 2005).

The obstructive pressure due to encephalisation has affected females only. Whereas male pelvises need to be adapted just to bipedal locomotion, female pelvises need to be adapted to both bipedal locomotion and giving birth (Wittman and Wall, 2007). Hence, the resulting pelvic shape is a compromise shape between bipedal locomotion, larger newborns, and possibly thermoregulation (Gruss and Schmitt, 2015; Wells, DeSilva, and Stock, 2012). The changes in the female pelvis have to lower the likelihood of obstructed labor. These different challenges led to the human sexual dimorphism in pelvic shape (Wittman and Wall, 2007).

The sexual dimorphism shows features concerning mainly the shape of the greater sciatic notch and the pelvic inlet. The male hip bones show greater coxal height, relatively larger and deeper hip joints, a deeper true pelvis, greater ischial length, greater upper iliac height, a larger auricular surface, and a more posteriorly placed anterior margin of the greater sciatic notch. The coxal bones of females display a closer position of the deepest point of the sciatic notch to the posterior superior iliac spine, a larger height of the sciatic notch, subtense of the iliopectineal chord, a more posterior position of the auricular surface relative to the acetabulum and the anterior iliac margin, a longer pubic bone, and generally a greater length of the coxal bones (Arsuaga and Carretero, 1994). These differences in shape are claimed to be sex differences independent of body height. Body height is therefore not the only important determinant of sex difference in pelvic shape (Arsuaga and Carretero, 1994). Aside from these differences in the pelvic shape between the sexes, the three dimensions – the transverse diameter of the bispinous midplane, the transverse diameter of the outlet, and the anteroposterior diameter of the inlet – of the female pelvis are larger than in the male pelvis (Correia et al., 2005).

1.4.2 Obstructed labor - Obstetric dilemma

The birth process of humans is not only more complicated than the mechanism of birth in other great apes, but also more dangerous (Rosenberg and Trevathan, 2002). The cause of this might be the change of the human skeleton during evolution.

Due to bipedal locomotion, the now more prominent ischial spines provide a larger attachment sites for ligaments. The ligaments support the abdominal viscera while standing upright. This modification in the ischial spines causes a restriction in the midplane of the pelvis and therefore lower the dimension of the pelvis (Wittman and Wall, 2007).

In humans the newborn has to rotate during delivery. The infant's head faces laterally at the beginning and rotates until it's facing backwards. This special feature can just be seen in humans and not in apes (Gruss and Schmitt, 2015). Compared to archaic humans, the proportions of the birth canal in *Homo sapiens* changed. In females, the anterior posterior dimensions in the midplane and outlet became larger, while the medioalteral orientation of the inlet stayed the same. The rotational birth seemed therefore to evolve not until the origin of *Homo sapiens* (Ruff, 2010; Weaver and Hublin, 2009). The change in the dimensions increased the birth canal in females. Without widening the pelvis, females may now be pregnant with a larger-brained infant (Gruss and Schmitt, 2015).

According to different studies, there is an association between Caesearen section, as a possible consequence of birth complications, and the body size of the mother and the size of the newborn. Shorter women have a higher risk for Caesearen section than taller women (Chan and Lao, 2009; Kirchengast and Hartmann, 2007; Merchant, Villar, and Kestler, 2001). Female body height and parental height difference are well known predictors of birth complications. The greater the difference, the higher the risk. The likelihood of pregnancy complications is higher for shorter females due to the on average taller partner. The newborn's size is not only linked to the mother's size, but also to the father's size and can thus be larger than "expected" (Stulp, Verhulst, Pollet, Nettle, and Buunk, 2011). The obstetric selection pressure on shorter females is stronger and, hence, their birth canal may be more adapted towards obstetrics. Additionally, females with a large head circumference are on a higher risk for obstetric labor. Their newborns may have also a large head circumference and therefore, the newborns' dimensions may be larger than the maternal pelvic dimensions.

For the surviving of a species, delivery is an important process and is under strong selective pressure. Adaptations to lower the risk of the birth process are expected to be seen on the bony pelvis of females and might be linked to the size of the females (Wells, 2015).

Considering the thermoregulation theory, not only the bipedal locomotion and the encephalisation have an impact on the pelvic shape. In tropical hot areas, the obstetric and thermoregulatory pressures may be a conflict for the morphology of the pelvis. Broadening the pelvis is not possible for an efficient thermoregulation considering the surface-to-volume ratio. The challenges of delivery and thermoregulation are in these cases opposed (Gruss and Schmitt, 2015).

1.5 Khoisan

Khoisans are a large constellation of ethnic groups including hunter-gatherers as well as herder-hunter-gatherers. The word Khoisan is a combination of 'San' for the hunter-gatherers and of 'Khoi' for Khoikhoi or 'Khoe' for Khoekhoe the herder-hunter-gatherers. In older literature, the Khoi have also been named 'Hottentots' and the San 'Bushmen'; both names were considered offensive and politically incorrect and are therefore no longer used(Barnard, 2007). Besides the notation Khoisan also Khoi San, Khoe San, and Khoesan can be found in the literature. In this work I used the spelling Khoisan.

In the nineteenth century, the interest in the Khoisans for collection issues arose. One of the first systematic studies was done by Shrubsall in 1898. Similar work of other scientists describing the skeletal anatomy followed. From 1907 to 1909, Rudolf Pöch, later a professor at the University of Vienna, traveled through the western Transvaal, northern Botswana, central Namibia, and the northern Cape to collect anthropological and ethnographic specimens. He produced sound recordings and photographs and collected skeletons. Some of the skeletons were excavated by himself, though the most were donated by local residents (Morris, 1987). Still, the largest collection of Khoisan skeletons outside of Africa belongs to the University of Vienna and represents the late 19th and early 20th century (Botha and Steyn, 2014). As part of historical revision, some skeletons of Pöch's collection has been considered as unethically collected. Thus, some individuals of the collection were returned to their homeland (Botha and Steyn, 2014; Fröschl, Müller, Olechowski, and Schmidt-Lauber, 2015).

1.6 Covariation between human pelvic shape, stature, and head size in a Caucasian sample

In a recent study by Barbara Fischer and Philipp Mitteröcker in 2015, the association between human pelvic shape, head size, and body stature was examined. Their sample included 99 individuals, representing the US population regarding body weight and size. By using different methods of geometric morphometrics, they found the typical pattern of sexual dimorphism in the pelvis: an on average broader and flatter pelvis for females than for males and a wider and shallower pelvic cavity for females than for males. In their sample, Fischer and Mitteröcker found an association of body height and head circumference with the shape of the pelvis. The pelvic inlet tended to be more oval-shaped for individuals with a smaller head, whereas the pelvic inlet of individuals with a larger head was rounder. The same shape patterns were also associated with the stature of the individuals. The pelvic inlet of taller individuals was, on average, more oval than of smaller individuals. This effect was found both in females and males. Gender comparisons showed a sacrum that was tilted more backwards with increasing head circumference in females. This association wasn't found in males (Fischer and Mitteroecker, 2015).

1.7 Aim

In my study, I wanted to transfer the work by Fischer and Mitteröcker to a sample of Khoisans. Using geometric morphometrics, I examined if the association between pelvic shape, body height, and head circumference can also be found in a sample containing individuals from South Africa who are known to have a lower degree of sexual dimorphism than Caucasian populations. Additionally the Khoisan population is, on average, shorter than Caucasian populations. The optimal pelvic shape, which fits best to the evolutionary requirements of bipedalism and encephalisation, may not only be not uniform within a population but also not uniform between different populations.

I wanted to study the variation of pelvic shape between the two sexes. Hence, I was interested if the pattern, Fischer and Mitteröcker found, can also be extended to the Khoisan sample and what a possible consensus or a possible mismatch of the results would mean for the evolutionary change of pelvic shape and the obstetric dilemma.

2 Material and Methods

2.1 Material

For this project, the so called S collection of the Department of Anthropology in Vienna was examined. The collection was established by Rudolf Pöch. The skeletons were collected during his journey through South Africa from 1907 to 1909. Some skeletons had been exhumed by Pöch, other skeletons had been donated to him by local European residents (Morris, 1987) or "purchased" by him (Pacher, 1962).

The collection contains more than 150 individuals but not all of them were used for my project. Damaged, incomplete skeletons, and skeletons of children were excluded from this study. The final sample contained 72 individuals, of which the pelvic bones were well enough preserved. An overview of the measured skeletons can be found in Table 2.3. I classified all individuals as Khoisans and made no difference between San and Khoikhoi.

2.2 Collecting Landmarks

To examine the 3D pelvic shape, the isolated ilium, ischium, and pubis were put together in their correct anatomic location by using plasticine, fimo modeling clay, and elastic bands. During the measurements, the elastic bands should prevent small movements of the single bones. 41 landmark coordinates and 15 curves were collected using the MicroScribe 3D digitizer G2. This digitizer has been designed to create three-dimensional coordinates. After calibrating the digitizer, the telescopic stylus was put on each single landmark and by pressing the connected foot pedal the coordinates were transfered to an Excel file. The Excel files were designed earlier using Microsoft Excel 2010 and contained the names of all landmarks. Each individual had its own file to prevent possible mistakes like overwriting the data.

The definitions of landmarks were based on the book "Spatial Geometry of the Human Pelvis" (Reynolds, Snow, Young, of Aviation Medicine, and (U.S.), 1982). See Table 2.1

and 2.2. During the measurements, no difference based on the type of landmark was made. The semilandmarks of the curves were gathered on the same way as the other landmarks.

Table 2.1: Landmarks of the pelvis measured by the digitizer MicroScribe

	Landmark name	
Sacrum	Promontorium	unpaired
	Posterior Point on first sacral vertebral body	unpaired
	Sacral Canal anterior wall	unpaired
	Center of First Sacral Vertebral Body	unpaired
	Sacral Canal anterior Roof	unpaired
	Caudion, deepest point	unpaired
	Caudion, lateral	paired
	Inferior Sacroiliac Junction	paired
	Lateral Alar-Auricular Point	paired
	Posterior Alar-Auricular Point	paired
	Anterior Alar Point	paired
	Center of the Superior Articular Facet	paired
Ilium-Ischium-Pubis	Left Superior Pole, Pubic Symphysis	paired
	Inferior Symphyseal Pole	paired
	Anterior Symphyseal Point	paired
	Posterior Symphyseal Point	paired
	Ischio-Spinale	paired
	Posterior Superior Iliospinale	paired
	Iliospinale, Anterior Inferior	paired
	Pubotubercle	paired
	Ischial Tuberosity, deepest point	paired
	Iliocristale, highest point	paired

During the later analysis, the two landmarks ischial tuberosity, deepest point, and iliocristale, highest point, defined as landmark type 3, were excluded. These points are locally defined extrema and are therefore not well enough defined for further analysis (Bookstein, Grayson, Cutting, Kim, and McCarthy, 1991). The final number of landmarks type 1 was 37, the final number of semilandmarks was 209.

Table 2.2: Curves measured on the pelvis using the digitizer MicroScribe

	Curve description	Number of Semilandmarks
Sacrum	Curve along the lower Sacrum from the right Inferior Sacroiliac Junction to the left Inferior Sacroiliac Junction	15
Ilium-Ischium-Pubis	Curve from the Superior Tuberosity Point to the Inferior Symphyseal Pole posterior	10
	Curve from the Superior Tuberosity Point to the Inferior Symphyseal Pole anterior	10
	Curve along the Acetabulion	15
	Curve along the Obturatur Foramen	10
	Curve from the Ischio-Spinale to he Posterior Superior Iliospinale	10
	Curve from the Iliocristale to the Iliospinale medial	15
	Curve from the Iliocristale to the Iliospinale lateral	15
	Linea terminalis from the Anterior Alar Point to the Posterior Symphyseal Point	10

2.3 Missing Landmarks

In most cases it was not possible to collect all landmarks. Sometimes parts of the bones were missing or damaged. In the end, I had 28 individuals with missing landmarks. Most of the time the ischio-spinale was broken off. It was missing on the right side in nine cases, on the left side in eleven cases. 93 different landmarks were missing and had to be estimated. Therefore, I used the software Mathematica 10.0 (Wolfram Research, Inc.). Based on the landmarks and semilandmarks, I computed a thin-plate spline interpolation for the complete and incomplete individuals. During the estimation, the semilandmarks and the landmarks were treated equally. By warping all the landmarks from the mean of the reference individuals to the incomplete individuals the missing landmarks were estimated (Gunz and Mitteroecker, 2013; Gunz, Mitteroecker, Neubauer, Weber, and Bookstein, 2009).

2.4 Semilandmarks

Semilandmarks enable us to measure and to analyze homologous curves between individuals (Gunz and Mitteroecker, 2013). For the analysis, the semilandmarks needed to be defined as such and to slide within the curves. The sliding of these landmarks was necessary to distribute them equally on the curves to avoid misleading differences between the individuals. By sliding the landmarks all semilandmarks of all individuals were spaced within the curve to minimize the bending energy. The sliding can be computed based on the Procrustes superimposition or on the thin-plate spline (TPS) deformation (Gunz and Mitteroecker, 2013).

First, the semilandmarks were defined and for every semilandmark a vector was computed on which it was allowed to slide. Each vector was determined through the landmarks next to the semilandmark along one curve. Second, each semilandmark slid along the associated vector to minimize the bending energy between the individual and the template. As a template I used the Procrustes Shape mean. Third, I computed a Procrustes Superimposition based on the new semilandmarks. Fourth, the semilandmarks were allowed to slide again but this time the new average Procrustes shape was used as the template. The third and fourth steps were repeated until the movements of each point were small.

To prevent the semilandmarks from sliding over the end of one curve the movement was limited at the beginning and the new coordinates were visual controlled by plotting them together with the original coordinates.

2.5 Additional information

To analyze the association of pelvic shape, body height, and head circumference, I also needed data about these features. For body height, the estimations by Pacher were adopted. To determine the body height, Pacher followed the rules established by Pearson (Pearson, 1898). To review Pacher's measurements concerning the head circumference, I also measured the head circumference using a measuring tape. The largest difference between Pacher's and my own measurements were 5 mm whereas the mean circumference of all skulls were 500.5 mm. The measurements from Pacher were therefore seen as reliable. The mean of both measurements for the head circumferences was used for further analysis. Also the gender estimation, based on osteological features, and the population group determination were adopted (Pacher, 1962).

Out of the 72 individuals, I had an estimated body height for 55 individuals and a measured head circumference for 65 individual (Pacher, 1962). The gender was determined by Pacher in 59 cases. Botha and Steyn (2013) examined the S collection in Vienna and were consistent in the sex determination with Pacher. Additionally, Botha determined the sex for three further individuals (personal communication with Botha). For 54 individuals I had all three traits – body height, head circumference, and sex. Table 2.3 outlines the information about the measured individuals.

The body height determination from Pacher was not given for all individuals. Thus, I measured the maximum length of the right and left femur using a measure board as a proxy for the body size. To lower my measuring error the average femur length was used in further analysis. For 70 individuals of the S collection this was possible to measure at least one femur. For 67 individuals I had the gender determination as well as the femur length. Femur length, gender determination, and head circumference were given for 52 individuals.

Table 2.3: Individuals measured by the MicroScribe digitizer: Gender, body height in mm, head circumference in mm, and average femur length in mm. Gender determination by Pacher except for * marked individuals. For additional information see Chapter 2.5

S-number	Gender	Body height	Head circumference	Average femur length
001	male	1620	508	411.0
002	female	1500	490	unknown
003	male	1610	499	424.5
004	female	1520	507	422.0
005	male	1510	503	463.5
006	male	1610	525	429.5
007	male	1570	494	390.5
008	male	1680	500	414.5
010	male *	1610	519	423.0
012	male	1700	544	475.5
013	female	1440	468	382.0
022	male	1590	506.5	420.0
024	male	1540	503	397.0
025	female	1480	503	400.0

continued …

. . . continued

S-number	Gender	Body height	Head circumference	Average femur length
026	female	1540	498.5	419.0
027	male	unknown	unknown	401.0
028	female	1520	512.5	418.0
029	male	1670	526	457.0
038	female	1490	476	395.5
040	female	1560	474	421.0
044	female	unknown	502.5	400.0
045	female	1490	495.5	405.5
046	female	1530	488.5	410.0
047	female	unknown	unknown	421.0
048	male	1610	516	424.5
049	female	1500	491	400.0
052	female	1560	489.5	424.0
053	male	unknown	unknown	455.0
054	male	1630	unknown	446.0
055	male	1510	492.5	405.5
058	male	1560	482	405.0
059	male	1660	490	420.0
061	male	1580	517.5	427.0
063	female	1580	502	441.5
065	male	1710	513.5	477.0
066	male	1680	532	456.5
067	male *	1690	530	462.0
068	male	1510	511	388.0
074	female	1490	511.5	397.5
075	female	1520	494.5	412.5
076	male	1640	491	unknown
084	unknown	unknown	518	451.5
086	unknown	unknown	510	434.0
087	unknown	unknown	503	465.5
094	unknown	unknown	538	498.5
095	male	1650	486	429.0

continued . . .

. . . continued

S-number	Gender	Body height	Head circumference	Average femur length
099	female	1530	469	431.0
102	female	1480	501.5	389.5
104	male	1560	495	418.5
105	female	1470	480	394.5
107	female *	1470	493.5	390.5
108	female	1480	477.5	499.5
109	male	1620	522.5	443.0
110	male	1550	481	410.0
111	male	1580	506	421.0
112	female	1490	491	407.0
113	female	1470	489	388.0
115	female	1470	486	386.5
119	male	1560	500	409.5
120	male	1580	478	418.5
123	male	1510	491	unknown
126	unknown	unknown	493	421.0
128	unknown	unknown	521	477.0
129	unknown	unknown	514	unknown
135	unknown	unknown	unknown	496.0
137	unknown	unknown	518	513.0
138	unknown	unknown	498	416.0
140	male	1570	509.5	420.5
142	female	1600	477.5	443.5
143	male	unknown	unknown	470.5
151	unknown	unknown	unknown	450.0
152	unknown	unknown	517	439.0

2.6 Analysis

For the analysis only the individuals for which all three traits – body height, head circumference, and sex – are known were considered. To visualize sexual dimorphism in the pelvis, I computed the average female and male pelvis of my sample. To remove all information about size, localization, and orientation a Generalized Procrustes Analysis was performed to receive Procrustes shape coordinates (Mitteroecker and Gunz, 2009). A vector plot was created to have a first look on the differences between female and male Khoisan. To evaluate the sexual dimorphism I performed a bootstrap analysis. The length of the sexual dimorphism vector was here used as the evaluation criterion.

Because of the small number of individuals, the following analysis was additionally performed for female and male together. To avoid the effects of the sexual dimorphism, a pooled regression was computed. By pooling the mean centered male and female data the effect of sex on the pelvic shape was avoided.

A multivariate multiple regression was computed with body height and head circumference as independent variables, and the landmark coordinates as the depending variables. An extrapolation of the pelvic shape was performed for body height and for head circumference. This enabled me to visualize the effect of the independent variables on the pelvic shape. For the extrapolation of the impact of body height and head size on the pelvic shape, the vector of the regression coefficients was added to the mean shape of each sex. To make the shape change more obvious the vector was multiplied by 20 cm or by three times the standard deviation of the independent variable.

I computed permutation tests for the regressions of body height and head circumference using the explained variance as test statistic and 5000 random permutations.

To enlarge the sample size and to review the height estimation by Pacher, the femur length was used as a proxy for body height. This enlarged the sample from 54 to 57 individuals. The analysis was repeated with the femur length as independent variable, first with the individuals separated by the sex, and second with the individuals pooled again.

2.7 Visualization

To present the shape difference in the pelvis most effectively I created surface models (Klingenberg, 2013; Mitteroecker and Gunz, 2009). Using the software Amira Version 6.0 (FEI Visualization Sciences Group) I collected landmarks and semilandmarks on a 3D surface model of an articulated pelvis (www.turbosquid.com, product ID 710664, Oormi Creations). The landmarks were the same 246 as collected earlier using the MircoScribe. The model was then deformed to the target landmark configurations by TPS interpolation. The created 3D surface models showed the impact of body height, head circumference, or femur length on the pelvic shape. Additionally one surface model showing the sexual dimorphism in the pelvic shape of this sample was created.

3 Results

3.1 Descriptive Statistics: body height and head circumference

My sample consisted of 54 individuals of Khoisans, for which I collected body height, head circumference, and sex. Out of the these 54, 24 individuals were determined as females and 30 individuals as males (Botha, 2016; Pacher, 1962). The average body height and head circumference can be seen in Table 3.1 (for the distribution of body height and head circumference see Figure 3.1 and 3.2). The correlation between body height and head circumference for females was 0.04 and for males 0.49. Figure 3.3 shows the relationship of body height and head circumference, separated for males and females.

Table 3.1: Descriptive statistic for body height and head circumference, separately for males and females

	Females		Males	
Measure	Mean	SD	Mean	SD
Body height (mm)	1508	39	1601	60
Head circumference (mm)	490	13	506	17

3.2 Descriptive Statistics: femur length

The correlation between femur length and body height was 0.94 for females and 0.66 for males. The high correlation especially in females supports the computed body height done by Pacher (1962). Considering the femur length instead of body height, I had 25 female and 32 male individuals. The average values are given in Table 3.2. The distribution of femur length and head circumference can be seen in Figure 3.5 and 3.6.

Table 3.2: Descriptive statistic for femur length and head circumference, separately for males and females

Measure	Females Mean	Females SD	Males Mean	Males SD
Femur length (mm)	407	17	427	24
Head circumference (mm)	491	13	507	17

3.3 Sexual dimorphism in the Khoisan pelvis

Figure 3.8 illustrates the sexual dimorphism in the pelvis of this Khoisan sample. The shape difference between the adjacent surface models was based on one standard deviation of the sexual dimorphism. The well-known patterns of sexual dimorphism can already be seen in the average male and female pelvic shape in the middle. On average the pelvis of females was broader, the subpubic angle was larger, the coxal height was smaller, the Os Sacrum was longer, and the pelvic inlet was rounder.

The principal components analysis of the Procrustes data showed, by plotting the principal component 1 against principal component 2, a distribution of the two sexes. Males seem to be more variable concerning the pelvic shape than females. Also, a large area of overlapping is visible (see Figure 3.9). In Figure 3.10 the distribution along principal component 3 versus prinicpal component 4 is illustrated. No group patterns based on the sex noticeable. Both sexes overlapped, whereas the male individuals had again a larger variance along the principal component 3 than the female individuals.

As the evaluation criterion for the bootstrap analysis, the norm of the sexual dimorphism vector was used. The bootstrap analysis was computed based on 1000 randomly

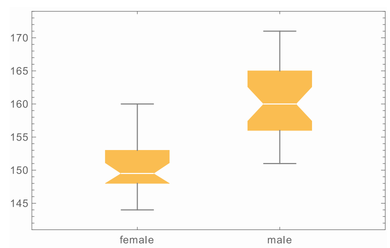

Figure 3.1: Box-Whiskey-Plot of the body height distribution in males and females in cm

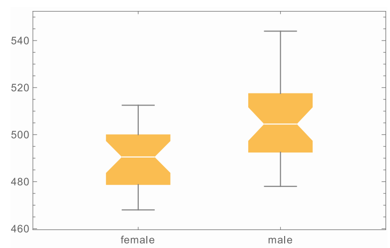

Figure 3.2: Box-Whiskey-Plot of the head circumference distribution in males and females in mm

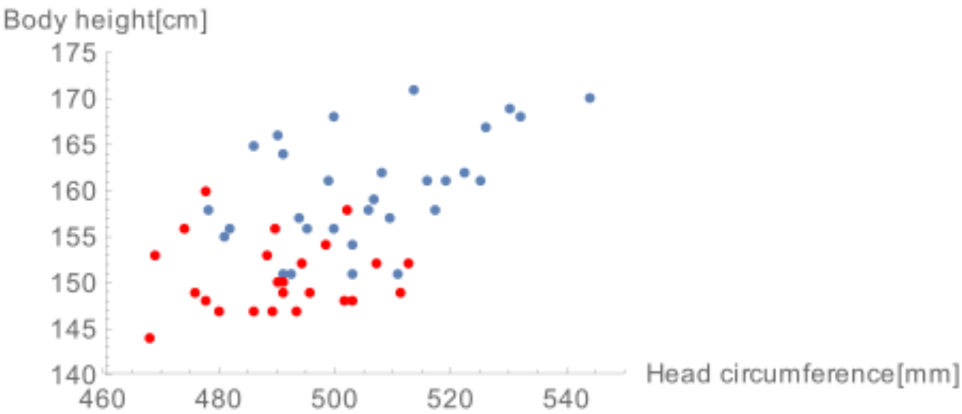

Figure 3.3: Distribution of body height and head circumference. The red dots represent females, the blue dots males.

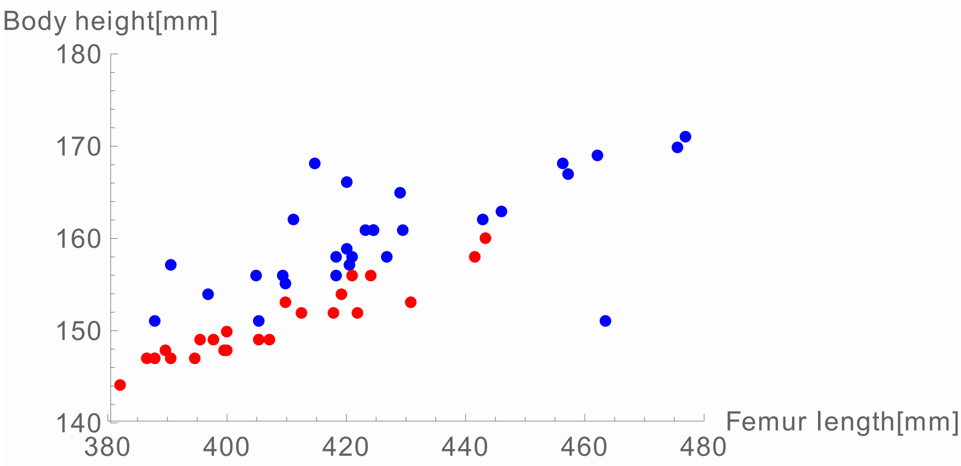

Figure 3.4: Distribution of femur length and body height. The red dots represent females, the blue dots males.

chosen subsamples. The length of the vector in my original sample was 0.060. The bootstrap analysis calculated an average norm of 0.063 and a standard deviation of 0.008. The results of the bootstrap analysis were visualized in histogram 3.11. Therefore, there seemed to be no obvious outliers, and perhaps no false sex determination.

3.4 Allometry based on body height

The association of body height on the pelvic shape can be seen in Figure 3.12. The extrapolation between the two pelvic shapes of both sexes corresponds to the linear regression coefficients for body height from the shape regressions. The shape difference was here based on a change in body height of +/- 20 cm from the average pelvic shape.

The female pelvic shape was clearly associated with body height extrapolation in many parts. The subpubic angle was larger and the complete width of the lower pelvic part was larger for shorter females. Also a rounder pelvic inlet and a longer and more backwards bent sacrum could be seen. The iliac blades of shorter females were straighter. The upper part of the pelvis was more elongated, whereas the lower part of the pelvis seemed to be shortened compared to the pelvis of taller females.

Similar patterns were found in males. For shorter males the iliac blades were straighter and more upward folded. The upper part of the pelvis was also more stretched, the lower part didn't seem to be influenced by a change in body height. The pelvic inlet was more oval-shaped for shorter males than for taller males and the sacrum was more bent backwards, whereas no obvious change in the sacrum length was detected.

3.5 Within-sex allometry based on body height

The allometry patterns of the pelvic shape, independent of the sex, are shown in Figure 3.13. The 3D reconstructions here are based on the pooled pelvic shapes. The column on the left shows the average pelvic shape of individuals, who are 20 cm shorter than the mean. The column on the right shows the average pelvic shape of individuals who are 20 cm taller than the mean.

The figure illustrates the larger subpubic angle, the straighter iliac blades, a slightly more round shaped pelvic inlet, and a more backwards bent sacrum for shorter individuals. The results here are independent of sex.

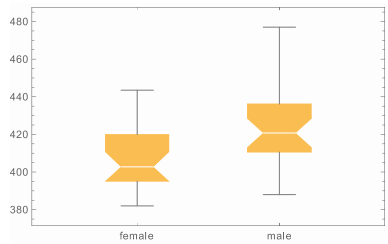

Figure 3.5: Box-Whiskey-Plot of the femur length distribution in males and females in mm

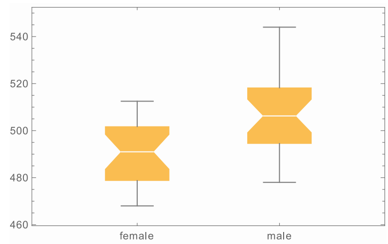

Figure 3.6: Box-Whiskey-Plot of the head circumference distribution in males and females in mm

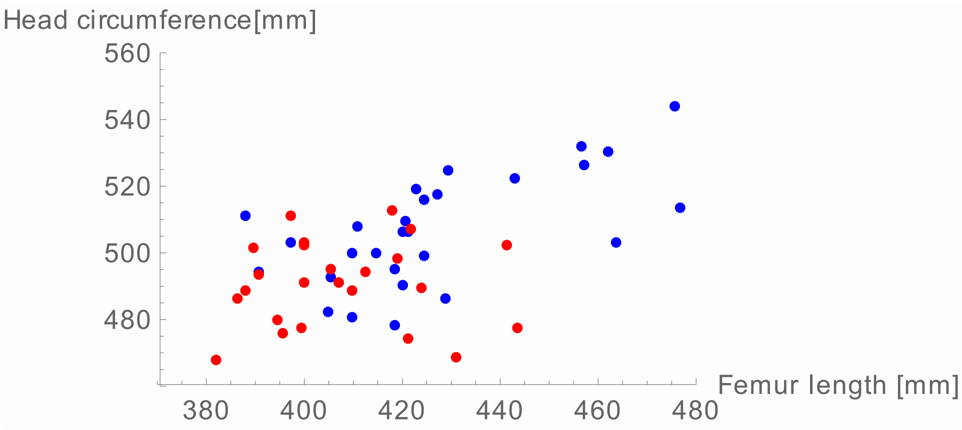

Figure 3.7: Distribution of femur length and head circumference, both in mm. The red dots represent females, the blue dots males.

3.6 Allometry based on femur length

The association of femur length and pelvic shape is visualized in Figure 3.14. Within one sex, the extrapolation of femur length is based on three times the standard deviation of the femur length.

Females with a shorter femur length have wider iliac blades, a larger subpubic angle, a rounder pelvic inlet, and a more backwards bent sacrum. A shorter femur length in males is connected with a larger subpubic angle, a more oval-shaped pelvic inlet, and a more backwards bent sacrum.

3.7 Shape regression on body height and head circumference

Figure 3.15 illustrates the association of head circumference with pelvic shape. Within one sex the extrapolation of head circumference based on three times the standard deviation of the head circumference.

For females with a smaller head, the pelvic inlet is more oval-shaped, the iliac blades are straighter upwards, and the ilium is more bent backwards. Males with a smaller head show also a sacrum, which is more bent backwards, whereas the pelvic inlet is more round-shaped. A clear change in the subpubic angle in males can be seen. The angle is smaller for males with larger heads. For both sexes the iliac blades seem to be wider in case of larger head circumference.

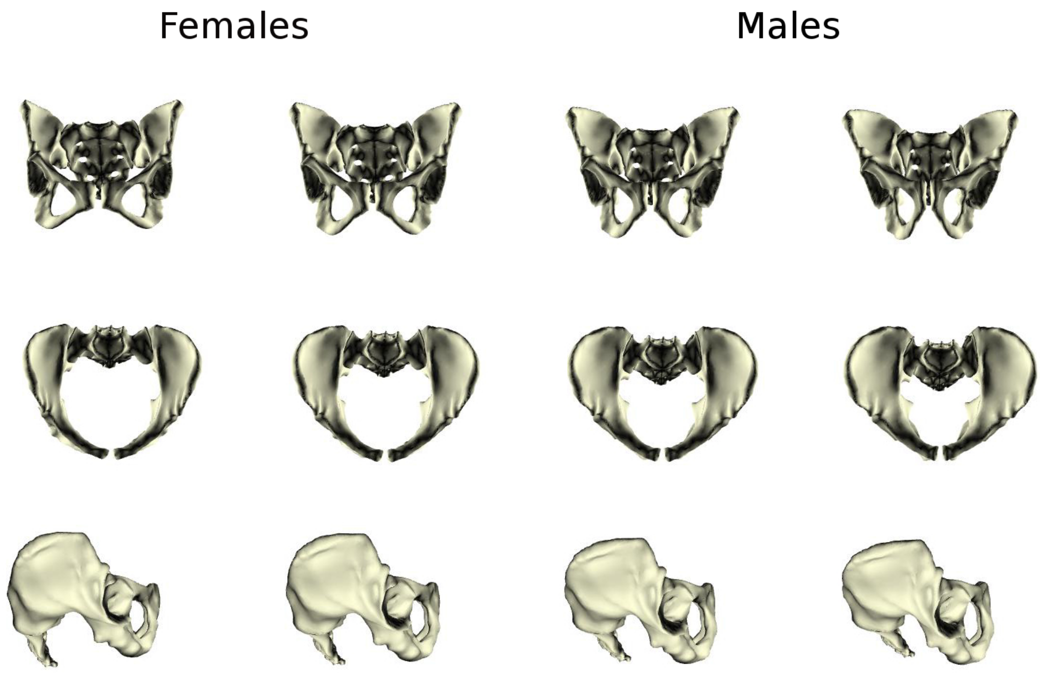

Figure 3.8: Sexual dimorphism in the pelvis: On the left side is the average female pelvis, on the right the average male pelvis. The second and third columns show the average female and the average male pelvis, the first and fourth columns show the extrapolation. The pelvic shapes are shown in anterior, superior, and lateral view.

By using head circumference as a co-variable in the regression (multivariate multiple regression of Procrustes shape coordinates on body height and head circumference), it is possible to extrapolate the impact of body height independent of head circumference. In Figure 3.16 the extrapolation of body height based on a height difference of +/- 20 cm from the average pelvic shape can be seen.

For the short females the pelvic inlet is rounder, the sacrum is larger and more bent backward, the subpubic angle is wider, and the iliac blades are straighter. The upper part of the pelvis seems more stretched whereas the lower part seems compressed.

The impact of the change in body height on the sacrum seems smaller in males. Also the sacrum is bent backwards for shorter males but no size difference is clearly visible. Shorter males have a more oval-shaped pelvic inlet and straighter and larger iliac blades. The change in pelvic shape in males is less pronounced than that in females.

In both sexes the association of pelvic shape with body height and head circumference was significant. The correlation of the pelvic shape scores with body height was 0.66

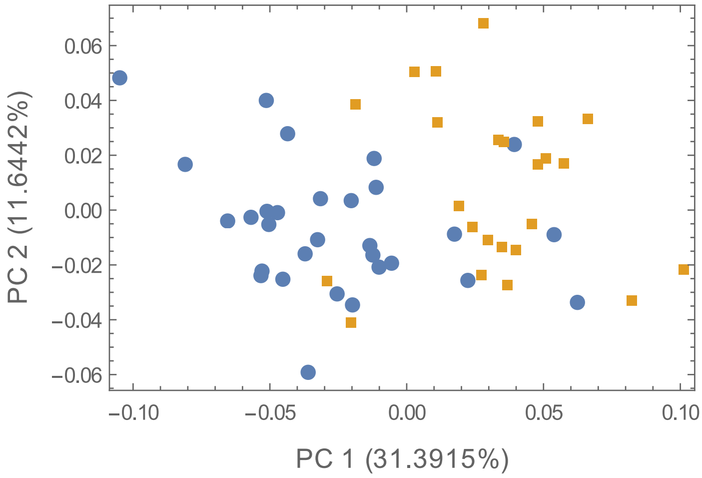

Figure 3.9: Principal components analysis of the Procrustes data. Yellow squares represent females, blue dots males. Shown is the principal component 1 against the principal component 2.

for females and 0.71 for males. The correlation with the head circumference was 0.68 for females and 0.70 for males. The correlation was therefore slightly larger for males. The explained variance was highest for the correlation between male pelvises and head circumference (11.96%) and lowest for the correlation between female pelvises and body height (5.55%). See Table 3.3 for details.

Table 3.3: Results of the regression of pelvic shape on body height and head circumference, separately for females and males

	Body height			Head circumference		
Sex	Correlation	Explained variance [%]	P-value	Correlation	Explained variance [%]	P-value
Females	0.66	5.55	¡0.001	0.68	8.92	¡0.001
Males	0.71	6.46	¡0.001	0.70	11.96	¡0.001

3.8 Shape regression on femur length and head circumference

The effect of femur length, with head circumference as co-variable, can be seen in Figure 3.17. Between the average female pelvises in the first two columns, the femur length varies by three times the standard deviation of the femur length. This also applies for the average male pelvises in the last two columns.

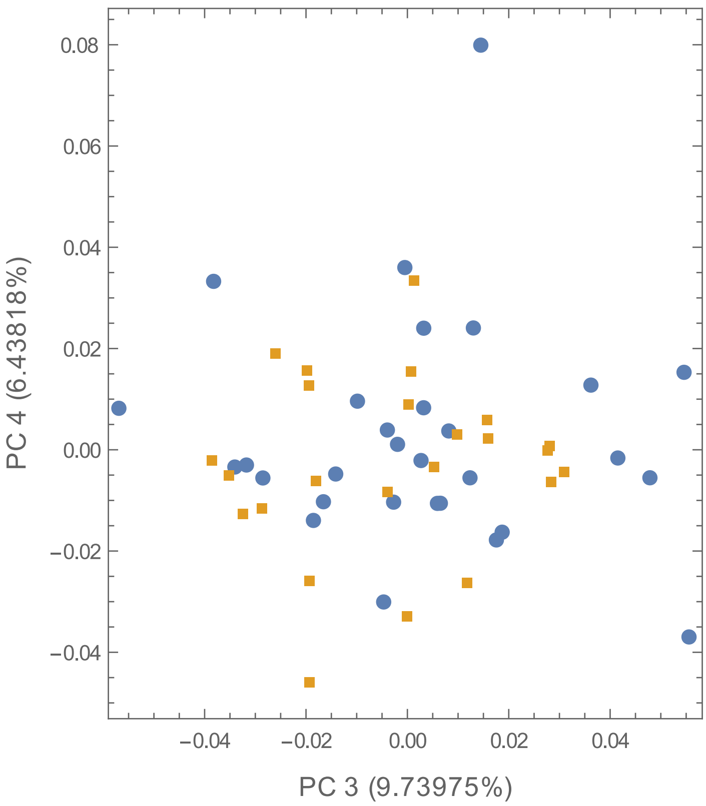

Figure 3.10: Principal components analysis of the Khoisan pelvic shape. Yellow squares represent females, blue dots males. Shown is the principal component 3 against the principal component 4

Females with a shorter femur length seem to have a larger subpubic angle, a rounder pelvic inlet, and a more backwards bent sacrum. The sacrum of males with shorter femur length is also more bent backwards and the pelvic inlet is more oval-shaped. A round pelvic inlet can be seen either in females with shorter femur length or in males with large femur length.

Figure 3.18 illustrates the different pelvic shapes based on a change of head circumference. The extrapolation for the female pelvises in the first two columns and for the male pelvises in the last two columns is based on three times the standard deviation of the head circumference. Females with a smaller head have a larger subpubic angle, straighter iliac blades, an oval-shaped pelvic inlet, and a more backwards bent sacrum. Males with a smaller head also have a larger subpubic angle, straighter iliac blades, and a more backwards bent sacrum. The pelvic inlet, on the other hand, is more round-shaped.

The association of pelvic shape with head circumference was significant for both sexes. The association with femur length was just significant for males. The correlation of the

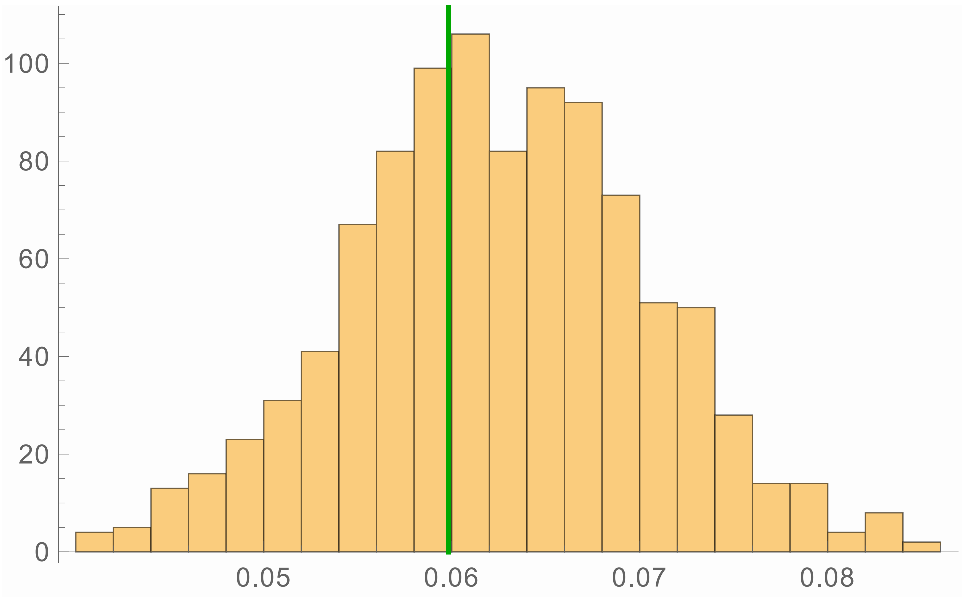

Figure 3.11: Histogram of the bootstrap results. The green line represents the length of sexual dimorphism vector in my sample.

pelvic shape scores with femur length was 0.61 for females and 0.70 for males. The correlation with the head circumference was 0.68 for females and 0.73 for males. The correlation was here also slightly larger for males. The explained variance was for this sample again highest for the correlation between male pelvises and head circumference (13.41%). Whereas it was lowest for the correlation of female pelvises and head circumference (9.51%). Details can be seen in Table 3.4.

The explained variance in males was in all cases larger than in females. When using the femur length instead of the body height, the explained variance was even higher in males (see Table 3.3 and 3.4).

Table 3.4: Results of the regression of pelvic shape on femur length and head circumference, separately for females and males

	Femur length			Head circumference		
Sex	Correlation	Explained variance [%]	P-value	Correlation	Explained variance [%]	P-value
Females	0.61	3.85	0.97	0.68	9.51	¡0.001
Males	0.70	12.20	¡0.001	0.73	13.41	¡0.001

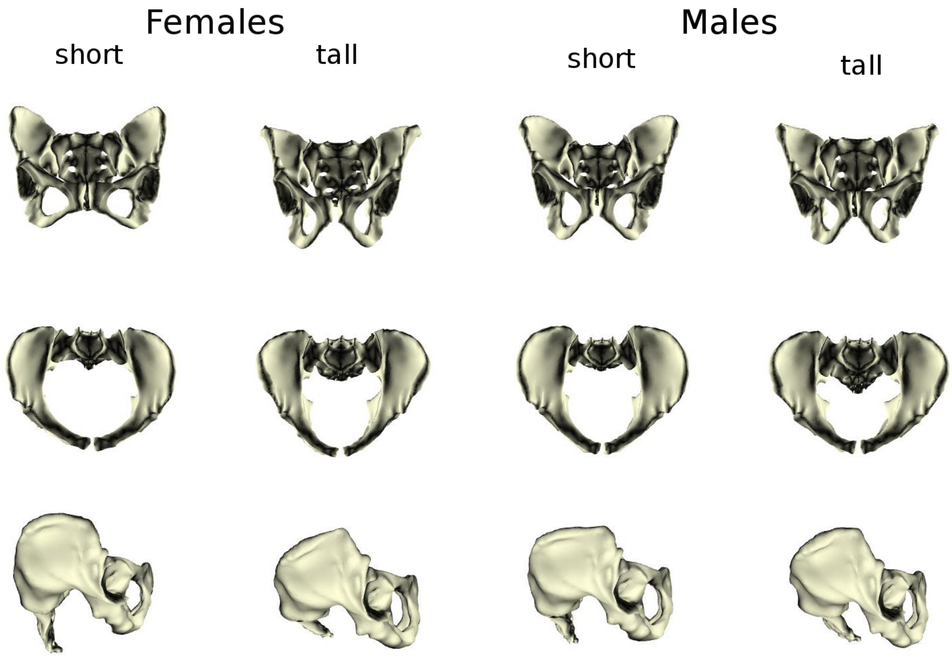

Figure 3.12: Allometry in the pelvis based on body height: Association between body height and pelvic shape, separately for females and males. On the left side are the female pelvises, on the right the male pelvises. The first and third columns show the average pelvis of a short individual, the third and fourth columns the average pelvis of a tall individual. The extrapolation based on the linear regression coefficients for stature from the shape regression. The pelvic shapes are shown in anterior, superior, and lateral view.

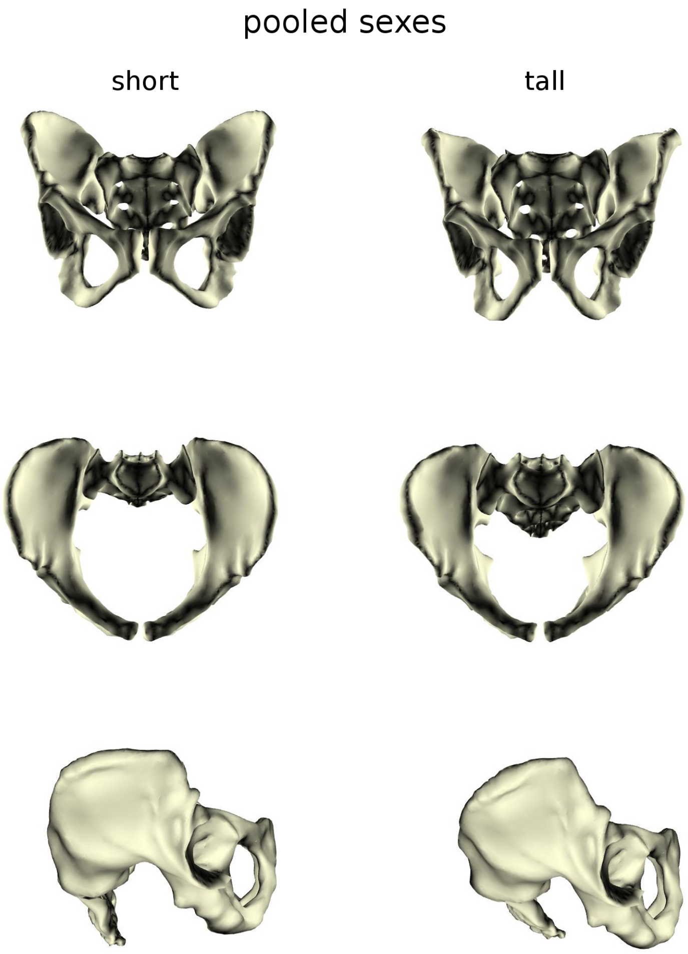

Figure 3.13: Allometry in the pelvis based on body height, independent of sex: Association between body height and pelvic shape for pooled pelvises. The first shows the average pelvis of a short individual, the second column the average pelvis of a tall individual. The extrapolation based on the linear regression coefficients for body height from the shape regression. The pelvic shapes are shown in anterior, superior, and lateral view.

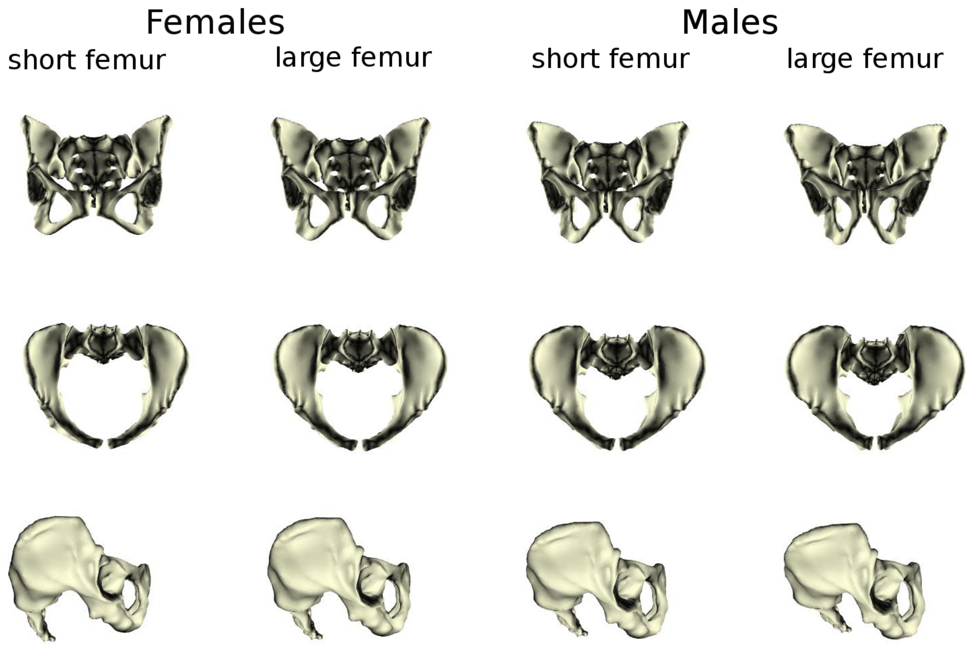

Figure 3.14: Allometry in the pelvis based on femur length: Association between femur length and pelvic shape, separately for females and males. On the left side are the female pelvises, on the right the male pelvises. The first and third columns show the average pelvis of individuals with a short femur, the third and fourth columns the average pelvis of individuals with a large femur. The extrapolation based on the linear regression coefficients for femur length from the shape regression. The pelvic shapes are shown in anterior, superior, and lateral view.

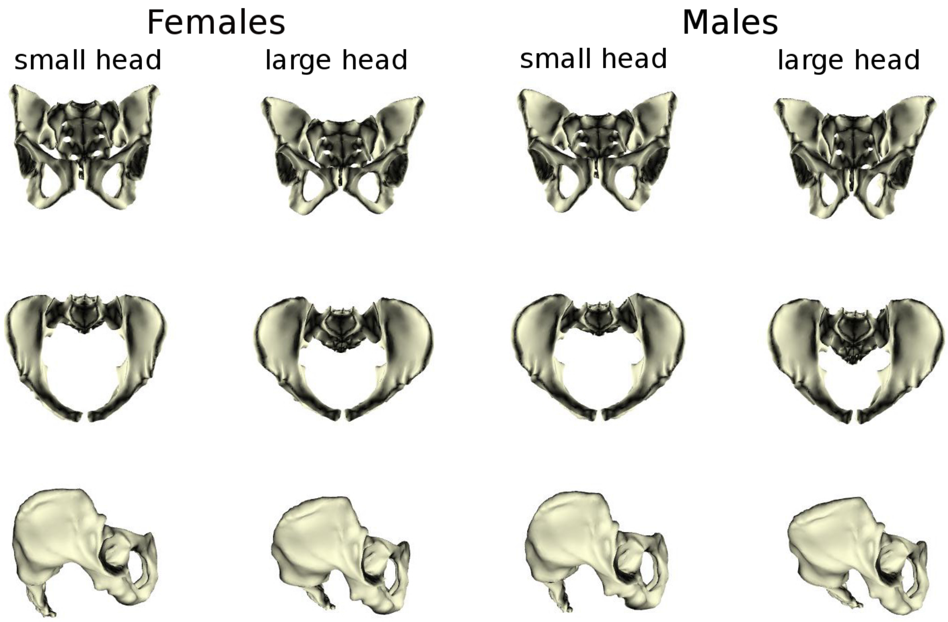

Figure 3.15: Association between head circumference and pelvic shape separately for females and males: The first and third columns show the average pelvis of an individual with a smaller head circumference, the third and fourth columns the average pelvis of an individual with a larger head circumference. The extrapolation is based on the partial linear regression coefficients for head circumference from the multivariate multiple regression of Procrustes shape coordinates on body height and head circumference. The pelvic shapes are shown in anterior, superior, and lateral view.

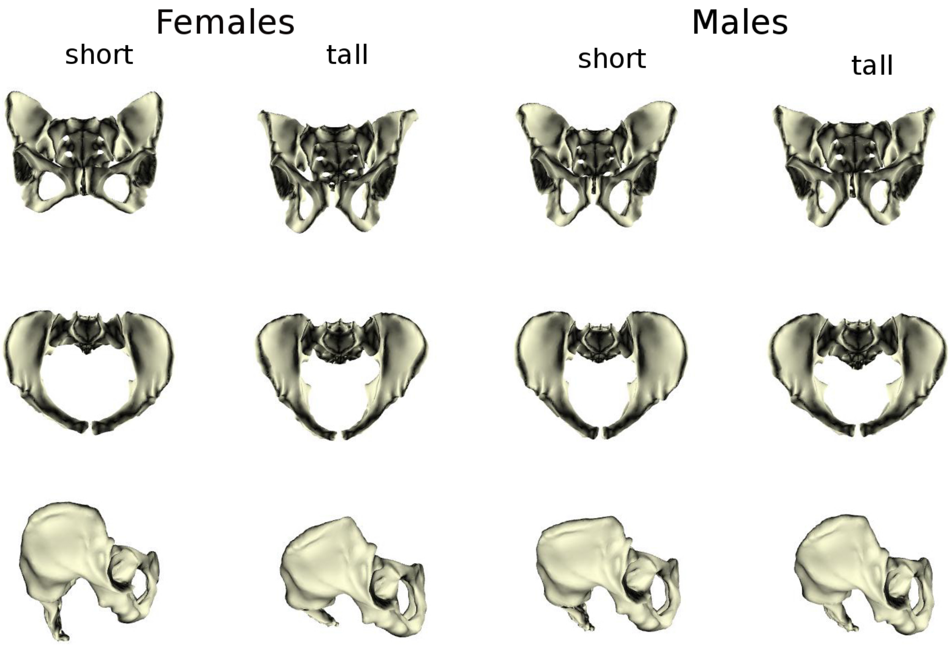

Figure 3.16: Association between body height and pelvic shape, separately for females and males: The first and third columns show the average pelvis of a short individual, the third and fourth columns the average pelvis of a large individual. The extrapolation is based on the partial linear regression coefficients for body height from the multivariate multiple regression of Procrustes shape coordinates on body height and head circumference. The pelvic shapes are shown in anterior, superior, and lateral view.

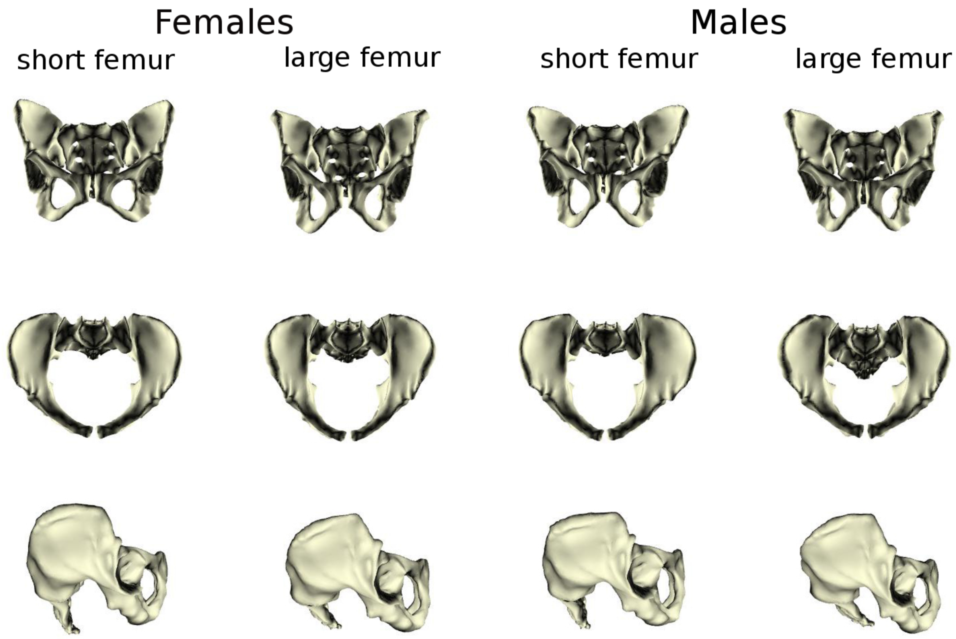

Figure 3.17: Association between femur length and pelvic shape, separately for females and males: The first and third columns show the average pelvis of an individual with a shorter femur, the third and fourth columns the average pelvis of an individual with a longer femur. The extrapolation is based on the partial linear regression coefficients for femur length from the multivariate multiple regression of Procrustes shape coordinates on femur length and head circumference. The pelvic shapes are shown in anterior, superior, and lateral view.

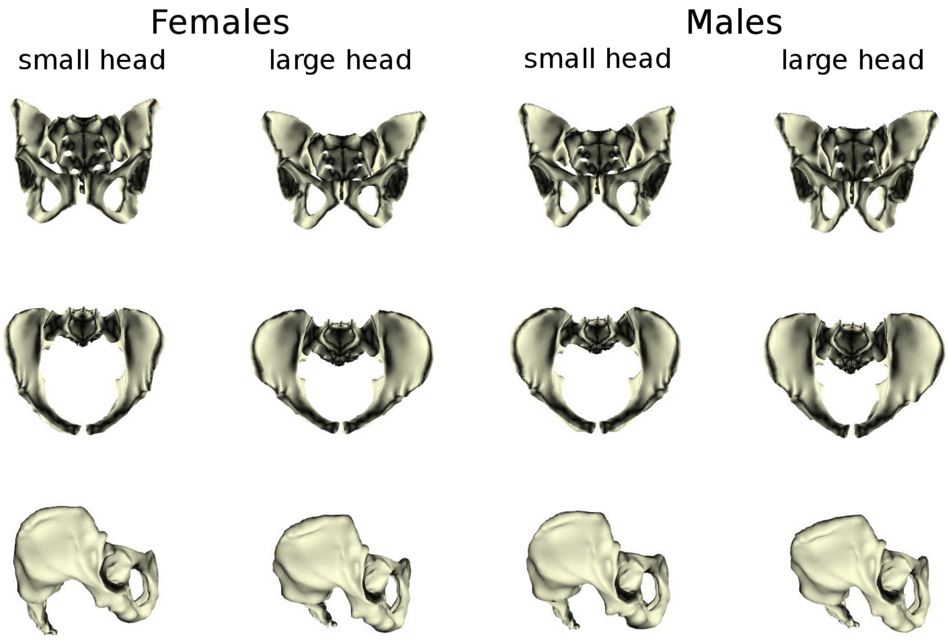

Figure 3.18: Association between head circumference and pelvic shape, separately for females and males: The first and third columns show the average pelvis of an individual with a smaller head circumference, the third and fourth columns the average pelvis of an individual with a larger head circumference. The extrapolation is based on the partial linear regression coefficients for head circumference from the multivariate multiple regression of Procrustes shape coordinates on femur length and head circumference. The pelvic shapes are shown in anterior, superior, and lateral view.

4 Discussion

The aim of my study was to examine sexual dimorphism in the pelvis and the association between head circumference, body height, and pelvic shape in a sample of Khoisans from South Africa. The main question was: which adaptations can be found in the pelvis to lower the risk of obstructed labor?

The obstetric selection pressure depends on the size of the mother and father, and on the head size of the newborn. On special risk are shorter females, which may give birth to a comparably large newborn because of the genetic correlation with the father, who may be much taller than the mother, and females with a large head cirumference. Fischer and Mitteröcker found a significant association between different body traits and pelvic shape in a Caucasian sample (Fischer and Mitteroecker, 2015).

I predicted that this association can also be found in a sample of Khoisans from South Africa. The Khoisans are known to have a, on average, shorter stature and a lower degree of sexual dimorphism than Caucasian populations.

4.1 Body height and head circumference

The average body height of females in this sample was 150.9 cm and for males 159.8 cm. In the literature, average female body heights of 136.0 cm (Toerien, 1954), 147.4 cm (Tobias, 1962), and 150.1 cm (Truswell and Hansen, 1976) for different South African populations are reported. In the same populations, average male body heights were 149.1 cm (Toerien, 1954), 157.9 cm (Tobias, 1962), 158.1 cm (Tobias, 1962), and 160.9 cm (Truswell and Hansen, 1976). The body height of my sample therefore resembled that of other known samples.

The distributions of body height, femur length, and head circumference show the well-known patterns of sexual dimorphism, where males are, on average, taller than females and therefore also have a larger head circumference (see Figure 3.3 and 3.7). The high correlation between body height and femur length supported the body height estimation by Pacher (1962). The correlation between body height and head circumference was 0.04

for females and 0.49 for males and, hence, lower than expected. Possible explanation for the low correlations can be a false assignment of the postcranial skeletons to the individual crania. In the literature I couldn't find any evidence for this assumption but the history of the S collection is still in some parts not well known.

Fischer and Mitteröcker had in their sample an average body height for females of 1,596.7 mm and for males of 1,731.2 mm (standard deviation was 65.8 mm and 76.8 mm, respectively) and an average head circumference for females of 532.2 mm and 552.4 mm for males (standard deviation was 23.1 mm and 18.9 mm, respectively) (Fischer and Mitteroecker, 2015). Compared to my sample, the average female in their sample was 88 mm taller and the average male was 130 mm taller. Also, the head circumference for females was 42 mm larger and for males 47 mm larger (see Table 3.1). The Khoisan sample differed therefore clearly in body height and head circumference from the Caucasian sample.

4.2 Sexual dimorphism

The results of the bootstrap analysis showed no obvious outliers and, hence, supported the sex determination by Pacher (see Figure 3.11). The principal component analysis of the pelvic shape showed by plotting PC1 against PC2 and PC3 against PC4 an overlapping area for females and males. The males in my sample were more variable than the females, especially by plotting PC3 against PC4. The relatively large area of overlapping indicated that the differences between the two sexes in the Khoisan pelvic shape are small and the sexual dimorphism in the pelvis is therefore low. The principal component analysis showed again no obvious outliers and supported the sex determination by Pacher (see Figure 3.9 and 3.10). Additionally, the sex determination by Botha matched Pacher's findings (Botha, 2016; Pacher, 1962). The sex determination by Pacher was therefore used for further analysis.

Compared to the study done by Fischer and Mitteröcker my sample partly showed the same patterns of sexual dimorphism in pelvic shape (Fischer and Mitteroecker, 2015). The average male pelvis had a flatter and broader shape, a larger subpubic angle, and slightly smaller acetabula than the average female pelvis. On the other side, this sample showed, in contrast to the Caucasian sample, in females a slightly longer and broader sacrum, less wide and straighter ilia, and an almost similar hip bone length in both sexes. The high consensus of sexual dimorphism patterns was mainly found in the lower part of the pelvis, which is also called the "true" pelvis. This would support the

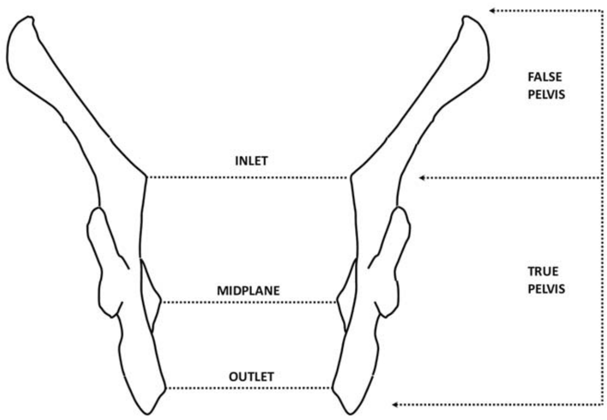

Figure 4.1: Figure of the “true” and “false” pelvis. Inlet, midplane, and outlet. Figure was taken from Betti, 2013

hypothesis that the obstetric selective pressure is especially high on the “true” pelvis and therefore its shape is more preserved, whereas the “false” pelvis may not be under such a strong obstetric selective pressure (Betti, von Cramon-Taubadel, Manica, and Lycett, 2013). One explanation of the difference in the “false” pelvis can be inferred from the thermoregulation theory. According to this theory, humans need to regulate their body temperature to keep it within a certain range independent of the outside temperature. Central is here the surface-to-volume ratio. According to Bergmann’s Rule, individuals in colder areas will be, on average, larger-bodied, whereas individuals in warmer areas will be, on average, smaller-bodied. Additionally, Allen’s Rule states that in colder areas individuals will have, on average, shorter extremities, whereas individuals in warmer areas will have, on average, larger extremities. Following Bergmann’s and Allen’s Rule, individuals in warmer areas are lighter, narrower, and have larger extremities. Therefore, the surface-to-volume ratio for these individuals increases. In hot areas, like in South Africa, the surface-to-volume ratio has to be high. Therefore, people in these areas are assumed to have an, on average, smaller body size. To increase the ratio even more a narrower pelvic shape is preferred (Bergmann, 1848; Katzmarzyk and Leonard, 1998; Ruff, 1994).

4.3 Allometry

The visualization of allometric effects on the pelvic shape showed for shorter females a larger subpubic angle, a broader lower pelvic part, a rounder pelvic inlet, a longer and more backwards bent sacrum, and straighter iliac blades. The visualization showed for shorter males an oval-shaped pelvic inlet, a more backwards bent sacrum, and straighter iliac blades.

The association of either body height or femur length with pelvic shape showed the same patterns. This was in line with my expectations because the calculated body height was based, among other bone measurements, also on the femur length. Therefore, a change in femur length would result in a corresponding change in the estimated body height.

In both cases the allometric patterns of pelvic shape were similar in males and in females.

To increase the sample size, the allometric pattern was also visualized for both sexes together. Small individuals had a larger subpubic angle, a rounder pelvic inlet, and a more backwards bent sacrum. The changes in pelvic shape for the pooled individuals resembled the allometric shape patterns in females.

Both pelvic size and shape differed between short and tall Khoisans. Different body sizes are associated with different demands on the human skeleton. By increasing only the size of the skeleton, without changing the shape, some requirements won't be fulfilled. This variation in pelvic shape is due to energetically efficient bipedal locomotion, thermoregulation, or the obstetrical dilemma in females.

4.4 Association of Body height and head circumference with pelvic shape

As already mentioned in Chapter 1.4.2, the human pelvis had to accommodate two major steps in evolution: the evolution of bipedal locomotion and of encephalisation. These two adverse demands caused different selection pressures on the pelvic structure depending on the sex. Therefore, a sexual dimorphism in the pelvic shape can be expected and was also seen in my study (see Section 4.2).

Based on the multiple linear regression of pelvic shape on body height and head circumference, short females showed a rounder pelvic inlet and a more backwards bent sacrum. Females with a smaller head circumference had a more oval-shaped pelvic inlet and a more backwards bent sacrum. The bending of the sacrum associated with body height or head circumference, was the same in males, whereas the shape of the pelvic inlet differed between males and females. Females with a large head or short females had a round-shaped pelvic inlet, also males with a smaller head circumference or large males had a round-shaped pelvic inlet (see Figure 3.15 and 3.16).

The patterns of change in pelvic shape associated with body height and head circumference matched the patterns associated with femur length and head circumference. The influence of body height on pelvic shape was, therefore, also well represented by using the femur length.

A round-shaped pelvic inlet could be seen for short females or females with large head circumference. These females are under greater selective pressure because of their higher risk of obstructed labor (Chan and Lao, 2009; Kirchengast and Hartmann, 2007; Toh-adam, Srisupundit, and Tongsong, 2012). This shape of the pelvic inlet is also known as “gynecoid” pelvis. The round pelvic inlet has the broadest midplane and may lower the probability of a dangerous deformation of the newborn’s head. A round pelvic inlet seems to be the optimal shape for vaginal birth, whereas an oval-shaped pelvic inlet may increase the probability of obstructed labor (Caldwell and Moloy, 1938; Lopez-Zeno, 2008; Salk, Cetin, Salk, and Cetin, 2015).

Additionally, the dimensions of the pelvis have an impact not only on the obstructed labor but also on the health of a newborn. During birth, the neonate rotates to fit through each pelvic dimension. This is a unique feature in humans across primates (Correia et al., 2005; Rosenberg, 1992). Different deformations of the fetal head during delivery have different impacts on the neonate. Borell and Fernstroem (1958a,5) found that a deformation in the occipito-frontal diameter had no negative impact on the neonate, whereas deformation in the biparietal diameter could cause major injuries and thus lead to the death of the newborn. The diameter of the female pelvis should thus fit to the biparietal diameter of the neonatal head, and the sexual dimorphism in this diameter should be most pronounced. Hence, the pelvis should be as broad as possible in the midplane to lower the risk of deformation in the biparietal diameter of the newborn (Correia et al., 2005). Increasing this diameter in the midplane may increase the population’s mean fitness by lowering the probability of injured newborns.

Even though an association of body height and head circumference with the pelvic inlet shape was present in both sexes, some shape patterns were only seen in females and were therefore sex-specific. By decreasing the body height of females, the average pelvis showed an increased subpubic angle and a more backwards bent sacrum. These patterns can only be seen in females associated with body height. The same shape patterns were associated with head circumference, both in females and in males. There were no sex-specific shape patterns associated with head circumference.

By tilting the sacrum more backwards, the size of the birth canal is increased. In my sample, short females and females with a smaller head circumference had, on average, a more backward bent sacrum and therefore a larger lower pelvic capacity. These individuals are more likely to give birth to relatively large neonates or to neonates who had a larger head than expected by their own stature, because of a much taller father. The likelihood of obstructed labor is therefore higher for shorter females than for taller females. The pelvic shape of shorter females has to be more adopted to a possible obstetrical dilemma than the pelvic shape of taller females. This adaptation may be due to a differently shaped pelvic inlet, a differently bent sacrum, a differently subpubic angle or differently shaped ischial spines (Salk et al., 2015; Stulp et al., 2011). This was partly also visible in my sample. Based on the association of body height with pelvic shape, shorter females had, on average, a rounder pelvic inlet and a more backwards bent sacrum. The illustrated shape patterns therefore supported this hypothesis (see Figure 3.16). The shape patterns associated with body height were sex-specific. The association of head circumference with pelvic shape were not sex-specific. Although the sacrum bent more backwards and, hence, supported the hypothesis, the pelvic inlet for smaller head circumference was more oval-shaped (see Figure 3.15).

Compared to the study by Fischer and Mitteroecker (2015), the pelvic shape patterns of both studies matched only in some parts. In both studies, shorter females had a round pelvic inlet and a more backwards bent sacrum, also shorter males had a more backwards bent sacrum. In contrast to the Caucasian sample, shorter females of the Khoisan sample had a clearly longer sacrum, whereas shorter males of the Khoisan sample had an oval-shaped pelvic inlet and no obviously shorter sacrum. In both samples, females with smaller head circumference had an oval-shaped pelvic inlet, whereas the sacrum bent in different directions. In both sampels, males with smaller head circumference had a similar bent sacrum, whereas the sacrum in the Khoisan sample was bent even more and also the pelvic inlet shape differed.

5 Conclusion

An association between body height, head circumference, and pelvic shape was found in the Khoisan sample. Partly, the shape patterns were sex-specific. Evidently, the sex-specific patterns in some parts of the female pelvises reduced the risk of obstructed labor and are therefore beneficial for giving birth. The probability of obstructed labor in humans is rather high. Therefore, the obstetric selective pressure led to different modifications to reduce the risk for the mother and the newborn. One adaptation was the rotation of the fetal head during labor, another may be the association of the pelvic shape, especially the pelvic inlet, with body height and head circumference in females.

Compared to a Caucasian sample, the Khoisan sample showed a high consensus in the shape patterns of the pelvic inlet in females but different shape patterns of the sacrum. Even though the bending and the length of the sacrum may influence the lower pelvic capacity, the pelvic inlet may have an even higher impact on the risk of obstructed labor and may therefore be more conserved between different populations.

List of Figures

List of Tables

Bibliography

Arsuaga, J. L. and J. M. Carretero (1994). Multivariate analysis of the sexual dimorphism of the hip bone in a modern human population and in early hominids. *American Journal of Physical Anthropology 93*(2), 241–257.

Barnard, A. (2007). *Anthropology and the Bushman.* Oxford: Berg Publishers.

Bergmann, C. (1848). *Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Größe*. Götteningen Studien.

Betti, L., N. von Cramon-Taubadel, A. Manica, and S. J. Lycett (2013). Global geometric morphometric analyses of the human pelvis reveal substantial neutral population history effects, even across sexes. *PloS one 8*(2), e55909.

Bookstein, F. L., B. Grayson, C. B. Cutting, H.-C. Kim, and J. G. McCarthy (1991). Landmarks in three dimensions: Reconstruction from cephalograms versus direct observation. *American Journal of Orthodontics and Dentofacial Orthopedics 100*(2), 133 – 140.

Borell, U. and I. Fernstroem (1958a). Die umformung des kindlichen kopfes bei engem becken. *Geburtsh. Frauenheilkd 18*, 1156–1166.

Borell, U. and I. Fernstroem (1958b). Die umformung des kindlichen kopfes waehrend normaler entbindung in regelrechter hinterhauptslage. *Geburtsh. Frauenheilkd 18*, 1245–1256.

Botha, D. (2016). *Personal Communication with Deona Botha MSc from the University of Pretoria via Mail (Deona.Botha@up.ac.za).*

Botha, D. and M. Steyn (2013). Khoe-san skeletal colletions in vienna and paris: Origin, history and context. *Goodwin Series 11.*

Botha, D. and M. Steyn (2014). A palaeopathological assessment of the late 19th and early 20th century khoesan. *International Journal of Osteoarchaeology*, n/a–n/a.

Caldwell, W. and H. Moloy (1938). Anatomical variations in the female pelvis: Their classification and obstetrical significance:(section of obstetrics and gynæcology). *Proceedings of the Royal Society of Medicine 32*(1), 1.

Chan, B. C.-P. and T. T.-H. Lao (2009). The impact of maternal height on intrapartum operative delivery: A reappraisal. *Journal of Obstetrics and Gynaecology Research 35*(2), 307–314.

Correia, H., S. Balseiro, and M. D. Areia (2005). Sexual dimorphism in the human pelvis: Testing a new hypothesis. *{HOMO} - Journal of Comparative Human Biology 56*(2), 153 – 160.

Fischer, B. and P. Mitteroecker (2015). Covariation between human pelvis shape, stature, and head size alleviates the obstetric dilemma. *Proceedings of the National Academy of Sciences of the United States of America 112*(18), 5655—5660.

Fröschl, Karl Anton, .-H., .-H. Müller, Gerd B., .-H. Olechowski, Thomas, and .-H. Schmidt-Lauber, Brigitta (2015). *Reflexive Innensichten aus der Universität; Disziplinengeschichten zwischen Wissenschaft, Gesellschaft und Politik.* 650 Jahre Universität Wien – Aufbruch ins neue Jahrhundert / hrsg. von Friedrich Stadler ; 4. Zsfassungen in engl. Sprache.

Gruss, L. T. and D. Schmitt (2015). The evolution of the human pelvis: changing adaptations to bipedalism, obstetrics and thermoregulation. *Philosophical Transactions of the Royal Society of London B: Biological Sciences 370*(1663).

Gunz, P. and P. Mitteroecker (2013). Semilandmarks: a method for quantifying curves and surfaces. *Hystrix, the Italian Journal of Mammalogy 24*(1), 103–109.

Gunz, P., P. Mitteroecker, S. Neubauer, G. W. Weber, and F. L. Bookstein (2009). Principles for the virtual reconstruction of hominin crania. *Journal of Human Evolution 57*(1), 48 – 62.

Harcourt-Smith, W. (2007). 5 the origins of bipedal locomotion. In W. Henke and I. Tattersall (Eds.), *Handbook of Paleoanthropology*, pp. 1483–1518. Springer Berlin Heidelberg.

Katzmarzyk, P. T. and W. R. Leonard (1998). Climatic influences on human body size and proportions: ecological adaptations and secular trends. *American Journal of Physical Anthropology 106*(4), 483–503.

Kirchengast, S. and B. Hartmann (2007). Short stature is associated with an increased risk of caesarean deliveries in low risk population. *Acta Medica Lituanica 14*(1), 200.

Klingenberg, C. (2013). Visualizations in geometric morphometrics: how to read and how to make graphs showing shape changes. *Hystrix, the Italian Journal of Mammalogy 24*(1), 15–24.

Lopez-Zeno, J. (2008). Presentation and mechanisms of labor. *Glob Libr Womens Med DOI:10.3843/GLOWM.10126.*

Lovejoy, C. (2005). The natural history of human gait and posture: Part 1. spine and pelvis. *Gait & Posture 21*(1), 95 – 112.

Martin, R. D. (1983). *Human brain evolution in an ecological context. Fifty-second James Arthur lecture on the evolution of the human brain. American Museum of Natural History.*

Merchant, K. M., J. Villar, and E. Kestler (2001). Maternal height and newborn size relative to risk of intrapartum caesarean delivery and perinatal distress. *BJOG: An International Journal of Obstetrics & Gynaecology 108*(7), 689–696.

Mitteroecker, P. and P. Gunz (2009). Advances in geometric morphometrics. *Evolutionary Biology 36*(2), 235–247.

Morris, A. G. (1987). The reflection of the collector: San and khoi skeletons in museum collections. *The South African Archaeological Bulletin 42*(145), pp. 12–22.

Pacher, H. (1962). *Anthropologische Untersuchungen an den Skeletten der Rudolf Pöch'schen Buschmannsammlung.* Number Bd. 1 in Rudolf Pöchs Nachlass: Physische Anthropologie. Böhlau in Komm.

Pearson, K. (1898). Mathematical contributions to the theory of evolution. v. on the reconstruction of the stature of prehistoric races. *Phil. Transact. R. Soc. London. Ser. A 192*, 169 – 245.

Reynolds, H. M., C. C. Snow, . Young, John W., U. S. O. of Aviation Medicine, and C. A. I. (U.S.) (1982). *Spatial geometry of the human pelvis.* Washington, D.C. : The Office ; Springfield, Va. : National Technical Information Service [distributor.

Rosenberg, K. and W. Trevathan (2002). Birth, obstetrics and human evolution. *BJOG: An International Journal of Obstetrics & Gynaecology 109*(11), 1199–1206.

Rosenberg, K. R. (1992). The evolution of modern human childbirth. *American Journal of Physical Anthropology 35*(S15), 89–124.

Ruff, C. (2010). Body size and body shape in early hominins – implications of the gona pelvis. *Journal of Human Evolution 58*(2), 166 – 178.

Ruff, C. B. (1994). Morphological adaptation to climate in modern and fossil hominids. *American Journal of Physical Anthropology 37*(S19), 65–107.

Ruff, C. B., E. Trinkaus, and T. W. Holliday (1997, May). Body mass and encephalization in pleistocene homo. *Nature 387*(6629), 173–176.

Salk, I., M. Cetin, S. Salk, and A. Cetin (2015). Determining the incidence of gynecoid pelvis using three-dimensional computed tomography in nonpregnant multiparous women. *Medical principles and practice: international journal of the Kuwait University, Health Science Centre 25*(1), 40–48.

Stulp, G., S. Verhulst, T. V. Pollet, D. Nettle, and A. P. Buunk (2011, 06). Parental height differences predict the need for an emergency caesarean section. *PLoS ONE 6*(6), e20497.

Tobias, P. V. (1962). On the increasing stature of the bushmen. *Anthropos 57*(3/6), 801–810.

Toerien, M. (1954). *The physical characters of the Lake Chrissie Bushmen.* University of the Witwatersrand.

Toh-adam, R., K. Srisupundit, and T. Tongsong (2012). Short stature as an independent risk factor for cephalopelvic disproportion in a country of relatively small-sized mothers. *Archives of gynecology and obstetrics 285*(6), 1513–1516.

Trevathan, W. (2015). Primate pelvic anatomy and implications for birth. *Philosophical Transactions of the Royal Society of London B: Biological Sciences 370*(1663).

Truswell, A. S. and J. D. Hansen (1976). Medical research among the! kung. *Kalahari hunter-gatherers*, 166–194.

Weaver, T. D. and J.-J. Hublin (2009). Neandertal birth canal shape and the evolution of human childbirth. *Proceedings of the National Academy of Sciences 106*(20), 8151–8156.

Wells, J. C., J. M. DeSilva, and J. T. Stock (2012). The obstetric dilemma: An ancient game of russian roulette, or a variable dilemma sensitive to ecology? *American Journal of Physical Anthropology 149*(S55), 40–71.

Wells, J. C. K. (2015). Between scylla and charybdis: renegotiating resolution of the 'obstetric dilemma' in response to ecological change. *Philosophical Transactions of the Royal Society of London B: Biological Sciences 370*(1663).

Wittman, A. and L. Wall (2007). The evolutionary origins of obstructed labor: bipedalism, encephalization, and the human obstetric dilemma. *Obstet Gynecol Surv 62(11)*(0029-7828 (Linking)), 739–748.