

**THE MORPHOLOGY OF THE UPPER THORAX OF *AUSTRALOPITHECUS*
SEDIBA WITHIN THE CONTEXT OF SELECTED HOMINOIDS**

by

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A thesis submitted to the Faculty of Science, University of the Witwatersrand,
Johannesburg, in fulfilment of the requirements for the degree of Doctor of
Philosophy

Johannesburg 2013

DECLARATION

I declare that this dissertation is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

A handwritten signature in black ink, appearing to be 'S. M.', written over a dotted line. Below the signature is a solid horizontal line.

27 day of September 2013

ABSTRACT

The thoracic skeletal morphology of homininae is poorly known and understood. As a result of the representative fossil record of ribs and vertebrae being rare, distorted, fragmentary or unrecognised even when recovered, very little is known about the variability of rib and vertebral morphology when compared to the other cranial and postcranial elements in this lineage. Yet the costal skeleton forms a substantial part of the postcranial skeleton and thus ribs and vertebrae are therefore potentially numerous in the fossil record; but in comparison with other skeletal elements, and for the reasons mentioned above, very little is known about vertebrate and especially hominin rib morphology. The assessment of the structure of the thoracic skeletal elements and its evolutionary and ecological significance, particularly in the Homininae, poses a challenge but is still important as the shape and form of the rib cage has numerous functional and behavioural implications. The present study analysed the ribs of selected primate and non-primate mammalian species by examining fifteen variables, seven indices and eight osteological non-metric features. These observations and measurements were compared to ribs found in the fossil record in order to determine if there are any structural correlates between the extant and the extinct hominin and mammalian species and in order to create a template for the identification of hominin ribs within an abundant and diverse mammalian assemblage. The results suggest that the 1st rib, due to its unique morphology, may be considered most diagnostic in differentiating various taxa. In addition, a template for the morphology of the proximal end of the first rib has been created to be used for both the general as well as the specific identification of fossilised fragments, and to

determine thoracic shape. The recently recovered costal elements of the *Australopithecus sediba* fossils were also examined as one of the most abundant assemblages of the elements in the early hominin record in order to add to our understanding of the morphology, and evolution of this poorly known area of hominin anatomy. The thorax of *Australopithecus sediba* demonstrates a medio-laterally narrow, ape-like upper thoracic shape, which is different from the broad upper thorax of *Homo* that has been associated with to the locomotor pattern of endurance walking and running. The lower thorax, however, is less laterally-flared than that of apes, and more closely approximates the morphology found in humans. This indicates a mosaic morphology of the thorax during the human evolutionary lineage.

ACKNOWLEDGEMENTS

To my supervisors, Prof. Lee Berger and Dr Bernhard Zipfel

– Lee, you initiated me on my journey and provided the initial spark and insight that stimulated my interest in the study of humanity– I thank you for all the help in especially the crucial stages of the development and the critical evaluation of this thesis.

- Bernhard, you are my mentor and guide through this journey, my eternal gratitude for providing insight and assistance, and for your invaluable words of advice, guidance and leadership during often challenging times – thank you

To Prof. Steven Churchill and Dr. Peter Schmid for the invaluable discussion, insight and input in increasing my understanding of thoracic morphology and functionality.

To Peter Schmid and Eveline Weissen for the osteological data and graphs related to *Australopithecus sediba* as well as the related comparative materials studied.

To Dr. Kristian J. Carlson – for being the sounding board of ideas and insight and especially your assistance with the statistics, data analysis and interpretation.

To Prof. Bruce Rubidge and Prof. Marion Bamford of the Bernard Price Institute for Palaeontological Research (BPI) - thank you for words of support and advises

To Andrea Leenen and Palaeontological Scientific Trust (PAST) for the generous financial support.

To Ann Smilkstein of PAST– for the cups of coffee and encouraging words that provided more than warmth on a cold day.

To Dr. Bonita De Klerk – for your words of constant encouragement

To Wilma Lawrence – for all the administrative support

To Prof. Andre Swart, Dean of the Faculty of Health Sciences, University of Johannesburg for your words of encouragement and support.

To Elaine Swanepoel, Nkosi Xhakaza, Henriette Matthews and colleagues of the Department of Human Anatomy and Physiology, Faculty of Health Sciences, University of Johannesburg – thank you for your support during my study

To the University of Witwatersrand Fossil Access Advisory Committee and Stephany Potze of the Ditsong (formerly Transvaal) Museum of Natural History for allowing access to housed fossil material.

To Dr Shaw Badenhorst of the Ditsong (formerly Transvaal) Museum of Natural History, to Brendon Billings of University of the Witwatersrand School of Anatomical Sciences and to the Evolutionary Study Institute (ESI) (formerly Bernard Price Institute for Palaeontological Research (BPI)) for making modern faunal material available for study.

To my fellow students and peers of BPI and Institute of Human Evolution (IHE) (now known as Evolutionary Study Institute, ESI) especially Natasha Barbolini – thank you for the chats, support and been a part of my journey through this project.

To Carol Ward, Andrew Gordon and James Ohman for their assistance in obtaining some of the literature for this study.

To the Centre for Professional Academic Staff Development, Division: Academic Development & Support, University of Johannesburg for funding from Staff Qualification Project (SQP).

To Neil De Villiers and Statkon (UJ) – for assistance with the statistics and data analysis.

DEDICATION

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To my parents: Abubukker and Sabera

my wife: Fatima

my children: Muhammad, Ameera, Ammaarah and Yusuf

and my siblings

Thank you for all the love and support that I could ever have desired

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CHAPTER 1 INTRODUCTION AND LITERATURE REVIEW

1.1. Background to the current study

The cranial and postcranial skeletal remains of most terrestrial mammals exhibit many common macroscopic features that fit into a “general mammalian body plan”. It thus follows that a basic mammalian morphological pattern is also shared by almost all of the costal elements or ribs, be they of primate or non-primate mammalian species (Jellema *et al.* 1993).

The costal skeleton of the thoracic cage forms a substantial component of the postcranial mammalian skeleton (Williams 1995). Ribs therefore have the potential of being numerous in the fossil record. These elements in the fossil record, however, have been poorly studied due to them being fragile, distorted or typically fragmentary when recovered or simply deemed too difficult to identify and associate with any particular species. In the hominin fossil record, the costal elements are particularly rare perhaps for the reason that they have not been identified as being hominin; researchers being unable to discriminate their morphology from those of animals of similar body size.

The perceived paucity and fragmentary nature of rib material in the hominin fossil record makes it difficult not only to identify the ribs in these extinct species, but to correctly sequence and position them in order to study the evolutionary morphology of the thoracic region. The fragmentary nature of the sample at present also reduces the possibility of obtaining standard costal measurements or thoracic dimensions of

the different taxa for comparison and analysis. As a result, very little is known about the variability in fossil primate rib morphology as compared to other elements of the cranial and postcranial skeleton even though it should be far more representative barring taxonomic issues of representation (Brain 1981). Therefore the assessment of the skeletal structure of the thorax and its evolutionary and ecological significance, particularly in hominins has presented a challenge (Weinstein 2008).

A number of earlier studies of the thoracic region and associated ribs of primates as well as non-primates have largely been descriptive qualitative studies (Owen 1854, Struthers 1875, 1893 and Getty 1975).

Hominin rib elements are known in the fossil record but even the identification of rib fragments, in order to discriminate them from other post-cranial remains has also proved to be problematic, and at least in one case a marine mammal rib fragment has been confused with a hominin clavicle (Boaz 1980), or in a laboratory with other long bone elements particularly when fragmentary (White *et al.* 1983, Larson *et al.* 2007). Additionally, due to relatively limited comparative work in the literature, most studies of hominin ribs tend to initially be extremely superficial. As an example, Carretero *et al.* (1999), in a study of *Homo antecessor*, reported only the presence of ribs with no further description, but stated that a more complete and detailed analysis of the ribs would be necessary recognising their potential importance. This was followed by Gomez-Olivencia *et al.* (2010) who provided a more detailed morphological description and metric analysis of the costal elements of the *Homo*

antecessor. They also compared these costal elements to those of other fossil hominins and extant modern mammalian groups, both primate and non-primate. Demonstrating the difficulty of working with fragmentary material of this nature, they still concluded that there was still uncertainty as to the size and shape of the thorax of *Homo antecessor* when compared to that of Neanderthals (Gomez-Olivencia *et al.* 2010).

The examination of the thorax of the partial *Australopithecus afarensis* skeleton, AL 288-1 or Lucy, by Schmid (1983), which suggested that contrary to previous suggestions, the thoracic shape of this species was more ape-like than human-like prompted significant debate and highlighted the potential importance of understanding thoracic shape in the fossil hominin record. Publications examining the remarkably complete thoracic remains of the Kebara 2 Neanderthal (Arensburg 1991) and the Nariokotome *Homo erectus* juvenile (Jellema *et al.* 1993) further challenged earlier ideas of the dimension and shape of the hominin thorax and its evolution. These studies have stimulated further paleoanthropological interest in the evolution of thoracic morphology, particularly in hominins (Franciscus and Churchill, 2002; Weinstein, 2007 and 2008; Kagaya *et al.*, 2008; Gomez-Olivencia *et al.*, 2009 and 2010). But the problem of the paucity of the hominin fossil rib record remains the greatest single challenge to our understanding of the morphology and evolution of this region.

Yet, ribs and rib fragments are abundant in most mammalian fossil assemblages but their specific identification has been deemed extremely difficult. If, however, the complete or fragmentary ribs of the various mammalian species could be reliably discriminated from one another, and more identifiable rib material could be recovered, then the inclusion of additional ribs could potentially expand greatly the understanding of the present fossil record of rare mammal species including hominins. The positive identification of rib fragments to the family, genus and species level therefore is of some considerable importance, especially in the field of primate evolutionary studies.

1.2. Current areas of research concerning ribs

Ribs, like other postcranial elements, have been proven to be useful in archaeological, paleontological as well as forensic studies in order to:

- i. determine the shape of the thorax and thus the position of the appendicular skeleton relative to it, e.g. Schmid (1983 and 1991), Franciscus and Churchill (2002), Kagaya *et al.* (2008 and 2009), Gomez-Olivencia *et al.* (2010) and
- ii. estimate the age at death of a particular human individual, e.g. Rios and Cardoso (2009) looked at three anatomical locations of a rib for epiphyseal union: the head, the articular tubercle and the non-articular tubercle. They noted that the age at which epiphyseal union occurred in the following sequence:

- a. at the non-articular tubercle (females, 11–19 years; males, 11–19 years);
 - b. at the articular tubercle (females, 11–20 years; males, 16–20 years) and
 - c. at the head (females, 15–24 years; males, 16–22 years), which can still show incomplete epiphyseal closure at 25 and 24 years for females and males, respectively.
- iii. determine the sex of an individual e.g. Bellamare *et al.* (2006). In this study they found that females have relatively longer ribs than males and that, in contrast to males, the length of the ribs in females is not significantly associated to the length of the axial skeleton. They suggested that different factors govern the growth of ribs in males and females.
 - iv. understanding the evolution of the respiratory system in the human species (Gea 2008).

Thus there is significant information that could be gleaned from a larger record of hominin rib material as each of these areas of study holds potentially important information as to the behaviour of early hominins, sex differences, development and the mode and tempo of hominin evolution.

1.3. Review of the costal arch

1.3.1. Comparison of the ribs of selected mammalian species

The available literature on the morphology of ribs of various mammalian species is mostly descriptive. As early as 1878, Gegenbaur (1878) compared the anatomy of various species of the vertebrate taxa. Yet this descriptive account was not detailed in terms of the osteology and morphology of the ribs of specific species only - a general rather than detailed description of the vertebrate ribs was given.

Subsequently Flower (1885) expanded on these descriptions by including specifically the osteology of the ribs in mammalia in general. He noted details of the morphology and number of the ribs that included:

- i. “among the higher Simiina, the ribs do not differ very notably from those of Man except in number”;
- ii. “lower forms especially of Lemurina resemble those of the Carnivora” and
- iii. a brief description on the typical forms of the “Carnivora and Ungulata”.

Shortly thereafter, Jayne (1898) added considerable detail when he compared the morphology of the domestic cat skeleton to that of humans by comparing osteological features, as well as producing the first examination of the linear metrical nature of the ribs. It was also noted for the first time that the size and degree of development of the ribs were dependent on the size and strength of the entire skeleton. In particular and

importantly a detailed description was undertaken of the fifth rib and special features of the other numbered ribs were noted (see Figure 1.1) (Jayne 1898).

Since these 19th century studies, there has largely existed a consensus that among most groups of vertebrates, rib structure is rather uniform and apparently sub-serves an established set of functional requirements (Getty 1975). Yet, it has been frequently noted that the functional aspects of the thoracic musculoskeletal system as a whole are incompletely understood and the significance of any observed rib specializations in various taxa are even more difficult to understand and interpret (Slijer 1946, Jenkins 1970, Napier and Napier 1967, O'Regan and Kitchener 2005, Kagaya *et al.* 2008 and 2009).

Ribs have also been largely ignored by faunal analysts. Brain (1974) in his seminal work on zooarchaeological methodology never mentioned ribs. Getty (1975) in Sisson and Grossmans' "Osteology of the domestic animals" described the osteology of a horse, an ox, the domestic pig and the domestic dog. However, even of this seminal examination, descriptions are not detailed except for that of the horse. No metrical analyses of the ribs were undertaken in this study of Getty. Voigt (1983) included ribs under "unidentified specimens" primarily due to their fragmentary nature that made it difficult to glean additional information from these bones. Plug (1988, 2001) included ribs into "unidentified remains" together with "miscellaneous skeletal fragments and bone flakes".

TABLE.	
Tubercle, with articular facet, present.	
Head with single facet.	
High tubercle. The shortest rib; very straight . . .	1
Head with two facets.	
Sternal end of body with great cephalo-caudal diameter.	
Rib very straight, tubercular facet small	2
Rib more curved, tubercular facet larger, and cir- cular. Length regularly increases . . .	3, 4, 5, 6
Sternal end of body smaller, more rounded. Tuber- cular facet oval, continued inward on neck.	
Length gradually increases	7, 8, 9
Length the same or decreases	10
No tubercle with articular facet.	
Head with single facet.	
Length and degree of curvature decrease gradually .	11, 12, 13

Figure 1.1: Tabulated features of the ribs of a cat (*Felis catus*) (After Jayne, 1898).

1.3.2. Morphology of the human rib

The ribs of vertebrates in general are described as being semi-elastic arches, connected posteriorly with the vertebral column and variably connected anteriorly, forming in conjunction with the vertebrae, much of the thoracic skeleton (Williams 1995). Hominins, of which humans are a member, follow the general vertebrate pattern of rib morphology, but due to the acquisition of bipedalism, there are unique features of the morphology of hominin ribs. As a benchmark, the human ribs are described below.

1.3.2.1. The “typical” human rib.

The non-pathological “typical” human thoracic cage exhibits twelve ribs on each side for a total of twenty-four ribs in the adult male and female. The number may be variable with supernumerary ribs in either the cervical or the lumbar regions (White 1999).

Human ribs are classified as:

- i. Vertebro-sternal ribs – numbers 1 to 7 that articulate via costal cartilages to the sternum;
- ii. Vertebro-chondral ribs – numbers 8 to 10 that articulate via costal cartilages with the costal cartilage of the preceding rib and
- iii. Floating ribs – numbers 11 and 12 that remain non-articulate anteriorly.

All ribs articulate posteriorly with the thoracic vertebral column with their associated thoracic vertebrae with rare instances of lower cervical and upper lumbar articulations (Drake *et al.* 2009).

Williams (1995) and White (1999) describe the typical human rib usually in the middle of a rib sequence (numbers 3 to 9), as being comprised of a shaft with posterior and anterior ends (see Figure 1.2).

The following description of the typical human rib was adopted from Williams (1995) and added to by the authors' observations:

The posterior or vertebral end of a typical rib has a *head*, a *neck*, a *tubercle* and a *shaft*. The *head* presents two facets (or demifacets), separated by the transverse crest of the head. The superior and smaller facet articulates with the body of the preceding vertebra. The inferior and larger facet articulates with the body of the corresponding vertebra. The crest attaches to the intervertebral disc above it (See Figure 1.3a and 1.3b).

The *neck* is a flattened part distal to the head and is positioned anterior to the corresponding vertebral transverse process. It lies obliquely facing antero-superiorly. The postero-inferior surface is rough and pierced by numerous small foramina. The superior border is the sharp *crest of the neck* and its lower border is rounded.

The *tubercle* is located postero-external and inferiorly. It is the junction of the neck with the shaft and is more prominent in the upper sequence of ribs. It has 2 parts that form it, namely a medial *articular* part and a lateral *non-articular* process (See Figure 3a). The articular part bears a small, oval facet for the transverse process of the corresponding vertebra. The non-articular process is roughened for the attachment of the lateral costo-transverse ligament (see Figure 1.3b).

The part distal to the tubercle is referred to as the *shaft* of the rib. The *shaft* is thin in cross-section and flattened with an external (convex) and an internal (concave) surface as well as superior and inferior borders. It is curved and bent at the *posterior angle*, located distal from the tubercle. The shaft is also twisted about its long axis to produce torsion of the rib. The part posterior to the angle inclines supero-medially; its external surface thus faces postero-inferiorly. In front of the angle, the shaft faces slightly superiorly; it is convex and smooth, and is crossed near the tubercle by a rough line, directed infero-laterally, at the posterior angle. This line corresponds with the attachment of the *iliocostalis* muscle.

The internal or medial surface is smooth and marked by the *costal groove*, bounded below by the inferior border. The groove commences at the inferior aspect of the neck. The groove is most prominent on ribs 5 to 7. The superior border of the groove continues behind the lower border of the neck and terminates anteriorly at the junction of the middle and anterior thirds of the shaft. The groove is absent anterior to

this junction. The inferior border of the shaft is sharp in contrast to its rounded superior border.

The anterior or sternal end has a small concave depression, the *costal pit*, for the corresponding costal cartilage's lateral end.

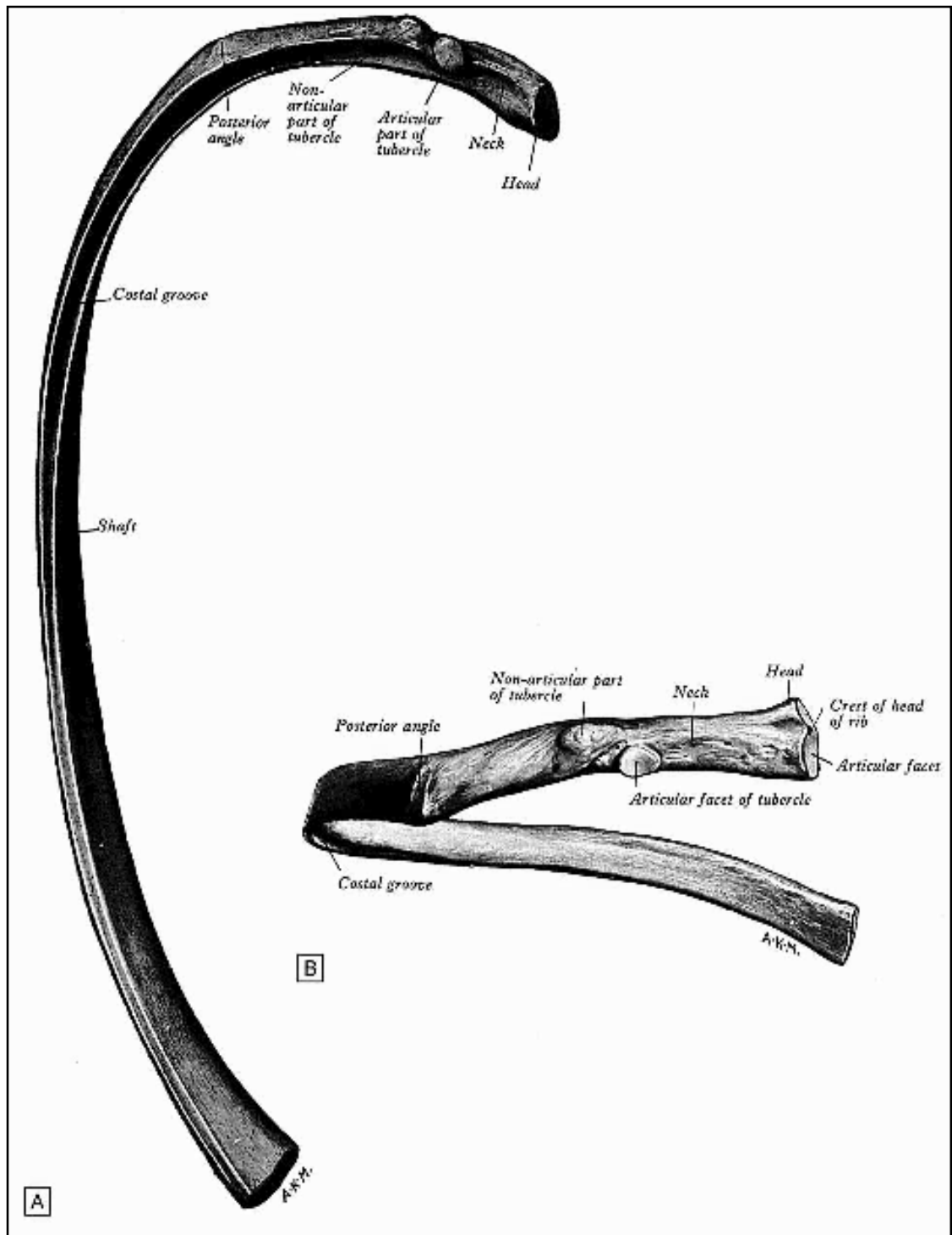
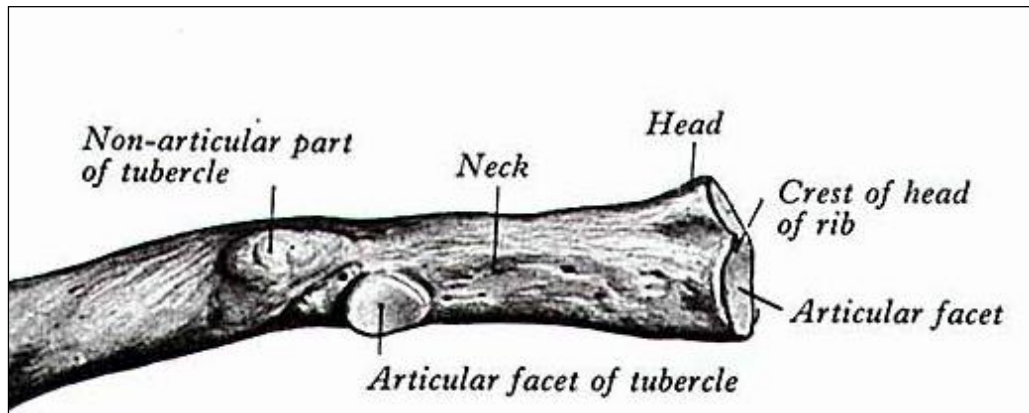
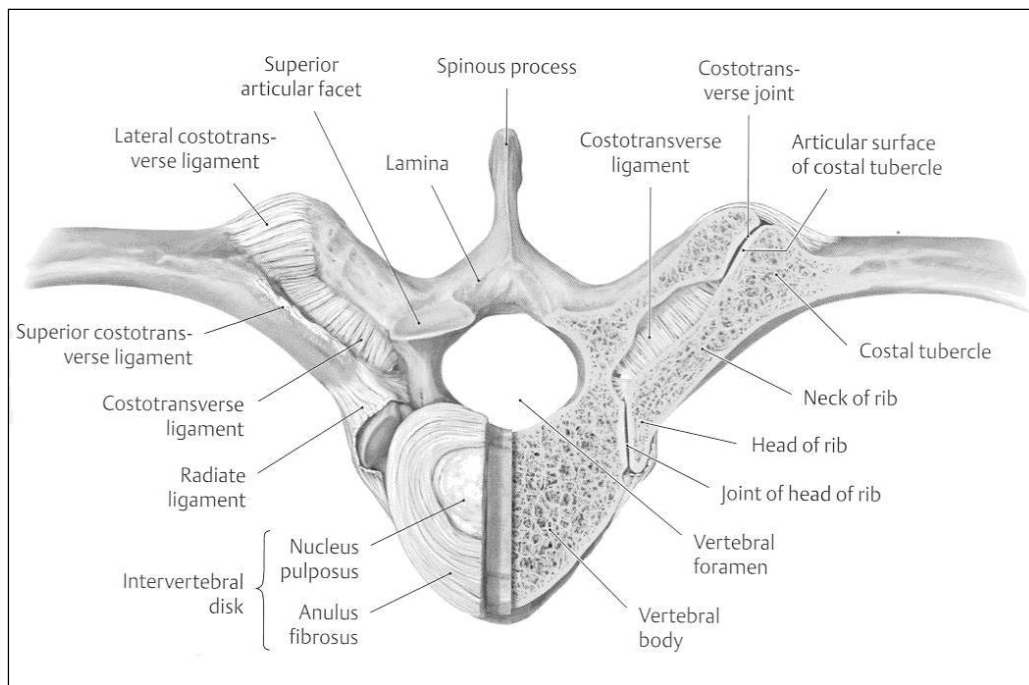


Figure 1.2: A typical human rib of the left side: A. Inferior aspect; B. Posterior aspect. (After Williams 1995).



(a)



(b)

Figure 1.3: (a) The proximal end of a typical human rib (After Williams 1995)
 (b) The costovertebral articulation joint showing the articulations between the head and the tubercle of a rib and the associated ligaments (After Drake *et al.* 2009).

1.3.2.1. The “atypical” human rib

The special or atypical ribs in humans are ribs 1, 2, 10, 11 and 12. These ribs are classified as such due to the osteological features that differ from the typical ribs as described above.

First (1st) rib

The 1st rib is most easily differentiable in human as a short, broad, supero-inferiorly flattened and tightly curved rib. A single facet is present on the head is for the articulation with the 1st thoracic vertebra. The neck of the 1st rib is typically rounded; its tubercle and posterior angle correspond. The shaft has a superior surface that is grooved (for the subclavian vessels) and roughened for muscle attachments.

The superior surface is associated with the overlying clavicle. It exhibits the following features, commencing from the proximal end:

- i. a roughened area for the attachment of *scalenus medius* muscle;
- ii. two grooves separated by a scalene tubercle – the posterior groove for the subclavian artery and trunks of the brachial plexus; an anterior groove for the subclavian vein;
- iii. antero-laterally, the attachment of the costoclavicular ligament and
- iv. anteriorly, at the margin of the costal pit, is the attachment of the *subclavius* muscle.

Figure 1.4 shows the features observed on the superior surface of the human 1st rib. The inferior surface is smooth due to coming in contact with the parietal pleura. It does not exhibit any costal groove or any other prominent osteological features.

The medial margin is concave and has a small bony elevation, situated approximately midway along its length, called the *scalene tubercle*. This tubercle is for the attachment of the *scalenus anterior* muscle. The lateral margin is convex and has the roughened attachment of the *serratus anterior* muscle (1st digitation) situated opposite to the scalene tubercle.

Second (2nd) Rib

Figure 1.5 shows the human 2nd rib.

The 2nd rib is transitory between the 1st and 3rd ribs.

On its head are two facets. The superior facet is for the articulation with the inferior costal demifacet of thoracic vertebra 1. The inferior facet is for the articulation with the superior costal demifacet of thoracic vertebra 2. The crest of the head provides for the attachment of the intra-articular ligament between the costocapitular ridge and the intervertebral symphysis.

The shaft of the rib lies at an angle that is between the vertical and the horizontal planes.

Ribs 10, 11 and 12

The 10th rib is typical except for the single facet on its head. The 11th and 12th ribs have a single facet on the head and exhibit rudimentary costal features.

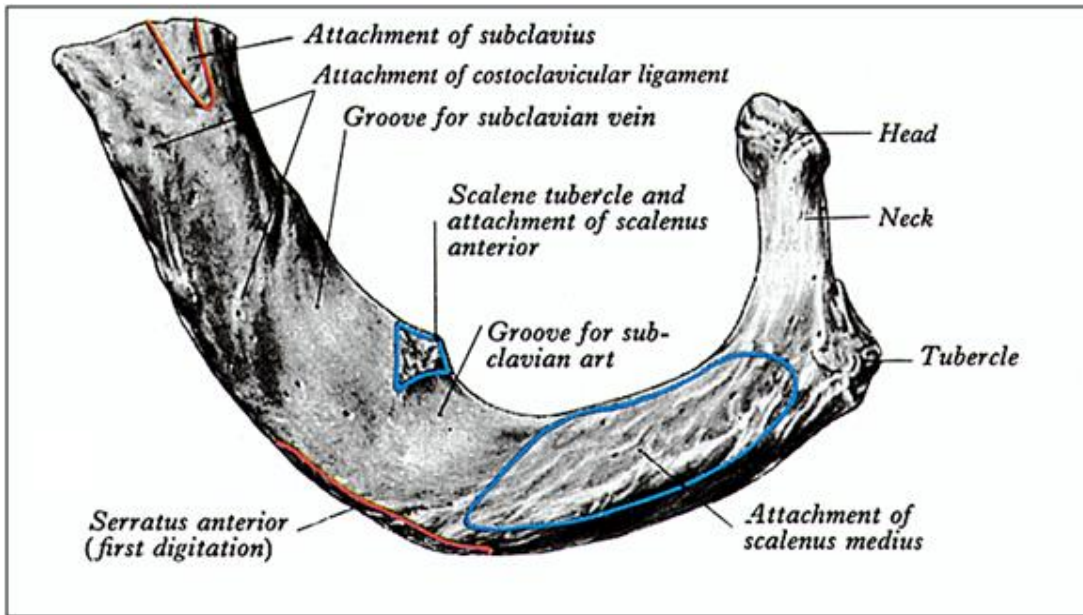


Figure 1.4: Superior surface of the human 1st rib (After William 1995).

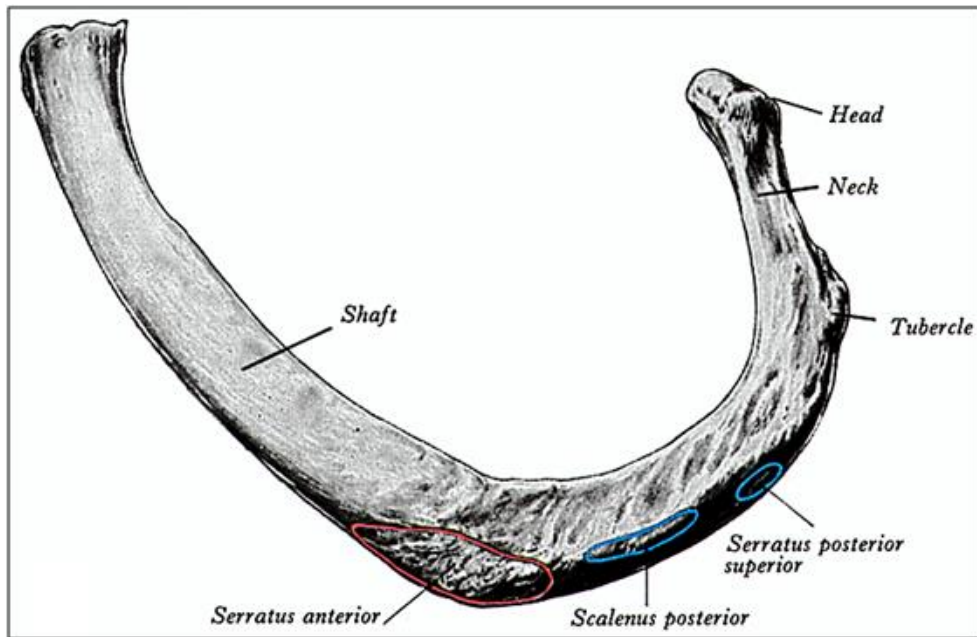


Figure 1.5: Superior view of the human 2nd rib (left) (After Williams 1995).

1.3.3. A comparison of the primate rib features and thoracic morphology

The incompleteness of fossil rib remains, and the consequent difficulty in accurately reconstructing the overall shape of a complex anatomical region that is made up of a large number of bones, has impeded the study of the evolution of human thoracic form and function. Very little literature exists on studies of the thoracic and rib morphology amongst extant non-human primates, and the literature is surprisingly sparse even when comparing the various species of hominoids.

Owen (1835) provided a description of the skeleton of chimpanzees and orangutans and compared them to those of humans. Very little information concerning the features of the ribs is contained in his description and only the differences in the number of ribs are mentioned. Struthers (1875 and 1893) observed the variations of the vertebrae and ribs in a number of specimens of *Homo sapiens* and *Gorilla gorilla*. Once again, individual specimens were described as to their variation rather than determining the general morphology of the primate rib. Struthers (1893) stated that in his observation it was rare to find a facet on the 7th cervical vertebra for articulation with the head of the 1st thoracic rib. He concluded that the 1st rib has only a single facet on its head in humans.

Tredgold (1897) looked at the variations of ribs in primates but concentrated primarily on the number of ribs present in each species.

De Palmer (1950) studied the relationship between the thoracic shape and the position of the upper limb elements. He observed that several factors are responsible for the changing relationship of the articular surfaces of the humerus. Development of the orthograde forms was accompanied by antero-posterior flattening of the thoracic cage and dorsal displacement of the scapula. The glenoid fossa is now directed laterally (Figure 1.6).

Bouvier (1967) assessed the structural differences between the 1st ribs of humans and other primates. This detailed study analysed the 1st rib by looking at 24 variables as well as various morphological features e.g. torsion of the head versus shaft of the rib. Jenkins (1970) studied the ribs of edentates and primates by looking at the functional implications of one rib specialisation, namely the antero-posterior expansion in diameter of the shaft of the rib. Gloobe and Nathan (1970) undertook anatomical observations of the costovertebral joints of various mammals and observed 3 distinct patterns of articulation between the head of a rib and the thoracic vertebral column.

This was followed by a study by Stern and Jungers (1990) who concentrated their research on the capitular joint of the 1st rib in primates. They observed that the uni-vertebral pattern of the head of the 1st rib was common in siamangs, occasionally found in gibbons and was typical of the larger indriids. The bi-vertebral pattern observed on the heads of all the other ribs of human and non-human primates is considered to be a typical mammalian condition (Stern and Jungers 1990).

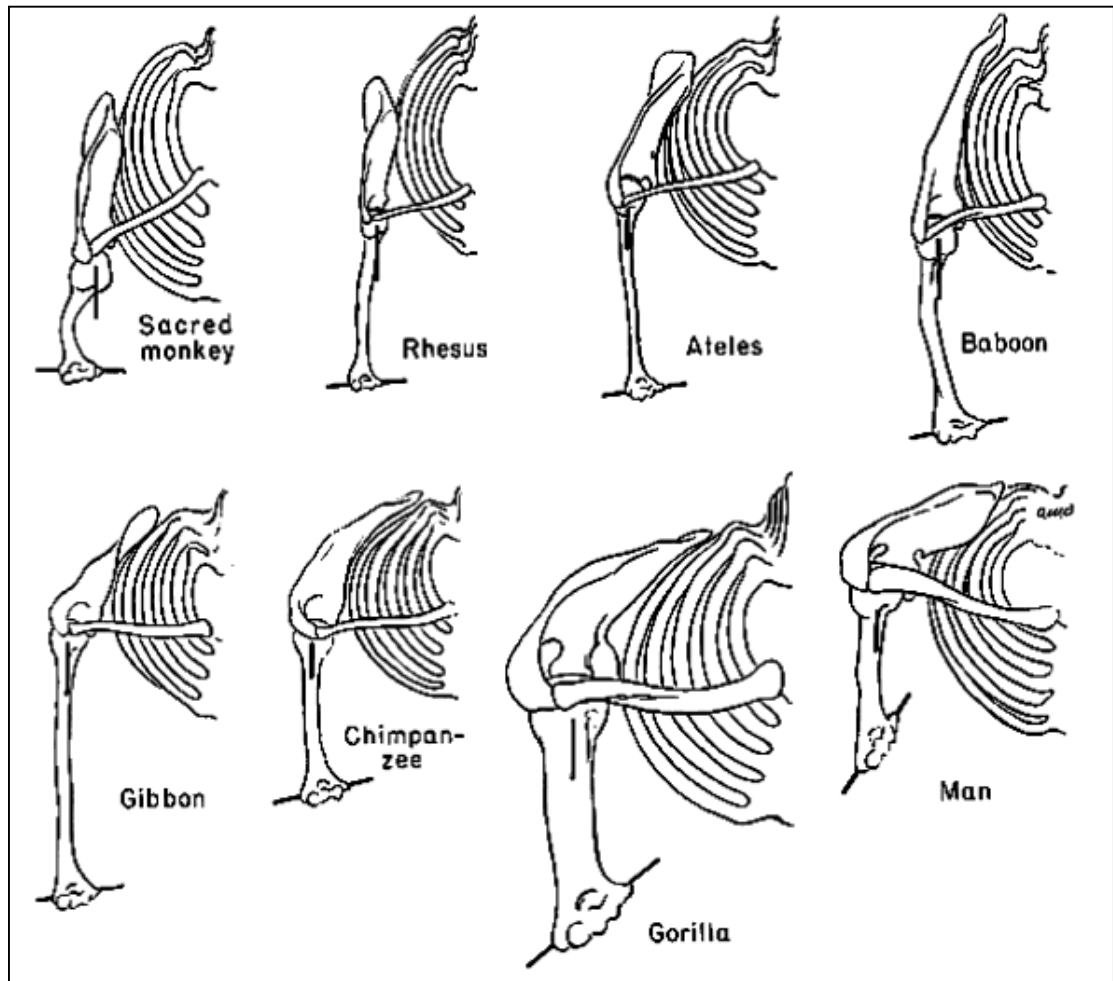


Figure 1.6.: Variations in the morphology of the upper limb related to the thoracic cage, the scapula and the humerus, in successive stages from the pronograde to the orthograde (After De Palmer 1950).

A quantitative analysis of the differentiation of primate ribs was undertaken by May and Martins (1985). In this study they looked at 13 measurements taken off the ribs of nine human and six non-human primates (four *Pongidae* and two *Cercopithecoidea*).

Key findings of this study were

- i. that human ribs were intermediate in size between the other species;
- ii. that the cranio-caudal trend of various measurements showed a similarity of the upper four ribs between the *Pongidae* and the humans;
- iii. there was greater similarity in the non-human primates with regards to the lower ribs and
- iv. that it was difficult to differentiate the 7th to 10th ribs of all the specimens studied.

More recently, Gea (2008) studied the evolution of the respiratory system in humans and the resultant effect on the shape and dimensions of the thoracic cage. It was concluded in this study that the upright posture, the consequent freeing of the upper limbs and vocalisation probably led to the development of a thorax that was mechanically more efficient due to shape changes observed.

Kagaya *et al.* (2008 and 2009) recently studied the elements of the thoracic cage of the anthropoid apes and the nonhuman hominoids. By studying thoracic width, rib curvature and rib orientation, they were able to assess the shape of the thoracic cage as well as the orthograde positional behaviour in the non-human hominoids. They concluded that all hominoids shared two distinct features in the upper half of the

thorax, namely, (1) a pronounced dorsal protrusion of the proximal part of the rib in accordance with ventral displacement of the thoracic spine and (2) a relatively medially projecting sternal end. Thus the structure of the rib looked at individually or as part of a sequence, will have an influence on the overall morphology of the trunk in especially the determination of the shape of the trunk. The impact of the shape will in turn influence the postural capability of that particular species.

Some authors studied only the costal elements that are represented within the Plio-Pleistocene fossil record or compared specific features thereof to that observed in modern human and non-human primates. Ohman (1984) for example studied only the first rib of hominoids and concluded that modern humans are unique among extant hominoids in that they display a single facet pattern for the first rib; that is, the head of the first rib articulates only with the body of the first thoracic vertebra. He further stated that all other hominoids display a bi-vertebral pattern; that is, the head of the first rib articulates with the bodies of the seventh cervical and the first thoracic vertebrae, as well as the intervening disk. He interpreted the uni-vertebral pattern of the head as a derived trait (Ohman, 1984).

Ohman (1986) in a later study stated that two fossil hominin partial first ribs, A.L. 288-lax and A.L. 333-118, showed that the uni-vertebral pattern was fully established in the hominin lineage by the time of the appearance of *Australopithecus afarensis*. This study also supported the hypotheses that (1) the uni-vertebral head of the 1st rib is a consequence of the more barrel-shaped thorax in hominins and (2) the uni-

vertebral head of the 1st rib is a consequence of modifications in hominin first rib motion while breathing in an upright stance (Ohman 1986).

Ohman (1986) further postulated that the 1st rib uni-vertebral pattern may also be due to the following factors:

- i. lengthening of the cervical region and the resultant laryngeal descent;
- ii. the shape of the thorax – more barrel shaped as observed in modern humans and hylobatids, reflecting an upright posture;
- iii. the increase in the space between the 1st rib and the clavicle to accommodate the neurovascular structures from the cervical region to the axilla e.g. subclavian vessels and brachial plexus trunks and
- iv. facilitation of the biomechanics of the glenohumeral joint.

Schmid (1991) points out that Ohman's (1986) description of Lucy's first rib as having only one facet on its head was contradicted by the initial description of Lucy's postcranial skeletal by Johanson *et al.* (1982), who indicated that the 1st rib has a distinct double facet separated by a central ridge. For more on this difference, see the results section of this current study (Chapter 5).

1.4. Influence of rib morphology on thoracic shape

Owen (1835, p. 353) was one of the first to examine differences in thorax shape among primates when he described the thorax of chimpanzees as having a transverse diameter that exceeds the antero-posterior diameter but not to the same extent as in

humans. This he ascribed to the requirement of an “ample developed respiratory system to allow for the agile and powerful locomotive actions of the chimpanzee”.

Such studies of shape, and their importance, however, would not be significantly examined further until Schultz (1950, 1969a, 1969b) illustrated the marked contrasts in thoracic shape between hominoids and cercopithecoids. Schultz (1969a and 1969b) was first to demonstrate that hominoids have broad trunks with transversely-wide and sagittally-narrow thoracic cavities compared with cercopithecoids, whose transverse and sagittal thoracic diameters are equal in length. Schultz (1969a and 1969b) also illustrated that the “barrel-shaped” chest of humans differs from the “funnel-shaped” thorax of African apes and orangutans, a contrast due in part to differences in lengths and curvatures of the ribs. He demonstrated clearly, and for the first time, that human ribs increase more rapidly in length from superior to inferior and exhibit more curvature as compared with the ribs of other great ape species.

Preuschoft (2004) highlighted the most important factor that influences the thoracic shape is the curvature of the ribs in sequence from superior to inferior. According to Barker and Ward (2008) four aspects of the ribs influence the shape of the thorax.

They postulate that thoracic shape is determined by the:

- i. curvature of the ribs at their vertebral ends;
- ii. length of the rib;
- iii. angle formed by the neck and the shaft of the rib and
- iv. area outlined by the rib.

Yet, the general shape of the primate rib cage has been described by researchers as being variable among primates, with little accomplished in the way of defining objectively shape and form (Schmid 1983 and 1991, Jellema *et al.* 1993, Franciscus and Churchill 2002, Weinstein 2008, Kagaya 2008). In monkeys and prosimians the rib cage has been described as being generally narrow (Aiello and Dean, 1996). Schmid, first suggested in 1983, that the *Australopithecus afarensis* thorax might be more conical in shape, and Zihlman (1984) in her reconstruction of Lucy (AL288-1), also supports such an assertion by stating that the rib cage of the A.L. 288-1 partial skeleton was remarkably chimp-like.

In general, the rib cage shape of hominins has been described as being characteristically wide and barrel shaped although this was the first study to recognise the potential of conical shape of early hominin rib cages (Schmid 1983), an observation that seems to have been supported by many subsequent studies (Ohman 1984, Arensburg 1991, Jellema *et al.* 1993, Churchill 1994, Aiello and Dean 1996, Franciscus and Churchill 2002, Kagaya *et al.* 2008, Gomez-Olivencia *et al.* 2009). In apes the morphology of the thorax affects the function of the upper limb in arboreal locomotion and positional behaviours (Ward 1993; Chan 2007), and thus reconstruction of thoracic shape in early hominins is central to resolving questions about the degree of arborality practiced by members of the human lineage prior to the genus *Homo* (Ward 2002). Human thoraces are more barrel-shaped: the upper rib cage is medio-laterally broad, such that relatively little additional lateral flaring occurs moving inferiorly. Furthermore, the lower ribs in the series have greater

curvatures than the homologous ribs in apes (Jellema *et al.* 1993), resulting in a rib cage overall that is more cylindrical (barrel-shaped) rather than the funnel shape characteristic of apes.

Clearly however, the identification of additional hominin ribs in the Plio-Pleistocene fossil record could aid in understanding the mode and tempo of this evolutionary process.

Direct information regarding any variability in the costal skeleton of fossil hominins is scanty, and this is exacerbated by the lack of information regarding thoracic variation in recent humans as well (Weinstein 2008). Furthermore, specifically among hominins, it has been hypothesised that major evolutionary changes have taken place in rib form and structure and this impacted on the overall shape of the thoracic cage (Schmid 1983 and 1991, Franciscus and Churchill 2002, Weinstein 2008; Gomez-Olivencia 2009).

Schultz (1961) states that extant apes and modern humans share many features not seen in monkeys, such as a transversely broad thoracic cage, a vertebral column set deeply within the rib cage, a dorsally-placed scapula, and a laterally-facing shoulder joint. He further states that the thorax of great apes widens towards the base, like an inverted funnel, and it is matched inferiorly by correspondingly flared ilia to accommodate a large gut in a short trunk. He notes that the pongid rib cage is also shaped like an inverted funnel, i.e. narrow at the top and wide at the bottom.

This configuration has been linked to arboreal climbing and suspension, in that it effectively positions the ribs so as to best resist large bending moments generated either by the forceful contraction of thoracoscapular and thoraco-humeral muscles during support and acceleration of body mass with the upper limbs during climbing and suspension (Preuschoft 2004) or by gravity operating on body mass during suspension (Hunt 1991).

The shape of the thorax of early hominins has for three decades been a matter of debate and interpretive study. Due to the generally fragmentary nature of fossil hominin ribs, there have been few specimens recovered that have complete enough rib remains to allow accurate reassembly of thoracic shape, thus leaving open the question of when the barrel-shaped chest of humans and their immediate ancestors evolved (Schmid 2013). Even the most complete preserved early hominin rib cages, such as those of the two *Australopithecus afarensis* partial skeletons A.L. 288 (Lucy) (Johanson *et al.* 1982) and KSD-VP-1/1 (Woranso-Mille) (Haile-Selassie *et al.* 2010) or the *Australopithecus africanus* partial skeleton Sts 14 (Robinson 1972), preserve only fragmentary elements.

Schmid (1991) states that the shape of the thorax, though very broad in all hominoids, is quite different in humans and in the great apes. In the latter the thorax is clearly funnel-shaped, whereas in humans and gibbons it is nearly barrel-shaped. In the funnel-shaped thorax the first few pairs of ribs increase in size more gradually than in the barrel-shaped one, in which this increase is more abrupt, particularly in the second

ribs. Most of the mid-thoracic ribs of the great apes have a rounded cross-section and are rather massive. In modern humans, the ribs of the mid-thorax have a compressed cross-section. They are broad cranio-caudally but thin in the transverse dimension. Most of the human ribs are characterised by a torsion which is basically responsible for the typical barrel-shaped form (Schmid, 1983).

See Figure 1.7 which shows the generalised shape of the thoracic cage in some of the extant primate species.

Haile-Selassie *et al.* (2010) noted that the lateral and distal portions of each human rib descend more obliquely from their vertebral origins than in African apes. Such declination increases thoracic transverse diameter and elongates the thorax (Schultz 1969a, Latimer and Ward 1993, Jellema *et al.* 1993). Declination also induces more flexed costal angles (each rib head is more inferiorly angled relative to its corpus), as well as torsion and flattening of each rib body, although the latter characters are highly variable. African apes lack rib obliquity, and their greatly reduced lumbar columns and iliocostal spaces prevent significant rib declination (Latimer and Ward 1993, Jellema *et al.* 1993). Their ribs exhibit more rounded cross-sections and have little or no axial torsion (Jellema *et al.* 1993).

As quoted in Leakey *et al.* (1992), Schmid (1983) observed that the ribs of “Lucy” were more rounded in cross-section as compared to those seen in apes. Schmid (1983) noted that the human ribs are flatter. Leakey *et al.* (1992) point out that Schmid (1983) could apparently not fit the ribs of “Lucy” into the barrel shaped human rib cage but rather into the conical shaped rib cage of apes. Schmid (1983) went into further detail in claiming that the rib cage of *Australopithecus afarensis* was voluminous and retained the inverted funnel shape typical of great apes as indicated by the apelike rounded cross-section and absence of flattening in the middle section of the body of fossil rib fragments.

Barker and Ward (2008) support that humans differ from great apes in having a “barrel-shaped” (i.e. cranially expanded/caudally restricted) rather than “cone-shaped” (i.e. cranially restricted/caudally expanded) thorax. Aiello and Wheeler (1995), in contrast, state that the barrel-shaped modern human thorax is more uniform in width from top to bottom, with the narrower and more curved contour of the lower rib cage and ilia, thus allowing the abdomen to accommodate the relatively small and short modern human gut.

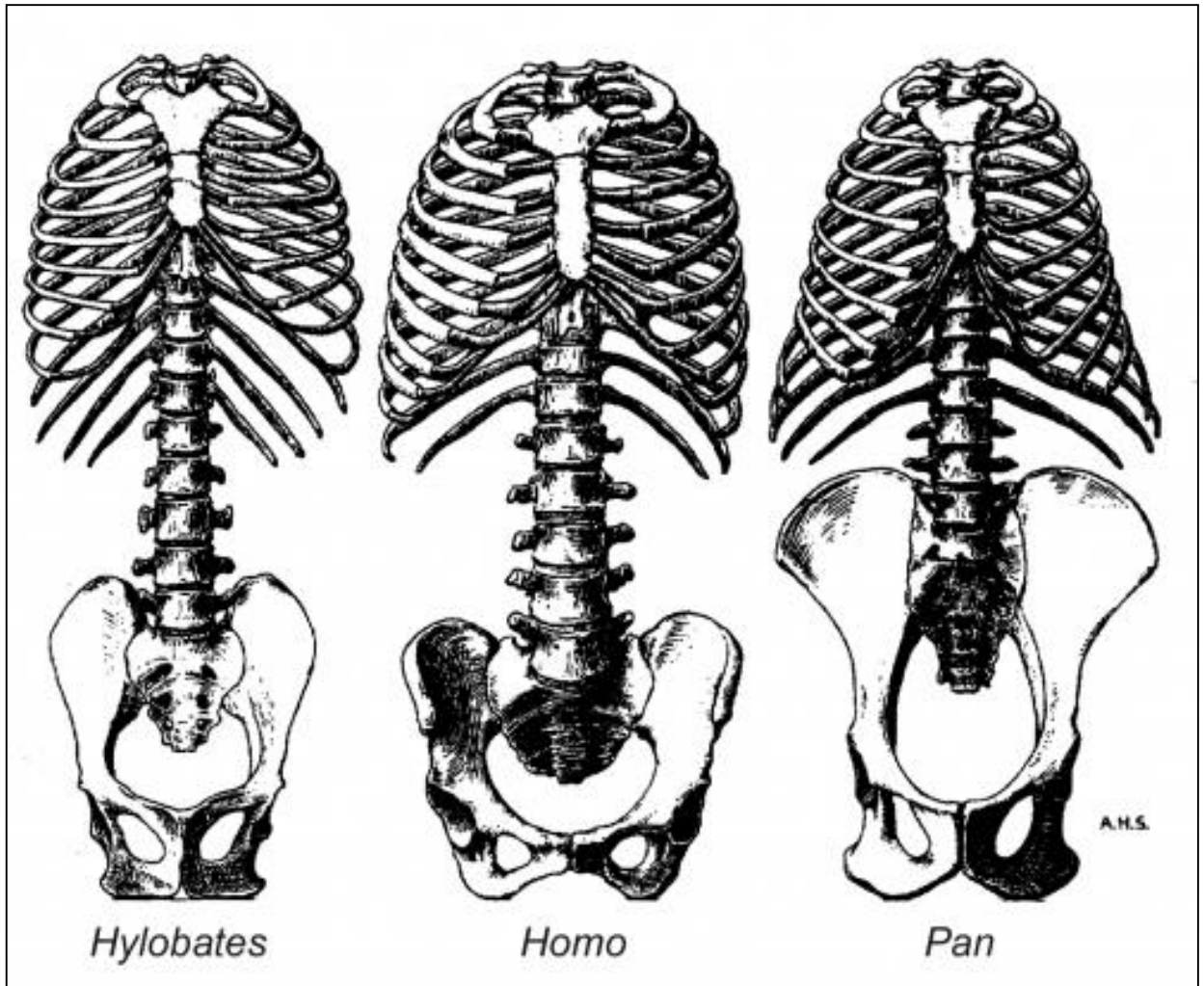


Figure 1.7: Differences in primate thoracic shape – Gibbons (*Hylobates*), Human (*Homo sapiens*) and Chimpanzee (*Pan troglodytes*) (After Schultz 1961).

It has thus become widely accepted that the rib cages of modern humans and the great apes are only broadly similar in shape, with a wide transverse diameter and a smaller ventro-dorsal diameter. This gives rise to a flattened section of the rib and the rib cage in the antero-posterior direction. The rib cage of the other primates, on the other hand, is elongated in the antero-posterior direction, and this affects respiratory mechanics in specific ways (Kagaya *et al.* 2008)

McHenry and Berger (1998) concluded that early hominin postcranial material that they studied revealed a resemblance to more pongid-like features of Stw 431 as well as of *Homo habilis* (OH 62 and KNM-ER 3735) than to the human pattern. The close relationship between the positions of the limbs impacted by posture, relative to the axial skeleton, will thus possibly show a similar resemblance in the associated axial skeletal morphology of which the thoracic skeleton forms a large proportion of.

Modelling of the thorax as a dynamic structural system has received some attention in the literature in recent years. Franciscus and Churchill (2002) found that the ribcage of Neanderthals and likely of earlier *Homo* differed in several anatomical details from those of anatomically modern humans. They also highlighted the importance of more completely assessing the full range of variability in all thoracic features among early modern and recent human samples in addition to those of pre-modern hominin fossils.

Later in the Pleistocene fossil hominin record, the Neanderthal body has also been described as having been remarkably stout, including a broad rib cage, long clavicle and wide pelvis, and the limb bones are generally robust with well-developed muscle insertions (Trinkaus 1986; Stringer & Gamble 1993). Since the first discoveries of Neanderthal postcranial remains, their thoracic shape has been repeatedly described as been “barrel-chested”, based primarily on qualitative estimates of the relative lack of curvature of their rib fragments in comparison with modern humans (Schaafhausen 1858; Boule 1911–13; Hrdlic̃ka 1930; Loth 1938; Coon 1962 and Smith 1976).

It has been inferred that the Neanderthal thorax is wide antero-posteriorly and medio-laterally when compared to humans, as seen from isolated fragments of ribs, clavicles, and sterna (Boule 1911 -1913; McCown and Keith 1939; Coon 1962; Vallois 1965; Endo and Kimura 1970; Heim 1976; Franciscus 1989; Arensburg 1991; Churchill 1994; Franciscus and Churchill 2002).

Thus the general patterns observed are that human ribs increase more rapidly in length from superior to inferior and exhibit more curvature compared with those of great apes (Gea 2008). Other skeletal correlates of the human barrel-shaped thorax include a narrow and curved lower thoracic cavity resulting in shorter and more curved inferior ribs, an expanded cranial third of the thoracic cage, the ventral invagination of the thoracic vertebral column into the thoracic cage, and the inferior sloping of the ribs (Jellema *et al.* 1993; Franciscus and Churchill 2002).

1.5. Detailed overview of the ribs of fossil homininae

There are relatively few hominin ribs known from the fossil record, most elements are isolated remains, but a few are associated with partial skeletons and for obvious reasons, these specimens are the most valuable where comparisons of form, shape and function are undertaken. Those fossil hominin skeletons that possess ribs that have been studied and reported in the literature include:

- i. *Ardipithecus ramidus* (Lovejoy *et al.* 2009);
- ii. *Australopithecus afarensis* represented by Woranso-Mille (Haile-Selassie 2010) and Lucy (A.L. 288) (Johanson *et al.* 1982, Lovejoy *et al.* 1982);
- iii. *Australopithecus africanus* represented by Sts 14 (Broom and Robinson 1947, Robinson 1972) and Stw 431 (Toussaint *et al.* 2003);
- iv. *Homo erectus* represented by the Nariokotome juvenile or Turkana boy (Jellema *et al.* 1993);
- v. early *Homo* from Dmanisi (Lordkipanidze *et al.* 2002) and
- vi. *Homo neanderthalensis* represented by Shanidar 3 (Solecki 1960, Franciscus and Churchill 2002) and Kebara 2 (Gomez-Olivencia *et al.* 2009).

More recently, complete rib and rib fragments have been found as part of the postcranial remains of *Australopithecus sediba* MH 1 and MH 2 (Berger *et al.* 2010) and new elements have been described for a possible male *Australopithecus afarensis* skeleton from Ethiopia (Haile-Selassie *et al.* 2010).

1.5.1. *Ardipithecus ramidus* (ARA-VP-6/500)

The skeleton of this “hominin” ancestor was found in 1992 in Afar, Ethiopia. Among the postcranial remains of this female skeleton was a single first rib (Lovejoy 2009).

Neither detailed analysis of any metric data nor morphological description of this fragmentary rib is available in the current literature.

1.5.2 *Australopithecus afarensis*

1.5.2.1. Woranso-Mille (KSD-VP-1/1)

KSD-VP-1/1 refers to the postcranial skeleton of a large male *Australopithecus afarensis* individual found in February 2005 from the Korsi Dora vertebrate locality 1 (KSD-VP-1) in the Woranso-Mille paleontological study area of the Afar region, Ethiopia (Haile-Selassie *et al.* 2010). Six ribs including a complete 2nd left rib formed the costal remains of the skeleton.

Figure 1.8 shows the postcranial remains of KSD-VP-1/1 with the costal elements.

A study of these costal elements showed the following features of these ribs:

- i. marked costal angles indicating deeper vertebral column invagination into the thorax than in apes;
- ii. cross-sectional flattening with deeply marked subcostal grooves and sharp inferior pleural margins and
- iii. axial torsion consistent with inferior declination and cranio-caudal elongation.

Utilisation of these features leads the authors to conclude that:

- i. the upper thoracic shape of the KSD-VP-1/1 was very similar to that observed in *Homo* and
- ii. thoracic shape in the *Australopithecine* differed substantially from that observed in the extant African apes.



Figure 1.8: Postcranial skeleton of KSD-VP-1/1 (After Haile-Selassie *et al.* 2010).



Figure 1.9: The ribs of KSD-VP-1/1. S15-S17. (After Haile-Selassie *et al.* 2010)

Specimens shown here (top to bottom) are KSD-VP-1/1n (left second rib; reversed), KSD-VP- 1/1q (right 5th, 6th, or 7th rib), KSDVP- 1/1s (middle rib fragment), KSDVP- 1/1o (right 7th or 8th rib), KSDVP- 1/1p (right 8th or 9th rib), and KSD-VP-1/1r (left 11th rib).

1.5.2.2. A.L. 288-1ax (or “Lucy”)

The remains of this fossil hominin were found by Donald Johanson and Tom Gray in 1974 in the Afar locality of Hadar, Ethiopia.

The postcranial remains includes a complete but distorted right 1st rib as well as a number of fragmentary rib specimens of the shaft of a number of ribs (Figure 1.8).

Johanson *et al.* (1982) have described the morphology of the 1st rib in very little detail. The key features that they noted concerning the 1st rib were that

- i) the rib has a modern human form;
- ii) it exhibits the presence of 2 facets on the head of the rib and
- iii) the internal margin does not display a scalene tubercle.

The fossil skeletal remains of Lucy are shown in Figure 1.10 with the prominent costal remains.

To date no detailed metrical analysis has been carried out on the ribs of A.L. 288-1 although the morphological descriptions and analyses of these have been done by Schmid (1983) and Ohman (1984).

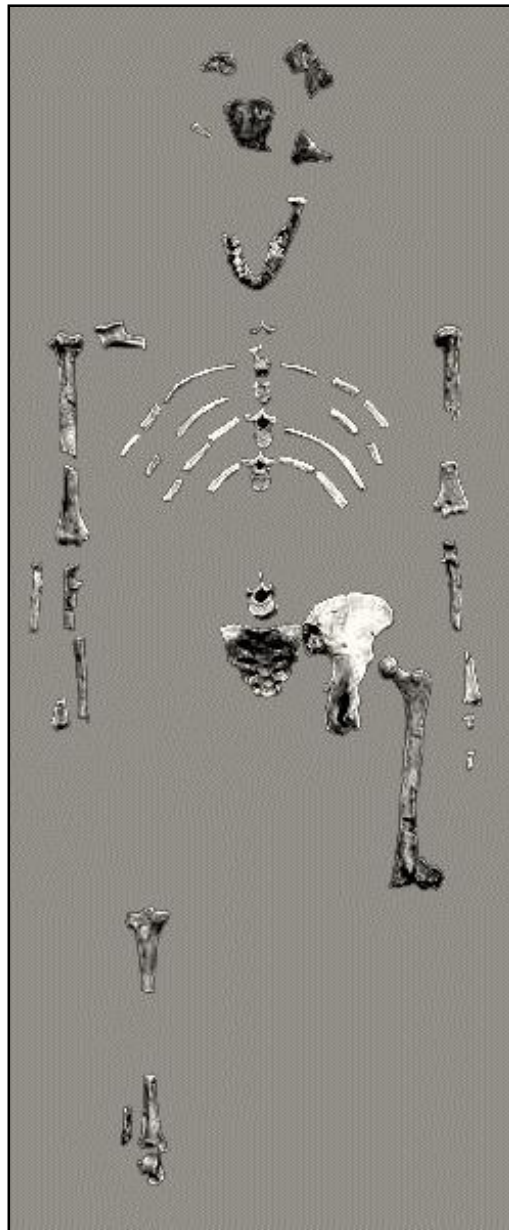


Figure 1.10: The skeleton of “Lucy” showing the postcranial remains including the costal elements (After Johanson and Taieb 1976).

1.5.3. *Australopithecus africanus* (Sts 14)

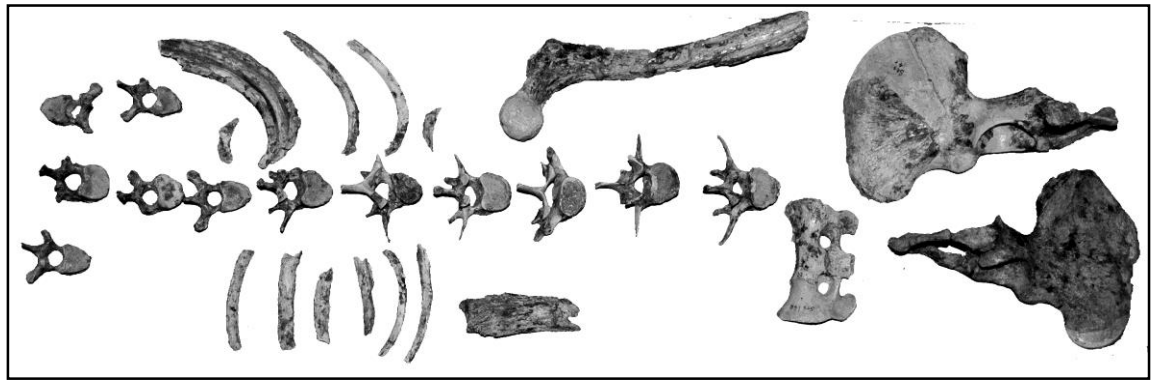
This fossil hominin skeleton was discovered by Robert Broom in 1947 at Sterkfontein. It is composed of vertebral, costal, pelvic and femoral elements. The costal elements comprise 13 fragments (3 fused and 8 separate) of partial ribs, ranging from the proximal ends of a rib to sections of the shafts of the ribs. These fragments are from both sides of the thoracic cage, the majority coming from the left hand side. The preservation of the fossils is poor and show post excavation acid preparation damage.

A brief description of the “most complete” rib fragments was given by Robinson (1972). In this description, the main observations made were:

- i. one rib is rib 12 on the right hand side;
- ii. four of the ribs belong to the lower thoracic cage;
- iii. four of the ribs are thinner and yet more robust than those of humans, orangutans and chimpanzees and
- iv. thoracic shape is broad and shallow, as observed in hominoids in general, rather than narrow and deep.

Figure 1.11 shows the postcranial remains of Sts 14 and the associated costal elements related to the postcranial remains.

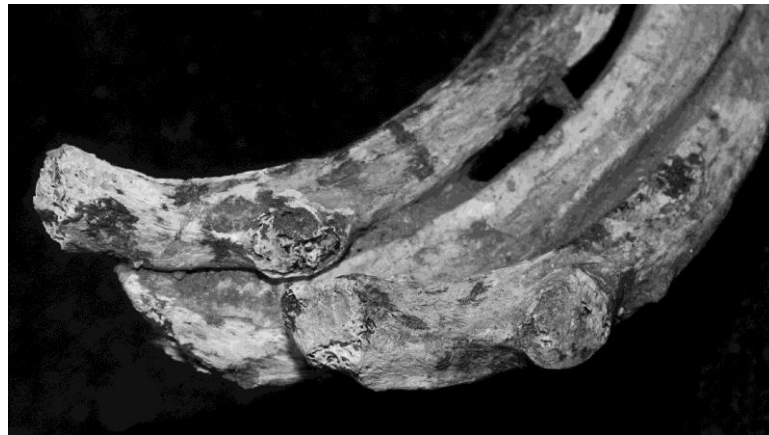
To date neither metrical analysis nor any detailed morphological description has been carried out on the rib fragments belonging to Sts 14.



(a)



(b)



(c)

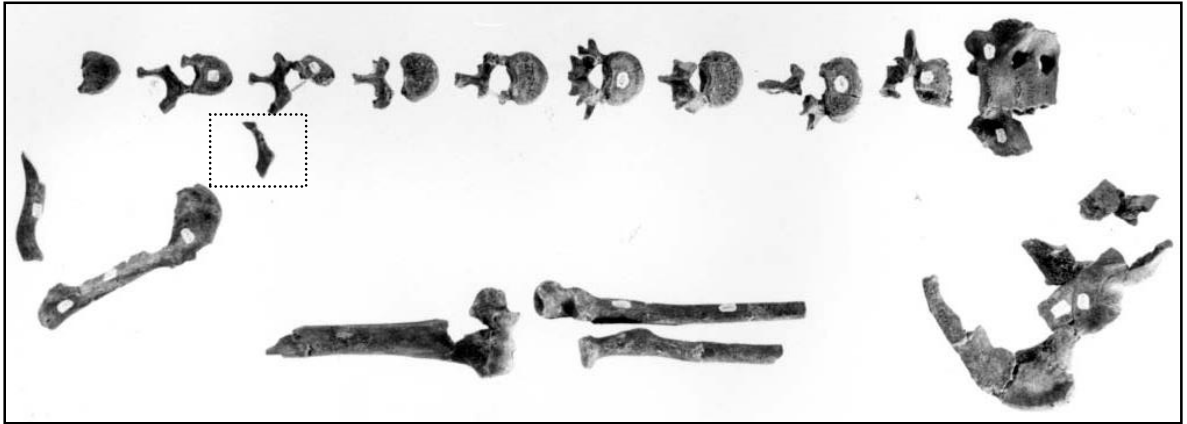
Figure 1.11: The postcranial remains of Sts 14 showing (a) the postcranial skeleton, (b) some of the costal fragments and (c) the proximal ends of the right ribs that are still united by breccia. Visible in (c) are the articular facet of the costal tubercle.

1.5.4. *Australopithecus africanus* (Stw 431)

The 1987 excavations of Member 4 of Sterkfontein resulted in the discovery of the postcranial skeleton of a single Late Pleistocene hominin, Stw 431. This individual is composed of a number of postcranial elements inclusive of one rib fragment (See Figure 1.12) that has been described as being a “dorsal third of right rib” (Toussaint, *et al.* 2003). They further stated that no specific diagnostic features are discernible on the preserved head, neck and tubercle of one right rib fragment found.

1.5.5. *Australopithecus sediba*

Berger *et al.* (2010) described *Australopithecus sediba* from a sample of African Plio-Pleistocene hominins comprising partial skeletons of a juvenile male (Malapa Hominin 1 or MH1) and adult female (Malapa Hominin 2 or MH2) (Figure 1.13). Each skeleton has costal elements associated with it, either complete e.g. 1st rib in MH2 or fragmentary as in most of the remaining ribs. The detailed study of the skeletal morphology of this hominin has been recently studied and analysed (Berger (2012), Berger (2013), Berger *et al.* (2010), Carlson *et al.* (2011), De Ruiter *et al.* (2013), De Silva *et al.* (2013), Irish *et al.* (2013), Kibii *et al.* (2011), Kivell *et al.* (2011), Schmid *et al.* (2013), Williams *et al.* (2013) and Zipfel *et al.* (2011)). Morphological descriptions and the metric analyses of the Malapa costal remains are described in this thesis.



(a)



(b)

Figure 1.12: (a) The postcranial remains of Stw 431 showing the single rib fragment (in box) (After Toussaint 2003). (b) A cranial view of the Stw 431 rib fragment.

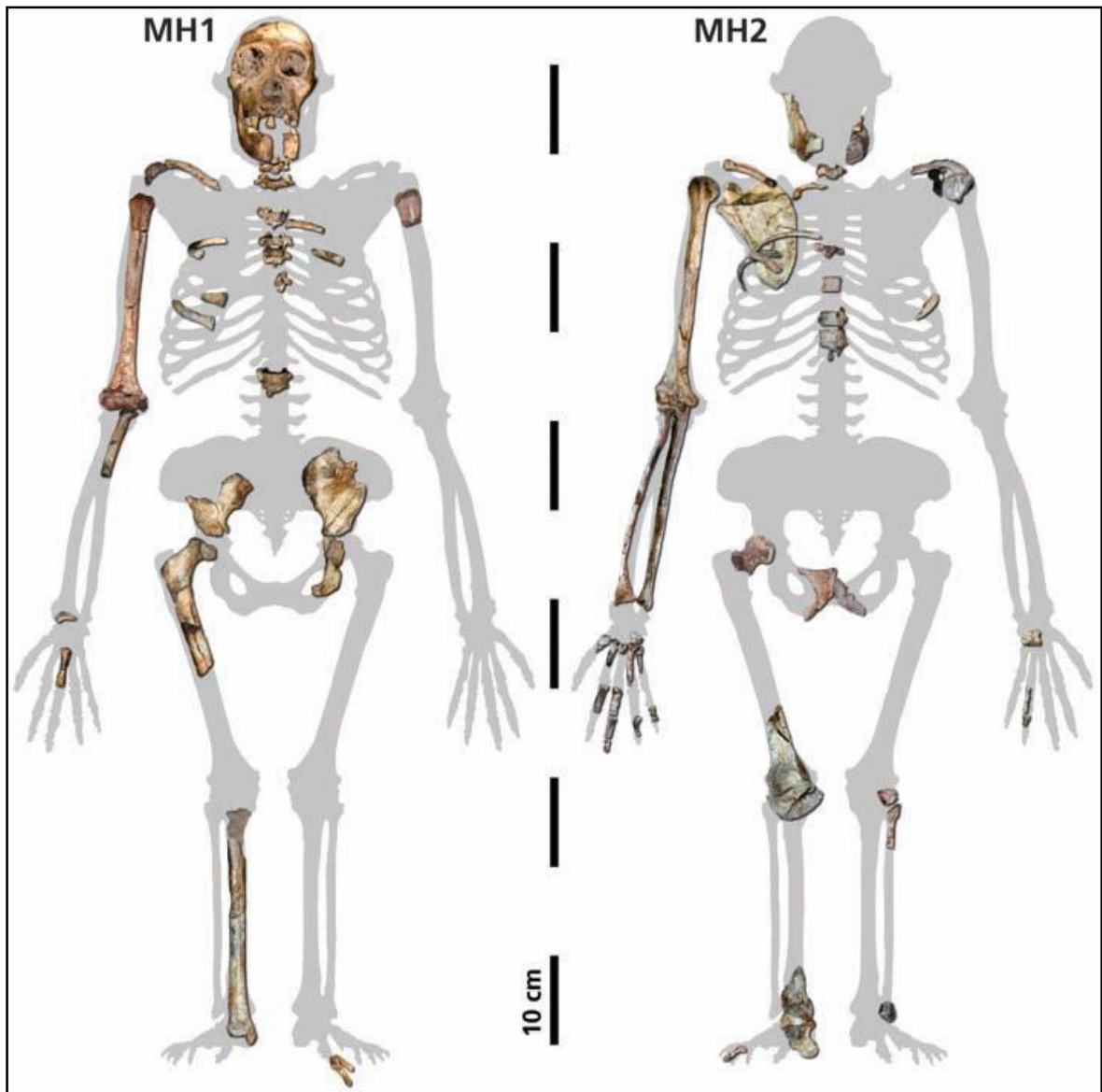


Figure 1.13: The skeletal remains of the juvenile male (MH1) and adult female (MH2) (After Berger *et al.* 2010)

1.5.6. *Homo erectus* (KNM-WT 15000 or “Nariokotome Child” or “Turkana Boy”)

These fossil remains were discovered by Kamoya Kimeu in 1984 at Nariokotome near Lake Turkana in Kenya (Walker *et al.* 1993). This is an almost complete skeleton of an 11 or 12 year old boy, the only major omissions being the hands and feet. It is the most complete known specimen of *H. erectus*, and also one of the oldest, at 1.6 million years (see Figure 1.12). Morphological description and metrical analysis of the ribs of this specimen has been covered in detail in Jellema *et al.* (1993). When describing the proposed posture and locomotion of “Turkana Boy”, it was noted that the presence of a barrel-shaped rib cage observed was like that of modern humans rather than a funnel-shaped one of apes. In fact the ribs as well as the thoracic shape were found to be indistinguishable from that observed in modern humans (Jellema *et al.* 1993). The shape of the thorax was also found to correspond to the anatomically reorganised human-like pelvis; both these features indicated that the Turkana Boy was fully adapted to habitual upright walking.



Figure 1.14.: The skeleton of “Turkana Boy” (After Walker *et al.* 1993).

1.5.7. *Homo sp.*

The *Homo* skeletons of Dmanisi, Georgia studied by Lordkipanidze *et al.* (2007) have the following ribs as part of the recovered postcranial remains:

- i. the subadult individual has the left and right 1st ribs as well as 11th rib from an undetermined side and
- ii. the adult has a right 2nd rib.

Figure 1.15. shows the costal remains of the Dmanisi *Homo*.

No further information is available as to whether these ribs have been further analysed.

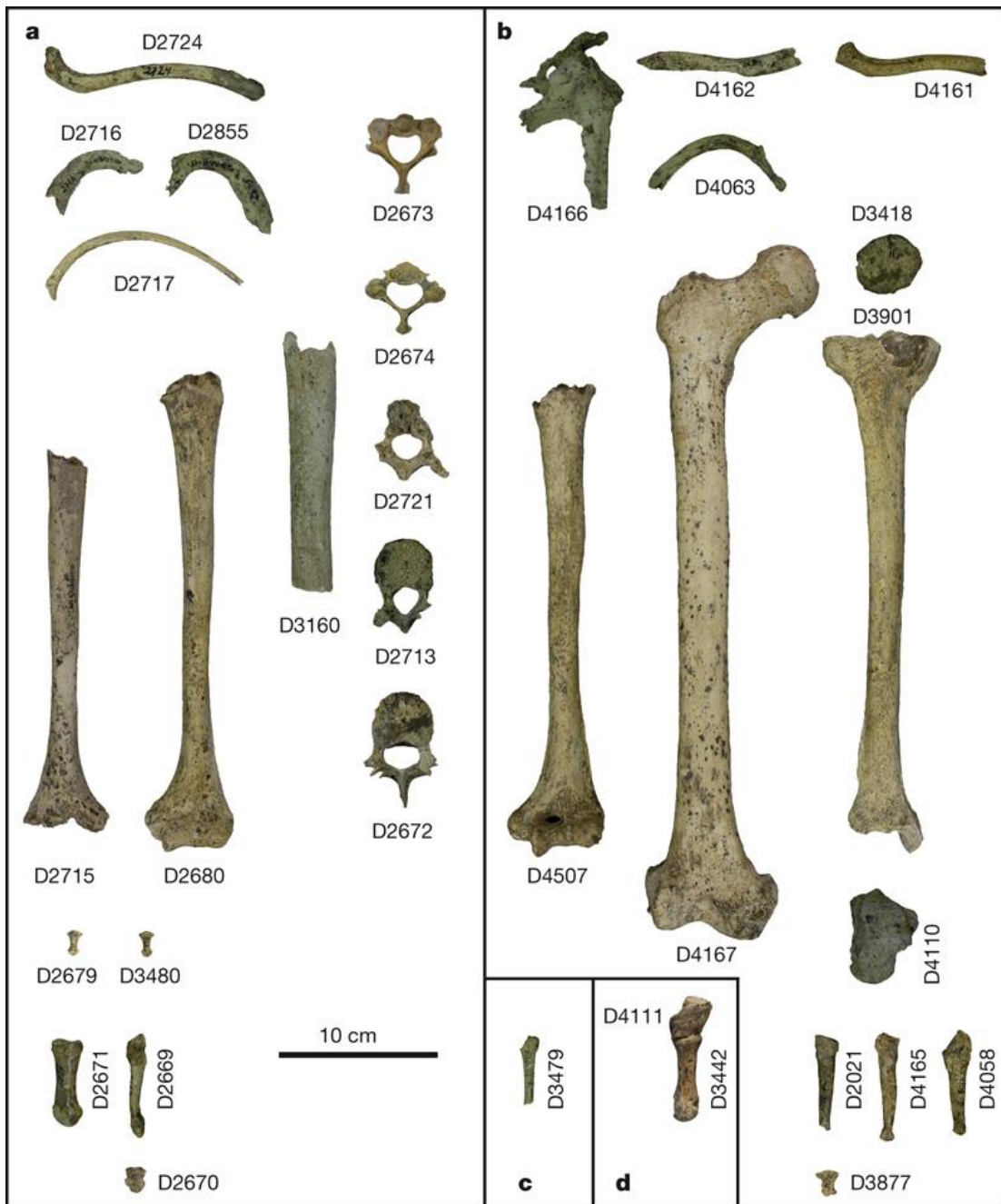


Figure 1.15: Post cranial remains of the Dmanisi *Homo* skeletons showing the ribs: of the subadult individual (D2716/D2855 – right and left 1st ribs; D2717 – eleventh rib) and of the adult individual (D4063 – right second rib) (After Lordkipanidze *et al.* 2007).

1.5.8. *Homo neanderthalensis* (Neanderthals)

Several Neandertals retain ribs with varying degrees of completeness. Among the more complete are Kebara 2 (Arensburg, 1991, Gomez-Olivencia *et al.* 2009), La Ferrassie 1 and 2 (Heim, 1976), Tabun C1 (McCown & Keith, 1939) and La Chapelle-aux-Saints 11 (Boule, 1911-13). The most complete fossilised Neanderthal ribs, both in number as well as structure belong to those skeletons of Kebara 2 and Shanidar 3 (Solecki 1960, Franciscus and Churchill 2002) (Figure 1. 14 and 1.15).

When compared with those of recent modern humans, the ribs of Neanderthals are interpreted as being more robust with a triangular or rounded cross-section, more open in curvature at the posterior angle, and with a large and shallow costal groove (Arensburg 1991).

Franciscus and Churchill (2002) found that the thorax of Shanidar 3, a male Neanderthal, is larger in length, curvature and area at rib eight and at the midshaft diameters of the superior ribs compared with other Pleistocene *Homo* fossils and recent humans. They also conclude that the

- i. rib curvature, posterior angle and midshaft cross-sectional size and shape, and muscle scarring varies considerably among Neanderthals and across all samples when considered in isolated ribs.
- ii. normalised metric and discrete patterning across the greater thorax clearly distinguishes Neanderthals from all comparative samples. These are most

marked in the inferior thorax where Neanderthals, and probably earlier *Homo*, exhibit larger, more rounded and rugose ribs and greater thoracic volume.

- iii. greater lower rib cross-sectional robusticity (indicating greater bending moments) and more rugose muscle scarring suggest elevated inspiratory levels.

Gomez-Olivencia *et al.* (2009) also analysed the ribs of Kebara 2 (K2) using standard anthropometric techniques as well as using the variables utilised by Franciscus and Churchill (2002). In this study K2 showed significant metric and morphological differences in comparison to a wide range of modern human comparative samples. The main results of this study showed that when compared with those of recent modern humans, the ribs of this Neanderthal are found to be more robust with a triangular or rounded cross-section, more open in curvature at the posterior angle, and with a large and shallow costal groove. This confirmed the observations noted by Arensburg (1991) concerning the ribs of K2.



Figure 1.16: The partial skeleton of the Kebara 2 Neanderthal (After Arensburg 1991).

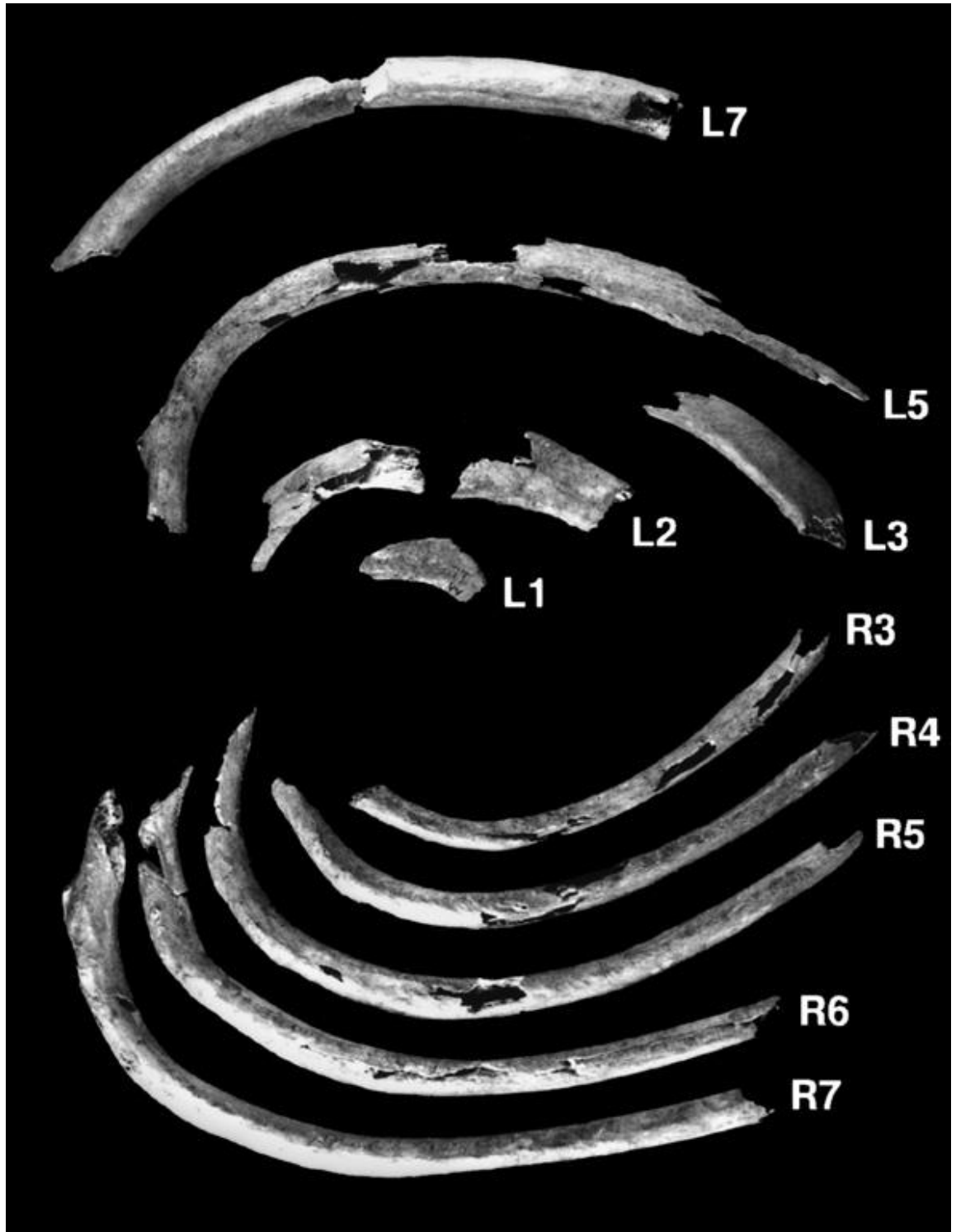


Figure 1.17: Some of the ribs of Shanidar 3 (After Franciscus and Churchill 2002).

Table 1.1: Summary of the fossil hominins with associated ribs.

Fossil	Taxa	Fossil number	Chronological Age	Locality
Ardi	<i>Ardipithecus ramidus</i>	ARA-VP-6/500	4.4 Ma	Middle Awash, Ethiopia
Woranso-Mille	<i>Australopithecus afarensis</i>	KSD-VP-1/1	3.58 Ma	Afar, Ethiopia
Lucy	<i>Australopithecus afarensis</i>	AL 288-1	3.2 Ma	Hadar, Ethiopia
Sts 14	<i>Australopithecus africanus</i>	Sts 14	2.6 – 2.8 Ma	Sterkfontein, South Africa
Stw 431	<i>Australopithecus africanus</i>	Stw 431	1.5 -2.8 Ma	Sterkfontein, South Africa
Malapa	<i>Australopithecus sediba</i>	MH 1 and MH 2	1.95 – 1.78 Ma	South Africa
Nariokotome Child/ Turkana boy	<i>Homo erectus/ergaster</i>	KNM WT 15000	1.6 Ma	Kenya
Dmanisi	<i>Homo</i>	D 2716, 2717,2855, 4063	1.77 Ma	Dmanisi, Georgia
Tabun C1	<i>Homo neanderthalensis</i>		120 ka	Mount Carmel, Israel
La-Chapelle-aux-Saints	<i>Homo neanderthalensis</i>		60 ka	France
Shanidar 3	<i>Homo neanderthalensis,</i>	32 - 57	75 – 50 ka	Iraq
Kebara 2	<i>Homo neanderthalensis,</i>	KMH 2	60 ka	Mount Carmel, Israel
Mladec	<i>Homo neanderthalensis</i>	11 - 20	31 ka	Czechoslovakia
Regourdou 1	<i>Homo neanderthalensis</i>		35 ka	France

1.6. The current study

The current project was designed to qualify and quantify the similarities, and the differences which may exist in the proximal/axial rib morphology of selected medium sized African mammals in order to produce a template of the typical costal morphology. The data obtained were then compared to that of fossil hominin specimens to see if any structural affinities between these taxa could be discriminated.

1.7. Objectives of the current study

The objectives of this study are:

- i. To compare and differentiate the thoracic morphology of the various extant species of African medium-sized mammals including humans by assessing the metrical variables and non-metrical features of the axial or proximal aspect of the costal arch;
- ii. To assess the morphological affinities of the extant species to extinct primate species using metrical variables and non-metrical features of the axial end of a costal arch that were identified and developed in this study;
- iii. To create a comparative and comprehensive template for the identification of the costal elements of selected extant and extinct species;
- iv. To assess the current costal elements that are related to especially the following fossil hominins: Stw 431, Sts 14, MH 1 and MH 2;

- v. To determine the thoracic shape (primarily upper) of *Australopithecus sediba* and
- vi. To relate hominin thoracic shape in the process of the postural evolution (e.g. evolution of human-like bipedalism) and physiology (e.g. respiratory functionality in the different modalities of locomotion).

The identification, differentiation and interpretation of the discovered fossil elements, especially ribs, when in the field are indicated by the sequence of the objectives outlined above.

CHAPTER 2 MATERIALS AND METHODS

2.1. Introduction

This study was broadly divided into four parts:

- i. a non-metric study of the proximal end of the vertebro-sternal ribs of the selected primate and non-primate species;
- ii. a metric study of the proximal end of vertebro-sternal ribs of preselected primates namely, the hominoidea represented by extant humans, great apes (chimpanzees, bonobo, gorillas and orangutans) and the cercopithecoidea, represented by baboons;
- iii. a metric study of the fossilised rib or rib fragments of extinct hominin individuals and
- iv. a non-metric study, examining the various morphological features of the proximal or vertebral end of fossilised extinct hominin complete rib or rib fragments.

2.2. Materials for the primate study

Metrical data were collected and non-metrical observations were made on the axial/vertebral ends of the right true or vertebro-sternal ribs (ribs 1 to 7) of the following samples or remains:

- a) Modern human (*Homo sapiens*) skeletons housed in the Raymond Dart Collection, School of Anatomical Sciences, University of the Witwatersrand.

These skeletons were preselected for age, sex and population classification.

The extant human population sample comprised the following skeletons

Zulu:	– 20 individuals (10 male; 10 female)
Sotho:	– 20 individuals (10 male; 10 female)
“European”:	– 20 individuals (10 male; 10 female)

(Total: 60 skeletons)

The Zulu and Sotho samples are representative of two Bantu-speaking groups of southern Africa (Zipfel 2004). The “European” sample represents a diverse South African group of European descent (Zipfel 2004, Dayal *et al.* 2009). It is important to note that these designations were largely based on hospital records of the language group of these individuals at the time of death and may not precisely reflect their true source population group.

b) Representative specimens of African non-human primate skeletons:

African Apes:

Bonobo (<i>Pan paniscus</i>)	– one individual
Chimpanzee (<i>Pan troglodytes</i>)*	– 21 individuals (14 male; seven female)
Gorilla (<i>Gorilla gorilla</i>)	– six individuals (three male and three female)

Non-African Apes

Orangutan (<i>Pongo pygmeus</i>)*	– 20 individuals (eight male; 12 female)
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*Lar gibbon (Hylobates lar)** - 20 individuals (10 male; 10 female)

Cercopithecoids

Baboon (*Papio ursinus*) – 20 individuals (10 male; 10 female)

Vervet monkey (*Cercopithecus aethiops/pygerythrus*) - 20 individuals (12 male; 8 female)

These specimens were obtained from the primate collections housed at the following institutions, namely:

- (a) Evolutionary Studies Institute (ESI) (formerly the Bernard Price Institute for Palaeontological Research (BPI));
- (b) the Hunterian Museum (Wits Comparative lab) and the Philip Tobias Fossil Primate and Hominin Laboratory (Wits Fossil Lab), both at the School of Anatomical Sciences, University of the Witwatersrand and
- (c) the Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria.
- (d) *from the Schultz Collection at the University of Zurich (data and analysis made available courtesy Eveline Weissen and Peter Schmid.)

See Appendix 1 for the details of some of the primate specimens used in this study.

2.3. Materials for the non-primate study

Non-metric descriptions of the ribs were carried out on the axial/vertebral end and shaft of the right ribs 1 to 7 of the following representative extant mammals housed at the ESI, Wits Comparative Lab, Wits Fossil Lab and the Ditsong National Museum of Natural History:

- 1) Domestic dog (*Canis lupus familiaris*) representing the Canidae;
- 2) Domestic pig (*Sus domesticus*) representing the Suidae;
- 3) Impala (*Aepyceros melampus*) representing the Bovidae;
- 4) Leopard (*Panthera pardus*) representing the Felidae and
- 5) Spotted hyena (*Crocuta crocuta*) representing the Hyaenidae

These taxa were selected because of the similar body size of the thorax to that observed in some of the extant primate species.

Appendix 2 indicates the specimens used in this part of the study.

2.4. Materials for the fossil study

Metric and non-metric observations were carried out on the following fossil hominin material:

- i. the right rib fragment of Stw 431, *Australopithecus africanus*;
- ii. a cast of the right first rib of AL 288 (Lucy), *Australopithecus afarensis*

These are housed in the Philip Tobias Primate and Hominin Laboratory of the School of Anatomical Sciences, University of the Witwatersrand Medical School;

- iii. the rib material of Sts 14 (*Australopithecus africanus*) housed at the Ditsong (formerly Transvaal) Museum, Pretoria. The rib fragments are from both sides of the body,
- iv. the ribs of *Homo erectus* (Turkana boy or KNM-WT 15000) and
- v. the costal remains of the Malapa fossils (*Australopithecus sediba*): juvenile male (MH1) and adult female (MH2) housed in the Institute for Human Evolution (IHE), University of the Witwatersrand, Johannesburg.

For the analysis of the fossilised hominin material, the original fossil material as well as casts and photographs of the originals were used.

2.5. Problem with the size of the non-primate samples

The postcranial skeletons of many animals are generally destroyed for a number of reasons (e.g. spread of disease, lack of storage space, etc.) and have not been maintained in comparative collections. In specimens originating from zoos, for example, the skeleton is destroyed to prevent the spread of disease and illness.

Wildshot specimens are also mainly represented by cranial material as the postcranial material is generally not collected (Zipfel 2004). The problems encountered when examining the fossil costal elements was that most of these are fragile, distorted and fragmentary and even when retained are often in a poor condition making it difficult to obtain measurements from the same anatomical points of reference (Brain 1974, Plug 1988).

2.6. Methods

2.6.1. Identification and sequencing of the primate ribs

The identification of the side of the body to which a particular rib belongs to and the sequencing of the 1st, 2nd, 10th, 11th and 12th rib is usually a relatively simple task and this study followed the methods suggested by previous researchers (see Jellema *et al.*, 1993).

The criteria applied in this study for identification and sequencing the typical ribs of the human sample were adapted and modified from Franciscus *et al.* (2002). These criteria were an adaptation of earlier studies by Mann (1993), Dudar (1993), Jellema *et al.* (1993) and Hoppa (1998). The same criteria were applied to the non-human primates ribs as to the human ribs where possible.

The criteria used to identify the rib number in the human sample include:

- i. Distance between the costo-transverse tubercles and the *iliocostalis* line; this typically increases sequentially in ribs 3–11;
- ii. Differential shaft shape: the shafts of ribs 3–6 increase steadily in relative width medio-laterally (i.e., internal to external surfaces); beginning with rib 7 they then gradually become relatively narrower and more “bladelike” caudally to rib 12;
- iii. Differential rib length and cross-sectional size: typically ribs increase sequentially in length and overall cross-sectional size (the latter more

important for fragmentary ribs) to a maximum typically at rib 7, After which they decrease steadily in both parameters;

- iv. Rib declination: in anatomical position, the angle of the lateral segment of the shaft (i.e., mid-shaft of the rib body) relative to the transverse plane increases sequentially in ribs 3–10 as each lateral shaft is slightly more inferiorly declinated than the preceding rib;
- v. Degree and form of shaft torsion: as rib declination sequentially increases, the torsion of the rib (i.e., spiralling of the shaft about its long axis) will result in different orientations of the external border of the mid-shaft. In ribs 3–10 this will result in a sequential gradation in which the superior part of the border is first medially inclined, then vertically aligned with the inferior border, and finally laterally inclined in the most caudal ribs;
- vi. Posterior angle: the posterior angle of the rib becomes sequentially more obtuse in ribs 3–12. The posterior angle is a common landmark in discussions of rib morphology. The posterior angle is defined as the point of intersection of the *iliocostalis* line with the caudal margin of the shaft. This point is usually coincident with the area of greatest flexion of the shaft and
- vii. Costal groove prominence: the costal groove is most prominent (i.e. deepest) on ribs 5, 6 and 7.

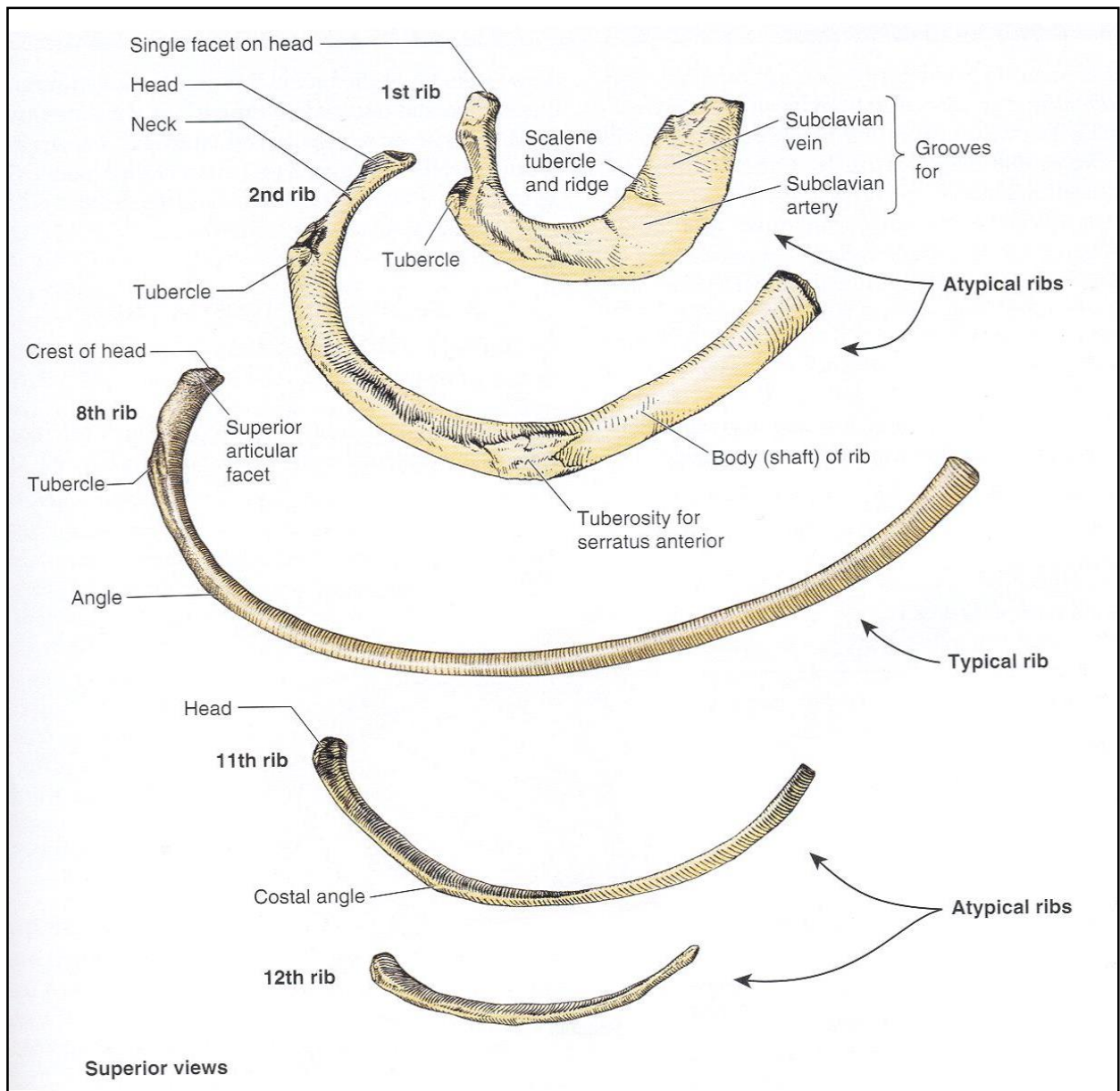


Figure 2.1: The human ribs showing the features of typical and atypical true ribs
(After Moore *et al.* 2009).

2.6.2 Definitions of the non-metrical features

The following non-metrical features were observed on the primate and non-primate ribs and scored as described in the following section. Utilising the scores, a comparative analysis of these scores was undertaken.

- a. Number of articular facets on head of rib (FACET)
 - i. scored 1 for a single facet
 - ii. scored 2 for a double facet separated by the crest of the head.

- b. Presence of crest of head of rib (CREST)
 - i. scored 0 for absence
 - ii. scored 1 for presence

- c. Position of the costal tubercle (TUBERCLEpos)
 - i. scored 1 if the articular facet was situated at the superior margin of the crest of rib
 - ii. scored 2 if the articular facet was situated at the inferior margin of the crest of rib

- d. Orientation of the tubercle facet (TUBERCLEor)
 - i. scored 1 if the articular facet was oriented to face postero-medially
 - ii. scored 2 if the articular facet was oriented to face infero-laterally

- e. Presence of the non-articular ligamentous attachment of lateral costotransverse ligament (LIGatt)
 - i. scored 0 if the attachment is absent
 - ii. scored 1 if the attachment is present

- f. Position of the non-articular ligamentous attachment of the lateral costo-transverse ligament (LIGpos)
 - i. scored 1 if the ligamentous attachment is situated at superior margin of the tubercle of the rib
 - ii. scored 2 if the ligamentous attachment is situated at inferior margin of the tubercle of the rib

- g. Beginning of costal groove (GROOVE)
 - i. scored 0 if the costal groove begins immediately adjacent to the tubercle
 - ii. scored 1 if the costal groove begins more lateral to the tubercle

- h. Depth of costal groove (CGD)
 - i. scored 0 where there was a beginning of a depression
 - ii. scored 1 if the costal groove was shallow
 - iii. scored 2 if the costal groove was deep

- i. Soft tissue attachments (TISSUEATTACH) as observed by the texture that is produced by soft tissue muscles and ligaments if they attach to the surfaces of the rib
 - i. scored 0 if no elevations are visible and the surfaces are smooth
 - ii. scored 1 if small elevations are observed
 - iii. scored 2 if larger and more distinctive elevations are observed

Osteological features of the 1st to 7th ribs of some of the primate and non-primate species were written as a description, commencing from the most proximal or vertebral end of the rib i.e. the head until a point just distal to the posterior angle on the shaft of a particular rib.

The human rib was utilised as the standard reference for comparisons of the other species that were studied.

2.6.3. Note on the orientation and terminology of the terms used to describe a rib

The description of the modern human rib was considered the standard point of reference against which the ribs of the other extant species were compared. It is important to note that the positions of the features of the human rib are all referenced against the standard anatomical position.

Figure 2.2. depicts the differences in orientation of bipedal and quadrupedal species and introduces some of the essential terminology that is used in discussions of skeletal anatomy. The positions of the costal features in the non-human or non-bipedal skeletons are referenced against the quadruped position of the skeleton (See Figure 2.3). The terms relating to the human anatomical position and the quadruped position needs to be noted for especially the measurements taken off the ribs.

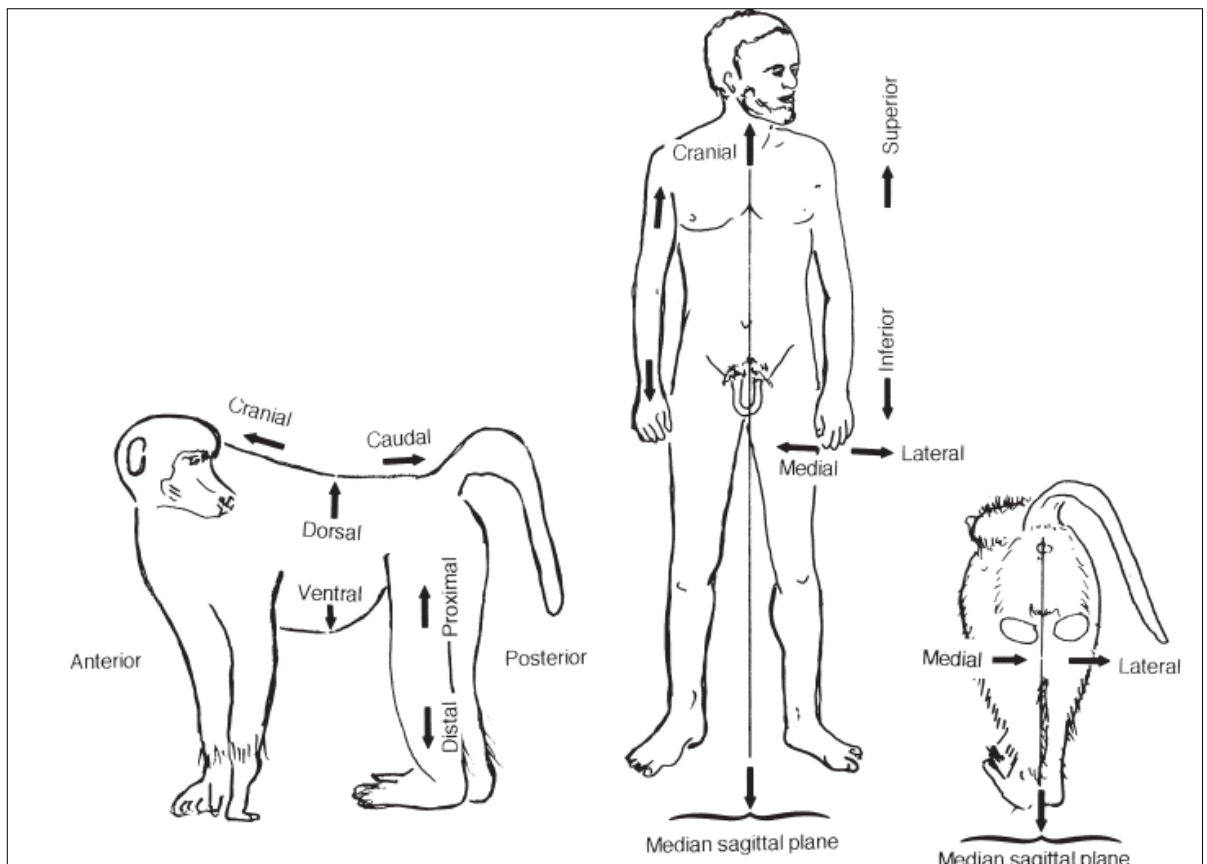


Figure 2.2: The standard reference quadruped specimen that was used to orientate features of the rib in a quadruped animal (After Ankel-Simons 2000).

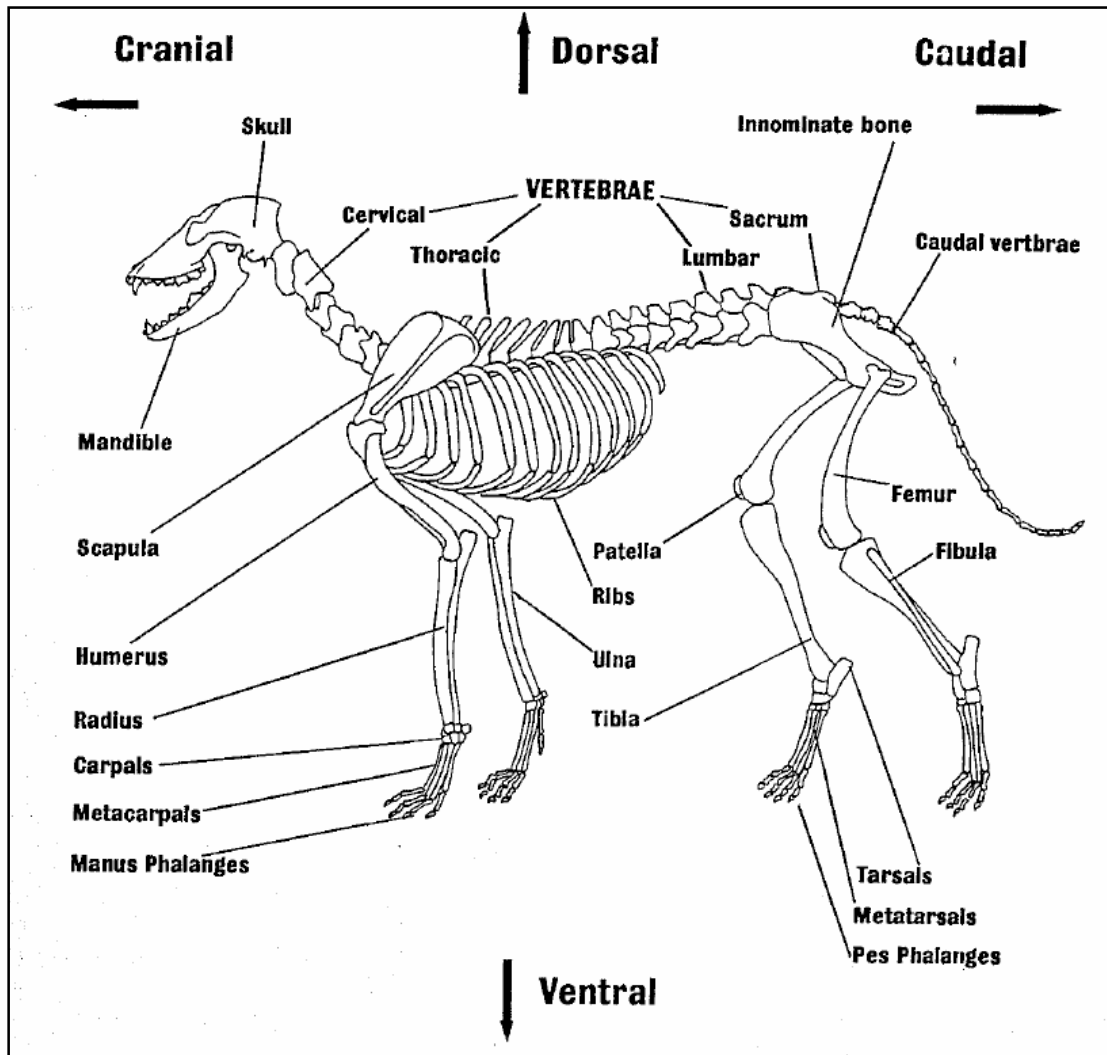


Figure 2.3: The standard reference quadruped specimen that was used to orientate features of the rib in a quadruped animal (After Hillson 1992).

2.7. Definitions of the linear variables used in the primate and non-primate study

The two standard types of measurements taken were:

- i. Breadth measurements – measurements from the most medial to the most lateral aspects of a particular region or part of the rib and
- ii. Length measurements – measurements from the most proximal to the most distal aspects of a particular region of part of the rib.

The following linear (metrical) measurements, corresponding to or modified from Franciscus and Churchill (2002), were taken from the rib material studied (see also Table 2.1. and Figure 2.4),

- i. *Head superior facet height (HSH)* is the maximum height of superior facet as measured between the most superior and inferior edges of the superior facet of the head;
- ii. *Head superior facet width (HSW)* is the maximum width of superior facet as measured between the most medial and lateral edges of the superior facet of the head, perpendicular to measurement (1) above;

Note that for the first rib of the human sample, only a head facet height and width is measured because there is only a single facet on the head of the first rib.

- iii. *Head inferior facet height (HIH)* is the maximum height of inferior facet as measured between the most superior and inferior edges of the inferior facet of the head;
- iv. *Head inferior facet width (HIW)* is the maximum width of inferior facet as measured between the most medial and lateral edges of the inferior facet of the head, perpendicular to measurement (iii) above;
- v. *Neck length (NL)* is the linear distance between the most lateral edge of the superior articular facet of head to the most medial edge of articular facet of the tubercle;
- vi. *Neck (Superior-Inferior diameter) at Head (NH)* is the maximum height of neck adjacent to the superior facet of the head;
- vii. *Neck (Superior-Inferior diameter) at Tubercle (NT)* is the maximum height of neck close to articular facet of the tubercle at its most medial point;
- viii. *Neck (Anterior-Posterior diameter) at Head (NHA)* is the maximum distance between the internal and external aspects of the neck of the rib at the part closest to the most lateral part of the head, perpendicular to measurement (vi) above;

- ix. *Neck (Anterior-Posterior diameter) at Tubercle (NTA)* is the maximum distance between the internal and external aspects of the neck of the rib at the part closest to the medial edge of the articular facet of the tubercle, perpendicular to (vii) above;
- x. *Tubercle facet height (TFH)* is the maximum height between the most superior and inferior edges of the articular facet of the tubercle;
- xi. *Tubercle facet width (TFW)* is the maximum width between the most medial and lateral edges of the articular facet of the tubercle, perpendicular to (x) above;
- xii. *Tubercle – iliocostal line distance (outer or inferior) (TILO)* measured from the most lateral edge of articular facet of the tubercle to the posterior angle (iliocostal line) on the external or inferior aspect of costal shaft;
- xiii. *Tubercle - iliocostal line distance (inner or superior) (TILI)* measured from the most lateral edge of articular facet of the tubercle to the posterior angle (iliocostal line) on the internal or superior aspect of costal shaft;
- xiv. *Shaft maximum height at posterior angle (SHPA)* is the maximum distance between the superior and inferior edges of the shaft of the rib at the posterior angle (iliocostal line) and

- xv. *Shaft maximum width at posterior angle (SWPA)* is the maximum distance between the internal and external surfaces of the shaft of the rib at the posterior angle (iliocostal line).

2.8. Definitions of the linear variables used in determination of the thoracic shape in *Australopithecus sediba*

For this aspect of the study, the following linear measurements were taken off the ribs and indices calculated in order to quantify relevant morphometric information from homologous points of incomplete ribs (Jellema *et al.* 1993; Franciscus and Churchill 2002):

- (1) *Tubercle-iliocostal line distance (TID)*: straight-line distances from the center of the articular tubercle to the furthest extend of the iliocostal line (i.e. the inferior costal point);
- (2) *Posterior angle chord (PAC)*: straight-line distance measured from the center of the articular tubercle to a point on the inferior aspect of the shaft, whose ventral linear distance from the iliocostal line is equidistant to the TID;
- (3) *Posterior angle subtense (PAS)*: the subtense from the inferior iliocostal point to the chord PAC. The value for the subtense is geometrically derived from a right triangle whose base is $1/2$ PAC and whose hypotenuse is TID;

- (4) *Posterior angle index (PA-INDEX)*: $(PAS/PAC)*100$. Relatively larger values for this index reflect a less “open” (i.e. more acute) posterior angle;
- (5) *Shaft maximum diameter at angle (SMXD)*: measured at the posterior angle of the ribs. In all cases, the calipers are oriented for maximum reading (for rib 12, the measurement is taken at the extend of the Mm. erector spinae line);
- (6) *Shaft minimum diameter at angle (SMND)*: minimum reading as in (5);
- (7) *Shaft index at angle (SH-INDEX)*: $(SMND/SMXD)*100$. Relatively larger values for this index reflect a more “circular” or “rounded” shaft cross section at the posterior angle;
- (8) *Mid-shaft maximum diameter (MMXD)*: maximum diameter at the estimated mid- shaft position;
- (9) *Mid-shaft minimum diameter (MMND)*: minimum reading as in (10);
- (10) *Mid-shaft index (MS-INDEX)*: $(MMND/MMXD)*100$. Relatively larger values for this index reflect a more “circular” or “rounded” shaft cross section at the midpoint of the rib body;
- (11) *Neck-length (NL)*: straight-line distance between the midpoint of the articular tubercle and the distal articular margin of the head;
- (12) *Neck S-I diameter (NSID)*: superoinferior height of neck (minimum reading);

- (13) *Neck index* (NCK-INDEX): $(NSID/NL)*100$. Relatively larger values for this index reflect a superoinferiorly wider rib neck and/or shorter neck length;
- (14) *Tuberculo-ventral chord* (TVC): straight-line distance between the ventral-most margin of the articular tubercle to the ventral-most point of the sternal end of the rib;
- (15) *Tuberculo-ventral subtense* (TVS): perpendicular distance from TVC to the lateral-most extends of the shaft of the rib;
- (16) *Total rib curvature index* (TRC-INDEX): $(TVS/TVC)*100$.
Relative larger values for this index reflect a less “open” curvature, with less mediolateral expansion and
- (17) *Humerus length* (HL): Maximum length of the humerus in order to standardise rib measurements.

Table 2.1: The variables that were measured off the vertebro-sternal ribs of all material studied.

(corresponding to variables in Franciscus and Churchill 2002 are in bold).

	METRICAL FEATURE	ACRONYM	LANDMARKS AT WHICH MEASUREMENTS WERE TAKEN
1	Head Superior facet height	HSH	maximum height of superior facet as measured between the most superior and inferior edges of the superior facet of the head
2	Head Superior facet width	HSW	maximum width of superior facet as measured between the most medial (tip of proximal end of crest of head) and lateral edges of the superior facet of the head
3	Head Inferior facet height	HIH	maximum height of superior facet as measured between the most superior and inferior edges of the inferior facet of the head
4	Head Inferior facet width	HIW	maximum width of superior facet as measured between the most medial (tip of proximal end of crest of head) and lateral edges of the inferior facet of the head
5	Neck length	NL	Maximum distance between the most lateral edge of the superior articular facet of head to the most medial edge of tubercle
6	Neck (S-I diameter) at Head	NH	maximum height of neck close to the superior facet of the head
7	Neck (S-I diameter) at Tubercle	NT	maximum height of neck close to tubercle at its most medial point
8	Neck (A-P diameter) at Head	NHA	maximum distance between the internal and external aspects of the neck of the rib at the part closest to the most lateral part of the head perpendicular to NH

Table 2.1 (continued): The variables that were measured off the vertebro-sternal ribs of all material studied.

	METRICAL FEATURE	ACRONYM	LANDMARKS AT WHICH MEASUREMENTS WERE TAKEN
9	Neck (A-P diameter) at Tubercle	NTA	maximum distance between the internal and external aspects of the neck of the rib at the part closest to the medial edge of the tubercle facet measured perpendicular to NT
10	Tubercle facet height	TFH	maximum height between the most superior and inferior edges of the tubercle facet perpendicular to TFW
11	Tubercle facet width	TFW	maximum width between the most medial and lateral edges of the of tubercle facet perpendicular to TFH
12	Tubercle – iliocostal line distance (outer)	TILO	maximum distance from most lateral edge of tubercle facet to posterior angle (iliocostal line) on inferior edge of costal shaft
13	Tubercle - iliocostal line distance (inner)	TILI	maximum distance from most lateral edge of tubercle facet to posterior angle (iliocostal line) on superior edge of costal shaft
14	Shaft maximum height at posterior angle	SHPA	maximum distance between the superior and inferior parts of the shaft of the rib at the posterior angle (iliocostal line)
15	Shaft maximum width at posterior angle	SWPA	maximum distance between the internal and external aspects of the shaft of the rib at the posterior angle (iliocostal line)

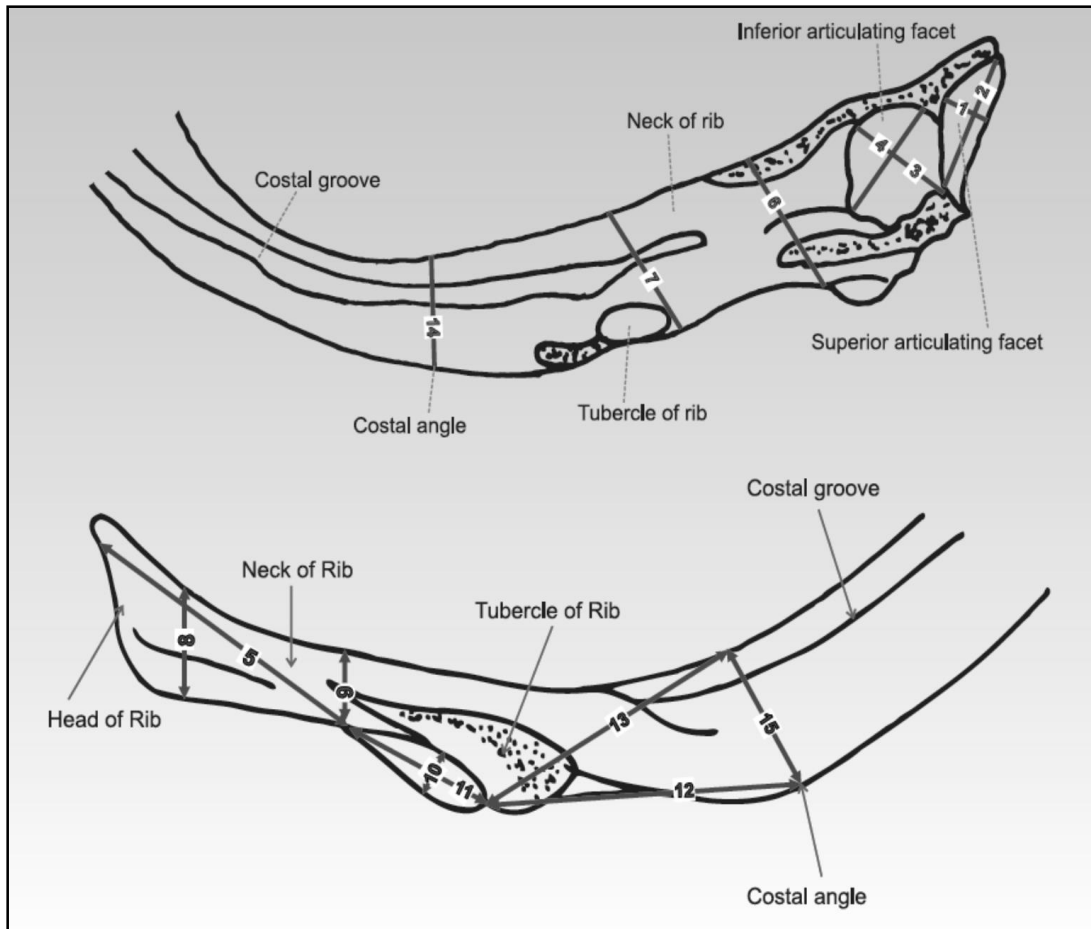


Figure 2.4: Schematic line diagrams of the proximal end of a rib showing the variables measured. Refer to the numbers in Table 2.2. for a descriptions of the linear measurements taken.

2.9. Methods employed in obtaining measurements of the bone

Linear measurements were obtained using standard digital sliding calipers. Readings were taken in millimeters and recorded to 0.01mm. Measurements were entered directly into a *Microsoft Excel*[®] spread sheet at the site of measurement. This reduced any sources of error associated with data transfer at a later date. All measurements were taken with the rib or rib fragment held and orientated by hand.

2.10. Assessment of error and its impact reduction

Every attempt to eliminate error was made whilst taking measurements on the rib or rib fragments. However, there is an inherent component of error if measuring bone utilizing landmarks that may not be equally visible on all bone specimens. This problem of systematic error had been eliminated to a great degree by ensuring:

- i. the utilisation of clearly and carefully defined reference positions and measured variables and
- ii. all the measurements were collected personally.

2.11. Indices calculated from the linear measurements

An index is a percentage value that describes measurements in relation to one another. By utilising indices, the variable of size is reduced to some extent while shape becomes more important (Hrdlic̃ka 1920).

The following eight indices were formulated and adapted by the author (see Hrdlic̃ka 1930; Franciscus and Churchill 2002) so as to quantify relevant metrical information from homologous points on the proximal ends of incomplete ribs. Subsequently these were calculated utilising the results of the measured variables defined above.

**Table 2.2: Indices in this study calculated from the measurements taken
(corresponding to Franciscus and Churchill 2002 are in bold)**

INDEX	ACRONYM	FORMULA
Superior Facet of rib head	SFHI	HSH/HSW x 100
Inferior Facet of rib head	IFHI	HIH/HIW x 100
Neck	NI	NH/NL x 100
Neck at head (S-I diameter vs. A-P diameter)	NHI	NH/NHA x 100
Neck at tubercle (S-I diameter vs. A-P diameter)	NTI	NT/NTA x 100
Tubercular facet	TFI	TFH/TFW x 100
Tubercle – iliocostal line distance	TICI	TILO/TILI x 100
Shaft height at the posterior angle	SHI	SHPA/SWPA x 100

2.12. Statistical analysis of the metrical measurements and indices

Statistical analyses of the metrical data obtained in this study were carried out using PASW Statistics 18 (SPSS Inc.). Analysis of the measurements was carried out only on the first (1st), second (2nd), fourth (4th) and seventh (7th) ribs.

This was done for the following reasons:

- i. the 1st is an atypical vertebro-sternal rib and is unique in its structure as compared to the other ribs;
- ii. the 2nd rib is an atypical vertebro-sternal rib and is a rib that exhibits transitional features in its morphology;
- iii. the 4th rib was selected because it represents a typical vertebro-sternal ribs and
- iv. the 7th rib is the last rib vertebro-sternal rib of the thoracic cage and is thus at the junction between the vertebro-sternal and vertebro-chondral ribs.

2.12.1. Univariate analysis

The analysis of data commenced with a simple Univariate analysis. This was undertaken for the following reasons:

- i. to identify any erroneously recorded data;
- ii. to obtain a broad comparison of the size and variance of each variable in different groups and
- iii. is a requirement for the subsequent multivariate analysis and the interpretation thereof.

Data from the groups being compared were examined in terms of the standard Univariate descriptors of arithmetic mean and standard deviation.

2.12.1. A. The arithmetic mean

The arithmetic mean is derived by adding the values of all the measures of the data and dividing this sum by the number of items.

The arithmetic mean may be expressed by the formula:

$$\text{Mean} = m_x = Sx/n$$

Where: m = arithmetic mean

S = the sum of

x = the individual measurements

n = number of measurements

2.12.1. B. The standard deviation

The standard deviation (SD) is the indicator of the dispersion of data around their mean and is expressed by the formula:

$$SD = \sqrt{\sum (x^2 - m)^2 / n - 1}$$

Where: x = variable value

m = mean value of all variables in the sample

n = number of specimens in the sample

\sum = the sum of

The standard deviation is the square root of the variance. The reason for using the $n - 1$ instead of n in the standard deviation is complex. However, for the purpose of the

current study, $n - 1$ in the denominator produces a more accurate estimate of the true population standard deviation and has desirable mathematical properties for statistical inferences (Dawson and Trapp 2001). This is more important in small sample sizes (as is the case in the current study) where differences may show a greater magnitude in variance.

2.12.2. Testing for normality of distribution

Any meaningful interpretation of patterns of morphological variation in a sample such as bone dimensions can be made only when it is assumed that the distribution shape described by individual dimensions are approximately normal. If the sample from which data to be analysed were to violate one or more of the normality test assumptions, the results of the analysis may be incorrect or misleading (Allan 1982).

In order to perform any further multivariate analyses of the variables, a verification as to whether the data distributions for the human as well as non-human primates differed significantly from normal distributions was done using one-sample Kolmogorov - Smirnov (KS) tests.

The Kolmogorov–Smirnov test (K–S test) is a form of minimum distance estimation used as a nonparametric test of equality of one-dimensional probability distributions used to compare a sample with a reference probability distribution (one-sample K–S test), or to compare two samples (two-sample K–S test) (Allan 1982). The Kolmogorov–Smirnov statistic quantifies a distance between the empirical

distribution function of the sample and the cumulative distribution function of the reference distribution, or between the empirical distribution functions of two samples.

Significance was tested at the 95 percentile. Any KS value resultant from the test less than 0.05 was deemed to be significant and thus the data was deemed to be not normally distributed. Therefore the null hypothesis, which states that the data is normally distributed, will be rejected.

2.12.3. Multivariate analysis

The Analysis of Covariance (ANCOVA) and the Analysis of Variance (ANOVA) were used to further analyse the data.

2.12.3. A. Analysis of Variance (ANOVA)

Analysis of variance (ANOVA) is a collection of statistical models, and their associated procedures, in which the observed variance is separated into components due to different explanatory variables (Allan 1982). In its simplest form, ANOVA gives a statistical test of whether the means of several groups are all equal, and therefore generalises Student's two-sample t-test to more than two groups. ANOVAs are helpful because they possess a certain advantage over a two-sample t-test. Doing multiple two-sample t-tests would result in a largely increased chance of committing a type I error i.e. reject a null hypothesis instead of accepting it. For this reason, ANOVAs are useful in comparing three or more means.

One-way ANOVA is used to test for differences among variances between two or more independent groups. Typically, however, the one-way ANOVA is used to test for differences among at least three groups, since the two-group case can be covered by a t-test. When there are only two means to compare, the t-test and the F-test are equivalent; the relation between ANOVA and t is given by $F = t^2$.

The variance (or average variation) is indicated by the following formula:

$$\text{Average variation} = \frac{S(x - m)^2}{n - 1}$$

where S = sum of

x = random variable or value of items in set of data

m = mean of the values

n - 1 = number of items in sample (for small samples)

2.12.3. B. Analysis of Covariance (ANCOVA)

Analysis of covariance (ANCOVA) is a general linear model with one continuous outcome variable (quantitative) and one or more factor variables (qualitative).

ANCOVA is a merger of ANOVA and regression for continuous variables.

ANCOVA tests whether certain factors have an effect on the outcome variable After removing the variance for which quantitative predictors (covariates) account. The inclusion of covariates can increase statistical power because it accounts for some of the variability (Allan 1982).

As in any statistical procedure, ANCOVA makes certain assumptions about the data entered into the model. Only if these assumptions are met, at least approximately, will ANCOVA yield valid results. Specifically, ANCOVA, just like ANOVA, assumes that the errors are normally distributed and homoscedastic. Further, since ANCOVA is a method based on linear regression, the relationship of the dependent variable to the independent variable(s) must be linear in the parameters.

The ANCOVA was undertaken and a general linear model was selected when evaluating group differences.

This was carried out as follows:

- i. Choose the Univariate analysis - General Linear Model;
- ii. Select the following:
 - a. “dependent variable” = variable that is been compared from the sample;
 - b. “fixed factor” = Populations or groups that is been selected and
 - c. “co-variate” = sex of the individuals within the group/s
- iii. In the “Model” window the fixed factor, the covariate and the interaction effect between the fixed factor and co-variate was documented. Thus the analyses of the 3 elements were performed for every variable;
- iv. In the “Options’ window, descriptive statistics, homogeneity and estimates of effects size were options chosen;
- v. If the interaction effect was non-significant ($p > 0.05$) and group variances were not significantly different for the dependent variable, then the ANCOVA

was repeated with the interaction effect excluded from the model and the new results were reported;

- vi. If either the interaction effect was significant ($p < 0.05$), or group variances were significantly different for the dependent variable, then cases were ranked and the ANCOVA was rerun and the new results were reported;
- vii. The new results as obtained in (e) above were then assessed by means of ANOVA to evaluate group differences that exist in the variables observed;
- viii. Group variances were also assessed using the Levene's test for homogeneity of variances;
- ix. Post Hoc analyses, that indicated the interaction between the groups been analysed, were done as part of the ANOVA test and
- x. Least Significant Difference (LSD), Bonferroni and Tamhane comparisons were resultant from the ANOVA test. These assessed the differences in the means between the groups investigated. If the Levene's test was not-significant, the LSD and Bonferroni comparisons are used. If the Levene's test was significant, then the Tamhane comparison was used.

All results were deemed to be significant if the level of confidence or p value was less than 0.05.

CHAPTER 3 - RESULTS - RIB DESCRIPTIONS OF EXTANT SPECIES

This chapter describes the osteological non-metric observations of the

- a) complete first rib and
- b) the vertebral or proximal end, defined as being at a point proximal to the *iliocostalis thoracis* line, of the second to seventh ribs of the following groups and species:

A) Primates

- 1) Human (*Homo sapiens*);
- 2) Baboon (*Papio ursinus*);
- 3) Chimpanzee (*Pan troglodytes*) and
- 4) Gorilla (*Gorilla gorilla*).

B) Non-primates

- 1) Domestic dog (*Canis lupus familiaris*) representing the Canidae;
- 2) Domestic pig (*Sus domesticus*) representing the Suidae;
- 3) Impala (*Aepyceros melampus*) representing the Bovidae;
- 4) Leopard (*Panthera pardus*) representing the Felidae and
- 5) Spotted hyena (*Crocuta crocuta*) representing the Hyaenidae.

3.1. Human (*Homo sapiens*)

The following observations were made on the ribs of the human sample studied.

a) 1st rib

The human 1st rib is an atypical and a vertebro-sternal (true) rib that is flattened and broad. It has an acute curvature and is the shortest of the rib series of the human thoracic cage.

See Figures 3.1 and 3.2 for views of the human 1st rib.

i) *Head*

The rounded head exhibits a single vertebral facet that is round and flattened. This facet is for the articulation with a complete facet on the lateral aspect of the body of thoracic vertebra 1.

ii) *Neck*

The neck appears rounded in cross-section and is elongated. Its supero-posterior surface is roughened and inferior surface is smooth. The neck is oriented at an angle to the transverse plane, and ascends in postero-lateral direction towards the tubercle.



Figure 3.1: a) Superior view of the human right 1st rib.
 b) Inferior view of the human right 1st rib.

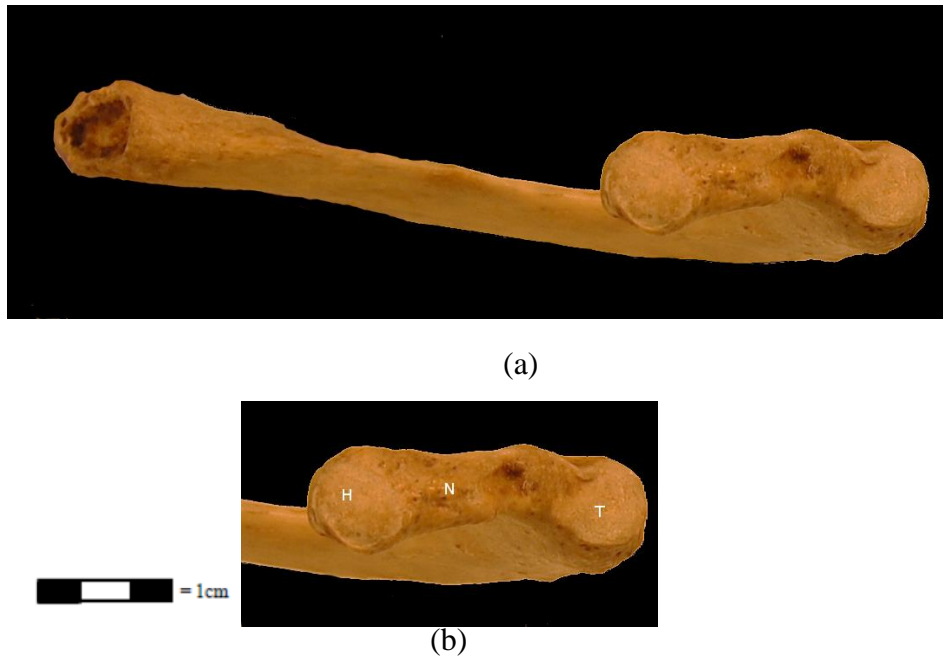


Figure 3.2: a) Postero-medial view of the human right 1st rib.
 b) The vertebral end of the human right 1st rib showing the head (H), neck (N) and tubercle (T).

iii) *Tubercle*

The tubercle is wide and has a single circular or oval articular facet for the articulation with the costal facet on the transverse process of thoracic vertebra 1. The articular facet is orientated to face postero-medially. Infero-lateral to the articular facet is a small roughened area for the attachment of the lateral costo-transverse ligament. This is referred to as the non-articular part of the tubercle.

The tubercle is in a superior position relative to the head of the rib. This feature assists in establishing to which side of the body the 1st rib belongs.

iv) *Angle*

The angle of the rib coincides with the tubercle. The *iliocostalis thoracis* muscle attachment is visible as part of the tubercle complex.

iv) *Shaft*

The shaft is flattened supero-inferiorly and has two surfaces (superior and inferior) as well as two margins (medial/internal and lateral/external).

The superior surface exhibits the following features, commencing from the proximal end:

- a roughened area for the attachment of the *scalenus medius* muscle;
- two grooves separated by the scalene tubercle – the posterior groove for the subclavian artery and upper trunk of the brachial plexus; and an anterior groove for the subclavian vein;

- antero-laterally, the attachment of the costoclavicular ligament and
- anteriorly is the attachment of the *subclavius* muscle.

The inferior surface is smooth due to its relationship with the parietal pleura. It does not exhibit any costal groove or any other osteological features. The medial margin is deeply concave and has the scalene tubercle protruding from it. The lateral margin is convex and has the roughened attachment of the *serratus anterior* muscle (1st digitation) situated opposite to the scalene tubercle. The shaft widens as the costal pit is approached distally.

v) Costal pit

The costal pit is a wide oval concavity.

b) 2nd rib

This is another atypical as well as vertebro-sternal (true) rib. It has a similar curvature to the 1st rib and is longer than the 1st rib. Its characteristic feature is that its shaft lies at an angle that is transitory between the atypical 1st rib and the typical 3rd rib.

i) *Head*

The head has two facets that are separated by a well-developed crest of the head. The facets lie at an obtuse angle to each other.

ii) *Neck*

The neck is flattened antero-posteriorly, producing two surfaces (anterior/internal and posterior/external) and two margins (superior/crest of the neck and inferior). It is elongated but shorter than that of the 1st rib. Its superior margin provides attachment for the superior costotransverse ligament.

iii) *Tubercle*

The convex and oval articular facet is situated towards the postero-inferior margin. The non-articular roughened part for the attachment of the lateral costo-transverse ligament lies more superiorly and further laterally.

iv) *Angle*

The angle of the rib is presented distal to the tubercle. The angle is visible as the juncture at which the neck of the rib changes direction to continue as the shaft. The *iliocostalis thoracis* muscle attachment is visible as a separate osseous elevation distal to the angle (see below).

v) *Shaft*

The shaft lies at an angle relative to the horizontal plane i.e. it is obliquely flattened. It exhibits the external and internal surfaces as well as the superior and inferior borders. The external surface is convex and is oriented supero-laterally. It has a slight elevation which corresponds to the attachment of the *iliocostalis thoracis* muscle.

This elevation runs from the angle in a supero-medial direction towards the crest of the neck.

The internal surface is concave, smooth and oriented infero-medially. There is a shallow costal groove on the inner surface, extending along the length of the shaft. The superior border is rounded as compared to the inferior border that is sharp due to the “bony overhang” produced by the costal groove.

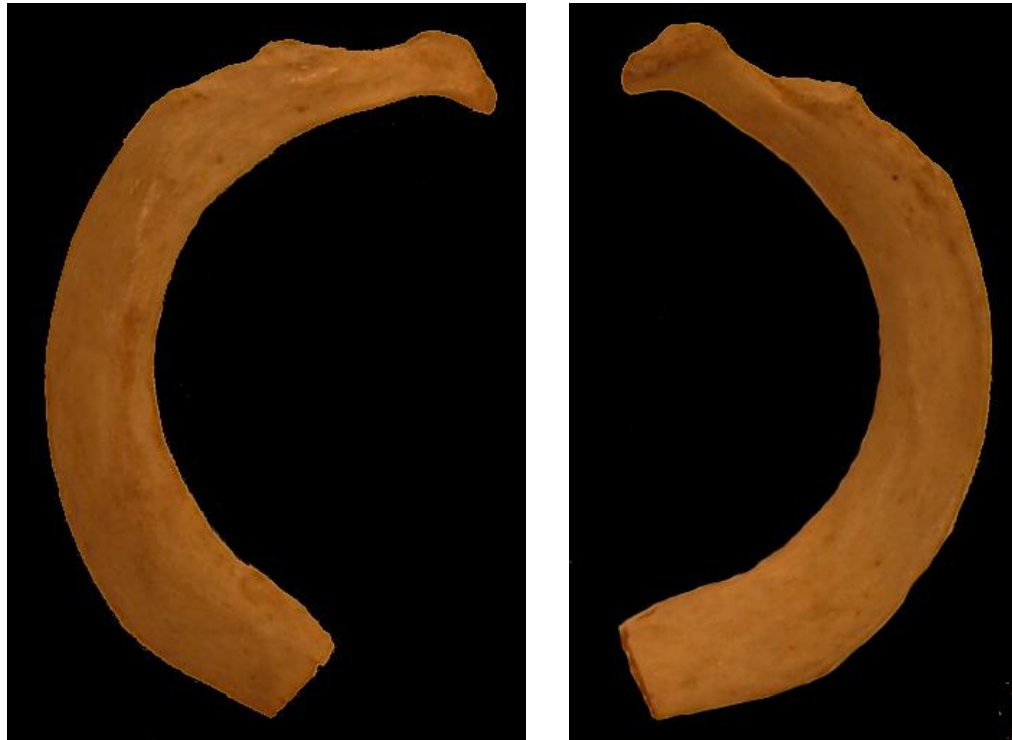
Figure 3.3 shows the osteology of the 2nd rib.

c) Ribs 3 to 7

These ribs are classified as typical vertebro-sternal (true) ribs. They outline a thoracic region that appears to be more circular and barrel-shaped. These ribs are progressively longer from rib 3 to 7 (Figure 3.4).

i) *Head*

The head exhibits two facets separated by a well developed crest. The facets of the head lie at an obtuse angle when compared to the 2nd rib. This produces a saddle-shaped area of articulation with the costal demifacets of the related thoracic vertebra.



 = 1cm

(a)

(b)

Figure 3.3: a) Superior view of the human right 2nd rib.

b) Inferior view of the human right 2nd rib.

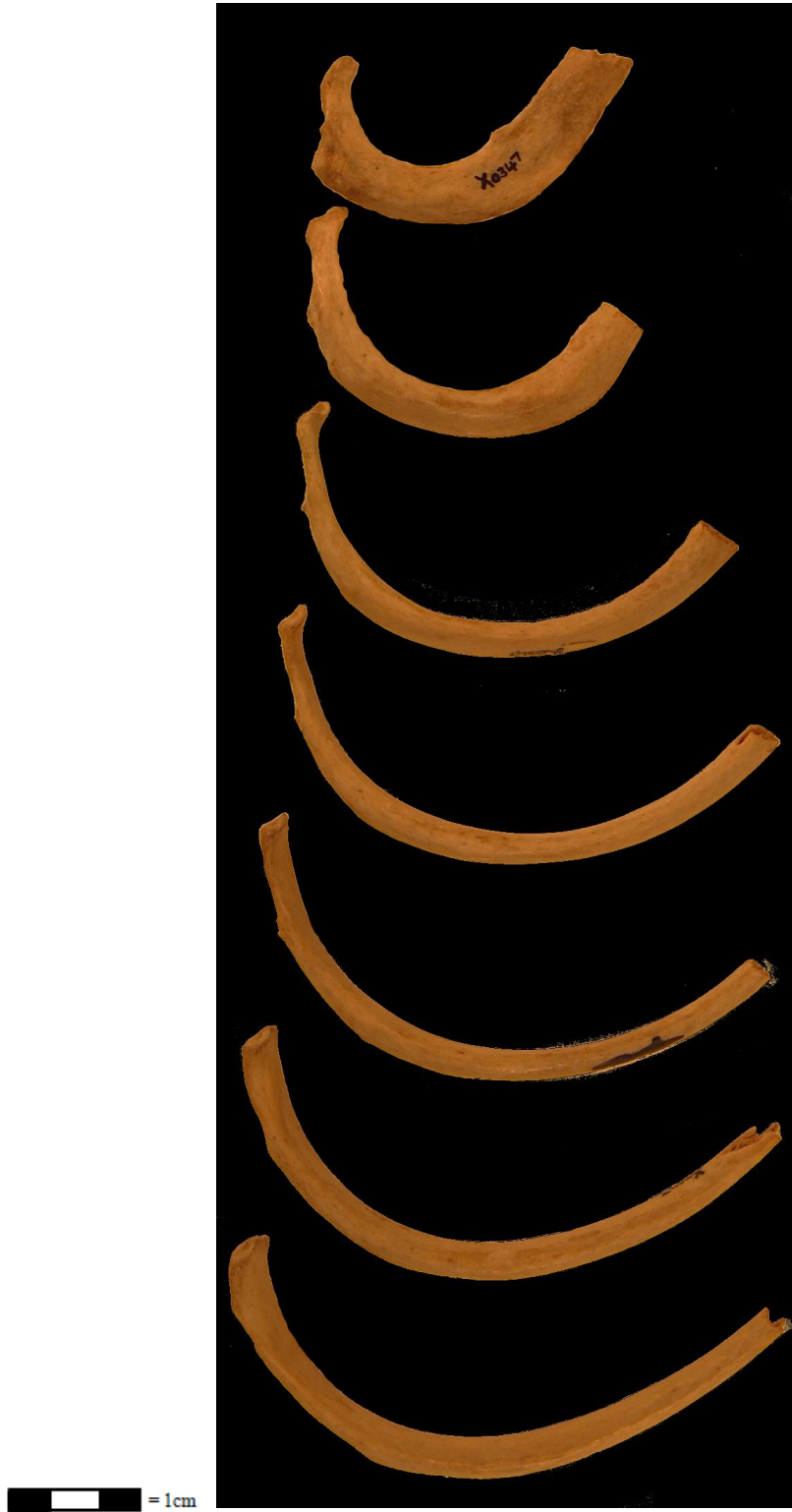


Figure 3.4: Human 1st to 7th ribs (from top to bottom Superior view, Right side).

ii) *Neck*

The neck is flattened in an antero-posterior direction. The neck is short.

It is also oriented that the internal surface faces antero-superiorly.

The superior border is well defined and has a well developed crest of the neck.

The inferior border of the neck exhibits the commencement of the costal groove.

iii) *Tubercle*

The convex articular facet appears on the inferior margin. It is be more rounded and oriented to face infero-medially.

The non-articular ligamentous attachment is well developed and is located supero-laterally to the articular facet.

iv) *Angle*

The angle is well defined. The angle is located progressively more lateral to the tubercle as one moves from rib 3 to rib 7.

v) *Shaft*

The shaft is flattened perpendicular to the long axis of the rib and produces two surfaces (medial/internal and lateral /external) and two borders (superior and inferior).

Its cross-sectional area is elongated been wider in a supero-inferior direction than in the medio-lateral direction. The *iliocostalis thoracis* attachment is located progressively further distally along the shaft as one moves sequentially from rib3 to

rib 7. The superior border of the shaft is rounded and the inferior border is sharp. The costal groove is well defined on the internal and inferior surface and extends for a distance along the shaft.

3.2. Baboon (*Papio ursinus*)

The following observations were made on a representative sample of the *Papio ursinus*.

a) 1st rib

The general appearance of the 1st rib as observed in all the rib specimens is described below. (See Figures 3.5. and 3.6)

i) *Head*

The head exhibits a single convex rounded facet. There is a rim of bone around the circumference of the head.

ii) *Neck*

The neck is rounded in its proximal half and is flattened in a cranio-caudal direction in its distal half. It is narrowing immediately distal to the head and widens as it approaches the shaft. The cranial surface of the neck is roughened and the caudal surface is smooth.

iii) *Tubercle*

The tubercle is well developed and exhibits a convex articular facet that is flattened in the horizontal plane i.e. the length is greater than the width. The articular facet faces posteriorly and slightly medially. There is a slightly developed non-articular part lateral to the articular facet for the lateral costo-transverse ligament. The tubercle lies cranial to the head relative to the horizontal plane.

iv) *Angle*

The angle coincides with the tubercle. The angle that is produced by the neck with the shaft appears to be slightly more obtuse than that observed in the human 1st rib.

v) *Shaft*

The shaft is flattened in a cranio-caudal direction.

Its distal third is wider than the proximal two-thirds. The distal third also is at an angle so that the cranial surface faces cranio-laterally. The cranial surface is smooth. The caudal surface exhibits, medially, a shallow and wide groove that extends for three quarters of the length of the shaft. The internal or medial margin does not show the scalene tubercle.

v) *Costal pit*

The costal pit is a wide oval concavity that articulates, via a costal cartilage, to the manubrium of the sternum.



 = 1cm

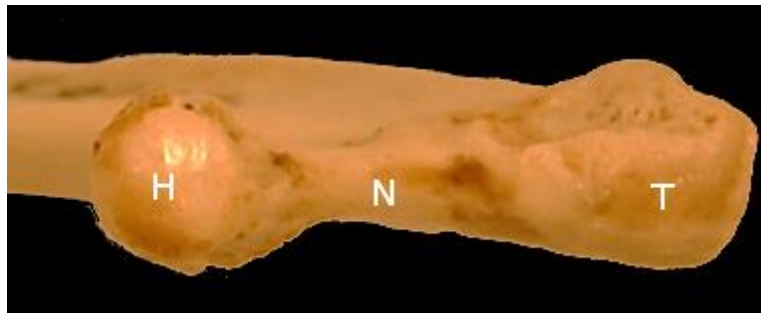
(a)



(b)

Figure 3.5: a) Cranial view of the *Papio ursinus* right 1st rib.

b) Caudal view of the *Papio ursinus* right 1st rib.



 = 1cm

Figure 3.6: The vertebral end of the *Papio ursinus* 1st rib showing the head (H), neck (N) and tubercle (T).

b) 2nd rib

i) *Head*

The head is round. There are two convex articular facets on the head separated by a slight protruding crest of the head

ii) *Neck*

The neck is rounded. Proximally on the cranial rim of the neck is a tubercle of bone that extends cranially.

iii) *Tubercle*

The convex articular facet of the tubercle is oval and oriented in a postero-caudal direction. The non-articular ligamentous attachment is located further distally and on the infero-lateral aspect of the tubercle.

iv) *Angle*

There is a slight angle distal to the tubercle.

v) *Shaft*

The shaft is flattened obliquely. The external surface faces cranio-laterally. It is smooth along its length except for a slight proximal roughened area for the attachment of the *iliocostalis thoracis* muscle. The internal surface has a deep costal groove extending from the articular facet of the tubercle to the middle of the shaft.

The cranial border is round. The caudal border is sharp due to the “bony overhang” of the costal groove (Figure 3.7).

c) Ribs 3 to 7

These ribs appear elongated when viewed from a cranial aspect. The thoracic shape that is outlined by the ribs is one where the antero-posterior width is greater than the medio-lateral width (See Figure 3.8).

i) *Head*

The triangular shaped head exhibits two convex articular facets separated by a slight crest of the head. The proximal part of the head has a sharp pointed “arrowhead tip” that will extend into the intervertebral space of the adjacent thoracic vertebrae.

ii) *Neck*

The neck is flattened in an antero-posterior direction, thus producing two surfaces (anterior and posterior) as well as two borders (cranial/crest of the neck and caudal). The anterior surface is smooth. The posterior surface is roughened for the attachment of the costo-vertebral ligament. It is medio-laterally elongated and lies in the horizontal plane. The crest of the neck is sharp. The caudal border is sharp.



(a)



(b)



Figure 3.7: a) Cranial view of the *Papio ursinus* left 2nd rib.

b) Caudal view of the *Papio ursinus* left 2nd rib.

iii) *Tubercle*

The tubercle has a concave articular facet that is oriented postero-medially. The non-articular roughened area for the ligamentous attachment is located infero-lateral to the articular facet. The neck and the shaft meet at a well defined angle at the tubercle.

iv) *Angle*

The angle is clearly defined.

v) *Shaft*

The shaft is flattened obliquely and appears triangular in cross-section.

The apex of the triangle forms the cranial border of the shaft and the caudal border/base is formed by a deep, well developed costal groove. The bony overhang is well developed and sharp and extends from the caudal border. The attachment of the *iliocostalis thoracis* muscle is visible on its external surface. The elevation produced by the attachment lies at an angle relative to the vertical axis of the shaft of the rib.



Figure 3.8: *Papio ursinus* 1st to 7th ribs (from top to bottom, Cranial view, Right side).

3.3. Chimpanzee (*Pan troglodytes*)

a) 1st rib

The 1st rib of the chimpanzee appears very human-like when viewed from the cranial and caudal aspects (Figure 3.9).

i) *Head*

The head has two well developed oval shaped convex articular facets that are separated by a crest of the head. The cranial facet appears smaller than the caudal facet. The crest of the head lies in a transverse plane, almost parallel to the longitudinal axis of the shaft of the rib. The angle between the two facets is acute. The cranial facet articulates with the costal demifacet of cervical vertebra 7.

ii) *Neck*

The neck is elongated and rounded. On the anterior surface of the neck is a line of continuation from the medial margin of the shaft of the rib. This line splits the neck into a cranial and caudal surface. On its postero-cranial surface, the neck exhibits a roughened attachment site for costo-vertebral ligaments. Distally and on the dorsal margin of the neck, a fossa is visible.

iii) *Tubercle*

The tubercle is well developed. There is a single large convex articular facet for the transverse process of the thoracic vertebra 1. A non-articular ligamentous attachment is visible immediately distal to the articular facet.

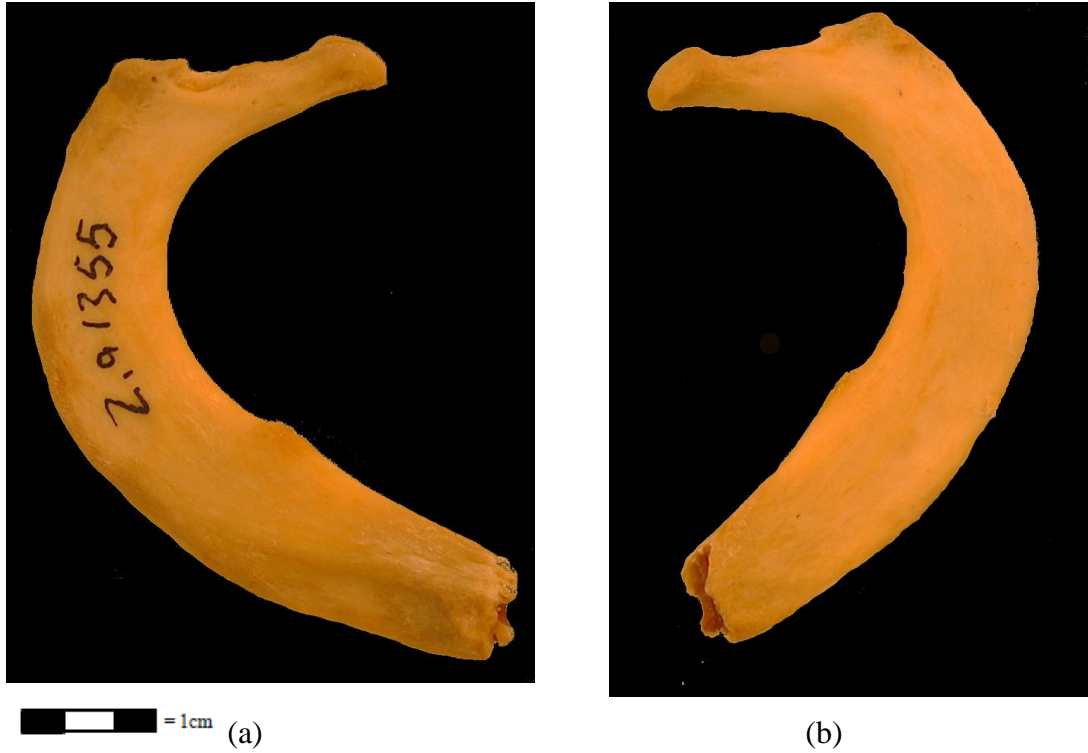


Figure 3.9: a) Cranial view of the *Pan troglodytes* right 1st rib.
 b) Caudal view of the *Pan troglodytes* right 1st rib.

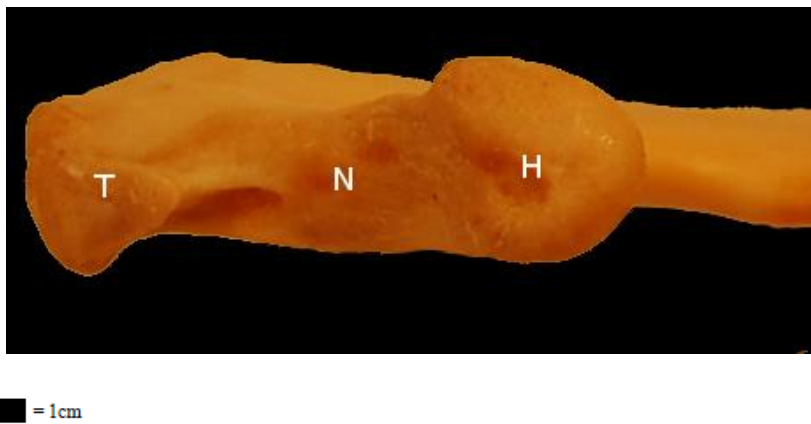


Figure 3.10: The vertebral end of the *Pan troglodytes* right 1st rib showing the head (H), neck (N) and tubercle (T).

The tubercle lies in a slightly more cranial position relative to the head when viewed in the same horizontal plane.

iv) *Angle*

The angle coincides with the tubercle. The angle appears more obtuse than that observed in human and baboon first ribs.

v) *Shaft*

The shaft is flattened in a cranio-caudal direction, resulting in 2 surfaces (cranial and caudal) and two margins (medial/internal and lateral/external). Both surfaces are smooth. The medial margin is concave and the lateral margin is convex. The margins are parallel to each other for the entire length of the shaft. Proximally on the lateral margin there is the *iliocostalis thoracis* muscle attachment. A tubercle that corresponds to the scalene tubercle of the human rib is visible on the cranio-medial margin of the 1st rib.

v) *Costal pit*

The costal pit is a round concavity that articulates, via a costal cartilage, to the manubrium of the sternum.

b) 2nd rib

i) *Head*

The head exhibits two concave facets separated by a visible crest of the head. The facets appear to be similar in size and shape.

ii) *Neck*

The neck is cranio-caudally flattened and elongated. The cranial surface is smooth. On its posterior surface is a ligamentous attachment area.

iii) *Tubercle*

The tubercle exhibits an oval, concave articular facet for the transverse process of the corresponding thoracic vertebra and a non-articular area for ligamentous attachment. The facet is located towards the posterior margin of the rib and oriented to face posteriorly. The ligamentous area is located cranial to the articular facet.

iv) *Angle*

The angle is visible as the juncture at which the neck of the rib changes direction to continue as the shaft.

v) *Shaft*

The shaft is obliquely flattened to produce two surfaces (cranial and caudal) and two margins (external and internal). The cranial surface is roughened. The caudal surface has a shallow costal groove that begins distal to the tubercle articular facet. The

external margin is convex and rounded. The internal margin is concave and sharp (Figure 3.11).

c) Ribs 3 to 7

i) *Head*

The head shows the presence of two oval concave articular facets separated by a well developed crest of the head. The cranial facet appears larger than the caudal facet.

The angle between the facets is acute and produces a sharp, arrow-head pointed proximal tip of the head, similar to that observed in gorilla.

ii) *Neck*

The neck is narrow and elongated. It is flattened in an antero-posterior plane, producing two surfaces (anterior/internal and posterior/external) as well as two borders (cranial/crest of the neck and caudal). The anterior surface is smooth. The posterior is roughened for the attachment of the costo-vertebral ligament. The crest of the neck is round. The caudal border has the commencement of the costal groove.

The angle between the neck and shaft at the tubercle is obtuse.

iii) *Tubercle*

The tubercle is located on the posterior margin of the rib. There is a well defined concave articular facet for the transverse process of the corresponding vertebra. The facet is oriented to face posteriorly. A non-articular ligamentous process lies lateral to the articular facet.



(a)



(b)



Figure 3.11: a) Cranial view of the *Pan troglodytes* right 2nd rib.
b) Caudal view of the *Pan troglodytes* right 2nd rib.

iv) *Angle*

The posterior angle is well defined and has the *iliocostalis thoracis* line related to it.

The distance between the tubercle and the angle increases from ribs 3 to 7.

v) *Shaft*

In cross-section, the shaft is flattened in the vertical plane to produce two surfaces (external and internal) and two borders (cranial and caudal). The external surface is convex and slightly roughened. The internal surface is concave and smooth. It has the continuation of the costal groove from the neck region. The cranial border is round. The caudal border is flattened with the bony extension of associated with the costal groove becoming more pronounced as one progresses distally along the shaft (See Figure 3.12.)



Figure 3.12: *Pan troglodytes* 1st to 7th ribs (from top to bottom, Cranial view, Right side).

3.4. Gorilla (*Gorilla gorilla*)

a) 1st rib

i) *Head*

The head has two well developed oval shaped convex articular facets that are separated by a well developed crest of the head. The cranial facet appears smaller than the caudal facet. The angle between the two facets is acute. The crest of the head lies in a transverse plane, almost parallel to the longitudinal axis of the shaft of the rib (Figure 3.13).

ii) *Neck*

The neck is short and rounded. The neck has a cranial and caudal surface as well as anterior and posterior margins. The cranial and caudal surfaces appear smooth. On its postero-cranial surface, the neck exhibits a roughened attachment site for costo-vertebral ligaments.

iii) *Tubercle*

The tubercle is well developed. There is a single large convex articular facet for the transverse process of the thoracic vertebra 1. No clearly defined non-articular ligamentous attachment is visible.

The tubercle lies in a slightly more cranial position relative to the head when viewed in the same horizontal plane.

iv) *Angle*

The angle coincides with the tubercle.

v) *Shaft*

The shaft is flattened in a cranio-caudal direction, resulting in two surfaces (cranial and caudal) and two margins (medial/internal and lateral/external) (Figure 3.14). Both surfaces are smooth. Proximally on the lateral margin there is the *iliocostalis thoracis* muscle attachment. The internal margin is concave and the external margin is convex. The margins are parallel to each other for the entire length of the shaft. No scalene tubercle is visible on the internal margin.

v) *Costal pit*

The costal pit is a wide oval concavity that articulates, via a costal cartilage, to the sternum.

b) 2nd rib

i) *Head*

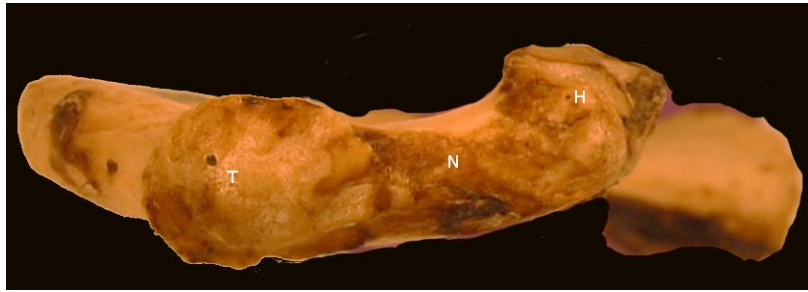
The head exhibits two concave facets separated by a well developed crest of the head. The facets appear to be similar in size and shape.

ii) *Neck*

The neck is antero-posteriorly flattened and short. The anterior surface is smooth. On its posterior surface is a ligamentous attachment area.



(a)



(b)



Figure 3.13: a) Postero-medial view of the *Gorilla gorilla* right 1st rib.
b) The vertebral end of the *Gorilla gorilla* right 1st rib showing the head (H), neck (N) and tubercle (T).



(a)



(b)

 = 1cm

Figure 3.14: a) Cranial view of the *Gorilla gorilla* right 1st rib.

b) Caudal view of the *Gorilla gorilla* right 1st rib.

iii) *Tubercle*

The tubercle exhibits a well developed oval, concave articular facet for the transverse process of the corresponding thoracic vertebra and a non-articular area for ligamentous attachment. The facet is located towards the caudal edge of the rib and oriented to face postero-medially. The ligamentous area is located cranial to the articular facet.

iv) *Angle*

The angle is visible as the juncture at which the neck of the rib changes direction to continue as the shaft.

v) *Shaft*

The shaft is obliquely flattened to produce two surfaces (external and internal) and two borders (cranial and caudal). The external surface is convex and faces cranio-laterally. The internal surface is concave and has a shallow costal groove that begins distal to the tubercle articular facet. The cranial border is rounded whereas the caudal border is sharp



(a)



(b)

 = 1cm

Figure 3.15: a) Cranial view of the *Gorilla gorilla* right 2nd rib.

b) Caudal view of the *Gorilla gorilla* right 2nd rib.

c) Ribs 3 to 7

i) *Head*

The head shows the presence of two oval concave articular facets separated by a well developed crest of the head. The cranial facet appears larger than the caudal facet.

The angle between the facets is acute and produces a sharp, arrow-head-like pointed proximal tip of the head.

ii) *Neck*

The neck is short and broad. It is flattened in an antero-posterior plane, producing two surfaces (anterior/internal and posterior/external) as well as two borders (cranial/crest of the neck and caudal). The anterior surface is smooth. The posterior is roughened for the attachment of the costo-vertebral ligament. The crest of the neck is round. The caudal border has the commencement of the costal groove.

iii) *Tubercle*

The tubercle is located on the caudal margin of the rib. There is a well defined concave articular facet for the transverse process of the corresponding vertebra. The facet is oriented to face infero-medially. A well developed non-articular ligamentous process lies lateral to the articular facet.

iv) *Angle*

The posterior angle is well defined and has the *iliocostalis thoracis* line related to it.

v) *Shaft*

In cross-section, the shaft is flattened in the vertical plane to produce two surfaces (external and internal) and two borders (cranial and caudal). The external surface is convex and slightly roughened. The internal surface is concave and smooth. It has the continuation of the costal groove from the neck region. The cranial border is round. The caudal border is flattened with the bony extension of associated with the costal groove becoming more pronounced as one progresses distally along the shaft (Figure 3.16).



 = 1cm

Figure 3.16: *Gorilla gorilla* 1st to 7th ribs (from top to bottom, Cranial view, Right side).

3.5. Impala (*Aepyceros melampus*)

See Figure 3.17 for the vertebro sternal ribs of the impala.

a) 1st rib

i) *Head*

The round head has two semicircular, convex articular facets separated by a crest of the head. The crest of the head lies in a plane almost perpendicular to the longitudinal axis of the shaft of the rib.

ii) *Neck*

The neck is round. The dorsal aspect of the neck has a deep concavity produced by the large articular part of the tubercle. The neck meets the shaft at an angle that is obtuse; approximately 130°.

iii) *Tubercle*

The tubercle is well developed and extends markedly from the junction between the neck and shaft of the rib. It has a large single convex facet that is round in shape. It is situated on the dorsal margin of the rib.

iv) *Angle*

The tubercle and the angle coincide. No attachment of *iliocostalis* muscle visible.

v) *Shaft*

The shaft is obliquely flattened and produces two surfaces (cranial and caudal) and two margins (medial/internal and lateral/external). The shaft is straight for its dorsal/proximal half to two-thirds. There is a twist in the shaft distally/ventrally and it is here that it then starts to bend medially. The ventral/distal half to one third of the cranial surface is everted cranio-laterally. The dorsal/proximal half of the shaft is narrow. The ventral/distal half widens medio-laterally as it approaches the costal pit. The medial margin is concave and the lateral margin is convex.

The thorax shape in cross-section, produced by the elongated shaft, is that it longer than it is wider.

vi) *Costal pit*

The costal pit is flattened and medio-laterally elongated.

b) 2nd rib

i) *Head*

The head is round with two convex facets separated by the crest of the head. The cranial facet is smaller than the caudal facet. The crest is orientated parallel to the long axis of the shaft.

ii) *Neck*

The neck is flattened cranio-caudally. The cranial surface is rough as compared to the caudal surface. The dorsal margin is sharp and longer than the ventral margin. The ventral margin is rounded.

iii) *Tubercle*

The round concave articular facet faces dorso-caudally. The well developed non-articular ligamentous attachment is located dorso-lateral to the articular facet. The tubercle lies more cranial than the head.

iv) *Angle*

The angle coincides with the *iliocostalis thoracis* line and is located distal to the tubercle.

v) *Shaft*

The shaft is flattened in a cranio-caudal direction. The cranial surface is cranio-laterally everted. The ventral surface has, on its proximal half and medial, a shallow costal groove on its lateral edge.

The shaft is slightly narrower dorsally and proximal to the angle (iliocostal line) and wider along the distal length of the shaft. The medial and lateral margins are sharp and parallel to each other.

c) Ribs 3 to 7

i) *Head*

The round head has two convex articular facets separated by a crest of the head. The head is oriented medially.

ii) *Neck*

The neck has two surfaces (cranial and ventro-caudal) separated by two margins (dorsal and ventral). The cranial surface is rough and has a slight depression that is continuous with the costal groove on the cranial surface of the shaft. The ventro-caudal surface is smooth. The dorsal margin is rounded. The ventral margin is sharp.

iii) *Tubercle*

The concave articular facet is round in shape and oriented to face dorsally. It has the non-articular ligamentous attachment locate dorso-cranially. The tubercle lies more cranial than the head.

iv) *Angle*

The posterior angle occurs distal to the tubercle and coincides with the *Iliocostalis thoracis* line.

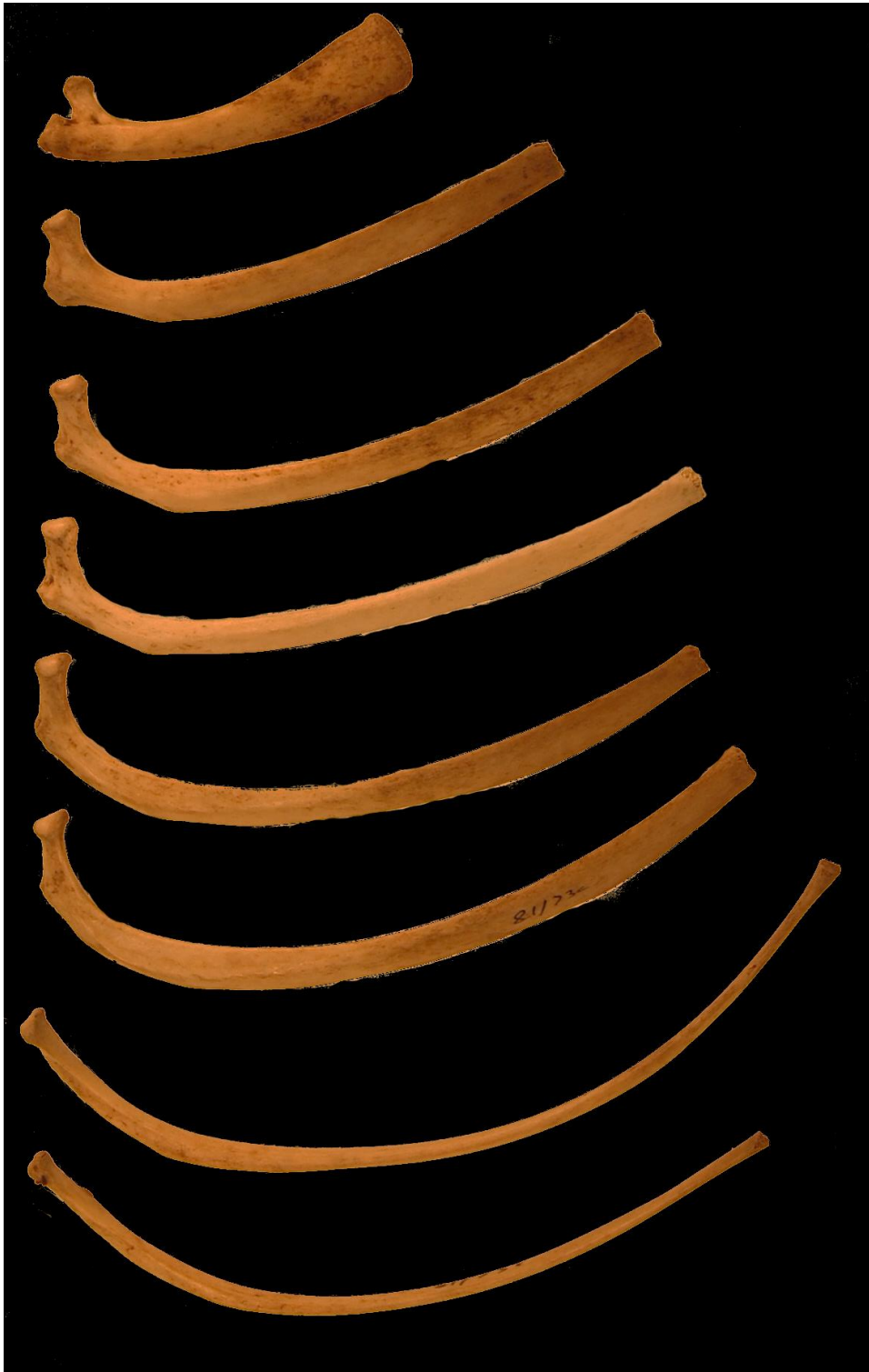


Figure 3.17: *Aepyceros melampus* 1st to 8th ribs (from top to bottom, Cranial view, Right side).

v) *Shaft*

The shaft is cranio-caudally flattened with two surfaces (medial and lateral) and two margins (cranial and caudal). The lateral surface is cranio-laterally everted.

Proximally and medially it has a shallow costal groove visible. The medial surface has, on its proximal half, a deep costal groove on its ventral edge that extends for half the length of the shaft. The costal groove commences at the tubercle articular facet.

The shaft is slightly narrower dorsally and proximal to the angle (iliocostal line) and wider along the distal length of the shaft. The cranial and caudal margins are sharp and parallel to each other.

vi) *Costal pit*

The costal pit is rounded to oval in shape.

3.6. Leopard (*Panthera pardus*)

See Figure 3.18 for the ribs of the leopard.

a) 1st rib

i) *Head*

The head is rounded with two convex articular facets separated by a crest of the head.

ii) *Neck*

The neck is oval in cross-section and short. The dorsal margin of the neck has a deep concavity between the head and tubercle. The ventral margin is straight. The neck widens from medial to lateral.

iii) *Tubercle*

The tubercle is prominent, projecting from the dorsal junction of the neck and shaft. The articular facet is oval in shape and convex. The non-articular ligamentous attachment is ventro-lateral to the articular facet.

iv) *Angle*

The angle coincides with the tubercle. The neck meets that shaft at the tubercle at an obtuse angle, i.e. greater than 90° .

v) *Shaft*

The proximal 1/5 and the distal 1/5 of the shaft is flattened in a cranio-caudal direction. The intermediate 3/5 is rounded. The distal end widens at the costal pit and is cranio-laterally everted. The medial/internal margin is concave and the lateral/external margin is convex. Neither costal groove nor scalene tubercle is visible.

vi) Costal Pit

The costal pit is oval in shape and large. It is obliquely flattened been cranio-caudally narrower and medio-laterally wider.

b) 2nd rib

i) *Head*

The head is rounded and has two convex facets separated by a well defined crest.

ii) *Neck*

The neck is short and flattened in a cranio-caudal direction. The cranial surface has a slight bony projection. It widens as it approaches the shaft at the tubercle.

iii) *Tubercle*

The tubercle articular facet is well developed, concave and dorso-medially oriented.

The non-articular ligamentous process is ventro-lateral to the articular facet.

iv) *Angle*

The angle coincides with the tubercle. The neck meets that shaft at the tubercle at an obtuse angle, i.e. greater than 90⁰.

v) *Shaft*

The shaft is flattened, proximally in a cranio-caudal direction and distally in a medio-laterally direction. A twist (torsion) is visible at the mid-shaft region to separate the

cranio-caudal from the medio-lateral oriented parts. The shaft is oval and elongated in cross section. The medial/internal margin is concave but this concavity is shallow as compared to the first rib. Thus the shaft appears straighter than it is curved.

c) Ribs 3 to 7

i) *Head*

The head has an arrowhead shape with two convex facets separated by a well defined crest.

ii) *Neck*

The neck is short and cubicle in cross-section. It has 4 surfaces viz. cranial, caudal, dorsal and ventral. The cranial and ventral surfaces are smooth. The caudal and dorsal surfaces are roughened.

iii) *Tubercle*

The articular facet is oval, concave and dorso-medially oriented. The non-articular ligamentous attachment is well developed.

iv) *Angle*

The distance between the tubercle and the neck increases from ribs 3 to 7.

v) *Shaft*

The shaft is cranio-caudally flattened proximally and rounded distally. The cranial surface is flat. A shallow costal groove is visible on the caudal surface. The groove commences distal to the articular facet of the tubercle. The groove has a caudally protruding lateral lip of bone. The medial/internal margin is round and concave but this concavity is deeper as compared to the first or second rib. The lateral margin is flattened.

vi) *Costal pit*

The costal pit is round.



 = 1cm

Figure 3.18: *Panthera pardus* 1st to 7th ribs (from top to bottom, Cranial view, Right side).

3.7. Domestic Dog (*Canis lupus familiaris*)

See Figure 3.19 for the ribs of the dog.

a) 1st rib

i) *Head*

The head is round and has two convex facets separated by an ill-defined crest of the head.

ii) *Neck*

The neck is short and rounded. The dorsal margin has the deep concavity separating the head from the tubercle. The neck meets the shaft at an obtuse angle.

iii) *Tubercle*

The tubercle is well developed and larger than the head. The articular facet is convex and oval in shape. The non-articular ligamentous attachment is reduced and located ventro-lateral to the articular facet. The head and tubercle lie in the same transverse plane.

iv) *Angle*

The angle and the tubercle coincide.

v) *Shaft*

The shaft is straight except for its distal end that bends internally/medially towards the costal pit. The shaft is round in cross-section. A deep groove is visible caudally where the neck meets the shaft.

vi) *Costal pit*

The costal pit is round.

b) 2nd rib

i) *Head*

The head is round with two convex articular facets separated by a well defined crest of the head.

ii) *Neck*

The neck is short and rounded. The dorsal aspect still exhibits the deep concavity between the head and tubercle. The neck meets the shaft at an acute angle.

iii) *Tubercle*

The tubercle and head are to be similar in size. The articular facet is convex, oval and oriented to face dorso-medially.

iv) *Angle*

The angle occurs distal to the tubercle.

v) *Shaft*

The shaft is flattened. Proximally it has two surfaces (cranial and caudal) and two margins (medial/internal and lateral/external). Distally, the shaft has a twist (torsion) that changes the orientation of the shaft i.e. has two surfaces (medial/internal and lateral/external) and two margins (cranio-medial and caudo-lateral). The internal surfaces are smooth. The internal margin is more concave than that of the 1st rib. The resultant cross-sectional thoracic shape is one that is dorso-ventrally elongated and medio-laterally narrow.

vi) *Costal pit*

The costal pit is rounded to oval and elongated.

c) Ribs 3 to 7

i) *Head*

The head is round with two convex facets separated by a crest of the head. The head and the tubercle lie in the same transverse plane.

ii) *Neck*

The neck is short and flattened in a cranio-caudal direction producing two surfaces (cranial and caudal) and two margins (dorsal and ventral). The cranial surface and the dorsal margin are rough. The caudal surface and the ventral margin are smooth.

iii) *Tubercle*

The articular facet of the tubercle is oval and convex. It is oriented dorso-medially.

The non-articular ligamentous attachment is distal to the articular facet.

iv) *Angle*

The angle is distal to the tubercle. The distance between the tubercle and the angle increases from rib 3 to 7.

v) *Shaft*

The shaft is flattened to form two surfaces (internal and external) and two margins (medial and lateral). The shaft is proximally flattened in a cranio-caudal direction and distally flattened medio-laterally. The external surface is rough when compared to the internal surface. A costal groove is not that well defined on the cranial or caudal surface. The internal margin is concave and the external is convex.

vi) *Costal pit*

The costal pit is rounded to oval and elongated.

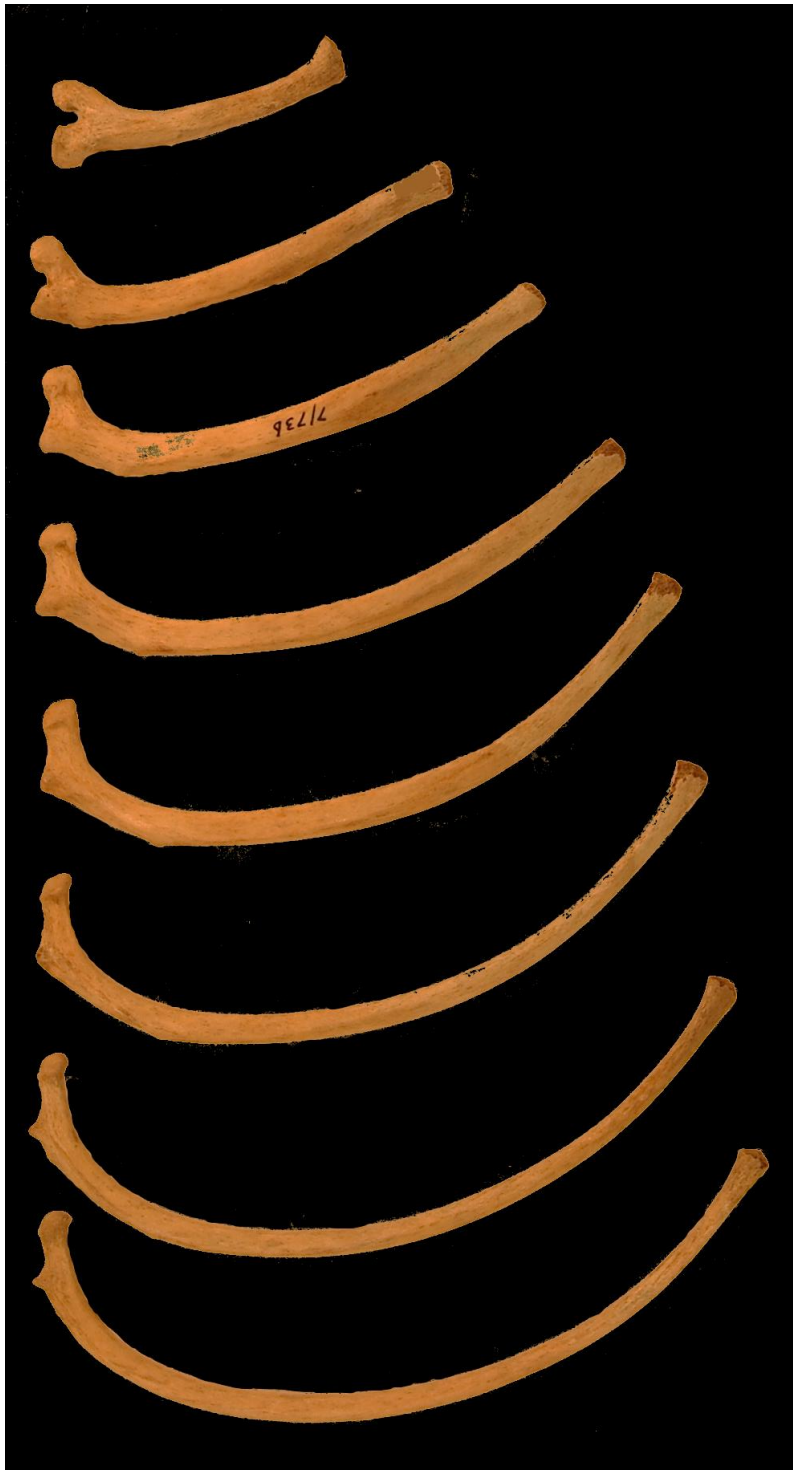


Figure 3.19: *Canis lupus familiaris* 1st to 7th ribs (from top to bottom, Cranial view, Right side).

3.8. Domestic Pig (*Sus domesticus*)

See Figure 3.20 for the vertebro-sternal ribs of the pig.

a) 1st rib

i) *Head*

The head is round and has two convex facets separated by an ill-defined crest of the head.

ii) *Neck*

The neck is short and rounded. The dorsal margin and cranial aspect shows a deep concavity separating the head from the tubercle. The neck meets the shaft at an obtuse angle.

iii) *Tubercle*

The tubercle is well developed and larger than the head. The articular facet is convex and oval in shape. The non-articular ligamentous attachment is visible and located distally and ventro-lateral to the articular facet. The head lies more caudal relative to the tubercle when observed in the transverse plane.

iv) *Angle*

The angle and the tubercle coincide.

v) *Shaft*

The shaft is straight except for its distal end that bends slightly internally/medially towards the costal pit. The shaft is very wide and is obliquely flattened in a medio-lateral direction along its entire length.

vi) *Costal pit*

The costal pit is oval and obliquely flattened.

b) 2nd rib

i) *Head*

The head is round with two convex articular facets that are separated by a slight groove dorsally and a crest of the head medially.

ii) *Neck*

The neck is short, broad and flattened. The dorsal aspect exhibits the deep concavity between the head and tubercle. The neck meets the shaft at an obtuse angle.

iii) *Tubercle*

The tubercle is smaller in size than the head. The articular facet is convex, oval and oriented to face dorso-medially. A non-articular ligamentous attachment is visible

iv) *Angle*

The angle occurs distal to the tubercle.

v) *Shaft*

The shaft is flattened and has two surfaces (external and internal) and two margins (cranio-medial and caudo-lateral). The shaft is narrow in a medio-lateral direction and broad in a cranio-caudal direction. The internal surfaces are smooth. The concavity outlined by the cranio-medial margin is very shallow.

The resultant cross-sectional thoracic shape is one that is dorso-ventrally elongated and medio-laterally narrow.

vi) *Costal pit*

The costal pit is rounded to oval and elongated.

c) Ribs 3 to 7

i) *Head*

The head is round with two convex facets separated by a slight cleft of the head. The head is located further cranially than the tubercle in the transverse plane.

ii) *Neck*

The neck is short and flattened. The cranial surface and the dorsal margin are rough.

The caudal surface and the ventral margin are smooth.

iii) *Tubercle*

The articular facet of the tubercle is oval and convex. It is smaller than that of the head. It is oriented dorso-medially. The non-articular ligamentous attachment is distal

to the articular facet and partially developed. There is a concavity located immediately distal to the ligamentous attachment.

iv) *Angle*

The angle is distal to the tubercle. The distance between the tubercle and the angle increases from rib 3 to 7.

v) *Shaft*

The shaft is flattened to form two surfaces (internal and external) and two margins (cranial and caudal). The shaft is proximally thicker. The external surface is rough when compared to the internal surface. A costal groove is clearly visible on the cranial as well as the caudal surfaces and commences at the neck of the rib. The groove is progressively better defined from rib 3 to 7. The internal margin is concave and the external is convex.

vi) *Costal pit*

The costal pit is rounded to oval and elongated.



 = 1cm

Figure 3.20: *Sus domesticus* 1st to 7th ribs (from top to bottom, Cranial view, Right side).

3.9. Spotted hyena (*Crocuta crocuta*)

Figure 3.21 shows the ribs of the spotted hyena.

a) 1st rib

i) *Head*

The head is round and has two convex facets separated by an ill-defined crest of the head.

ii) *Neck*

The neck is elongated and rounded. The dorsal margin has the deep concavity separating the head from the tubercle. The cranial aspect has osseous elevations that provide for the attachment of ligaments. The neck meets the shaft at an obtuse angle. The neck is wider distally.

iii) *Tubercle*

The tubercle is well developed and larger than the head. The articular facet is convex and oval in shape. The non-articular ligamentous attachment is well developed and located distally and ventro-lateral to the articular facet. The head and tubercle lie in the same transverse plane.

iv) *Angle*

The angle and the tubercle coincide.

v) *Shaft*

The shaft is straight except for its distal end that bends slightly internally/medially towards the costal pit. The shaft is slightly flattened in a cranio-caudal direction, proximally and is slightly flattened in a medio-lateral direction, distally. On the caudal surface there exists a line that is continuous distally with the caudal margin of the rib.

vi) *Costal pit*

The costal pit is oval.

b) 2nd rib

i) *Head*

The head is round with two convex articular facets that are separated by a well defined groove. There is no crest of the head.

ii) *Neck*

The neck is short and rounded. The dorsal aspect still exhibits the deep concavity between the head and tubercle. The neck meets the shaft at an acute angle.

iii) *Tubercle*

The tubercle and head are to be similar in size. The articular facet is convex, oval and oriented to face dorso-medially. A well developed non-articular ligamentous attachment is visible.

iv) *Angle*

The angle occurs distal to the tubercle.

v) *Shaft*

The shaft is flattened more distally than proximally. Proximally it has two surfaces (cranial and caudal) and two margins (medial/internal and lateral/external). Distally, the shaft has a twist (torsion) that changes the orientation of the shaft i.e. has two surfaces (medial/internal and lateral/external) and two margins (cranio-medial and caudo-lateral). The internal surfaces are smooth. The internal margin is more concave than that of the 1st rib. The resultant cross-sectional thoracic shape is one that is dorso-ventrally elongated and medio-laterally narrow.

c) Ribs 3 to 7

i) *Head*

The head is round with two convex facets separated by a crest of the head as well as a slight cleft of the head. The head and the tubercle lie in the same transverse plane.

ii) *Neck*

The neck is short and rounded. The cranial surface and the dorsal margin are rough.

The caudal surface and the ventral margin are smooth.

iii) *Tubercle*

The articular facet of the tubercle is oval and convex. It is oriented dorso-medially.

The non-articular ligamentous attachment is distal to the articular facet and is well developed.

iv) *Angle*

The angle is distal to the tubercle. The distance between the tubercle and the angle increases from rib 3 to 7.

v) *Shaft*

The shaft is flattened to form two surfaces (internal and external) and two margins (medial and lateral). The shaft is proximally thicker and flattened in a cranio-caudal direction. Distally it is thinner flattened medio-laterally. The external surface is rough when compared to the internal surface. A costal groove is clearly visible on the caudal surface and commences at the neck of the rib. The groove is progressively better defined from rib 3 to 7. The internal margin is concave and the external is convex.

vi) *Costal pit*

The costal pit is rounded to oval and elongated.



Figure 3.21: *Crocuta crocuta* 1st to 7th ribs (left to right, Cranial view, Right side.)

Table 3.1: Summary of the osteological features of the vertebro-sternal ribs in extant species.

		Species							
		Human	Baboon	Chimpanzee	Gorilla	Impala	Leopard	Domestic dog	Domestic pig
Osteological feature of the 1st rib	Number of facets on head	1		2					
	Head Shape	Round and flat		Pointed “arrow head tipped”		Round; Knob-like			
	Crest of the head	No crest		Well developed		Visible			
	Neck shape	Round	Round and narrow proximally; flattened and widens distally	Round; fossa visible on dorsal margin	Round/oval	Cylindrical, Deepened concavity on the dorsal aspect			
	Neck length	Elongated			Short				

		Species									
		Human	Baboon	Chimpanzee	Gorilla	Impala	Leopard	Domestic dog	Domestic pig	Spotted hyena	
Osteological feature of 1 st rib	Angle of neck and shaft at tubercle	Obtuse; approximately 110°		Obtuse; > than 110° but < 135°		Obtuse	Obtuse; approximately 110°	Obtuse;> 135°			
	Angle	Coincides with tubercle									
	Tubercle size	Narrow; Flattened			Large						
	Tubercle prominence	Clearly identifiable			Very well developed process						
	Shape of tubercle articular	Oval/circular	Flattened	Oval/circular	Oval	Round; Knob-like					
	Position of tubercle articular	Infero-lateral				Dorso-lateral					
	Orientation of tubercle articular	Postero-medial			Dorsal	Dorso-medial	Dorsal				

		Species								
		Human	Baboon	Chimpanzee	Gorilla	Impala	Leopard	Domestic dog	Domestic pig	Spotted hyena
Osteological feature of 1 st rib	Shaft orientation	Flattened supero-inferiorly; horizontal; curved	Flattened cranio-caudally; horizontal; proximally oblique; distally; curved	Flattened cranio-caudally; horizontal; curved		Flattened ; narrow dorsal half; widens and bends ventrally	Intermediate 3/5 rounded; curved ventrally	Round; dorsally straight then curves ventrally;	Flattened; narrow dorsal half; widens and curves ventrally	Flattened dorsal 1/4; Cylindrical and straight ventral 3/4
	Scalene tubercle	Present	Absent	Present	Absent					
	Shaft width from proximal to distal	Uniform	Narrow proximal; Widens distally	Uniform	Widens as the costal pit is approached	Narrow dorsally; widens substantial ventrally	Narrow dorsally; widens ventrally		Narrow dorsally; widens ventrally	Wide dorsally; narrows ventrally
	Costal Groove	Absent	Present	Absent						
	Costal groove depth	NA	Shallow	NA						

		Species							
		Human	Baboon	Chimpanzee	Gorilla	Impala	Leopard	Domestic dog	Domestic pig
Osteological feature of the 2nd to 7th rib	Number of facets on head	2							
	Head Shape	Saddle shaped; obtuse angle	Round	Pointed arrow-head; acute angle between facets		Rounded			
	Crest of the head	Visible	Visible	Well developed					
	Neck shape	Flattened antero-posteriorly			Flattened and thick	Deepened dorsal concavity separates head from tubercle			
	Neck length	Elongated in 2 nd ; Short and broad form 3 rd to 7 th	Elongated and narrow		Elongated in 2 nd to 4 th ; shorter and broader 5 th to 6 th	Short and Cylindrical			

		Species								
		Human	Baboon	Chimpanzee	Gorilla	Impala	Leopard	Domestic dog	Domestic pig	Spotted hyena
Osteological feature of 2nd to 7th rib	Angle of neck and shaft at tubercle	Obtuse > 90° but less than 135°				Obtuse closer to 180° in 2 nd to 4 th ; less obtuse in 5 th to 7 th				
	Tubercle shape	Wide	Flattened			Round				
	Tubercle prominence	Clearly identifiable	Very Prominent	Clearly identifiable	Well developed and knob like				Knob-like on 2 nd ; flattened on 3 rd to 7 th	
	Shape of tubercle articular facet	Oval/Round								
	Position of tubercle articular facet	Postero-inferior								

		Species								
		Human	Baboon	Chimpanzee	Gorilla	Impala	Leopard	Domestic dog	Domestic pig	Spotted hyena
Osteological feature of 2nd to 7th rib	Orientation of tubercle articular facet	Postero-medial/dorso medial								
	Angle	Progressively further distal to tubercle								
	Shaft orientation	Oblique in 2 nd ; Perpendicular to long axis from 3 rd to 7 th	Oblique and becoming progressively perpendicular to long axis 2 nd to 7 th	Oblique from 2 nd to 7 th	Oblique in 2 nd ; Perpendicular to long axis from 3 rd to 7 th	Oblique; cranio-medially inverted	Oblique from 2 nd to 7 th	Oblique from 2 nd to 7 th	Oblique; cranio-laterally everted	Oblique from 2 nd to 7 th
	Shaft features (proximal to distal)	Uniform width; deep concave internal margin; rounded cranial margin				Shallow concave internal surface; sharpened cranial and caudal margins				

		Species								
		Human	Baboon	Chimpanzee	Gorilla	Impala	Leopard	Domestic dog	Domestic pig	Spotted hyena
Osteological feature of 2nd to 7th rib	Costal Groove	Present; ends mid way of shaft			Present on both edges of rib			Present; ends mid way of shaft		
	Costal Groove depth	Shallow in 2 nd ; deepens in 3 rd to 7 th								

CHAPTER 4 – THE METRIC STUDY OF THE PRIMATE RIB

4.1. Non-Human Primate sample

4.1.1. Measurements of non-human primates

The sample size, mean value and standard deviation for each measurement from each group are contained in Tables 4.1 to 4.4.

The ANOVA and ANCOVA values and significant levels for the measurements are contained in Tables 4.6 to 4.9.

Results for the measurements of non-human primates between the sexes in each species of non-human primates

In all the ribs of the non-human primates analysed, viz. ribs 1, 2, 4 and 7, the majority of the linear measurements was found to exhibit a statistically significant sexual dimorphism.

The following measurements however did not show statistical significant sexual dimorphism for all the non-human primate species:

- (a) Neck (A-P diameter) at Tubercle (NTA) in the second rib and
- (b) Shaft maximum height at dorsal angle (SHPA) of the fourth and the seventh ribs.

A significant sexual difference was also observed in the following measurements for specific species:

- (a) Neck length (NL) of the first rib in baboon and
- (b) Head Cranial facet width (HSW) of the seventh rib in the baboon sample and the gorilla.

Refer to Table 4.11 that shows the sexual differences between the different population groups (After rank analysis due to significant interaction between population and sex)

For the first rib, a significant difference was observed between the sexes in the baboon sample in the measurement of the Neck length (NL) (see Table 4.11).

The female gorilla showed a significant difference when compared to the female baboon sample and chimpanzee sample in the measurement of the Neck length (NL) (see Table 4.12).

No significant difference between the males of the different species was observed in the measurement of the Neck length (NL) (see Table 4.13).

For the seventh rib, a significant difference was observed between the sexes in the baboon sample and in the gorilla in the measurement of the Head Cranial facet width (HSW) (See Table 4.11).

A significant difference between the female baboon sample and female gorilla existed in the measurement of the Head Cranial facet width (HSW) (see Table 4.12).

A significant difference between the males of the baboon sample and the gorilla and chimpanzee sample was observed in the measurement of the Head Cranial facet width (HSW) (See Table 4.13).

Comparisons between the species of non-human primates for each of the ribs analysed

The first rib As would be expected, given actual body size differences, the gorilla group exhibited the largest means all the measurements of the first rib followed by the chimpanzee sample and then the baboon sample.

The non-human primate species were significantly different from each other in the following measurements:

- (a) Head Cranial facet height (HSH);
- (b) Head Cranial facet width (HSW);
- (c) Neck (Cranial-Caudal diameter) at Tubercle (NT);
- (d) Neck (Ventral-Dorsal diameter) at Head (NHA) and
- (e) Neck (Ventral-Dorsal diameter) at Tubercle (NTA).

The gorilla and orangutan sample was significantly different from the baboon and vervet samples in the measurement of the Neck (Cranial-Caudal diameter) at Head

(NH). There was no significant difference of this measurement between the gorilla sample and the chimpanzee sample. This appears unusual at first glance but may be explained by looking at the postural, functional and locomotor similarities that these groups exhibit as reflected the skeletal structure.

The gorilla and orangutan sample was significantly different from the baboon, vervet and the chimpanzee samples in the following measurements:

- (a) Tubercle facet height (TFH);
- (b) Tubercle facet width (TFW);
- (c) Shaft maximum height at dorsal angle (SHPA) and
- (d) Shaft maximum width at dorsal angle (SWPA).

The second rib. The gorilla and orangutan group exhibited the expected result of exhibiting the largest means all the measurements of the second rib followed by the chimpanzee, the baboon and the vervet samples.

The non-human primate species was significantly different from each other for the following measurements:

- (a) Head Cranial facet height (HSH);
- (b) Head Cranial facet width (HSW);
- (c) Head Caudal facet height (HIH);
- (d) Head Caudal facet width (HIW);
- (e) Neck (Ventral-Dorsal diameter) at Head (NHA);

- (f) Tubercle facet height (TFH);
- (g) Tubercle – iliacostal line distance (outer) (TILO);
- (h) Tubercle - iliacostal line distance (inner) (TILI) and
- (i) Shaft maximum height at dorsal angle (SHPA)

The gorilla sample was significantly different from the baboon and vervet sample in the following measurements:

- (a) Neck (Cranial-Caudal diameter) at Head (NH);
- (b) Neck (Cranial-Caudal diameter) at Tubercle (NT) and
- (c) Neck (Ventral-Dorsal diameter) at Tubercle (NTA).

The gorilla sample was significantly different from the baboon, vervet, orangutan and the chimpanzee samples in the measurement of the Tubercle facet width (TFW).

The baboon and vervet samples was significantly different from the gorilla sample and the chimpanzee sample in the measurement of the Neck length (NL).

The baboon sample was significantly different chimpanzee sample in the measurement of the width of the shaft at the posterior angle (SWPA).

The fourth rib The gorilla group exhibited the largest means all the measurements of the fourth rib followed by the chimpanzee, the baboon and the vervet samples.

The non-human primate species was significantly different from each other for the following measurements:

- (a) Head Caudal facet width (HIW) and
- (b) the height of the shaft at the posterior angle (SHPA).

The gorilla sample was significantly different from the baboon, vervet and the chimpanzee samples in the following measurements:

- (a) Head Cranial facet height (HSH);
- (b) Head Cranial facet width (HSW);
- (c) Head Caudal facet height (HIH);
- (d) Neck (Cranial-Caudal diameter) at Tubercle (NT);
- (e) Neck (Ventral-Dorsal diameter) at Head (NHA);
- (f) Neck (Ventral-Dorsal diameter) at Tubercle (NTA);
- (g) Tubercle facet height (TFH);
- (h) Tubercle facet width (TFW);
- (i) Tubercle – ilioostal line distance (outer) (TILO) and
- (j) Tubercle - ilioostal line distance (inner) (TILI)

The gorilla and the orangutan samples were significantly different from the baboon and vervet sample in the following measurements:

- (a) Tubercle facet width (TFW) and
- (b) Shaft maximum width at posterior angle (SWPA).

The baboon and vervet sample was significantly different from the gorilla, orangutan and the chimpanzee samples in the following measurements:

- (a) Neck (Cranial-Caudal diameter) at Head (NH) and
- (b) Neck length (NL).

The seventh rib The gorilla group exhibited the largest means all the measurements of the seventh rib followed by the orangutan, the chimpanzee, the baboon and vervet samples.

The non-human primate species was significantly different from each other for the following measurements:

- (a) Head Cranial facet height (HSH);
- (b) Head Caudal facet width (HIW);
- (c) Neck (Cranial-Caudal diameter) at Head (NH);
- (d) Neck (Ventral-Dorsal diameter) at Head (NHA) and
- (e) Neck (Ventral-Dorsal diameter) at Tubercle (NTA).

The gorilla and orangutan samples were significantly different from the baboon and vervet sample and the chimpanzee sample in the following measurements:

- (a) Head Caudal facet height (HIH);
- (b) Tubercle facet height (TFH);
- (c) Tubercle facet width (TFW);
- (d) Tubercle – iliocostal line distance (outer) (TILO);
- (e) Tubercle - iliocostal line distance (inner) (TILI);
- (f) Shaft maximum height at posterior angle (SHPA) and
- (g) Shaft maximum width at posterior angle (SWPA).

The baboon and the vervet samples were significantly different from the gorilla, orangutan and the chimpanzee samples in the following measurements:

- (a) Neck length (NL) and
- (b) Neck (Cranial-Caudal diameter) at Tubercle (NT).

Table 4.1: Descriptive statistics of the non-human primate first rib measurements.

Variable		BABOON	GORILLA	CHIMPANZEE	VERVET	ORANGUTAN
HSH	Mean	4.30	8.96	4.23	2.49	6.86
	Std Deviation	0.77	0.95	1.01	0.14	0.63
HSW	Mean	4.57	12.48	8.34	2.67	11.18
	Std Deviation	0.79	4.18	2.23	0.41	1.24
NH	Mean	4.14	9.96	7.12	2.42	9.70
	Std Deviation	0.86	2.62	2.14	0.18	1.77
NL	Mean	12.24	18.08	14.02	7.27	16.26
	Std Deviation	2.43	3.35	1.90	0.89	3.41
NT	Mean	2.97	8.84	5.31	2.11	8.27
	Std Deviation	1.05	1.07	1.08	0.32	2.12
NHA	Mean	3.98	11.49	6.33	2.27	8.78
	Std Deviation	0.89	1.73	0.85	0.34	1.97
NTA	Mean	6.57	13.34	9.11	3.54	12.07
	Std Deviation	1.38	1.98	1.20	0.47	0.80
TFH	Mean	4.37	10.92	5.57	2.79	7.84
	Std Deviation	1.11	1.73	0.70	0.49	1.88
TFW	Mean	6.37	14.77	8.68	3.48	7.89
	Std Deviation	1.70	2.68	1.70	0.27	0.32
SHPA	Mean	4.25	10.19	5.47	2.60	6.58
	Std Deviation	0.87	1.85	0.82	0.28	1.31
SWPA	Mean	11.31	19.22	14.02	6.29	21.07
	Std Deviation	2.06	2.40	1.75	0.55	4.27

Table 4.2: Descriptive statistics of the non-human primate second rib measurements.

Variable		BABOON	GORILLA	CHIMPANZEE	VERVET	ORANGUTAN
HSH	Mean	3.22	8.57	6.26	1.89	7.41
	Std Deviation	0.69	1.77	1.46	0.20	0.58
HSW	Mean	4.97	11.71	8.15	2.65	10.74
	Std Deviation	0.91	2.67	1.03	0.12	2.41
HIH	Mean	3.65	8.59	5.72	1.87	7.09
	Std Deviation	0.70	1.88	1.09	0.26	0.10
HIW	Mean	4.80	12.15	7.93	2.73	11.17
	Std Deviation	1.01	3.00	1.27	0.17	1.58
NH	Mean	4.97	10.65	7.30	2.82	9.45
	Std Deviation	0.96	2.80	1.70	0.22	1.06
NL	Mean	10.90	16.96	15.30	6.45	16.98
	Std Deviation	1.78	3.08	2.25	1.01	4.26
NT	Mean	3.51	9.53	6.17	2.41	8.83
	Std Deviation	0.75	2.23	1.66	0.22	1.13
NHA	Mean	3.50	7.91	5.62	1.93	7.24
	Std Deviation	0.70	1.44	0.52	0.32	0.63
NTA	Mean	5.51	8.33	7.38	3.05	9.00
	Std Deviation	1.77	1.47	0.91	0.41	1.81
TFH	Mean	3.85	9.33	5.65	2.09	7.76
	Std Deviation	0.78	2.12	1.31	0.25	1.61
TFW	Mean	5.95	13.62	7.45	2.73	8.08
	Std Deviation	1.16	2.77	2.48	0.29	2.33
TILO	Mean	11.37	28.80	18.70	6.85	22.67
	Std Deviation	3.14	5.88	10.06	0.40	2.44
TILI	Mean	9.63	29.05	16.68	5.07	20.71
	Std Deviation	2.62	5.64	9.52	0.58	2.77
SHPA	Mean	3.37	10.69	5.58	1.98	7.26
	Std Deviation	0.62	1.49	0.41	0.22	0.35
SWPA	Mean	6.79	11.42	10.83	4.13	15.78
	Std Deviation	1.77	3.97	1.10	0.35	2.55

Table 4.3: Descriptive statistics of the non-human primate fourth rib measurements.

Variable		BABOON	GORILLA	CHIMPANZEE	VERVET	ORANGUTAN
HSH	Mean	3.50	9.59	5.37	2.00	6.77
	Std Deviation	0.55	1.30	0.93	0.41	1.30
HSW	Mean	5.25	14.43	9.41	2.90	12.24
	Std Deviation	1.13	2.37	2.04	0.33	0.74
HIH	Mean	4.01	9.67	5.91	1.87	7.09
	Std Deviation	0.77	2.43	1.21	0.15	1.28
HIW	Mean	5.32	14.57	8.97	2.82	10.69
	Std Deviation	1.18	3.18	0.77	0.17	1.84
NH	Mean	5.67	13.45	9.74	3.27	12.39
	Std Deviation	1.07	3.33	1.74	0.13	1.14
NL	Mean	11.36	19.72	14.27	6.89	14.29
	Std Deviation	1.77	3.98	1.32	1.09	5.51
NT	Mean	5.37	12.88	8.34	3.17	11.03
	Std Deviation	0.89	3.37	2.11	0.13	1.55
NHA	Mean	3.31	8.97	4.56	1.65	6.39
	Std Deviation	0.68	0.88	0.64	0.16	0.83
NTA	Mean	3.93	8.62	5.59	2.42	8.07
	Std Deviation	0.71	0.92	0.90	0.40	1.36
TFH	Mean	5.03	9.45	6.08	2.82	8.80
	Std Deviation	0.90	1.46	0.83	0.39	0.33
TFW	Mean	6.67	10.87	7.74	3.14	10.56
	Std Deviation	1.07	2.50	2.11	0.34	0.08
TILO	Mean	24.80	44.11	24.52	15.02	34.16
	Std Deviation	5.51	11.42	5.51	1.85	4.41
TILI	Mean	22.12	40.41	21.61	13.02	31.34
	Std Deviation	5.21	13.55	4.88	1.66	1.13
SHPA	Mean	3.63	12.99	6.86	2.05	9.39
	Std Deviation	0.57	3.45	0.57	0.17	1.78
SWPA	Mean	6.64	9.44	9.08	4.79	13.76
	Std Deviation	1.15	1.66	2.19	0.38	1.82

Table 4.4: Descriptive statistics of the non-human primate seventh rib measurements.

Variable		BABOON	GORILLA	CHIMPANZEE	VERVET	ORANGUTAN
HSH	Mean	4.59	10.70	6.23	2.55	9.19
	Std Deviation	0.98	3.09	0.46	0.31	1.52
HSW	Mean	5.87	17.66	11.15	3.15	12.79
	Std Deviation	1.24	2.73	2.72	0.50	2.22
HIH	Mean	5.21	12.23	6.47	2.44	9.84
	Std Deviation	1.06	2.06	0.21	0.22	2.03
HIW	Mean	5.82	17.12	10.42	3.10	9.98
	Std Deviation	1.18	2.66	1.74	0.52	1.29
NH	Mean	7.47	15.59	11.99	3.72	14.68
	Std Deviation	1.39	2.26	2.62	0.35	1.83
NL	Mean	11.87	19.56	16.16	6.86	15.55
	Std Deviation	1.75	4.83	1.50	0.79	1.23
NT	Mean	6.49	14.05	10.45	3.68	10.70
	Std Deviation	1.22	2.62	1.79	0.66	2.71
NHA	Mean	3.78	10.89	5.38	1.97	7.33
	Std Deviation	0.75	1.82	0.65	0.27	1.05
NTA	Mean	3.99	10.40	6.89	2.40	9.32
	Std Deviation	0.75	1.95	1.27	0.24	0.37
TFH	Mean	5.63	9.42	6.50	2.99	9.70
	Std Deviation	0.92	2.24	0.59	0.22	1.74
TFW	Mean	7.34	11.98	7.77	3.60	12.11
	Std Deviation	1.73	0.57	1.08	0.30	1.29
TILO	Mean	35.15	69.15	39.50	19.21	42.79
	Std Deviation	6.46	14.36	6.74	4.56	3.09
TILI	Mean	32.57	64.34	34.51	18.12	39.04
	Std Deviation	6.61	16.52	6.17	3.46	0.35
SHPA	Mean	4.36	13.96	10.70	2.79	10.23
	Std Deviation	0.72	3.59	2.69	0.47	1.83
SWPA	Mean	6.73	10.94	8.19	3.62	13.72
	Std Deviation	1.16	2.27	2.52	0.48	4.17

Table 4.5: ANCOVA and ANOVA for the non-human primate first rib measurements.

Variable		ANCOVA				ANOVA for Population			Population Comparison ²			
		F	df	Significance	Levene's Test	F	df	Significance				
HSH	Population	161.61	5	0.000	0.173	95.56	6	0.000	All significantly different			
	Sex	20.40	1									
HSW ³	Population	2.04	4		0.000	0.000				35.79		
	Sex	18.52	1									
NH	Population	4.28	4		0.000 ¹	5.72						Gorilla significantly different from Baboon and Vervet
	Sex	27.04	1									
NL ³	See Tables 4.11, 4.12 and 4.13											
NT	Population	87.11	4	0.000	0.001	61.48	6	0.000	All significantly different			
	Sex	9.33	1	0.004								
NHA	Population	14.05	4	0.000	0.016 ¹	5.88						
	Sex	55.03	1									
NTA	Population	133.33	5		0.004	78.08						
	Sex	24.01	1									
TFH	Population	106.57	5		5.87	56.22						
	Sex	27.89	1									
TFW	Population	71.93	5	10.79	49.52							
	Sex	11.21	1			0.002						
SHPA	Population	111.74	5	0.000	6.26	62.71						
	Sex	23.89	1									
SWPA	Population	6.15	4		0.650	5.5						
	Sex	23.34	1									

¹Levene's statistic is significant ²Post Hoc Test performed as part of ANOVA of population ³After performing rank analysis

Table 4.6: ANCOVA and ANOVA for the non-human primate second rib measurements. ¹Levene's statistic is significant ²Post Hoc Test performed as part of ANOVA of population ³After performing rank analysis

Variable		ANCOVA				ANOVA for Population			Population Comparison ²			
		F	df	Significance	Levene's Test	F	Df	Significance				
HSH	Population	6.65	4	0.000	0.000	6.39	6	0.000	All significantly different			
	Sex	13.21	1	0.001								
HSW	Population	4.65	4	0.000	0.000 ¹	21.28	0.000					
	Sex	47.23	1									
HIH ³	Population	11.99	4		0.000 ¹	10.08		0.000				
	Sex	20.62	1									
HIW	Population	6.15	4		0.000 ¹	18.06				0.000		
	Sex	23.87	1									
NH	Population	81.83	5		0.007 ¹	51.98					0.000	Gorilla & Orangutan significantly different from Baboon and Vervet
	Sex	15.39	1									
NL	Population	6.35	4		0.011	3.36			0.000			Baboon and Vervet sig different from Gorilla.Orangutan and Chimpanzee
	Sex	28.84	1									
NT	Population	91.06	5	0.000 ¹	56.82	0.000	Gorilla & Orangutan significantly different from Baboon and Vervet					
	Sex	6.66	1									
NHA	Population	168.51	5	0.002 ¹	23.36		0.000	All significantly different				
	Sex	38.65	1									
NTA	Population	29.01	5	0.888	7.79			0.002		Gorilla & Orangutan significantly different from Baboon & Vervet		
	Sex	4.30	1									
TFH ³	Population	5.89	4	0.001	4.76					0.000	All significantly different	
	Sex	32.11	1									
TFW	Population	81.79	5	0.000 ¹	55.41				0.000		Gorilla sig different from Baboon, Vervet and Chimpanzee	
	Sex	11.75	1									
TILO ³	Population	64.56	4	0.000	44.46	0.000					All significantly different	
	Sex	11.77	1									
TIL ³	Population	83.97	4	0.000	58.15		0.000					
	Sex	11.23	1									
SHPA	Population	223.40	4	0.010	165.30			0.000 ¹				
	Sex	7.13	1									
SWPA	Population	48.83	4	0.001	32.00					0.000 ¹		Baboon & Vervet sig different from Chimpanzee& Orangutan
	Sex	13.86	1									

Table 4.7: ANCOVA and ANOVA Table for the non-human primate fourth rib measurements

Variable		ANCOVA				ANOVA for Population			Population Comparison ²		
		F	df	Significance	Levene's Test	F	df	Significance			
HSH	Population	155.27	5	0.000	0.004 ¹	103.29	6	0.000	Gorilla & Orangutan significantly different from Baboon, Vervet and Chimpanzee		
	Sex	12.62	1	0.001							
HSW	Population	14.13	4	0.000	0.000 ¹	9.34	0.000	All significantly different			
	Sex	4.55	1	0.005							
HIH ³	Population	2.25	4	0.080		6.55				13.19	54.47
	Sex	39.35	1	0.000							
HIW	Population	7.80	4	0.000		5.46		57.94	133.19	Gorilla & Orangutan significantly different from Baboon & Vervet	
	Sex	13.68	1	0.001							
NH	Population	88.26	5	0.000		0.025		86.14	67.97	Gorilla & Orangutan significantly different from Baboon, Vervet and Chimpanzee	
	Sex	12.64	1	0.001							
NL	Population	8.35	4	0.000		0.000 ¹		17.38	10.39	Gorilla significantly different from Baboon, Vervet and Chimpanzee	
	Sex	55.34	1								
NT	Population	83.38	5	0.002		8.07		72.04	All significantly different		
	Sex	10.29	1								
NHA	Population	246.84	5	0.000	6.07	6.07	Gorilla & Orangutan significantly different from Baboon & Vervet				
	Sex	26.20	1								
NTA	Population	141.00	5	0.046	0.000 ¹	10.39	All significantly different				
	Sex	18.15	1								
TFH	Population	87.61	5	0.000	0.000 ¹	10.39	All significantly different				
	Sex	4.19	1								
TFW	Population	9.16	5	0.225	0.000 ¹	8.07	All significantly different				
	Sex	1.51	1								
TILO	Population	3.51	4	0.000	0.000 ¹	8.07	All significantly different				
	Sex	11.71	1								
TILI	Population	3.12	4	0.024	0.000 ¹	8.07	All significantly different				
	Sex	8.03	1								
SHPA	Population	93.78	5	0.000	0.000 ¹	8.07	All significantly different				
	Sex	2.98	1								
SWPA ³	Population	9.07	4	0.000	0.000 ¹	8.07	All significantly different				
	Sex	3.78	1								

¹Levene's statistic is significant ²Post Hoc Test performed as part of ANOVA of population ³After performing rank analysis

Table 4.8: ANCOVA and ANOVA for the non-human primate seventh rib measurements. ¹Levene's statistic is significant ²Post Hoc Test performed as part of ANOVA of population ³After performing rank analysis

Variable		ANCOVA				ANOVA for Population			Population Comparison ²										
		F	df	Significance	Levene's Test	F	df	Significance											
HSH ³	Population	1.27	4	0.291	0.000	9.46	6	0.000	All significantly different										
	Sex	25.64	1	0.000															
HSW	See Tables 4.11, 4.12 and 4.13																		
HIH ³	Population	10.14	4	0.000	0.000	10.84	6	0.000	Gorilla & Orangutan significantly different from Baboon, Vervet and Chimpanzee										
	Sex	29.08	1																
HIW	Population	20.66	4						0.004	4.04	0.000	0.000	All significantly different						
	Sex	22.66	1																
NH	Population	12.05	4						0.000	7.80			0.000	0.000	Baboon & Vervet significantly different from Gorilla, Orangutan and Chimpanzee				
	Sex	41.08	1																
NL ³	Population	4.15	4						0.001	7.99					0.000	0.000	All significantly different		
	Sex	15.61	1																
NT	Population	6.75	4						0.011	3.93							0.000	0.000	All significantly different
	Sex	18.04	1																
NHA ³	Population	12.16	4	0.001	8.55	0.000	0.000	All significantly different											
	Sex	21.48	1																
NTA ³	Population	15.70	4	0.021	46.81			0.000	0.000	All significantly different									
	Sex	13.27	1																
TFH	Population	79.58	5	0.000	10.96					0.000	0.000	Gorilla significantly different from Baboon, Vervet and Chimpanzee							
	Sex	19.88	1																
TFW	Population	12.66	4	0.000	0.006							0.000	0.000	All significantly different					
	Sex	9.57	1																
TILO ³	Population	6.68	4	0.009	7.80									0.000	0.000	Gorilla & Orangutan significantly different from Baboon & Vervet			
	Sex	18.37	1																
TILI ³	Population	3.86	4	0.002	53.12	0.000	0.000									Gorilla & Orangutan significantly different from Baboon & Vervet			
	Sex	10.55	1																
SHPA	Population	61.75	5	0.541	5.35			0.000	0.000							Gorilla & Orangutan significantly different from Baboon & Vervet			
	Sex	0.379	1																
SWPA	Population	1.28	4	0.000	0.001					0.000	0.000					Gorilla & Orangutan significantly different from Baboon & Vervet			
	Sex	38.71	1																

4.1.2. Indices for non-human primates

The sample size, mean value and standard deviation for the indices from each are contained in Tables 4.5.

The ANOVA and ANCOVA values and significant levels for the indices are contained in Tables 4.10.

Results of the indices for non-human primates between the sexes of the non-human primates

All the calculated indices did not show any significant sexual dimorphism except for the neck index (NI) for rib 1 and rib 7. This may be an anomaly because it was only this index in these two ribs that was analysed further by doing a rank analysis of the associated data.

The male baboon sample exhibited a significant difference for the Neck length of the first rib.

The female baboon sample and the female gorilla sample showed a significant difference in the Head Cranial facet width (HSW) of the seventh rib.

The male baboon sample also was significantly different from the male chimpanzee sample and male gorilla and orangutan samples for the Head Cranial facet width (HSW) of the seventh rib.

Results of the indices for non-human primates between the different non-human primate species looking at specific ribs

The first rib. The gorilla sample exhibited the largest mean for the following indices:

- (a) the neck index (NI);
- (b) the neck at tubercle index (NTI);
- (c) the tubercle facet index (TFI) and
- (d) the shaft height index (SHI).

The head facet index (FHI) was calculated for the first rib as a product of the height and width of the single facet in the baboon sample, and the cranial facet of the gorilla sample and chimpanzee sample. The baboon sample had the largest value for the mean of the head facet index (FHI). The chimpanzee sample was largest for the mean of the neck at head index (NHI). There was a significant difference in the head facet index of the baboon and vervet samples when compared to the chimpanzee, gorilla and orangutan samples.

The neck index (NI) was significantly different in the baboon sample when compared to the gorilla and the chimpanzee samples (see Table 4.9).

No significant difference was observed in the following indices:

- (a) index of the neck at head (NHI) and
- (b) index of the tubercle facet (TFI).

The gorilla sample was significantly different from the baboon and the vervet sample for the neck at tubercle index (NTI).

The gorilla sample was significantly different from the baboon sample and the chimpanzee sample for the shaft height index (SHI).

The second rib. The baboon sample had the largest mean for the following indices:

- (a) the caudal facet of rib head index (IFHI);
- (b) the neck at tubercle index (NTI) and
- (c) the tubercle-iliocostal line index (TICI).

The chimpanzee sample had the largest mean for the following indices:

- (a) the cranial facet of the head index (SFHI) and
- (b) the tubercle facet index (TFI)

The gorilla sample had the largest mean for the following indices:

- (a) the neck index (NI);
- (b) the neck at tubercle index (NTI) and
- (c) the shaft height index (SHI).

No significant difference was observed between the species in the following indices:

- (a) the cranial facet of head index (SFHI);
- (b) the caudal facet of head index (IFHI);
- (c) the neck at head index (NHI);

- (d) the tubercle facet index (TFI) and
- (e) shaft height index (SHI).

The gorilla sample was significantly different from the baboon sample in the following indices:

- (a) the neck index (NI);
- (b) the neck at tubercle index (NTI) and
- (c) the tubercle-iliocostal line index (TICI).

The fourth rib. The baboon sample had the largest mean value for the following indices:

- (a) the cranial facet of the head index (SFHI) and
- (b) the caudal facet of the head index (IFHI)

The gorilla sample had the largest mean value for the following indices:

- (a) the neck index (NI);
- (b) the tubercle facet index (TFI) and
- (c) the shaft height index (SHI).

The chimpanzee sample had the largest mean value for the following indices:

- (a) the neck at the head index (NHI);
- (b) the neck at the tubercle index (NTI) and
- (c) the tubercle-iliocostal line index (TICI).

There was no significant difference between the species or the following indices:

- (a) the cranial facet of head index (SFHI);
- (b) the caudal facet of head index (IFHI);
- (c) the neck at head index (NHI);
- (d) the neck at tubercle index (NTI);
- (e) the tubercle facet index (TFI) and
- (f) the tubercle-iliocostal line index (TICI).

The baboon and vervet sample was significantly different from the gorilla sample and the chimpanzee sample in the neck index (NI).

The gorilla sample was significantly different from the baboon sample and the chimpanzee sample in the shaft height index (SHI).

The seventh rib. The gorilla sample showed the largest mean value for the following indices:

- (a) the cranial facet of the head index (SFHI) and
- (b) the neck index (NI).

The baboon sample showed the largest mean value for the following indices:

- (a) the caudal facet of the head index (IFHI) and
- (b) the neck at the tubercle index (NTI).

The chimpanzee sample showed the largest mean value for the following indices:

- (a) the neck at head index (NHI);
- (b) the tubercle facet index (TFI);
- (c) the tubercle-iliocostal line index (TICI) and
- (d) the shaft height index (SHI).

There was significant difference in the following indices:

- (a) the tubercle facet index (TFI) and
- (b) the tubercle-iliocostal line index (TICI).

The gorilla sample was significantly different from the baboon, the vervet and the chimpanzee samples in the neck at head index (NHI).

The baboon sample was significantly different from the gorilla sample and the chimpanzee sample in the following indices

- (a) the cranial facet of head index (SFHI);
- (b) the caudal facet of head index (IFHI);
- (c) the neck at head index (NHI) and
- (d) the shaft height index (SHI).

The baboon sample was significantly different from the gorilla sample in the neck index (NI) only.

Trends observed in the indices for the non-human primates

The following describes the trends observed for each species in the value of the means of the indices calculated.

Facet of the Head Index (FHI). This index is only applicable for the first rib. It had the greatest value for all the facet indices calculated for the ribs 1, 2, 4 and 7.

Cranial facet of the Head Index (SFHI). This index showed the following trend:

The value increased from rib 2 to 7 in the baboon sample.

The value decreased from rib 2 to 7 in the gorilla sample.

The value decreased from rib 2 to 7 in the chimpanzee sample.

Caudal facet of the Head Index (IFHI). This value decreased from rib 2 to 4 and then increased to rib 7 in the baboon sample and the gorilla sample.

This value decreased from rib 2 to 7 in the chimpanzee sample.

Neck Index (NI). This value increased from rib 1 to 7 in the baboon sample and the gorilla sample.

This value decreased from rib 1 to 2 and then increased to rib 7 in the chimpanzee sample.

Neck at Head Index (NHI). This value increased from rib 1 to 7 in the baboon sample and the chimpanzee sample. This value increased from rib 1 to 4 and then decreased to rib 7 in the gorilla sample.

Neck at Tubercle Index (NTI). This value increased from rib 1 to 7 in the baboon sample and the chimpanzee sample.

This value increased from rib 1 to 4 and then decreased to rib 7 in the gorilla sample.

Tubercle facet Index (TFI). This value decreased from rib 1 to 2 and then increased to rib 7 in the baboon sample.

This value decreased from rib 1 to 2, increased to rib 4 and then decreased to rib 7 in the gorilla sample.

This value increased from rib 1 to rib 7 in the chimpanzee sample

Tubercle-Iliocostal line index (TICI). This value decreased from rib 2 to rib 7 in the baboon sample.

This value increased from rib 2 to 4 and then decreased to rib 7.

Shaft height at posterior angle Index (SHI). This value increased from rib 1 to rib 7 in the baboon sample.

This value increased from rib 1 to 4 and then decreased to rib 7 in the gorilla sample.

This value increased from rib 1 to rib 7 in the chimpanzee sample.

Table 4.9: Descriptive statistics of the non-human primate rib indices.

Rib number	Variable		BABOON	GORILLA	CHIMPANZEE	VERVET	ORANGUTAN	
1	FHI	Mean	94.71	77.27	68.23	94.45	61.48	
		Std Deviation	11.19	21.59	8.73	10.41	1.15	
	NI	Mean	34.19	57.30	50.29	33.81	59.87	
		Std Deviation	5.95	20.77	11.81	4.99	1.50	
	NHI	Mean	105.32	86.75	113.68	109.22	111.19	
		Std Deviation	16.55	16.89	35.32	18.79	4.20	
	NTI	Mean	45.61	67.15	57.94	60.76	67.93	
		Std Deviation	14.23	10.39	5.79	12.98	12.64	
	TFI	Mean	71.39	74.44	69.37	80.51	98.84	
		Std Deviation	19.16	6.65	20.51	14.80	19.36	
	SHI	Mean	37.69	53.00	38.94	41.61	31.23	
		Std Deviation	4.82	6.19	1.86	5.74	0.07	
	2	SFHI	Mean	65.51	73.78	76.32	71.31	70.40
			Std Deviation	12.30	6.49	12.37	6.93	9.21
IFHI		Mean	77.27	70.98	71.98	68.32	64.38	
		Std Deviation	10.78	5.44	4.61	8.13	9.19	
NI		Mean	45.93	63.46	49.08	44.52	56.84	
		Std Deviation	7.38	15.33	13.02	5.95	7.01	
NHI		Mean	145.49	133.73	129.57	148.97	130.28	
		Std Deviation	32.73	20.62	27.17	19.64	3.11	
NTI		Mean	75.53	120.48	86.27	80.38	98.96	
		Std Deviation	38.25	46.11	30.68	12.41	6.59	
TFI		Mean	66.02	68.62	78.24	77.00	97.43	
		Std Deviation	14.24	8.47	10.90	7.75	7.02	
TICI		Mean	118.65	99.52	114.57	137.02	109.69	
		Std Deviation	14.04	10.50	6.86	17.78	2.70	
SHI	Mean	51.09	108.89	51.72	48.05	46.97		
	Std Deviation	9.74	56.69	4.15	3.17	8.94		

Table 4.9 (contd.): Descriptive statistics of the non-human primate rib indices.

Rib number	Variable		BABOON	GORILLA	CHIMPANZEE	VERVET	ORANGUTAN
4	SFHI	Mean	68.20	67.09	58.15	70.32	55.07
		Std Deviation	10.68	8.30	10.42	18.99	7.09
	IFHI	Mean	76.32	66.21	66.25	66.48	66.24
		Std Deviation	10.87	5.74	15.35	6.37	0.52
	NI	Mean	50.01	68.63	68.21	48.52	92.52
		Std Deviation	6.08	13.52	10.83	7.38	22.63
	NHI	Mean	172.46	148.76	213.35	198.95	194.58
		Std Deviation	17.31	26.99	24.49	18.36	6.75
	NTI	Mean	137.92	148.86	150.15	134.07	137.19
		Std Deviation	17.40	34.48	38.28	18.78	3.64
	TFI	Mean	76.13	92.58	82.51	90.80	83.37
		Std Deviation	12.36	35.73	22.58	16.69	2.52
	TICI	Mean	112.68	111.59	115.07	115.84	108.77
		Std Deviation	6.61	10.31	13.43	8.98	9.94
	SHI	Mean	55.69	144.85	78.91	43.13	67.90
		Std Deviation	10.35	57.54	26.31	5.01	3.68
7	SFHI	Mean	79.03	59.76	58.05	83.80	71.87
		Std Deviation	11.76	9.59	12.57	20.53	0.56
	IFHI	Mean	90.45	71.66	63.47	80.29	98.05
		Std Deviation	14.41	6.89	10.88	11.46	7.13
	NI	Mean	63.25	82.27	73.72	54.67	94.17
		Std Deviation	9.88	15.44	11.58	6.37	4.13
	NHI	Mean	200.30	144.03	222.19	189.63	200.65
		Std Deviation	31.79	12.02	37.22	28.27	3.51
	NTI	Mean	164.22	137.21	152.59	153.71	114.10
		Std Deviation	23.50	23.92	16.47	24.23	24.03
	TFI	Mean	79.40	78.61	84.83	83.56	79.76
		Std Deviation	16.81	17.46	13.66	7.89	5.50
	TICI	Mean	108.41	108.81	114.59	105.72	109.68
		Std Deviation	5.43	7.04	1.49	12.70	8.95
	SHI	Mean	66.50	135.44	141.31	79.62	76.25
		Std Deviation	15.94	53.17	51.49	23.26	8.36

Table 4.10: ANCOVA and ANOVA of non-human primate rib indices.

Rib number	Variable		ANCOVA				ANOVA			Population Comparison ²
			F	df	Significance	Levene's Test	F	Df	Significance	
1	FHI	Population	1.93	5	0.195	1.11	0.70	0.571	Baboon and Vervet significantly different from Chimpanzee	
		Sex	2.72	1	0.130					
	NI ³	Population	5.14	4	0.002	3.29	3.29	0.012	Baboon and Vervet significantly different from Gorilla, Orangutan and Chimpanzee	
		Sex	5.44	1	0.024					
	NHI	Population	4.49	5	0.002	0.996	4.36	0.001	No significant difference	
		Sex	2.71	1	0.054					
	NTI	Population	4.55	5	0.002	0.140	3.85	0.003	Gorilla significantly different from Baboon & Vervet	
		Sex	0.46	1	0.500					
	TFI	Population	2.75	5	0.029	2.55	2.36	0.044	No significant difference	
		Sex	3.13	1	0.083					
	SHI	Population	8.27	5	0.000	3.15	7.14	0.000	Gorilla significantly different from Baboon, Vervet, Orangutan and Chimpanzee	
		Sex	2.81	1	0.100					
	2	SFHI	Population	3.91	5	0.005	2.40	3.10	0.012	No significant difference
			Sex	3.27	1	0.078				
IFHI		Population	9.39	4	0.000	5.24	0.57	0.001	No significant difference	
		Sex	0.01	1	0.916					
NI		Population	6.38	5	0.000	2.851	5.88	0.000	Gorilla & Orangutan significantly different from Baboon & Vervet	
		Sex	0.395	1	0.533					
NHI		Population	0.75	5	0.589	2.20	1.27	0.314	No significant difference	
		Sex	3.52	1	0.067					
NTI		Population	2.57	5	0.039	3.30	2.45	0.037	Gorilla significantly different from Baboon & Vervet	
		Sex	5.06	1	0.816					
TFI		Population	5.67	5	0.000	3.96	5.11	0.000	Gorilla significantly different from Baboon & Vervet	
		Sex	0.199	1	0.657					
TICI		Population	8.35	5	0.000	2.84	6.77	0.000	Gorilla significantly different from Baboon & Vervet	
		Sex	1.50	1	0.226					
SHI	Population	9.91	2	0.000	45.60¹	8.37	0.000	Gorilla significantly different from Baboon & Vervet		
	Sex	0.52	1	0.474						

¹Levene's statistic is significant ²Post Hoc Test performed as part of ANOVA of population ³After performing rank analysis

Table 4.10 (contd.): ANCOVA and ANOVA of non-human primate rib indices.

Rib number	Variable		ANCOVA				ANOVA			Population Comparison ²
			F	df	Significance	Levene's Test	F	df	Significance	
4	SFHI	Population	0.87	5	0.512	4.79	0.76	6	0.605	No significant difference
		Sex	0.19	1	0.665					
	IFHI	Population	2.78	5	0.028	3.01	2.50		0.035	
		Sex	0.31	1	0.580					
	NI	Population	12.81	4	0.000	6.47¹	0.78		0.000	Baboon significantly different from Gorilla and Chimpanzee
		Sex	8.99	1	0.004					
	NHI	Population	12.52	5	0.000	2.24	10.68		0.118	All significantly different
		Sex	0.053	1	0.819					
	NTI	Population	1.65	5	0.166	3.33	1.81		0.149	No significant difference
		Sex	0.07	1	0.793					
	TFI	Population	0.01	5	0.098	3.06	1.67		0.448	
		Sex	0.13	1	0.134					
TICI	Population	1.28	5	0.288	4.00	0.98	0.000	Gorilla sig different from Baboon, Vervet & Chimpanzee		
	Sex	1.63	1	0.207						
SHI ³	Population	22.23	5	0.000	19.14	18.86	0.047	No significant difference		
	Sex	0.28	1	0.601						
7	SFHI	Population	8.99	4	0.114	2.44	0.59	0.001	Baboon & Vervet sig different from Gorilla and Chimpanzee	
		Sex	2.59	1	0.002					
	IFHI	Population	5.00	5	0.001	1.53	4.46	0.000	Baboon and Vervet sig diff from Gorilla	
		Sex	0.398	1	0.531					
	NI ³	Population	16.36	5	0.000	1.54	12.81	0.001	Gorilla significantly different from Baboon and Chimpanzee	
		Sex	2.98	1	0.091					
	NHI	Population	5.84	5	0.000	1.54	4.95	0.026	Gorilla sig diff from Baboon	
		Sex	4.98	1	0.030					
	NTI	Population	3.07	5	0.018	0.183	2.66	0.891	No significant difference	
		Sex	1.44	1	0.236					
	TFI	Population	0.35	5	0.877	2.90	0.376	0.047		
		Sex	0.42	1	0.423					
TICI	Population	3.11	4	0.085	2.45	0.366	0.000	Baboon significantly different from Gorilla and Chimpanzee		
	Sex	4.12	1	0.002						
SHI	Population	5.73	5	0.000	17.03¹	5.93	0.000			
	Sex	0.35	1	0.555						

¹Levene's statistic is significant ²Post Hoc Test performed as part of ANOVA of population ³After performing rank analysis

Table 4.11: Sex differences amongst the different non-human primate species (After rank analysis; significant interaction between population and sex).

Rib Number	Variable	Population								
		Baboon			Gorilla			Chimpanzee		
		F	df	Significance	F	df	Significance	F	df	Significance
1	NL	6.68	1	0.019	6.39	1	0.065	16.03	1	0.057
7	HSW	53.10		0.000	10.29		0.033	12.03		0.074

Table 4.12: Non-human primate species differences amongst females.

Rib Number	Variable	F	df	Significance	Post hoc results
1	NL	64.56	2	0.000	Gorilla significantly different from Baboon and Chimpanzee
7	HSW	160.72			Significant difference between Baboon and Gorilla

Table 4.13: Non-human primate species differences amongst males.

Rib Number	Variable	F	df	Significance	Post hoc results
1	NL	1.10	2	0.365	No significant difference between species
7	HSW	219.46		0.000	Baboon significantly different from Chimpanzee and Gorilla

4.2. Human Population sample

4.2.1. Measurements of human sample

The human sample showed a normal distribution for all the measurements and indices as indicated by the calculated KS values (see Tables 4.14 to 4.18).

The sample size, mean value and standard deviation for each measurement from each group are contained in Tables 4.14 to 4.17.

The ANOVA and ANCOVA values and significant levels for the measurements are contained in Tables 4.19 to 4.22.

Results for the measurements of human sample between the sexes in the human sample

A statistical significant difference was observed in all the measurements for all the ribs analysed except for the following:

- (a) Neck length (NL) of the first rib;
- (b) Head Superior facet height (HSH) of the fourth rib;
- (c) Tubercle facet height (TFH) of the seventh rib and
- (d) Tubercle facet width (TFW) of the seventh rib.

More specifically, a significant sexual difference was also observed in the following measurements for each specific population group:

(a) Sotho;

- i. Neck length (NL) of the second and fourth ribs;
- ii. Neck (Anterior-Posterior diameter) at Tubercle (NTA) for the fourth rib and
- iii. Tubercle – ilio-costal line distance (inner) (TILI) for the seventh rib.

(b) Zulu and

- i. Neck (Superior-Inferior diameter) at Tubercle (NT) and Neck (Anterior-Posterior diameter) at Head (NHA) for the first rib;
- ii. Neck length (NL) of the second rib and
- iii. Head Superior facet width (HSW) of the seventh rib.

(c) European

- i. Neck (Superior-Inferior diameter) at Tubercle (NT) and Neck (Anterior-Posterior diameter) at Head (NHA) for the first rib;
- ii. Tubercle – ilio-costal line distance (outer) (TILO) for the second, fourth and seventh ribs;
- iii. Tubercle - ilio-costal line distance (inner) (TILI) for the second rib;
- iv. Neck length (NL) for the fourth rib;
- v. Head Superior facet width (HSW) for the seventh rib and
- vi. Shaft maximum width at posterior angle (SWPA) for the seventh rib.

Refer to Table 4.24 that shows the sexual differences between the different population groups (After rank analysis due to significant interaction between population and sex).

For the first rib, the European female group was significantly different from the Zulu female group for the Neck (Superior-Inferior diameter) at Tubercle (NT) and there was no significant difference among the females of all the population groups in the Neck (Anterior-Posterior diameter) at Head. (NHA). It was noted that the Sotho male was significantly different from the Zulu and European male groups for the Neck (Superior-Inferior diameter) at Tubercle (NT) and the Sotho male group also was significantly different from the European male group for the Neck (Anterior-Posterior diameter) at Head (NHA).

For the second rib, the European females also showed a significant difference from the Zulu and Sotho females for the following measurements:

- (a) Tubercle – iliocostal line distance (outer) (TILO) and
- (b) Tubercle - iliocostal line distance (inner) (TILI).

The European female Neck length (NL) also was significantly different from that of the Sotho female.

No differences were observed between males of the population groups for the same 3 measurements above.

For the fourth rib, the Sotho female was significantly different from the Zulu and European female concerning the Neck length (NL). The Zulu female was significantly different from the Sotho and the European female groups for the Neck (Anterior-Posterior diameter) at Tubercle (NTA). The European male was significantly different from the Sotho and Zulu males with regards to the Neck length (NL).

For the seventh rib, the Zulu female showed a significant difference from the Sotho and European for the Shaft maximum width at posterior angle (SWPA). The European male showed a significant difference from the Sotho male for the Head Superior facet width (HSW) and from the Zulu and Sotho male for the Shaft maximum width at posterior angle (SWPA).

Results for the measurements of human sample between the populations of the human sample for each of the ribs analysed

The first rib. The Sotho group had the largest mean for the Neck (Superior-Inferior diameter) at Tubercle (NTA).

The Zulu group had the largest mean for the following measurements:

- (a) Neck (Superior-Inferior diameter) at Tubercle (NT);
- (b) Tubercle facet height (TFH) and
- (c) Tubercle facet width (TFW).

The European group showed the largest mean values for the following measurements:

- (a) Head Superior facet height (HSH);
- (b) Head Superior facet width (HSW);
- (c) Neck (Superior-Inferior diameter) at Head (NH);
- (d) Neck length (NL);
- (e) Neck (Anterior-Posterior diameter) at Head (NHA);
- (f) Shaft maximum height at posterior angle (SHPA) and
- (g) Shaft maximum width at posterior angle (SWPA)

Table 4.19 shows that there were no statistically significant differences between the three population groups in any of the measurements except for the following:

- (a) Head facet height (HH) and
- (b) Neck (Superior-Inferior diameter) at Head (NH)

The second rib. The Sotho group had the largest mean for the following measurements:

- (a) Head Inferior facet height (HIH);
- (b) Head Inferior facet width (HIW);
- (c) Neck (Superior-Inferior diameter) at Head and
- (d) Neck (Anterior-Posterior diameter) at Tubercle (NTA).

The Zulu group had the largest mean for the following measurements:

- (a) Head facet height (HH);
- (b) Head facet width (HW);
- (c) Neck (Superior-Inferior diameter) at Tubercle (NT);
- (d) Neck (Anterior-Posterior diameter) at Head (NHA);
- (e) Tubercle facet height (TFH);
- (f) Tubercle – iliocostal line distance (outer) (TILO);
- (g) Tubercle - iliocostal line distance (inner) (TILI);
- (h) Shaft maximum height at posterior angle (SHPA) and
- (i) Shaft maximum width at posterior angle (SWPA).

The European group had the largest mean for the Neck length (NL) and the Tubercle facet width (TFW).

Statistically significant differences were observed only for the following measurements between the population groups:

- (a) Sotho and Zulu groups for the Head Inferior facet height (HIH) and
- (b) European group from the Zulu and Sotho for
 - i. Neck (Anterior-Posterior diameter) at Tubercle (NTA);
 - ii. Tubercle facet width (TFW) and
 - iii. Shaft maximum width at posterior angle (SWPA)

No further population differences were observed for the remaining measurements.

The fourth rib. The Sotho group had the greatest mean for the Head Inferior facet height (HIH).

The Zulu group had the largest mean for the following measurements:

- (a) Neck (Superior-Inferior diameter) at Head (NH);
- (b) Neck (Superior-Inferior diameter) at Tubercle (NT);
- (c) Neck (Anterior-Posterior diameter) at Tubercle (NTA);
- (d) Tubercle facet width (TFW);
- (e) Tubercle – iliocostal line distance (outer) (TILO);
- (f) Tubercle - iliocostal line distance (inner) (TILI) and
- (g) Shaft maximum height at posterior angle.

The European group showed the largest mean for the following measurements:

- (a) Head Superior facet height (HSH);
- (b) Head Superior facet width (HSW);
- (c) Head Inferior facet width (HIW);
- (d) Neck length (NL);
- (e) Neck (Anterior-Posterior diameter) at Head (NHA);
- (f) Tubercle facet height (TFH) and
- (g) Shaft maximum height at posterior angle (SHPA).

The European group was significantly different from the Zulu and Sotho for the Head Superior facet height (HSH).

The European group was significantly different from the Sotho group concerning the Head Superior facet width (HSW) and Neck (Anterior-Posterior diameter) at Head (NHA).

No significant differences were noted for the other measurements.

The seventh rib. The Sotho group had the largest mean for the following measurements:

- (a) Head Inferior facet height (HIH);
- (b) Tubercle – iliocostal line distance (outer) (TILO);
- (c) Tubercle - iliocostal line distance (inner) (TILI) and
- (d) Shaft maximum height at posterior angle (SHPA).

The Zulu population group had the largest mean for the

- (a) Neck (Anterior-Posterior diameter) at Tubercle (NTA);
- (b) Tubercle facet width (TFW) and
- (c) Shaft maximum width at posterior angle (SWPA).

The European group had the largest mean for the following measurements:

- (a) Head Superior facet height (HSH);
- (b) Head Superior facet width (HSW);
- (c) Head Inferior facet width (HIW);
- (d) Neck (Superior-Inferior diameter) at Head (NH);
- (e) Neck length (NL);
- (f) Neck (Superior-Inferior diameter) at Tubercle (NT);
- (g) Neck (Anterior-Posterior diameter) at Head (NHA) and
- (h) Tubercle facet height (TFH).

The European was significantly different from the Zulu and Sotho for the Neck length (NL).

No significant population differences were noted for the other measurements.

Table 4.14: Descriptive statistics of the human first rib measurements.

Variable		SOTHO	ZULU	EUROPEAN	TOTAL HUMAN	KOLMOGOROV-SMIRNOV TEST
HH	Mean	8.15	8.07	9.50	8.56	0.591
	Std Deviation	1.11	1.26	1.99	1.61	
HW	Mean	9.18	9.21	10.19	9.52	0.629
	Std Deviation	1.37	1.49	2.07	1.71	
NH	Mean	6.42	6.63	7.70	6.91	0.900
	Std Deviation	0.86	0.87	1.46	1.22	
NL	Mean	15.54	15.26	15.62	15.47	0.629
	Std Deviation	2.36	2.39	2.26	2.30	
NT	Mean	5.11	5.59	5.32	5.34	0.999
	Std Deviation	0.65	0.62	1.14	0.84	
NHA	Mean	7.80	7.41	8.31	7.84	0.991
	Std Deviation	1.23	1.40	2.11	1.64	
NTA	Mean	10.51	9.64	10.22	10.28	0.717
	Std Deviation	1.53	0.89	1.73	1.46	
TFH	Mean	6.01	6.72	6.48	6.41	1.000
	Std Deviation	0.95	1.19	1.24	1.14	
TFW	Mean	9.07	10.28	10.16	9.85	0.452
	Std Deviation	1.43	2.20	2.14	2.004	
SHPA	Mean	7.30	7.68	7.72	7.57	0.855
	Std Deviation	1.19	0.82	1.26	1.099	
SWPA	Mean	15.79	15.95	17.04	16.26	0.823
	Std Deviation	1.87	1.50	2.57	2.06	

Table 4.15: Descriptive statistics of the human second rib measurements.

Variable		SOTHO	ZULU	EUROPEAN	TOTAL HUMAN	KOLMOGOROV-SMIRNOV TEST
HSH	Mean	5.26	5.74	5.47	5.50	0.584
	Std Deviation	1.01	1.28	1.37	1.23	
HSW	Mean	8.33	8.83	8.42	8.53	0.766
	Std Deviation	1.04	1.22	1.73	1.36	
HIH	Mean	8.08	6.58	7.02	7.23	0.902
	Std Deviation	1.19	1.55	1.36	1.49	
HIW	Mean	10.15	9.69	9.36	9.74	0.763
	Std Deviation	1.46	1.85	1.49	1.62	
NH	Mean	8.74	8.37	8.57	8.56	0.869
	Std Deviation	1.74	1.27	1.90	1.63	
NL	Mean	19.17	19.04	20.66	19.61	0.821
	Std Deviation	3.76	2.83	2.29	3.06	
NT	Mean	6.97	6.99	6.54	6.84	0.653
	Std Deviation	0.83	1.10	1.06	1.01	
NHA	Mean	7.26	7.75	7.54	7.52	0.758
	Std Deviation	1.26	1.52	2.18	1.68	
NTA	Mean	8.27	8.18	7.20	7.89	0.643
	Std Deviation	0.95	0.83	1.22	1.10	
TFH	Mean	6.06	6.57	6.23	6.29	0.923
	Std Deviation	0.89	1.39	1.23	1.19	
TFW	Mean	8.37	8.30	9.27	8.64	0.999
	Std Deviation	1.45	1.36	1.58	1.50	
TILO	Mean	16.40	20.44	12.76	16.59	0.586
	Std Deviation	3.13	6.03	3.74	5.46	
TILI	Mean	13.81	18.00	11.08	14.36	0.059
	Std Deviation	2.05	6.07	3.42	5.07	
SHPA	Mean	8.46	8.50	7.84	8.27	0.540
	Std Deviation	1.43	1.94	0.97	1.52	
SWPA	Mean	11.87	11.97	10.74	11.53	0.951
	Std Deviation	1.31	1.70	1.40	1.56	

Table 4.16: Descriptive statistics of the human fourth rib measurements.

Variable		SOTHO	ZULU	EUROPEAN	HUMAN TOTAL	KOLMOGOROV-SMIRNOV TEST
HSH	Mean	5.14	5.60	5.95	5.56	0.747
	Std Deviation	0.75	1.10	1.01	1.01	
HSW	Mean	8.55	9.39	9.71	9.21	0.782
	Std Deviation	1.06	1.19	1.83	1.45	
HIH	Mean	7.50	7.13	6.85	7.16	0.994
	Std Deviation	1.33	1.35	1.64	1.45	
HIW	Mean	9.61	9.71	9.76	9.69	0.865
	Std Deviation	1.42	1.82	3.04	2.17	
NH	Mean	10.24	10.85	10.25	10.45	0.464
	Std Deviation	1.55	1.70	1.63	1.62	
NL	Mean	18.60	19.50	21.29	19.79	0.873
	Std Deviation	2.76	2.25	2.22	2.63	
NT	Mean	9.34	9.42	9.06	9.28	0.734
	Std Deviation	1.12	1.30	1.30	1.23	
NHA	Mean	5.86	6.15	6.91	6.30	0.522
	Std Deviation	0.95	1.00	1.69	1.31	
NTA	Mean	5.56	5.86	5.71	5.71	0.982
	Std Deviation	0.58	0.67	1.18	0.82	
TFH	Mean	7.07	6.97	7.80	7.27	0.560
	Std Deviation	0.83	1.72	1.36	1.39	
TFW	Mean	8.76	9.05	8.10	8.65	0.088
	Std Deviation	1.03	2.71	1.45	1.90	
TILO	Mean	29.31	30.18	28.82	29.45	0.840
	Std Deviation	2.65	5.70	4.76	4.53	
TILI	Mean	24.83	25.44	24.81	25.03	0.440
	Std Deviation	2.86	5.18	3.82	4.03	
SHPA	Mean	10.58	10.75	10.76	10.70	0.994
	Std Deviation	1.61	1.33	1.26	1.39	
SWPA	Mean	8.31	8.42	7.97	8.24	0.914
	Std Deviation	1.24	1.32	2.02	1.55	

Table 4.17: Descriptive statistics of the human seventh rib measurements.

Variable		SOTHO	ZULU	EUROPEAN	TOTAL HUMAN	KOLMOGOROV-SMIRNOV TEST
HSH	Mean	7.04	7.04	7.82	7.29	0.959
	Std Deviation	1.13	1.39	1.77	1.48	
HSW	Mean	10.07	9.99	10.61	10.22	0.888
	Std Deviation	1.06	1.73	2.23	1.73	
HIH	Mean	9.39	8.91	8.81	9.03	0.855
	Std Deviation	1.08	1.98	1.70	1.63	
HIW	Mean	10.78	10.29	10.82	10.63	0.955
	Std Deviation	1.15	1.96	2.01	1.74	
NH	Mean	13.65	12.85	13.90	13.46	0.956
	Std Deviation	1.47	1.31	1.87	1.60	
NL	Mean	20.27	20.06	22.11	20.80	0.945
	Std Deviation	2.33	2.68	2.34	2.59	
NT	Mean	11.44	11.09	11.81	11.44	0.726
	Std Deviation	1.36	1.55	1.58	1.52	
NHA	Mean	6.63	6.86	6.97	6.82	0.839
	Std Deviation	1.18	1.18	1.62	1.32	
NTA	Mean	6.23	6.50	6.37	6.37	0.999
	Std Deviation	0.94	0.99	1.55	1.17	
TFH	Mean	6.80	6.63	6.99	6.81	0.284
	Std Deviation	1.06	1.83	1.31	1.43	
TFW	Mean	8.79	8.88	8.50	8.77	0.847
	Std Deviation	0.92	1.32	1.45	1.24	
TILO	Mean	46.75	45.98	46.36	46.36	0.961
	Std Deviation	3.16	6.48	7.13	5.78	
TILI	Mean	41.68	39.84	41.04	40.84	0.951
	Std Deviation	4.15	5.90	7.00	5.76	
SHPA	Mean	14.54	12.88	13.65	13.68	0.998
	Std Deviation	2.39	3.26	1.85	2.62	
SWPA	Mean	8.09	9.52	8.93	8.86	0.261
	Std Deviation	1.30	2.14	3.17	2.37	

Table 4.18: ANCOVA and ANOVA for the human first rib measurements (E = European; S = Sotho; Z = Zulu).

Variable		ANCOVA				ANOVA for Population			Population Comparison ²
		F	df	Significance	Levene's Test	F	df	Significance	
HH	Population	7.20	2	0.002	0.088	5.799	2	0.005	E significantly different from Z & S
	Sex	16.94	1	0.000					
HW	Population	2.27	2	0.114	0.648	2.38		0.101	No significant difference
	Sex	17.05	1	0.000					
NH	Population	6.55	2	0.003	0.610	7.80		0.001	E significantly different from S & Z
	Sex	5.30	1	0.025					
NL	Population	0.13	2	0.882	0.942	0.135	0.874	No significant difference	
	Sex	0.46	1	0.502					
NT	See Table 4.24, 4.25 and 4.26								
NHA	See Table 4.24, 4.25 and 4.26								
NTA	Population	2.85	2	0.066	0.327	2.63	2	0.081	No significant difference
	Sex	9.62	1	0.003					
TFH	Population	2.59	2	0.084	0.266	2.09		0.13	
	Sex	11.19	1	0.001					
TFW	Population	2.58	2	0.085	0.448	2.33		0.106	
	Sex	5.43	1	0.023					
SHPA	Population	1.37	2	0.262	0.201	0.91	0.41		
	Sex	25.53	1	0.000					
SWPA	Population	2.71	2	0.075	0.104	2.26	0.11		
	Sex	14.55	1	0.000					

¹Levene's statistic is significant ²Post Hoc Test performed as part of ANOVA of population ³After performing rank analysis

Table 4.19: ANCOVA and ANOVA for the human second rib measurements (E = European; S = Sotho; Z = Zulu).

Variable		ANCOVA				ANOVA for Population			Population Comparison ²
		F	df	Significance	Levene's Test	F	df	Significance	
HSH	Population	1.11	2	0.336	0.858	0.79	2	0.457	No significant difference
	Sex	15.73	1	0.000					
HSW	Population	1.67	2	0.198	0.325	2.38	2	0.101	
	Sex	46.53	1	0.000					
HIH	Population	9.63	2	0.000	0.623	6.32	2	0.003	Z & S significantly different
	Sex	30.95	1	0.000					
HIW	Population	1.76	2	0.182	0.899	1.22	2	0.302	No significant difference
	Sex	25.96	1	0.000					
NH	Population	0.274	2	0.762	0.630	0.270	2	0.764	
	Sex	32.00	1	0.000					
NL ³	See Table 4.24, 4.25 and 4.26								
NT	Population	1.58	2	0.214	0.754	1.29	2	0.284	No significant difference
	Sex	10.95	1	0.002					
NHA	Population	0.66	2	0.521	0.026 ¹	1.26	2	0.649	
	Sex	18.65	1	0.000					
NTA	Population	9.50	2	0.000	0.584	6.95	2	0.002	E significantly different from Z & S
	Sex	20.55	1	0.001					
TFH	Population	1.23	2	0.300	0.051	0.95	2	0.394	No significant difference
	Sex	11.45	1	0.001					
TFW	Population	2.99	2	0.058	0.956	2.72	2	0.074	E significantly different from Z & S
	Sex	8.63	1	0.005					
TILO ³	See Table 4.24, 4.25 and 4.26								
TILI ³	See Table 4.24, 4.25 and 4.26								
SHPA	Population	1.23	2	0.300	0.127	2.71	2	0.313	No significant difference
	Sex	1.87	1	0.177					
SWPA	Population	4.90	2	0.011	0.351	4.23	2	0.019	E significantly different from Z & S
	Sex	8.51	1	0.005					

¹Levene's statistic is significant ²Post Hoc Test performed as part of ANOVA of population

Table 4.20: ANCOVA and ANOVA Table for the human fourth rib measurements (E = European; S = Sotho; Z = Zulu). ¹Levene's statistic is significant ²Post Hoc Test performed as part of ANOVA of population ³After performing rank analysis.

Variable		ANCOVA			ANOVA for Population			Population Comparison ²	
		F	df	Significance	Levene's Test	F	df		Significance
HSH	Population	3.50	2	0.037	0.551	3.49	2	0.037	E significantly different from Z & S
	Sex	1.11	1	0.297					
HSW	Population	6.77	2	0.002	0.801	3.64	2	0.032	E significantly different from S
	Sex	62.71	1	0.000					
HIH	Population	1.34	2	0.270	0.642	1.02	2	0.366	No significant difference
	Sex	18.57	1	0.000					
HIW	Population	0.027	2	0.973	0.763	0.02	2	0.978	
	Sex	64.13	1	0.000					
NH	Population	1.31	2	0.279	0.781	0.97	2	0.384	
	Sex	13.14	1	0.001					
NL ³	See Table 4.24, 4.25 and 4.26								
NT	Population	0.764	2	0.470	0.159	0.46	2	0.631	No significant difference
	Sex	26.37	1	0.000					
NHA	Population	2.98	2	0.059	0.577	3.70	2	0.031	E significantly different from S
	Sex	13.33	1	0.001					
NTA ³	See Table 4.24, 4.25 and 4.26								
TFH	Population	2.49	2	0.92	0.041 ¹	2.19	2	0.121	No significant difference
	Sex	11.61	1	0.001					
TFW	Population	1.56	2	0.219	0.368	1.34	2	0.270	
	Sex	7.10	1	0.010					
TILO ³	See Table 4.24, 4.25 and 4.26								
TILI	Population	0.20	2	0.816	0.015 ¹	0.156	2	0.856	No significant difference
	Sex	6.11	1	0.016					
SHPA	Population	0.18	2	0.836	0.553	0.104	2	0.901	
	Sex	24.41	1	0.000					
SWPA	Population	1.17	2	0.318	0.630	0.46	2	0.636	
	Sex	19.60	1	0.000					

Table 4.21: ANCOVA and ANOVA for the human seventh rib measurements (E = European; S = Sotho; Z = Zulu).

Variable		ANCOVA			ANOVA for Population			Population Comparison ²	
		F	df	Significance	Levene's Test	F	df		Significance
HSH	Population	2.60	2	0.083	0.223	1.93	2	0.155	No significant difference
	Sex	25.13	1	0.000					
HSW	See Table 4.24, 4.25 and 4.26								
HIH	Population	1.04	2	0.362	0.024 ¹	0.728		0.487	No significant difference
	Sex	30.01	1	0.000					
HIW	Population	0.855	2	0.431	0.413	0.587		0.559	
	Sex	49.29	1	0.000					
NH	Population	3.88	2	0.026	0.745	2.56		0.086	
	Sex	40.08	1	0.000					
NL	Population	5.36	2	0.007	0.038 ¹	4.27		0.019	E significantly different from Z & S
	Sex	18.43	1	0.000					
NT	Population	1.48	2	0.236	0.808	1.17	2	0.317	No significant difference
	Sex	24.71	1	0.000					
NHA	Population	0.62	2	0.544	0.419	0.34		0.716	
	Sex	41.94	1	0.000					
NTA	Population	0.76	2	0.470	0.025 ¹	0.28		0.758	
	Sex	63.86	1	0.000					
TFH	Population	0.30	2	0.741	0.541	0.32		0.729	
	Sex	1.63	1	0.207					
TFW	Population	0.48	2	0.621	0.041 ¹	0.50		0.612	
	Sex	1.44	1	0.235					
TILO	See Table 4.24, 4.25 and 4.26								
TILI	Population	0.60	2	0.553	0.012 ¹	0.53		0.589	No significant difference
	Sex	19.98	1	0.000					
SHPA ³	Population	2.06		0.136	0.083	2.12	2	0.129	
	Sex	21.40		0.000					
SWPA	See Table 4.24, 4.25 and 4.26								

¹Levene's statistic is significant ²Post Hoc Test performed as part of ANOVA of population ³After performing rank analysis

4.2.2. Indices of the human sample

The sample size, mean value and standard deviation for the indices from each group are contained in Table 4.18.

The ANOVA and ANCOVA values and significant levels for the indices are contained in Tables 4.23.

Results for the indices of the human sample between the sexes in each species of human sample

Statistically significant sex differences was observed only in the following indices for the first rib

- (a) Neck at head index (NHI) and
- (b) Neck at tubercle index (NTI)

For the second rib, the European female showed a significant difference as compared to the Sotho and Zulu female for the Neck index (NI).

Statistically significant differences were observed in the Superior Facet of rib head index (SFHI) and the Inferior Facet of rib head index (IFHI) of the fourth rib.

For the seventh rib, statistically significant differences were observed in the Neck at head index (NHI) and the Neck at tubercle index (NTI). The Zulu female group was significantly different from the Sotho female and European female groups for the Shaft height at the posterior angle index (SHI). The European male was significantly

different from the Sotho male and Zulu male groups for the Shaft height at the posterior angle index (SHI).

Results for the indices of the human sample between the populations of the human sample for each of the ribs analysed

The first rib. The European group was significantly different from the Sotho group for the Neck index (NI).

The Zulu group showed a significant difference from the Sotho and European group for the Neck at tubercle index (NTI).

The other indices did not show any significant differences between the population groups.

The second rib The Sotho was significantly different from the Zulu for the following indices:

- (a) Inferior Facet of rib head (IFHI) and
- (b) Tubercular facet (TFI).

The other indices did not show any significant differences between the population groups.

The fourth rib. The European group was significantly different from the Sotho and Zulu groups for the following indices:

- (a) Neck (NI);
- (b) Neck at head (NHI) and
- (c) Tubercular facet (TFI).

The other indices did not show any significant differences between the population groups.

The seventh rib. The European group was significantly different from the Sotho group for the Neck index (NI) only.

The other indices did not show any significant differences between the population groups.

Trends observed in the indices for the non-human primates

The following describes the trends observed for each species in the value of the means of the indices calculated.

Facet of the Head Index (FHI). This index is only applicable for the first rib. It had the greatest value for all the facet indices calculated for the ribs 1, 2, 4 and 7.

Superior facet of the Head Index (SFHI). This value decreased from rib 2 to rib 4 and then increased to rib 7 for all groups.

Inferior facet of the Head Index (IFHI). This value decreased from rib 2 to 4 and then increased to rib 7 in Sotho and European groups.

This value increased from rib 2 to 7 in the Zulu.

Neck Index (NI). This value increased from rib 1 to 7 in the Sotho and the Zulu.

This value decreased from rib 1 to 2 and then increased to rib 7 in the European group.

Neck at Head Index (NHI). This value increased from rib 1 to 7 for all groups.

Neck at Tubercle Index (NTI). This value increased from rib 1 to 7 in all groups.

Tubercle facet Index (TFI). This value increased from rib 1 to rib 4 and then decreased to rib 7 in all groups.

Tubercle-Iliocostal line index (TICI). This value decreased from rib 2 to rib 7 in the Sotho and the European.

This value increased from rib 2 to 4 and then decreased to rib 7 in the Zulu.

Shaft height at posterior angle Index (SHI). This value increased from rib 1 to rib 7 in all groups.

Table 4.22: Descriptive statistics of the human rib indices.

Rib number	Variable		SOTHO	ZULU	EUROPEAN	TOTAL HUMAN	KOLMOGOROV-SMIRNOV TEST
1	FHI	Mean	89.54	88.65	94.33	90.81	0.941
		Std Deviation	10.53	14.08	15.56	13.57	
	NI	Mean	42.26	44.19	50.18	49.52	0.698
		Std Deviation	8.86	7.58	10.77	9.60	
	NHI	Mean	84.16	92.39	95.18	90.60	0.854
		Std Deviation	16.94	20.57	15.67	18.21	
	NTI	Mean	49.01	58.22	50.60	52.70	0.963
		Std Deviation	6.58	6.14	7.49	7.79	
	TFI	Mean	67.59	66.20	64.78	66.19	0.689
		Std Deviation	14.09	8.74	10.82	11.26	
	SHI	Mean	46.68	48.38	45.73	46.96	0.989
		Std Deviation	8.36	5.61	6.73	6.95	
2	SFHI	Mean	63.03	65.73	65.77	64.86	0.614
		Std Deviation	9.86	14.35	13.49	12.60	
	IFHI	Mean	80.80	68.37	75.09	74.75	0.811
		Std Deviation	15.09	12.87	9.18	13.41	
	NI	Mean	46.46	44.27	41.67	44.13	0.932
		Std Deviation	8.29	5.65	8.73	7.77	
	NHI	Mean	124.04	110.98	118.30	117.66	0.766
		Std Deviation	32.59	22.68	26.13	27.45	
	NTI	Mean	85.51	86.39	93.24	88.35	0.717
		Std Deviation	14.27	17.80	19.90	17.54	
	TFI	Mean	74.22	79.27	67.73	73.83	0.745
		Std Deviation	15.87	12.22	10.22	13.62	
	TICI	Mean	118.75	115.44	116.50	116.87	0.207
		Std Deviation	13.95	17.46	12.08	14.54	
	SHI	Mean	71.75	74.58	74.23	73.54	0.011
		Std Deviation	12.88	35.17	13.85	22.96	

Table 4.22 (contd.): Descriptive statistics of the human rib indices.

Rib number	Variable		SOTHO	ZULU	EUROPEAN	TOTAL HUMAN	KOLMOGOROV-SMIRNOV TEST
4	SFHI	Mean	60.69	60.53	62.30	61.16	0.160
		Std Deviation	9.63	14.20	10.75	11.57	
	IFHI	Mean	77.86	74.38	72.97	75.07	0.598
		Std Deviation	6.42	13.12	14.92	12.03	
	NI	Mean	55.87	55.95	48.07	53.34	0.799
		Std Deviation	9.49	7.58	5.38	8.40	
	NHI	Mean	176.52	180.55	152.63	170.07	0.343
		Std Deviation	22.49	39.15	26.20	32.28	
	NTI	Mean	168.45	163.06	163.26	164.89	0.972
		Std Deviation	16.65	30.63	32.03	27.05	
	TFI	Mean	81.33	80.56	98.02	86.54	0.147
		Std Deviation	10.56	23.19	19.48	20.00	
	TICI	Mean	118.66	119.33	116.42	118.16	0.160
		Std Deviation	9.91	12.16	10.59	10.84	
SHI	Mean	129.45	129.91	141.27	133.48	0.898	
	Std Deviation	23.18	22.11	30.87	25.77		
7	SFHI	Mean	70.14	70.83	74.02	71.65	0.980
		Std Deviation	10.57	10.82	11.50	10.92	
	IFHI	Mean	87.30	86.87	81.90	85.38	0.675
		Std Deviation	7.93	13.22	10.00	10.77	
	NI	Mean	67.56	64.75	62.95	65.08	0.892
		Std Deviation	4.87	8.12	6.34	6.77	
	NHI	Mean	210.36	191.20	204.57	201.87	0.651
		Std Deviation	33.81	28.69	29.91	31.39	
	NTI	Mean	186.34	173.25	192.34	183.80	0.933
		Std Deviation	27.72	30.56	37.16	32.52	
	TFI	Mean	77.98	77.44	83.61	79.64	0.048
		Std Deviation	12.70	33.24	17.84	22.98	
	TICI	Mean	112.68	115.83	113.43	114.00	0.745
		Std Deviation	7.98	9.05	6.79	7.99	
SHI	Mean	182.90	143.81	167.52	164.40	0.822	
	Std Deviation	36.46	49.82	47.74	47.28		

Table 4.23: ANCOVA and ANOVA of human rib indices (E = European; S = Sotho; Z = Zulu).

Rib number	Variable		ANCOVA				ANOVA			Population Comparison ²
			F	df	Significance	Levene's Test	F	df	Significance	
1	FHI	Population	1.01	2	0.370	0.559	1.03	2	0.364	No significant difference
		Sex	0.002	1	0.965					
	NF ³	Population	3.90	2	0.260	0.207	4.09		0.022	E significantly different from S
		Sex	1.67	1	0.202					
	NHI	Population	2.19	2	0.121	0.548	2.06		0.137	No significant difference
		Sex	5.75	1	0.020					
	NTI	Population	12.88	2	0.000	0.816	10.97		0.000	S & E differ sig from Z, S no sig E
		Sex	9.34	1	0.003					
	TFI	Population	0.30	2	0.743	0.253	0.30		0.740	No significant difference
		Sex	0.01	1	0.760					
	SHI	Population	0.807	2	0.451	0.125	0.76		0.471	
		Sex	1.72	1	0.195					
SFHI	Population	0.30	2	0.743	0.375	0.31	0.738			
	Sex	0.01	1	0.931						
IFHI	Population	4.85	2	0.011	0.560	4.86	0.011	S significantly different from Z		
	Sex	0.77	1	0.383						
2	NI	See Table 4.24, 4.25 and 4.26								
	NHI	Population	1.20	2	0.310	0.090	1.18	0.316	No significant difference	
		Sex	0.70	1	0.406					
	NTI	Population	1.17	2	0.317	0.822	1.18	0.314		
		Sex	0.25	1	0.617					
	TFI	Population	4.11	2	0.021	0.840	4.06	0.022	S significantly different from Z	
		Sex	1.03	1	0.314					
	TICI	Population	0.26	2	0.771	0.244	0.268	0.766	No significant difference	
		Sex	0.02	1	0.887					
	SHI	Population	0.08	2	0.919	0.353	0.09	0.915		
Sex		0.425	1	0.517						

¹Levene's statistic is significant ²Post Hoc Test performed as part of ANOVA of population ³After performing rank analysis

Table 4.23 (contd.): ANCOVA and ANOVA of human rib indices (E = European; S = Sotho; Z = Zulu).

Rib number	Variable		ANCOVA				ANOVA			Population Comparison ²
			F	df	Significance	Levene's Test	F	df	Significance	
4	SFHI	Population	0.21	2	0.813	0.913	0.14	0.870	No significant difference	
		Sex	15.11	1	0.000					
	IFHI	Population	0.93	2	0.401	0.037 ¹	0.87	0.423		
		Sex	4.58	1	0.037					
	1NI	Population	7.12	2	0.002	0.006 ¹	7.03	0.002	E significantly different from S & Z	
		Sex	1.35	1	0.250					
	NHI	Population	4.93	2	0.011	0.042 ¹	5.02	0.010		
		Sex	0.23	1	0.634					
	NTI	Population	0.25	2	0.783	0.033 ¹	0.25	0.779	No significant difference	
		Sex	0.04	1	0.844					
	TFI	Population	5.58	2	0.006	0.058	5.68	0.006	E significantly different from S & Z	
		Sex	0.285	1	0.596					
	TICI	Population	0.38	2	0.684	0.443	0.39	0.677	No significant difference	
		Sex	0.10	1	0.748					
SHI	Population	0.77	2	0.470	0.990	1.38	0.260			
	Sex	0.46	1	0.502						
7	SFHI	Population	0.71	2	0.499	0.934	0.72	0.493	No significant difference	
		Sex	0.02	1	0.889					
	IFHI	Population	1.56	2	0.219	0.142	1.59	0.212		
		Sex	0.66	1	0.799					
	NI	Population	2.49	2	0.092	0.087	2.48	0.093	S significantly different from E	
		Sex	1.36	1	0.249					
	NHI	Population	2.43	2	0.097	0.731	2.09	0.133	No significant difference	
		Sex	6.97	1	0.011					
	NTI	Population	2.32	2	0.103	0.493	1.91	0.157		
		Sex	10.17	1	0.002					
	TFI	Population	0.431	2	0.652	0.270	0.44	0.647		
		Sex	2.63	1	0.110					
	TICI	Population	0.842	2	0.436	0.858	0.87	0.424		
		Sex	1.54	1	0.220					
	SHI ³	See Table 4.24, 4.25 and 4.26								

¹Levene's statistic is significant ²Post Hoc Test performed as part of ANOVA of population ³After performing rank analysis

Table 4.24: Sex differences amongst the different human population groups (After rank analysis; significant interaction between population and sex).

Rib Number	Variable	Population								
		Sotho			Zulu			European		
		F	df	Significance	F	df	Significance	F	df	Significance
1	NT	3.10	1	0.095	9.39	1	0.006	60.93	1	0.000
	NHA	0.91		0.353	4.67		0.044	30.59		
2	NL	10.55		0.004	4.43		0.050	0.15		0.705
	TILO	0.61		0.444	0.862		0.365	16.78		0.001
	TILI	2.79		0.112	1.62		0.219	20.89		0.000
	NI	0.81		0.380	0.28		0.603	10.10		0.005
4	NL	9.42		0.007	0.44		0.515	15.23		0.001
	NTA	13.21		0.002	0.11		0.746	16.17		
	TILO	0.87		0.378	0.002		0.976	21.83		
7	HSW	4.19		0.056	20.71		0.000	32.83		0.000
	TILO	7.73	0.012	0.77	0.392	29.03				
	SWPA	1.51	0.235	1.16	0.296	19.91				
	SHI	1.31	0.268	8.44	0.009	16.11	0.001			

Table 4.25: Population differences amongst human females (E = European; S = Sotho; Z = Zulu).

Rib Number	Variable	F	df	Significance	Post hoc results
1	NT	6.23	2	0.006	E significantly different from Z
	NHA	1.31		0.286	No significant difference
2	NL	4.86		0.016	E significantly different from S
	TILO	19.10		0.000	E significantly different from S & Z
	TILI	15.46		0.000	
NI	7.17	0.003			
4	NL	5.02		0.014	S significantly different from Z & E
	NTA	4.46		0.021	Z significantly different from S & E
	TILO	3.00		0.066	No significant difference
7	HSW	1.23		0.307	
	TILO	2.00		0.154	
	SWPA	9.86		0.001	
	SHI	10.98	0.000		

Table 4.26: Population differences amongst human males (E = European; S = Sotho; Z = Zulu).

Rib Number	Variable	F	df	Significance	Post hoc results
1	NT	8.16	2	0.002	S significantly different from Z & E
	NHA	7.11		0.003	E significantly different from S
2	NL	0.61		0.550	No significant difference
	TILO	2.29		0.121	
	TILI	2.85		0.076	
	NI	0.50		0.612	
4	NL	9.58		0.001	E significantly different from S & Z
	NTA	2.16		0.135	No significant difference
	TILO	1.14		0.336	
7	HSW	6.97		0.004	E significantly different from S
	TILO	2.79		0.079	No significant difference
	SWPA	4.64		0.019	E significantly different from S & Z
	SHI	6.53	0.005		

4.3. A comparison of the primate sample

4.3.1. Measurements of the human versus non-human primate sample

The ANOVA and ANCOVA values and significant levels for the indices are contained in Tables 4.27 to 4.34.

Between the sexes in each species of the primate species compared

See Tables 4.27 to 4.30.

Statistically significant sexual dimorphism was exhibited for all the variables for all the primate ribs except for the following:

- (a) Shaft maximum height at posterior angle (SHPA) for the second rib
- (b) Head Superior facet height (HSH) for the fourth rib

A statistically significant sexual dimorphism was also observed in the following specific variables of the ribs of the specific species:

- (a) Baboon and Vervet
 - i. Neck (Superior-Inferior diameter) at Head (NH) of rib 1;
 - ii. Tubercle – iliocostal line distance (outer) (TILO) and Tubercle - iliocostal line distance (inner) (TILI) of rib 2;
 - iii. Neck length (NL), Tubercle – iliocostal line distance (outer) (TILO) and Tubercle - iliocostal line distance (inner) (TILI) for rib 4 and
 - iv. Neck (Superior-Inferior diameter) at Head (NH) and Tubercle facet width (TFW) of the seventh rib

(b) Gorilla and Orangutan

- i. Neck (Superior-Inferior diameter) at Head (NH) of the seventh rib

(c) Chimpanzee

- i. Neck (Superior-Inferior diameter) at Head (NH) of the first rib and
- ii. Tubercle – iliocostal line distance (outer) (TILO) of the fourth rib

(d) Human

- i. Neck (Superior-Inferior diameter) at Head (NH) and Shaft maximum height at posterior angle (SHPA) of the seventh rib

The following observations were made for the specific ribs:

For the first rib, the gorilla and baboon female differed significantly from the human female in the following measurements:

- (a) Neck length (NL) and
- (b) Neck (Superior-Inferior diameter) at Head (NH)

No significant difference was observed for the male group for Neck length (NL). The baboon male group differed significantly from the human male group in the Neck (Superior-Inferior diameter) at Head (NH).

For the second rib, the female chimpanzee and the female baboon groups differed significantly from the female human group for the Tubercle – iliocostal line distance (outer) (TILO). Both sexes of the baboon group differed significantly from both sexes of the human group in the Tubercle - iliocostal line distance (inner) (TILI). The male gorilla group differed significantly from the male human group for the Tubercle - iliocostal line distance (outer) (TILO).

For the fourth rib, the female gorilla and the female baboon groups differed significantly from the female human group for the Neck length (NL). A significant difference was also observed for the Tubercle – iliocostal line distance (outer) (TILO) and Tubercle - iliocostal line distance (inner) (TILI) between the female baboon and female human groups. The male chimpanzee and the male gorilla groups differed from the male human for the Tubercle – iliocostal line distance (outer) (TILO) and Tubercle - iliocostal line distance (inner) (TILI), respectively.

For the seventh rib, the female gorilla and female baboon groups differed from the female human group for the Neck (Superior-Inferior diameter) at Head (NH) and Tubercle facet width (TFW). The female baboon differed significantly from the female human for the Shaft maximum height at posterior angle (SHPA). The male chimpanzee and the male baboon differed significantly from the human male for Shaft maximum height at posterior angle (SHPA). The male baboon differed significantly from the male human for Neck (Superior-Inferior diameter) at Head

(NH). The male gorilla differed significantly from the male human for the Tubercle facet width (TFW).

Between the ribs of the primate species compared

See Tables 4.27 to 4.30

The first rib. The chimpanzee and baboon differed significantly from the human in the measurement of Head Superior facet height (HSH).

The baboon differed significantly from the human in the measurement of Head Superior facet width (HSW).

The chimpanzee, gorilla and baboon differed significantly from the human in the measurement of the Shaft maximum height at posterior angle (SHPA).

The gorilla and the baboon differed significantly from the human for the following measurements:

- (a) Neck (Superior-Inferior diameter) at Tubercle (NT);
- (b) Neck (Anterior-Posterior diameter) at Head (NHA);
- (c) Neck (Anterior-Posterior diameter) at Tubercle (NTA);
- (d) Tubercle facet height (TFH);
- (e) Tubercle facet width (TFW) and
- (f) Shaft maximum width at posterior angle (SWPA).

No significant differences were observed in these measurements for the chimpanzee.

The second rib. The gorilla and the baboon differed significantly from the human for Head Superior facet height (HSH).

The baboon differed significantly from the human for the following measurements:

- (a) Head Superior facet width (HSW);
- (b) Head Inferior facet height (HIH);
- (c) Head Inferior facet width (HIW);
- (d) Neck (Superior-Inferior diameter) at Head (NH);
- (e) Neck (Anterior-Posterior diameter) at Tubercle (NTA);
- (f) Tubercle facet height (TFH) and
- (g) Shaft maximum width at posterior angle (SWPA)

The chimpanzee and baboon differed significantly from the human in the following measurement:

- (a) Neck length (NL);
- (b) Neck (Anterior-Posterior diameter) at Head (NHA);
- (c) Tubercle facet width (TFW) and
- (d) Shaft maximum height at posterior angle (SHPA).

The fourth rib. The baboon differed significantly from the human for the following measurements:

- (a) Head Inferior facet height (HIH);
- (b) Head Inferior facet width (HIW);
- (c) Neck (Superior-Inferior diameter) at Head (NH);
- (d) Neck (Superior-Inferior diameter) at Tubercle (NT);
- (e) Tubercle facet width (TFW) and
- (f) Shaft maximum width at posterior angle (SWPA).

The gorilla and the baboon differed significantly from the human for the following measurements:

- (a) Head Superior facet height (HSH);
- (b) Head Superior facet width (HSW);
- (c) Neck (Anterior-Posterior diameter) at Head (NHA);
- (d) Neck (Anterior-Posterior diameter) at Tubercle (NTA) and
- (e) Tubercle facet height (TFH).

The chimpanzee and baboon differed significantly from the human in the measurement of the Shaft maximum height at posterior angle (SHPA).

The seventh rib. All the primates showed a significant difference for the measurement of Head Inferior facet height (HIH).

The gorilla differed significantly from the human for the Tubercle facet height (TFH).

The baboon differed significantly from the human for the following measurements:

- (a) Head Superior facet height (HSH) and
- (b) Shaft maximum width at posterior angle (SWPA).

The chimpanzee and baboon differed significantly from the human in the measurement of the Neck length (NL).

The gorilla and the baboon differed significantly from the human for the following measurements:

- (a) Head Superior facet width (HSW);
- (b) Head Inferior facet width (HIW);
- (c) Neck (Superior-Inferior diameter) at Head (NH);
- (d) Neck (Superior-Inferior diameter) at Tubercle (NT);
- (e) Neck (Anterior-Posterior diameter) at Head (NHA);
- (f) Neck (Anterior-Posterior diameter) at Tubercle (NTA);
- (g) Tubercle – iliocostal line distance (outer) (TILO) and
- (h) Tubercle - iliocostal line distance (inner) (TILI).

Table 4.27: ANCOVA and ANOVA for the all primate first rib measurements (C = Chimpanzee; B = Baboon; G = Gorilla; V = Vervet; H= Human).

Variable		ANCOVA				ANOVA for Species			Species Comparison ²			
		F	df	Significance	Levene's	F	df	Significance				
HSH	Species	97.24	7	0.000	5.63 ¹	75.24	7	0.000	C & B significantly different from H			
	Sex	28.98	1		6.85 ¹	0.872				B & V significantly different from H		
HSW ³	Species	28.49	7						3.86		1	
	Sex	3.86	1									
NH	See Table 4.32 to 4.34											
NL												
NT	Species	7.81	7	0.000	5.78 ¹	69.39	7	0.000	G, B & V significantly different from H			
	Sex	42.87	1		8.52 ¹	59.79						
NHA	Species	6.78	7	0.001								
	Sex	40.10	1									
NTA	Species	100.49	7	0.000	3.70	79.45						
	Sex	26.48	1									
TFH	Species	69.84	7			3.38			51.79			
	Sex	33.78	1									
TFW	Species	50.99	7			4.12 ¹			44.41			
	Sex	14.42	1									
SHPA	Species	114.39	7			4.09	76.79			C, G, B & V significantly different from H		
	Sex	48.81	1									
SWPA	Species	7.32	7		0.004	3.99	0.893			G, B & V significantly different from H		
	Sex	29.79	1									

¹Levene's statistic is significant ²Post Hoc Test performed as part of ANOVA of Species ³After performing rank analysis

Table 4.28: ANCOVA and ANOVA for the all primate second rib measurements (C = Chimpanzee; B = Baboon; G = Gorilla; V = Vervet; H= Human). ¹Levene's statistic is significant ²Post Hoc Test performed as part of ANOVA of Species ³After performing rank analysis

Variable		ANCOVA			ANOVA for Species			Species Comparison ²	
		F	Df	Significance	Levene's	F	Df		Significance
HSH	Species	58.85	7	0.000	5.31 ¹	47.36	7	0.000	G, B & V significantly different from H
	Sex	24.55	1						
HSW	Species	5.89	7		8.60 ¹	0.917			B & V significantly different from H
	Sex	67.72	1						
HIH ³	Species	96.36	7		9.38 ¹	63.88			B & V significantly different from H
	Sex	50.60	1						
HIW	Species	103.54	7		7.12 ¹	70.88			C, B and V significantly different from H
	Sex	45.76	1						
NH	Species	61.45	7		5.93 ¹	47.59			B & V significantly different from H
	Sex	28.07	1						
NL	Species	84.80	7		3.26 ¹	68.06			C, B and V significantly different from H
	Sex	24.16	1						
NT	Species	92.41	7		7.58 ¹	78.60			B & V significantly different from H
	Sex	17.71	1						
NHA	Species	68.43	7	9.36 ¹	49.85	C, B and V significantly different from H			
	Sex	35.64	1						
NTA	Species	54.69	7	3.81 ¹	45.54	B and V significantly different from H			
	Sex	19.20	1						
TFH	Species	66.70	7	6.15 ¹	52.63	C, B & V significantly different from H			
	Sex	26.10	1						
TFW	Species	70.72		6.01 ¹	58.80	C, B & V significantly different from H			
	Sex	19.89							
TILO	See Table 4.32 to 4.34								
TILI									
SHPA	Species	94.50	7	0.000	4.51 ¹	90.49	7	0.000	C, B & V significantly different from H
	Sex	4.94	1						
SWPA	Species	75.31	7		7.10 ¹	61.41			B & V significantly different from H
	Sex	22.10	1						

Table 4.29: ANCOVA and ANOVA for the all primate fourth rib measurements (C = Chimpanzee; B = Baboon; G = Gorilla; V =Vervet; H= Human). ¹Levene’s statistic is significant ²Post Hoc Test performed as part of ANOVA of Species ³After performing rank analysis

Variable		ANCOVA			ANOVA for Species			Species Comparison ²		
		F	df	Significance	Levene’s	F	df		Significance	
HSH	Species	78.01	7	0.000	2.34	72.91	7	0.000	G & B significantly different from H	
	Sex	7.30	1	0.008						
HSW	Species	10.04	7	0.000	8.15 ¹	0.93	7	0.000		
	Sex	33.62	1		6.55 ¹	50.23				
HIH	Species	69.06	7		5.63 ¹	0.876				B & V significantly different from H
	Sex	36.31	1		6.87 ¹	70.90				
HIW	Species	30.26	7							
	Sex	4.52	1							
NH	Species	89.43	7							
	Sex	25.58	1							
NL ³	See Table 4.32 to 4.34									
NT	Species	104.92	7	0.000	10.88 ¹	77.96	7	0.000	B & V significantly different from H	
	Sex	34.57	1		8.07 ¹	69.49				
NHA	Species	90.40	7		3.06	73.21			G & B significantly different from H	
	Sex	29.27	1		4.61 ¹	45.74				
NTA	Species	98.74	7		1.96	32.58				B & V significantly different from H
	Sex	34.47	1							
TFH	Species	53.38	7							
	Sex	15.58	1							
TFW	Species	3.22	7							
	Sex	1.41	1							
TILO ³	See Table 4.32 to 4.34									
TILI ³	See Table 4.32 to 4.34									
SHPA	Species	166.70	7	0.000	6.94 ¹	133.21	7	0.000	C & B significantly different from H	
	Sex	25.87	1		4.16 ¹	0.761				
SWPA	Species	4.62	7						B & V significantly different from H	
	Sex	10.13	1							

Table 4.30: ANCOVA and ANOVA for the all primate seventh rib measurements (C = Chimpanzee; B = Baboon; G = Gorilla; V = Vervet; H= Human). ¹Levene's statistic is significant ²Post Hoc Test performed as part of ANOVA of Species ³After performing rank analysis

Variable		ANCOVA				ANOVA for Species			Species Comparison ²
		F	d	Significance	Levene's	F	df	Significance	
HSH ³	Species	1.34	7	0.000	5.97 ¹	0.847	7	0.000	B & V significantly different from H
	Sex	4.12	1	0.001					
HSW ³	Species	10.99	7	0.000	7.45 ¹	0.939	7	0.000	
	Sex	79.00	1						
HIH	Species	101.62	7	0.000	4.49 ¹	66.70	7	0.000	All significantly different
	Sex	50.75	1						
HIW	Species	9.98	7	0.001	3.06	0.931	7	0.000	G & B significantly different from H
	Sex	39.75	1						
NH	See Table 4.32 to 4.34								
NL	Species	131.51	7	0.000	4.22 ¹	97.94	7	0.000	C, B & V significantly different from H
	Sex	34.32	1						
NT	Species	112.82	7	0.000	1.30	83.24	7	0.000	G, B & V significantly different from H
	Sex	35.42	1						
NHA	Species	3.85	7	0.000	4.42 ¹	0.902	7	0.000	
	Sex	31.67	1						
NTA ³	Species	5.87	7	0.000	4.72	0.916	7	0.000	
	Sex	36.08	1						
TFH	Species	33.65	7	0.000	3.41	30.05	7	0.000	G significantly different from H
	Sex	10.51	1						
TFW ³	See Table 4.32 to 4.34								
TILO ³	Species	31.19	7	0.000	4.25	0.891	7	0.000	G, B & V significantly different from H
	Sex	4.11	1						
TILI ³	Species	22.43	7	0.000	6.02	0.860	7	0.000	
	Sex	4.68	1						
SHPA ³	See Table 4.32 to 4.34								
SWPA ³	Species	27.51	7	0.000	3.89	0.758	7	0.000	B & V significantly different from H
	Sex	6.32	1						

4.3.2. Indices of the primate species compared

The ANOVA and ANCOVA values and significant levels for the indices are contained in Tables 4.31.

Results between the sexes of the primate species compared

Statistically significant sexual dimorphism was exhibited for all the indices for all the primate ribs except for the following:

(a) for the first rib;

- i. Facet height index (FHI);
- ii. Neck at tubercle (S-I diameter vs. A-P diameter) (NTI) and
- iii. Tubercular facet (TFI).

(b) for the second rib;

- i. Neck (NI) and
- ii. Neck at head (S-I diameter vs. A-P diameter) (NHI).

(c) for the fourth rib and

- i. Inferior Facet of rib head (IFHI);
- ii. Neck at head (S-I diameter vs. A-P diameter) (NHI);
- iii. Neck at tubercle (S-I diameter vs. A-P diameter) (NTI);
- iv. Tubercular facet (TFI);
- v. Tubercle – iliocostal line distance (TICD) and
- vi. Shaft height at the posterior angle (SHI).

(d) for the seventh rib

- i. Neck at head (S-I diameter vs. A-P diameter) (NHI);
- ii. Neck at tubercle (S-I diameter vs. A-P diameter) (NTI);
- iii. Tubercular facet (TFI) and
- iv. Tubercle – iliocostal line distance (TICD).

Both sexes of baboon and vervet groups showed a significant difference from the human group for the Inferior Facet of rib head (IFHI) for rib 2.

For the Shaft height at the posterior angle index (SHI), a significant difference was only noted in rib 7 between the male baboon group and the male human group.

Results between the ribs of the primate species compared

See Table 4.31.

The first rib. No significant differences were noted for the following indices:

- (a) Facet height (FHI);
- (b) Neck at head (S-I diameter vs. A-P diameter) (NHI) and
- (c) Tubercular facet (TFI).

The baboon differed significantly from the human in the following indices:

- (a) Neck (NI) and
- (b) Neck at tubercle (S-I diameter vs. A-P diameter) (NTI)

The chimpanzee and the baboon differed from the human in the Shaft height at the posterior angle (SHI) only.

The second rib. No significant differences were noted for the following indices:

- (a) Superior Facet of rib head (SFHI);
- (b) Neck (NI);
- (c) Neck at tubercle (S-I diameter vs. A-P diameter) (NTI) and
- (d) Tubercle – iliocostal line distance (TICI)

The baboon differed significantly from the human in the following indices:

- (a) Neck at head (S-I diameter vs. A-P diameter) (NHI) and
- (b) Tubercular facet (TFI).

The chimpanzee, the baboon and the vervet groups differed from the human in the Shaft height at the posterior angle (SHI) only.

The fourth rib. No significant differences were noted for the following indices:

- (a) Superior Facet of rib head (SFHI);
- (b) Inferior Facet of rib head (IFHI);
- (c) Neck (NI);
- (d) Neck at head (S-I diameter vs. A-P diameter) (NHI);
- (e) Tubercular facet (TFI) and
- (f) Tubercle – iliocostal line distance (TICI).

The baboon differed significantly from the human in the following indices:

- (a) Neck at tubercle (S-I diameter vs. A-P diameter) (NTI) and
- (b) Shaft height at the posterior angle (SHI).

The seventh rib. All the primates differed significantly for the Superior Facet of rib head (SFHI).

The chimpanzee differed significantly from the human for the Inferior Facet of rib head (IFHI).

The gorilla differed from the human for the following indices:

- (a) Neck (NI);
- (b) Neck at head (S-I diameter vs. A-P diameter) (NHI) and
- (c) Neck at tubercle (S-I diameter vs. A-P diameter) (NTI).

The baboon differed significantly from the human for the Tubercle – iliacostal line distance (TICI).

The smaller bodied cercopithecoids (vervets in this study) differed non-significantly from the larger bodied ones (baboon).

Table 4.31: ANCOVA and ANOVA of all primate rib indices (C = Chimpanzee; B = Baboon; G = Gorilla; V =Vetvet; O = Orangutan; H= Human). ¹Levene's statistic is significant ²Post Hoc Test performed as part of ANOVA of Species ³After performing rank analysis

Rib number	Variable		ANCOVA				ANOVA			Species Comparison ²
			F	df	Significance	Levene's	F	df	Significance	
1	FHI	Species	1.93	7	0.195	1.11	1.04	7	0.388	No significant difference
		Sex	2.72	1	0.130					
	NI ³	Species	2.91	7	0.008	3.38	0.62	7	0.003	B & V significantly different from H
		Sex	5.98	1	0.016					
	NHI	Species	7.86	7	0.000	0.75	6.84	7	0.000	Significant difference
		Sex	8.41	1	0.005					
	NTI	Species	7.36	7	0.000	0.78	7.22	7	0.000	B & V significantly different from H
		Sex	4.18	1	0.044					
	TFI	Species	4.57	7	0.000	3.14 ¹	4.49	7	0.000	Significant difference
		Sex	2.45	1	0.120					
	SHI	Species	8.58	7	0.000	2.21	8.36	7	0.000	C, B & V significantly different from H
		Sex	4.31	1	0.040					

Table 4.31 (contd): ANCOVA and ANOVA of all primate rib indices (C = Chimpanzee; B = Baboon; G = Gorilla; V =Vetvet; O = Orangutan; H= Human). ¹Levene’s statistic is significant ²Post Hoc Test performed as part of ANOVA of Species ³After performing rank analysis

Rib number	Variable		ANCOVA				ANOVA			Species Comparison ²
			F	df	Significance	Levene’s	F	df	Significance	
2	SFHI	Species	2.86	7	0.009	2.11	2.75	7	0.012	No significant difference
		Sex	1.10	1	0.297					
	IFHI ³	See Table 4.32 to 4.34								
	NI	Species	6.66	7	0.000	2.08	6.72	7	0.000	Significant difference
		Sex	0.05	1	0.831					
	NHI	Species	5.37	7	0.000	2.12	5.03	7	0.000	B & V significantly different from H
		Sex	3.38	1	0.069					
	NTI	Species	3.20	7	0.004	3.51	3.24	7	0.004	Significant difference
		Sex	0.22	1	0.639					
	TFI	Species	4.93	7	0.000	1.67	4.97	7	0.000	B & V significantly different from H
		Sex	1.14	1	0.288					
	TICI	Species	6.33	7	0.000	1.87	6.29	7	0.000	Significant difference
		Sex	0.51	1	0.480					
	SHI	Species	8.21	7	0.000	7.13 ¹	8.35	7	0.000	C & B significantly different from H
Sex		0.92	1	0.339						

Table 4.31 (contd): ANCOVA/ANOVA all primate rib indices (C = Chimpanzee; B = Baboon; G = Gorilla; V =Vetvet; O = Orangutan; H= Human).¹Levene’s statistic is significant ²Post Hoc Test performed as part of ANOVA of Species³After performing rank analysis

Rib number	Variable		ANCOVA				ANOVA			Species Comparison ²
			F	df	Significance	Levene’s	F	df	Significance	
4	SFHI	Species	2.42	7	0.025	3.78	0.29	7	0.001	Significant difference
		Sex	0.097	1	0.756					
	IFHI	Species	2.38	7	0.027	1.52	2.42		0.024	No Significant difference
		Sex	1.95	1	0.166					
	NI	Species	9.33	7	0.000	5.56 ¹	0.641		0.000	Significant Difference
		Sex	5.75	1	0.018					
	NHI	Species	7.87	7	0.000	3.59 ¹	7.88		0.000	
		Sex	0.28	1	0.596					
	NTI	Species	5.16	7	0.000	3.47	5.21		0.000	B & V significantly different from H
		Sex	0.000	1	0.990					
	TFI	Species	2.94	7	0.008	2.36	2.95		0.007	No significant difference
		Sex	0.36	1	0.552					
	TICI	Species	1.38	7	0.220	2.66	1.33		0.245	
		Sex	1.18	1	0.280					
SHI	Species	22.23	7	0.000	17.09	18.85	0.000	B & V significantly different from H		
	Sex	0.28	1	0.601						
7	SFHI	Species	8.40	7	0.115	1.62	0.50	0.000	All significantly different	
		Sex	5.51	1	0.000					
	IFHI	Species	4.81	7	0.000	1.39	4.99	0.000	C significantly different from H	
		Sex	0.41	1	0.525					
	NI ³	Species	16.34	7	0.000	2.94	15.52	0.000	G significantly different from H	
		Sex	4.34	1	0.040					
	NHI	Species	4.23	7	0.000	1.36	4.25	0.000		
		Sex	0.29	1	0.593					
	NTI	Species	6.93	7	0.000	1.41	0.357	0.208	No significant difference	
		Sex	3.28	1	0.073					
TICI	Species	5.06	7	0.247	1.41	0.357	0.208			
	Sex	1.36	1	0.001						
SHI ³	See Table 4.32 to 4.34									

Table 4.32: Sex differences amongst the different species (After rank analysis; significant interaction between species and sex).

Rib Number	Variable	Species																									
		Baboon			Gorilla			Chimpanzee			Human																
		F	df	Significance	F	df	Significance	F	df	Significance	F	df	Significance														
1	NL	6.68	1	0.19	1	0.065	1	100.58	1	0.063	1	0.36	1	0.556													
	NH	4.59		0.000		2.40		0.196		0.69		0.558		0.006	0.939												
2	TILO	19.26		1.215		0.332		25.22		0.358		0.86		0.365													
	TILI	10.76		0.004		1.22		0.331		1.97		0.394		1.62	0.219												
	IFHI	5.41		0.032		0.203		0.676		17.92		0.148		2.81	0.111												
4	NL	30.23		1		0.000		39.26		1		0.119		1	0.377	1	0.44	1	0.515								
	TILO	29.50						2.727				0.174			0.02		0.916		0.002	0.967							
	TILI	38.99						3.06				0.155			0.16		0.965		0.09	0.773							
7	NH	42.33						1				0.000			17.20		1		0.014	1	0.238	1	11.30	1	0.003		
	TFW	12.82													0.002				1.29		0.319		1.03		0.496	1.90	0.184
	SHPA	4.24													0.054				0.003		0.957		0.003		0.968	20.20	0.000
	SHI	1.23													0.282				0.49		0.523		0.38		0.649	8.44	0.009

Table 4.33: Species differences amongst females (C = Chimpanzee; B = Baboon; G = Gorilla; V =Vervet; O = Orangutan; H= Human).

Rib Number	Variable	F	df	Significance	Post Hoc Results
1	NL	27.23	3	0.000	G & B significantly different from H
	NH	35.92			
2	TILO	18.63			C & B significantly different from H
	TILI	14.26		B & V significantly different from H	
	IFHI	6.37			0.003
4	NL	46.73		0.000	G, O & B significantly different from H
	TILO	8.09		0.001	B significantly different from H
	TILI	6.14		0.003	
7	NH	124.02		0.000	G & B significantly different from H
	TFW	27.32			
	SHPA	29.26		0.005	B significantly different from H
	SHI	5.62			No significant difference

Table 4.34: Species differences amongst males (C = Chimpanzee; B = Baboon; G = Gorilla; V =Vervet; O = Orangutan; H= Human).

Rib Number	Variable	F	df	Significance	Post Hoc Results
1	NL	0.89	3	0.463	No significant difference
	NH	24.98		0.000	B and V significantly different from H
2	TILO	11.72			G and O significantly different from H
	TILI	21.57		0.981	B and V significantly different from H
	IFHI	0.058			
4	NL	26.57		0.000	C significantly different from H
	TILO	16.96			G significantly different from H
	TILI	16.41			B and V significantly different from H
7	NH	65.30		0.010	G significantly different from H
	TFW	4.87			
	SHPA	41.27		0.000	C & B significantly different from H
	SHI	22..06			B and V significantly different from H

Table 4.35: Summary of interaction within non-human primate measurements (ns = not significant; significant if p<0.005).

Rib Number	Variable	ACRONYM	Species					
			Baboon		Gorilla		Chimpanzee	
			Gorilla	Chimpanzee	Baboon	Chimpanzee	Baboon	Gorilla
1	Head Superior facet height	HSH	Significant					
	Head Superior facet width	HSW						
	Neck length	NL	Significant female	ns	Significant female		ns	Significant female
	Neck (Superior-Inferior diameter) at Head	NH	Significant		Significant	ns		ns
	Neck (Superior-Inferior diameter) at Tubercle	NT	Significant					
	Neck (Anterior-Posterior diameter) at Head	NHA						
	Neck (Anterior-Posterior diameter) at Tubercle	NTA						
	Tubercle facet height	TFH	Significant	ns	Significant		ns	Significant
	Tubercle facet width	TFW						
	Shaft maximum height at posterior angle	SHPA						
	Shaft maximum width at posterior angle	SWPA						

Table 4.35. (cont.): Summary of interaction within non-human primate measurements (ns = not significant; significant if $p < 0.005$).

Rib Number	Variable	ACRONYM	Species					
			Baboon		Gorilla		Chimpanzee	
			Gorilla	Chimpanzee	Baboon	Chimpanzee	Baboon	Gorilla
2	Head Superior facet height	HSH	Significant					
	Head Superior facet width	HSW						
	Head Inferior facet height	HIH						
	Head Inferior facet width	HIW						
	Neck length	NL	Significant			ns	Significant	ns
	Neck (Superior-Inferior diameter) at Head	NH	Significant	ns	Significant	ns		
	Neck (Superior-Inferior diameter) at Tubercle	NT						
	Neck (Anterior-Posterior diameter) at Head	NHA	Significant					
	Neck (Anterior-Posterior diameter) at Tubercle	NTA	Significant	ns	Significant	ns		
	Tubercle facet height	TFH	Significant					
	Tubercle facet width	TFW	Significant	ns	Significant		ns	Significant
	Tubercle – iliacostal line distance (outer)	TILO	Significant					
	Tubercle - iliacostal line distance (inner)	TILI						
	Shaft maximum height at posterior angle	SHPA						
	Shaft maximum width at posterior angle	SWPA	ns	Significant	ns		Significant	ns

Table 4.35. (Cont): Summary of interaction within non-human primate measurements (ns = not significant; significant p<0.005).

Rib Number	Variable	ACRONYM	Species					
			Baboon		Gorilla		Chimpanzee	
			Gorilla	Chimpanzee	Baboon	Chimpanzee	Baboon	Gorilla
4	Head Superior facet height	HSH	Significant	ns	Significant	ns	Significant	
	Head Superior facet width	HSW						
	Head Inferior facet height	HIH						
	Head Inferior facet width	HIW	Significant					
	Neck length	NL	Significant	Significant	ns	Significant	ns	
	Neck (Superior-Inferior diameter) at Head	NH						
	Neck (Superior-Inferior diameter) at Tubercle	NT	Significant	ns	Significant	ns	Significant	
	Neck (Anterior-Posterior diameter) at Head	NHA						
	Neck (Anterior-Posterior diameter) at Tubercle	NTA						
	Tubercle facet height	TFH						
	Tubercle facet width	TFW						
	Tubercle – iliocostal line distance (outer)	TILO	Significant	ns	Significant	ns	Significant	
	Tubercle - iliocostal line distance (inner)	TILI	ns					
	Shaft maximum height at posterior angle	SHPA	Significant					
	Shaft maximum width at posterior angle	SWPA	Significant	ns	Significant	ns		

Table 4.35. (Cont): Summary of interaction within non-human primate measurements (ns = not significant; significant p<0.005).

Rib Number	Variable	ACRONYM	Species					
			Baboon		Gorilla		Chimpanzee	
			Gorilla	Chimpanzee	Baboon	Chimpanzee	Baboon	Gorilla
7	Head Superior facet height	HSH	Significant					
	Head Superior facet width	HSW	Significant male		Significant both sexes	ns	Significant	ns
	Head Inferior facet height	HIH	Significant	ns	Significant		ns	Significant
	Head Inferior facet width	HIW	Significant					
	Neck length	NL	Significant		Significant	ns	Significant	ns
	Neck (Sup-Inferior diameter) at Head	NH	Significant					
	Neck (Superior-Inferior diameter) at Tubercle	NT	Significant		Significant	ns	Significant	ns
	Neck (Anterior-Posterior diameter) at Head	NHA	Significant					
	Neck (Anterior-Posterior diameter) at Tubercle	NTA						
	Tubercle facet height	TFH	Significant	ns	Significant		ns	Significant
	Tubercle facet width	TFW						
	Tubercle – iliocostal line distance (outer)	TILO						
	Tubercle - iliocostal line distance (inner)	TILI						
	Shaft maximum height at posterior angle	SHPA	Significant	ns	Significant	ns		
	Shaft maximum width at posterior angle	SWPA						

Table 4.36.: Summary of interaction within non-human primate indices (ns = not significant; significant if p<0.005).

Rib Number	Index	ACRONYM	Species					
			Baboon		Gorilla		Chimpanzee	
			Gorilla	Chimpanzee	Baboon	Chimpanzee	Baboon	Gorilla
1	Superior Facet of rib head	SFHI	ns	Significant	ns		Significant	ns
	Neck	NI	Significant	ns	Significant	ns		
	Neck at head (S-I diameter vs. A-P diameter)	NHI	ns					
	Neck at tubercle (S-I diameter vs. A-P diameter)	NTI	Significant	ns	Significant	ns		
	Tubercular facet	TFI	ns					
	Shaft height at the posterior angle	SHI	Significant	ns	Significant		ns	Significant
2	Superior Facet of rib head	SFHI	ns					
	Inferior Facet of rib head	IFHI	ns					
	Neck	NI	Significant	ns	Significant	ns		
	Neck at head (S-I diameter vs. A-P diameter)	NHI	ns					
	Neck at tubercle (S-I diameter vs. A-P diameter)	NTI	Significant	ns	Significant	ns		
	Tubercular facet	TFI	ns		ns			
	Tubercle – iliocostal line distance	TICI	Significant		Significant			
Shaft height at the posterior angle	SHI	ns	ns					

Table 4.36.: (Cont): Summary of interaction within non-human primate indices (ns = not significant; significant if p<0.005).

Rib Number	Index	ACRONYM	Species					
			Baboon		Gorilla		Chimpanzee	
			Gorilla	Chimpanzee	Baboon	Chimpanzee	Baboon	Gorilla
4	Superior Facet of rib head	SFHI	ns					
	Inferior Facet of rib head	IFHI						
	Neck	NI	Significant		ns	Significant	ns	
	Neck at head (S-I diameter vs. A-P diameter)	NHI	Significant					
	Neck at tubercle (S-I diameter vs. A-P diameter)	NTI	ns					
	Tubercular facet	TFI						
	Tubercle – iliocostal line distance	TICI						
	Shaft height at the posterior angle	SHI	Significant	ns	Significant		ns	ns
7	Superior Facet of rib head	SFHI	Significant		Significant	ns	Significant	ns
	Inferior Facet of rib head	IFHI						
	Neck	NI	Significant	ns	Significant	ns		
	Neck at head (S-I diameter vs. A-P diameter)	NHI			Significant		Significant	ns
	Neck at tubercle (S-I diameter vs. A-P diameter)	NTI			Significant	ns		
	Tubercular facet	TFI	ns					
	Tubercle – iliocostal line distance	TICI						
	Shaft height at the posterior angle	SHI	Significant		ns	Significant	ns	

Table 4.37.: Summary of interaction within human measurements.

Rib Number	Variable	ACRONYM	Population Group					
			European		Sotho		Zulu	
			Sotho	Zulu	European	Zulu	European	Sotho
1	Head facet height	HSH	Significant		Significant	ns	Significant	ns
	Head facet width	HSW	ns					
	Neck length	NL						
	Neck (Superior-Inferior diameter) at Head	NH	Significant			ns	Significant	ns
	Neck (Superior-Inferior diameter) at Tubercle	NT	ns	Significant female	Significant male		Significant female	Significant male
	Neck (Anterior-Posterior diameter) at Head	NHA	Significant male	ns	Significant male	ns		
	Neck (Anterior-Posterior diameter) at Tubercle	NTA	ns					
	Tubercle facet height	TFH						
	Tubercle facet width	TFW						
	Shaft maximum height at posterior angle	SHPA						
Shaft maximum width at posterior angle	SWPA							

Table 4.37. (cont.): Summary of interaction within human measurements (ns = not significant; significant if p<0.005).

Rib Number	Variable	ACRONYM	Population Group					
			European		Sotho		Zulu	
			Sotho	Zulu	European	Zulu	European	Sotho
2	Head Superior facet height	HSH	ns					
	Head Superior facet width	HSW						
	Head Inferior facet height	HIH	ns		Significant	ns	Significant	
	Head Inferior facet width	HIW	ns					
	Neck length	NL	Significant female	ns	Significant female	ns		
	Neck (Superior-Inferior diameter) at Head	NH	ns					
	Neck (Superior-Inferior diameter) at Tubercle	NT						
	Neck (Anterior-Posterior diameter) at Head	NHA						
	Neck (Anterior-Posterior diameter) at Tubercle	NTA	Significant		ns	Significant	ns	
	Tubercle facet height	TFH	ns					
	Tubercle facet width	TFW	Significant		ns	Significant	ns	
	Tubercle – iliocostal line distance (outer)	TILO	Significant female			Significant female		
	Tubercle - iliocostal line distance (inner)	TILI						
	Shaft maximum height at posterior angle	SHPA	ns					
Shaft maximum width at posterior angle	SWPA	Significant Significant		ns	Significant	ns		

Table 4.37. (cont.): Summary of interaction within human measurements (ns = not significant; significant if p<0.005).

Rib Number	Variable	ACRONYM	Population Group					
			European		Sotho		Zulu	
			Sotho	Zulu	European	Zulu	European	Sotho
4	Head Superior facet height	HSH	Significant		Significant	ns	Significant	ns
	Head Superior facet width	HSW	Significant	ns		ns		
	Head Inferior facet height	HIH	ns					
	Head Inferior facet width	HIW						
	Neck length	NL	Significant both sexes	ns	Significant male and female		ns	Significant both sexes
	Neck (Sup-Inferior diameter) at Head	NH	ns					
	Neck (Sup-Inferior diameter) at Tubercle	NT						
	Neck (Anterior-Posterior diameter) at Head	NHA	Significant	ns	Significant	ns		
	Neck (Anterior-Posterior diameter) at Tubercle	NTA	ns	Significant female	ns	Significant female		
	Tubercle facet height	TFH	ns					
	Tubercle facet width	TFW						
	Tubercle – iliocostal line distance (outer)	TILO						
	Tubercle - iliocostal line distance (inner)	TILI						
	Shaft maximum height at posterior angle	SHPA						
Shaft maximum width at posterior angle	SWPA							

Table 4.37. (cont.): Summary of interaction within human measurements (ns = not significant; significant if p<0.005).

Rib Number	Variable	ACRONYM	Population Group					
			European		Sotho		Zulu	
			Sotho	Zulu	European	Zulu	European	Sotho
7	Head Superior facet height	HSH	ns					
	Head Superior facet width	HSW	Significant female	ns	Significant female	ns		
	Head Inferior facet height	HIH	ns					
	Head Inferior facet width	HIW						
	Neck length	NL	Significant			ns	Significant	ns
	Neck (Sup-Inferior diameter) at Head	NH	ns					
	Neck (Sup-Inferior diameter) at Tubercle	NT	ns					
	Neck (Anterior-Posterior diameter) at Head	NHA						
	Neck (Anterior-Posterior diameter) at Tubercle	NTA						
	Tubercle facet height	TFH						
	Tubercle facet width	TFW						
	Tubercle – iliocostal line distance (outer)	TILO						
	Tubercle - iliocostal line distance (inner)	TILI	ns					
	Shaft maximum height at posterior angle	SHPA	ns					
Shaft maximum width at posterior angle	SWPA	Significant male						

Table 4.38.: Summary of interaction within human indices (ns = not significant; significant if p<0.005).

Rib Number	Index	ACRONYM	Population Group					
			European		Sotho		Zulu	
			Sotho	Zulu	European	Zulu	European	Sotho
1	Facet of rib head	SFHI	ns					
	Neck	NI	Significant	ns	Significant	ns		
	Neck at head (S-I diameter vs. A-P diameter)	NHI	ns					
	Neck at tubercle (S-I diameter vs. A-P diameter)	NTI	ns	Significant	ns	Significant	Significant	
	Tubercular facet	TFI	ns					
2	Superior Facet of rib head	SFHI	ns					
	Inferior Facet of rib head	IFHI	ns			Significant	ns	Significant
	Neck	NI	Significant female			ns	Significant female	ns
	Neck at head (S-I diameter vs. A-P diameter)	NHI	ns					
	Neck at tubercle (S-I diameter vs. A-P diameter)	NTI	ns					
	Tubercular facet	TFI	ns			Significant	ns	Significant
	Tubercle – iliocostal line distance	TICI	ns					
	Shaft height at the posterior angle	SHI	ns					

Table 4.38. (Cont): Summary of interaction within human indices (ns = not significant; significant if p<0.005).

Rib Number	Index	ACRONYM	Population Group					
			European		Sotho		Zulu	
			Sotho	Zulu	European	Zulu	European	Sotho
4	Superior Facet of rib head	SFHI	ns					
	Inferior Facet of rib head	IFHI						
	Neck	NI	Significant		ns	Significant	ns	
	Neck at head (S-I diameter vs. A-P diameter)	NHI						
	Neck at tubercle (S-I diameter vs. A-P diameter)	NTI	ns					
	Tubercular facet	TFI	Significant		ns	Significant	ns	
	Tubercle – iliocostal line distance	TICI	ns					
	Shaft height at the posterior angle	SHI						
7	Superior Facet of rib head	SFHI	ns					
	Inferior Facet of rib head	IFHI						
	Neck	NI	Significant	ns	Significant	ns		
	Neck at head (S-I diameter vs. A-P diameter)	NHI	ns					
	Neck at tubercle (S-I diameter vs. A-P diameter)	NTI						
	Tubercular facet	TFI						
	Tubercle – iliocostal line distance	TICI						
	Shaft height at the posterior angle	SHI	Significant male	Significant both sexes	Significant female		Significant both sexes	Significant female

Table 4.39.: Summary of interaction primate measurements (ns = not significant; significant if p<0.005).

Rib Number	Variable	ACRONYM	Species		
			Human		
			Baboon	Gorilla	Chimpanzee
1	Head Superior facet height	HSH	Significant	ns	Significant
	Head Superior facet width	HSW			Significant female
	Neck length	NL	Significant	ns	
	Neck (Superior-Inferior diameter) at Head	NH			Significant
	Neck (Superior-Inferior diameter) at Tubercle	NT			
	Neck (Anterior-Posterior diameter) at Head	NHA			
	Neck (Anterior-Posterior diameter) at Tubercle	NTA			
	Tubercle facet height	TFH			
	Tubercle facet width	TFW	Significant	ns	
	Shaft maximum height at posterior angle	SHPA			
Shaft maximum width at posterior angle	SWPA	Significant	ns		

Table 4.39. (cont.): Summary of significant interaction within primate measurements (ns = not significant; significant if $p < 0.005$).

Rib Number	Variable	ACRONYM	Species			
			Human			
			Baboon	Gorilla	Chimpanzee	
2	Head Superior facet height	HSH	Significant		ns	
	Head Superior facet width	HSW	Significant	ns		
	Head Inferior facet height	HIH				
	Head Inferior facet width	HIW				
	Neck (Superior-Inferior diameter) at Head	NH				
	Neck length	NL				
	Neck (Superior-Inferior diameter) at Tubercle	NT				Significant
	Neck (Anterior-Posterior diameter) at Head	NHA				ns
	Neck (Anterior-Posterior diameter) at Tubercle	NTA				ns
	Tubercle facet height	TFH				Significant
	Tubercle facet width	TFW			Significant	
	Tubercle – iliocostal line distance (outer)	TILO	Significant female	Significant male	Significant female	
	Tubercle - iliocostal line distance (inner)	TILI	Significant	ns	ns	
	Shaft maximum height at posterior angle	SHPA			Significant	
Shaft maximum width at posterior angle	SWPA	ns				

Table 4.39. (cont.): Summary of significant interaction within primate measurements.

Rib Number	Variable	ACRONYM	Species		
			Human		
			Baboon	Gorilla	Chimpanzee
4	Head Superior facet height	HSH	Significant	Significant	ns
	Head Superior facet width	HSW		ns	
	Head Inferior facet height	HIH		Significant female	
	Head Inferior facet width	HIW		ns	
	Neck length	NL		Significant	
	Neck (Superior-Inferior diameter) at Head	NH		ns	
	Neck (Superior-Inferior diameter) at Tubercle	NT		Significant	
	Neck (Anterior-Posterior diameter) at Head	NHA		ns	
	Neck (Anterior-Posterior diameter) at Tubercle	NTA		Significant	
	Tubercle facet height	TFH		ns	
	Tubercle facet width	TFW		Significant male	ns
	Tubercle – iliocostal line distance (outer)	TILO		ns	Significant
	Tubercle - iliocostal line distance (inner)	TILI		ns	Ns
	Shaft maximum height at posterior angle	SHPA			
Shaft maximum width at posterior angle	SWPA				

Table 4.39. (cont.): Summary of significant interaction within primate measurements.

Rib Number	Variable	ACRONYM	Species			
			Human			
			Baboon	Gorilla	Chimpanzee	
7	Head Superior facet height	HSH	Significant	ns	Ns	
	Head Superior facet width	HSW				
	Head Inferior facet height	HIH				
	Head Inferior facet width	HIW				
	Neck length	NL				Significant
	Neck (Superior-Inferior diameter) at Head	NH				
	Neck (Superior-Inferior diameter) at Tubercle	NT		Significant	Ns	
	Neck (Anterior-Posterior diameter) at Head	NHA				
	Neck (Anterior-Posterior diameter) at Tubercle	NTA				
	Tubercle facet height	TFH				
	Tubercle facet width	TFW				
	Tubercle – iliocostal line distance (outer)	TILO				
	Tubercle - iliocostal line distance (inner)	TILI		ns	Significant males	
	Shaft maximum height at posterior angle	SHPA				
Shaft maximum width at posterior angle	SWPA	Ns				

Table 4.40.: Summary of significant interaction within primate indices (ns = not significant; significant if p<0.005).

Rib Number	Index	ACRONYM	Species		
			Human		
			Baboon	Gorilla	Chimpanzee
1	Facet of rib head	FHI	ns	ns	Ns
	Neck	NI	Significant		
	Neck at head (S-I diameter vs. A-P diameter)	NHI	ns		
	Neck at tubercle (S-I diameter vs. A-P diameter)	NTI	Significant		
	Tubercular facet	TFI	ns		
	Shaft height at the posterior angle	SHI	Significant		Significant
2	Superior Facet of rib head	SFHI	ns	ns	Ns
	Inferior Facet of rib head	IFHI	Significant		
	Neck	NI			
	Neck at head (S-I diameter vs. A-P diameter)	NHI	ns		
	Neck at tubercle (S-I diameter vs. A-P diameter)	NTI			
	Tubercular facet	TFI	Significant		
	Tubercle – iliocostal line distance	TICI	ns		
Shaft height at the posterior angle	SHI	Significant	Significant		

Table 4.40. (Cont): Summary of significant interaction within primate indices (ns = not significant; significant if p<0.005).

Rib Number	Index	ACRONYM	Species		
			Human		
			Baboon	Gorilla	Chimpanzee
4	Superior Facet of rib head	SFHI	ns	ns	
	Inferior Facet of rib head	IFHI			
	Neck	NI			
	Neck at head (S-I diameter vs. A-P diameter)	NHI			
	Neck at tubercle (S-I diameter vs. A-P diameter)	NTI	Significant		
	Tubercular facet	TFI	ns		
	Tubercle – iliocostal line distance	TICI			
Shaft height at the posterior angle	SHI	Significant			
7	Superior Facet of rib head	SFHI	Significant		Significant
	Inferior Facet of rib head	IFHI	ns	ns	
	Neck	NI		Significant	ns
	Neck at head (S-I diameter vs. A-P diameter)	NHI			
	Neck at tubercle (S-I diameter vs. A-P diameter)	NTI			
	Tubercular facet	TFI	Significant		
	Tubercle – iliocostal line distance	TICI		ns	
	Shaft height at the posterior angle	SHI	Significant male		

CHAPTER 5 - RESULTS - DESCRIPTIONS AND EVALUATION OF HOMININ FOSSIL RIBS

5.1. *Australopithecus africanus* –Stw 431

5.1.1. Morphological features of Stw 431

A detailed description of the “dorsal” or vertebral end of the single rib fragment of Stw 431, and its comparison to the extant primates, will assist in attempting to explain the form and shape of the thorax and thus body structure of Stw 431.

Head of the rib

The head of the rib of Stw 431 has two facets that are separated by a well-developed and prominent crest of the head. Facets are oval in shape and concave (see Figure 5.1 and 5.2). Angle between the facets of the head is acute resulting in the head having a pointed arrow-head shape.

Mammalian ribs all exhibit a double facet on the head of the rib, except for the first rib as is the case in humans (Ohman 1984).

There exists an acute angle between the facets of the head in the ribs of the chimpanzee and the gorilla, Figure 5.3 shows the typical appearance of a double facet on the head of the gorilla. The angulation of the facets to each other produces a head of the rib shaped like a pointed arrow-head (see Figure 5.4 and 5.5).

The angle between the facets in the modern human is more obtuse. The shape of the head thus produced is one that is saddle-shaped (see Figure 5.6).

Thus in a general superficial shape and form analysis, the conclusion drawn is that there is a greater similarity in the overall pattern of morphology of the head of the rib fragment of Stw 431 to that of the chimpanzee rib, as compared to those of humans and gorillas.

Neck of the rib

Figures 5.7 and 5.8 show the cranial and caudal views of the rib of Stw 431 showing specifically the neck region of the rib fragment.

The neck appears initially constricted. It is antero-posteriorly (ventro-dorsally) flattened to produce two surfaces (an anterior/internal and a posterior/external) and two margins (cranial and caudal). The neck widens as it approaches the tubercle.

The posterior surface is straight and exhibits a roughened texture (see Figure 5.9) that indicates the site of attachment of soft tissue ligaments of the costo-vertebral joint. The anterior surface is convex and smooth (see Figure 5.10)

The cranial margin, referred to as the crest of the neck, has a rounded edge and has a tubercle on its distal third. The caudal margin is slightly sharper when compared to the cranial margin.

The neck slopes infero-laterally towards the tubercle (see Figure 5.9).

The neck thus shows morphological features that are similar to the chimpanzee and human rather than the gorilla.

Tubercle of the rib

The tubercle of the rib of Stw 431 appears as a prominent bony extension extending from the dorsal aspect and cranial aspect of the fossil (see Figure 9).

The articular facet and the non-articular ligamentous attachments are not clearly distinguishable.

The morphology of the tubercle is similar to that observed in the chimpanzee second and third rib.

Shaft of the rib

A short proximal part of the shaft is present on this rib fragment.

The shaft is oval in cross-section and flattened to produce two surfaces (cranial and caudal) and two margins (internal/medial and external/lateral). The shaft is orientated at an angle to the horizontal so that the superior surface faces cranio-laterally.

Both surfaces are smooth. The internal margin is pointed and the external margin is rounded and smooth. The beginning of a shallow costal groove is visible on the inferior surface.

The angulation and morphological features of the shaft is similar to that observed in the chimpanzee second rib rather than the third rib (see Figure 10 and 11).



Figure 5.1: Cranial view of the dorsal rib fragment of Stw 431.



Figure 5.2: Caudal view of the dorsal rib fragment of Stw 431.

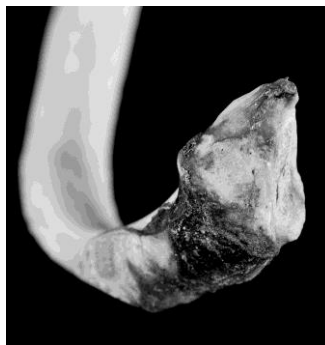


Figure 5.3: The head of the gorilla rib showing the two facets separated by a well developed crest. Note the pointed arrow head shape as a result of the angulation of the facets of the head.



Figure 5.4: The vertebral end of the chimpanzee right second and third rib (superior view).



Figure 5.5: The vertebral end of the gorilla right side second and third rib (superior view).



Figure 5.6: The vertebral end of the human right hand side second and third rib (superior view).



Figure 5.7: Cranial view of Stw 431 showing the neck region of the rib.



Figure 5.8: Caudal view of Stw 431 showing the neck region of the rib.



Figure 5.9: Posterior view of the vertebral end of the rib of Stw 431 showing the head and tubercle of the rib fragment.



Figure 5.10: Oblique view of the rib of Stw 431. The oval shape of the shaft in cross-section is visible.



Figure 5.11: Caudal views of the vertebral end of the right ribs of Stw 431 and chimpanzee showing the different morphology of the ribs.

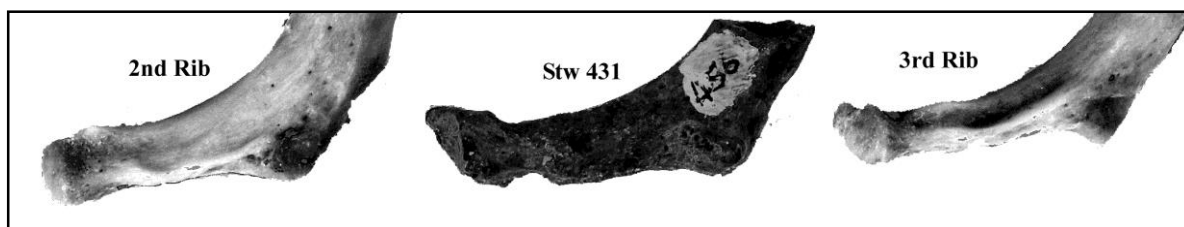


Figure 5.12: Cranial view of the vertebral end of the right ribs of Stw 431 and chimpanzee.

5.1.2. Measurements of the Stw 431 fragment and indices calculated

Head of the rib fragment

The dimensions, in millimetres, of the facets of the rib of Stw 431 are indicated below.

Height of Superior Head Facet (HSH)	Width of Superior Head Facet (HSW)	Height of Inferior Head Facet (HIH)	Width of Inferior Head Facet (HIW)
6.7	10.41	6.73	9.11

The indices that are calculated from the aforementioned variables are indicated below.

Superior Facet of Head Index (SFHI)	Inferior Facet of Head Index (IFHI)
64.36	73.87

Neck of Stw 431

The various variables of the neck are indicated in the Tables below.

Neck Height at Superior facet of Head (NH)	Neck Length (NL)	Neck Height at Tubercle (NT)
9.95	17.88	8.59

Neck Antero-posterior Diameter at Head (NHA)	Neck antero-posterior diameter at Tubercle (NTA)
5.07	9.27

The indices calculated for the neck are shown in the Table below.

Index of Neck Height – Neck Length (NI)	Neck Index at Head (NHI)	Neck Index at Tubercle (NTI)
55.65	196.25	92.66

Tubercle of Stw 431

The variables obtained from the tubercle and the index that is calculated is indicated below.

Tubercle Facet Height (TFH)	Tubercle facet Width (TFW)	Tubercle Facet Index (TFI)
9.2	6.94	132.56

Comparison of the variables and indices of Stw 431 to those of chimpanzee, gorilla and human second and third ribs

Table 5.1. shows the values of the variables and indices of the second and third ribs of the chimpanzee, gorilla and human species.

There exists an overlap between some of the ranges of variables of the chimpanzee, gorilla and human species. However, highlighted in Table 5.1 are the values of variables and indices of Stw 431 that

- fall into a particular range between the maximum and minimum for a particular species and
- are proximate to the mean and/or the median of that particular species

From these results, it is observed that, of the 11 variables and 6 indices of the rib fragment of Stw 431:

- seven variables (HSH, HSW, HIH, NL, NT, NHA, TFW) and four indices (IFHI, NI, NHI and NTI) are found in the chimpanzee range;
 - HSH, HIH, NHA and NI = rib 2 and
 - HSW, NL, NT, TFW, IFHI, NHI and NTI = rib 3.
- three variables (NH, NTA and TFH) and one index (SFHI) are found in the gorilla range and
 - NH and NTA = rib 2 and
 - TFH and SHFI = rib 3.
- One variable (HIW) and one index (NHI and TFI) are found in the human range
 - HIW = rib 2 and
 - TFI = rib 3.

Possible identification of Stw 431

Utilising the morphological descriptions made as well the variables and indices calculated, the following identification concerning the rib fragment of Stw 431 can be made:

- it closely resembles the vertebral end of the ribs of the great apes, viz. chimpanzee and gorilla;
- it more closely resembles the vertebral end of the ribs of the chimpanzee and
- it is most likely the vertebral end of the third rib.

Table 5.1: The variables and indices for the chimpanzee, gorilla and human second and third ribs.

		HSH	HSW	HIH	HIW	NH	NL	NT	NHA	NTA	TFH	TFW	SFHI	IFHI	NI	NHI	NTI	TFI
Chimpanzee second rib	Mean	6.94*	8.45	6.13*	8.35*	8.12	15.38	6.95	5.74*	7.04	6.22	8.43	82.38	73.44	53.92*	142.15	99.87	75.07
	Median	7.19*	9.04	5.89*	7.78*	8.25	16.12	7.16	5.55*	7.27	6.59	8.03	82.10	73.48	48.89*	142.34	103.30	77.97
	Max	7.43*	9.05	7.12*	9.69*	8.58	17.55	7.51	6.37*	7.63	6.76	10.45	85.52	77.81	66.16*	154.59	115.30	84.18
	Min	6.20*	7.25	5.37*	7.57*	7.53	12.47	6.18	5.29*	6.21	5.31	6.81	79.54	69.02	46.71*	129.51	81.00	63.06
Chimpanzee third rib	Mean	5.83	9.40*	5.47	8.26	8.80	17.96*	7.53*	4.39	6.93	6.42	6.61*	62.88	66.15*	49.19	201.45*	111.02*	97.49
	Median	5.74	9.73*	5.74	8.27	8.38	17.71*	7.51*	4.63	6.30	6.37	6.62*	58.99	69.21*	48.95	212.27*	105.39*	96.22
	Max	6.08	10.72*	5.89	8.51	10.07	20.57*	8.81*	4.80	8.55	6.98	6.93*	72.94	69.41*	53.68	217.49*	139.84*	110.97
	Min	5.66	7.76*	4.78	7.99	7.96	15.61*	6.26*	3.75	5.94	5.91	6.29*	56.72	59.82*	44.95	174.58*	87.84*	85.28
Gorilla second rib	Mean	8.57	11.71	8.56	12.15	10.65*	16.96	9.54	7.91	8.33*	9.33	13.62	73.78	70.98	63.46	133.73	120.48	68.62
	Median	8.21	11.41	8.15	11.38	10.13*	16.87	9.43	7.85	8.96*	9.06	12.85	74.25	71.55	66.44	132.11	105.91	68.26
	Max	11.43	15.09	10.96	16.23	14.18*	20.78	12.43	10.14	9.73*	11.95	17.59	82.10	78.74	80.25	161.32	188.61	82.41
	Min	6.34	8.62	6.10	8.30	6.47*	12.00	6.92	6.37	5.62*	6.84	10.51	64.08	63.00	41.05	101.57	77.40	56.43
Gorilla third rib	Mean	9.02	13.78	8.62	14.20	11.90	18.55	11.98	7.88	7.73	8.97*	11.61	65.05*	61.90	64.69	151.27	156.25	77.56
	Median	8.57	13.21	8.08	13.42	11.44	17.50	11.09	7.43	7.54	8.81*	10.46	65.40*	59.78	67.21	152.31	157.40	75.54
	Max	11.65	16.95	11.58	19.72	16.67	25.02	17.24	11.34	9.54	11.35*	14.73	71.08*	73.67	78.86	180.82	212.18	86.20
	Min	6.56	11.39	5.78	8.66	8.13	14.43	8.14	6.67	6.38	7.38*	10.01	55.69*	55.23	48.20	121.89	108.97	70.89
Human second rib	Mean	5.49	8.53	7.23	9.74*	8.56	19.61	6.84	7.52	7.89	6.29	8.64	64.86	74.75	44.14	117.66	88.35	73.83
	Median	5.34	8.56	7.39	9.71*	8.64	19.71	6.93	7.34	8.00	6.36	8.55	62.03	75.82	43.59	115.08	88.49	72.94
	Max	9.45	11.40	10.38	14.15*	13.02	25.34	9.70	11.69	10.03	9.58	12.25	100.42	123.49	62.21	187.37	139.64	121.61
	Min	2.76	5.27	4.42	7.11*	5.55	9.27	4.24	4.21	4.99	3.94	5.23	41.15	49.33	27.54	71.71	51.25	45.40
Human third rib	Mean	5.24	8.60	6.39	9.15	9.05	18.86	8.35	6.09	5.68	6.99	8.39	61.53	69.78	48.34	151.41	150.44	84.27*
	Median	5.19	8.36	6.40	9.20	8.97	19.09	8.28	6.06	5.65	6.67	8.38	58.73	69.93	48.81	149.00	146.96	80.38*
	Max	9.93	11.61	10.32	12.41	12.22	23.07	11.54	9.48	8.28	11.74	11.35	114.53	91.68	66.59	234.16	226.01	138.43*
	Min	3.15	6.16	3.43	5.60	5.49	12.96	5.39	3.99	3.15	4.59	4.93	40.59	44.63	27.85	97.64	92.99	57.83*

5.2. *Australopithecus afarensis* – A.L. 288-1ax or “Lucy”

5.2.1. Metric features of A.L. 288-1ax and Indices calculated

No detailed metric analysis of the first rib of A.L. 288-1ax can be found in the literature.

Table 4.2 shows the variables and indices of the first rib of the chimpanzee, gorilla and human species.

This study on the A.L. 288-1ax first rib has yielded the following variables and indices for the different parts of the rib.

Head

The dimensions, in millimeters, of the single facet of the head of the rib of A.L. 288-1ax are indicated below:

Height of Head Facet (HSH)	Width of Head Facet (HSW)	Facet of Head Index (FHI)
6.66	6.68	99.70

Neck

The various variables of the neck are indicated below:

Neck Height at Facet of Head (NH)	Neck Length (NL)	Neck Height at Tubercle (NT)	Neck Antero-posterior Diameter at Head (NHA)	Neck antero-posterior diameter at Tubercle (NTA)
6.26	9.95	5.65	4.58	8.16

The indices calculated for the neck are shown below:

Index of Neck Height – Neck Length (NI)	Neck Index at Head (NHI)	Neck Index at Tubercle (NTI)
62.91	136.68	69.24

Tubercle

The variables obtained from the tubercle and the tubercle facet index is indicated below:

Tubercle Facet Height (TFH)	Tubercle facet Width (TFW)	Tubercle Facet Index (TFI)
4.65	8.16	56.99

Shaft

The variables for the shaft and index calculated are indicated below:

Shaft Height at Posterior Angle (SHPA)	Shaft Width at the Posterior Angle (SWPA)	Shaft Height Index (SHI)
6.12	9.22	66.38

When these results are compared to those of the first rib observed in chimpanzee, gorilla and humans in Table 5.2, the following observations are made. There exists an overlap between the some of the ranges of variables of the first rib of the chimpanzee, gorilla and human species.

Highlighted in Table 5.2. are the values of variables and indices of A.L. 288-1ax that:

- fall into a particular range between the maximum and minimum for a particular primate species and
- lie within the ranges of the mean and/or the median of that particular primate species

Of the eleven variables and six indices of the first rib of A.L. 288-1ax:

- four variables (HSH, NT, NTA, SHPA) and two indices (NHI and TFI) are found in the chimpanzee range;
- two indices (NI and NTI) are found in the gorilla range;
- four variables (HSW, NH, TFH and TFW) and one index (FHI) are found in the human range and
- three variables (NL, NHA and SWPA) do not fall in a range for any of the comparative specimens.

Table 5.2: The variables and indices for the chimpanzee, gorilla and human first rib. (Bold values indicate the range for A.L.288-lax where there is overlap)

		HSH	HSW	NH	NL	NT	NHA	NTA	TFH	TFW	SHPA	SWPA	FHI	NI	NHI	NTI	TFI	SHI
Chimpanzee	Mean	5.98	9.14	8.11	14.49	5.74	6.29	9.61	5.86	9.99	5.80	14.65	66.58	56.10	130.24	59.70	59.65	39.61
	Median	5.61	9.53	7.91	14.81	5.59	6.79	9.51	5.73	10.45	5.56	14.12	63.12	56.24	135.35	62.81	55.23	39.64
	Max	6.83	10.82	9.19	16.34	6.58	6.98	10.43	6.39	11.57	6.47	16.32	77.76	58.64	142.04	63.09	68.89	41.15
	Min	5.49	7.06	7.23	12.33	5.06	5.09	8.90	5.47	7.94	5.37	13.51	58.87	53.41	113.32	53.21	54.83	38.03
Gorilla	Mean	8.96	12.48	9.96	18.08	8.84	11.49	13.34	10.92	14.77	10.19	19.22	77.27	57.30	86.75	67.15	74.44	53.00
	Median	8.82	11.03	8.80	18.04	8.50	11.97	13.56	11.00	14.84	9.89	18.91	80.51	53.77	93.17	62.33	76.24	53.49
	Max	10.52	18.91	14.24	22.12	10.37	13.48	16.05	13.45	18.26	13.49	23.37	105.04	92.89	105.64	85.50	82.82	60.55
	Min	8.01	8.76	7.87	13.51	7.55	9.11	10.07	8.39	11.15	8.23	16.30	50.49	35.58	64.83	59.59	63.64	42.93
Human	Mean	8.56	9.52	6.91	15.47	5.34	7.84	10.22	6.41	9.85	7.57	16.26	90.81	45.52	90.60	52.70	66.19	46.96
	Median	8.29	9.17	6.76	15.41	5.26	7.78	10.03	6.43	9.56	7.67	15.98	90.90	43.75	90.59	51.89	66.15	46.88
	Max	13.25	14.68	11.25	20.81	7.54	12.45	15.36	8.70	17.26	10.75	21.64	134.87	68.72	135.36	69.63	99.33	61.71
	Min	5.45	5.96	4.89	11.68	3.52	5.09	7.60	3.73	5.97	4.82	12.68	56.95	25.66	62.33	37.05	42.36	26.15

5.3. *Australopithecus africanus* - Sts 14

5.3.1. Morphological description of Sts 14 rib fragments

The rib fragments with certain complete features were the following:

- i. a proximal fragment of bone from the right hand side;
- ii. a proximal fragment of bone from the left hand side;
- iii. a single long fragment(Sts 14x) from the left hand side of the body that has a tubercle present and
- iv. a set of three ribs that are still in breccia and these are from the from the left hand side. Measurements could only be taken from the superior and inferior rib fragments.

The fragile condition of the fossilised ribs of Sts 14 as well as the adhesions between the attached rib fragments did not permit measurements to be taken for all variables. No casts of the rib material are available.

Figures 5.13, 5.14 and 5.15 show the rib specimens of Sts 14 utilised in this study.

The ribs of Sts 14 show the general structural appearance of the typical hominoid ribs.

The head of the right proximal fragment shows the typical double facet.

The neck is flattened to produce cranial and caudal margins as well as internal and external surfaces. The neck is orientated in a plane that is similarly observed in the human, chimpanzee and gorilla ribs.

The angle of the neck to the shaft appears obtuse as is similar to that observed in primates. The tubercle of the rib is well developed and rounded in appearance. It is positioned close to the superior margin of the rib, a feature that one does not observe in the hominoids. Its facet is orientated to face postero-medially. The shaft is obliquely orientated, a feature observed in the typical ribs of the chimpanzee but not human nor gorilla. It exhibits an internal and an external surface. It has a rounded superior margin and a sharper inferior margin.

5.3.2. Metrical observations of the Sts 14 rib fragments

Right hand side proximal fragment

These measurements, in millimetres, were obtained from the right hand side fragment of Sts 14 are indicated below.

Head. The dimensions of the superior and inferior facets of the head are indicated below:

Height of Head Superior Facet (HSH)	Width of Head Facet (HSW)	Superior Facet of Head Index (SFHI)	Height of Head Facet (HIH)	Width of Head Facet (HIW)	Inferior Facet of Head Index (IFHI)
3.86	6.67	57.87	7.8	6.64	117.47

Neck. The various measurements of the neck are indicated below:

Neck Height at Facet of Head (NH)	Neck Length (NL)	Neck Height at Tubercle (NT)	Neck Antero-posterior diameter at Head (NHA)	Neck antero-posterior diameter at Tubercle (NTA)
13.98	8.46	7.24	4.16	5.46

The indices calculated for the neck are shown below:

Index of Neck Height – Neck Length (NI)	Neck Index at Head (NHI)	Neck Index at Tubercle (NTI)
47.50	336.06	132.60

Tubercle. The variables obtained from the tubercle and the tubercle facet indexes are indicated below:

Tubercle Facet Height (TFH)	Tubercle facet Width (TFW)	Tubercle Facet Index (TFI)
5.34	7.29	73.25

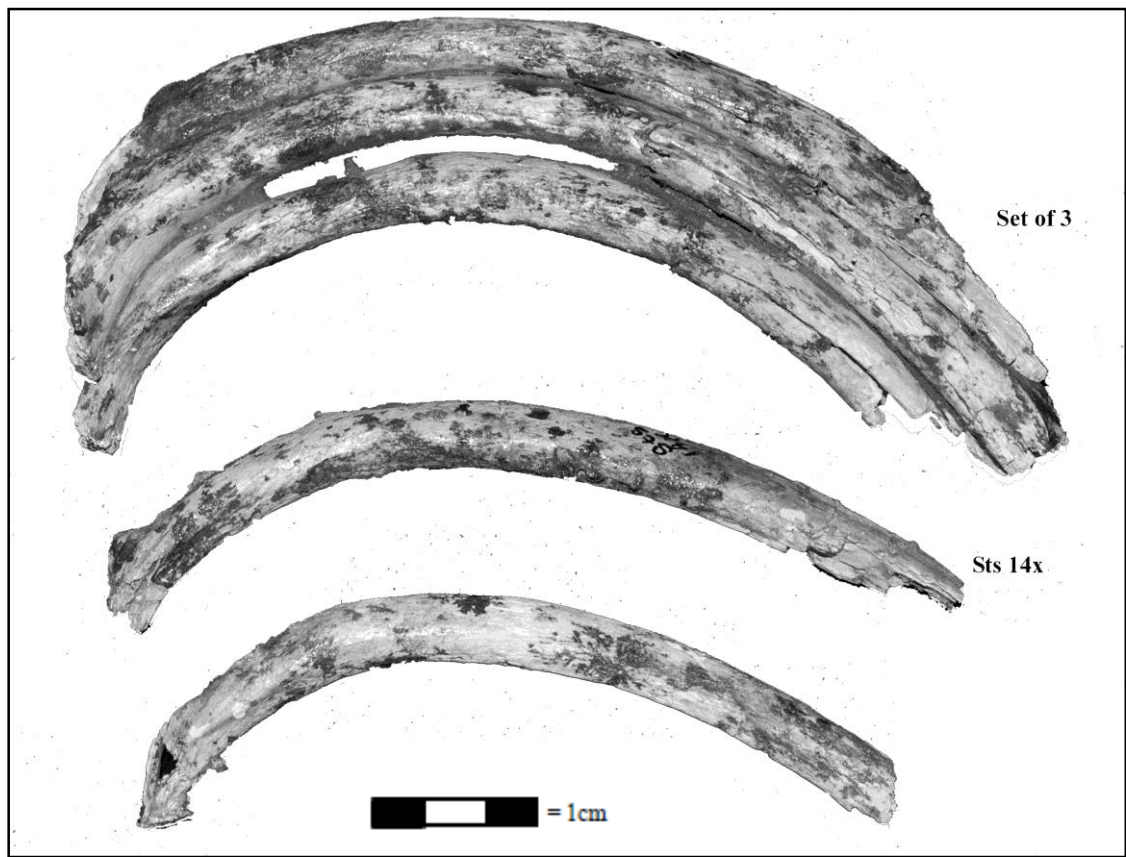
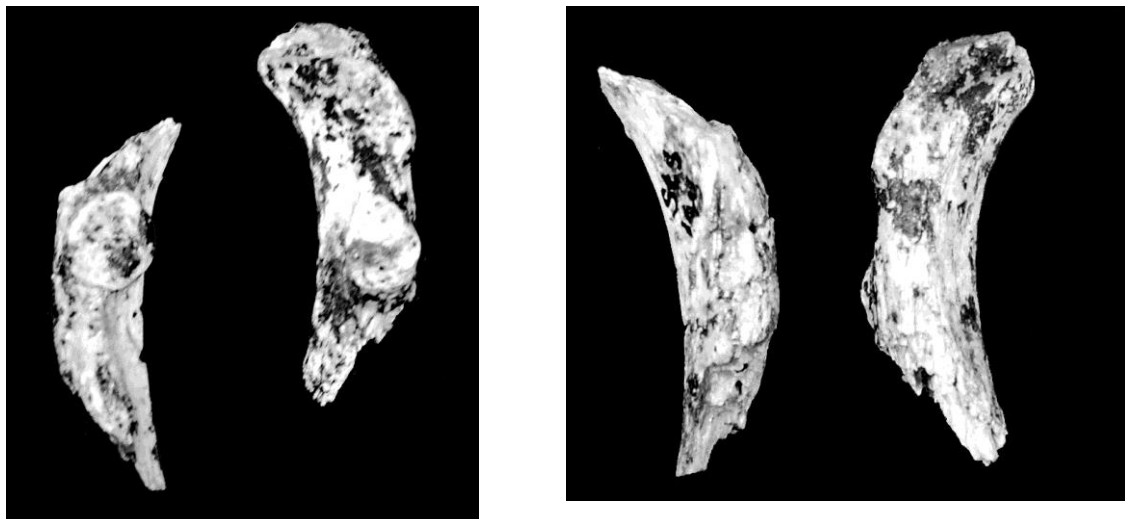


Figure 5.13: Some of the fragmented ribs of Sts 14.



(a)

(b)

Figure 5.14: The left and right fragments of the proximal ribs of Sts 14: (a) inferior and (b) superior views.



Figure 5.15: The proximal ends of the ribs of Sts 14 showing acid damaged head facets and the tubercles.

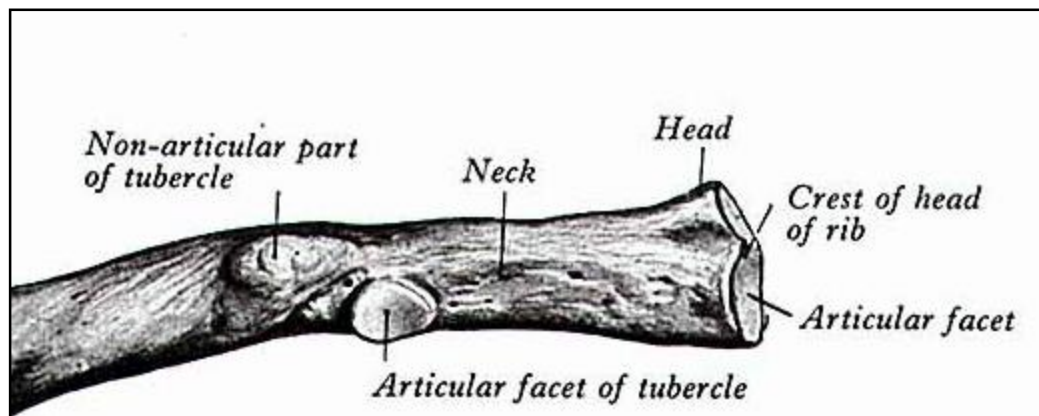


Figure 5.16: The proximal end of the typical human rib showing the position of the tubercle relative to the neck margins. (After Williams 1995).

Left hand side fragment, Sts 14x and the set of 3 ribs

The left hand fragment is a piece of rib that extends from point on the neck to a point distal to the tubercle. It is broken at both ends and thus only the tubercle could be measured. The ribs that form the “set of three” are still embedded and held together by breccia. For this reason as well as their state of disrepair, the only measurements that could be taken were from the tubercle.

The measurements and calculated indices of the tubercle of these ribs are:

Specimen	Tubercle Facet Height (TFH)	Tubercle facet Width (TFW)	Tubercle Facet Index (TFI)
Left fragment	6.82	7.58	89.97
Sts 14x	4.53	5.59	81.01
Superior rib of set	5.26	5.87	89.61
Inferior rib of set	5.81	7.17	81.03

When these measurements and indices of the right proximal fragment were compared to those of the extant primates (as reflected in Table 4.3.), the following trends are observed:

Variable	Comment on comparing the measurement obtained for Sts 14
SFHI	Falls between the ranges for all typical ribs in chimpanzee; ribs 5 to 7 in gorilla and ribs 4 to 5 in human
IFHI	Value is too high when compared to the other primates
NI	Falls between the ranges of the second and third human ribs
NHI	Value is too high when compared to other primates
NTI	Falls between the ranges of the second and third human ribs
TFI	Falls in the range of the second and third ribs for baboon, chimpanzee and gorilla and between the first and second ribs for human

When the tubercle facet index of the remaining ribs were compared to those of the extant primates (as reflected in Table 4.3), the following observations were noted

Rib	Comment on comparing the measurement obtained for Sts 14
Left proximal fragment	Falls in the range for third and fourth rib in chimpanzee; fourth to 5 th rib in human
Sts 14x	Falls in the range for 5 th to seventh rib for chimpanzee; fourth to seventh rib for gorilla and second to third for human
Superior of “set of 3”	Falls in the range for third and fourth rib in chimpanzee; fourth to 5 th rib in human
Inferior of “set of 3”	Falls in the range for 5 th to seventh rib for chimpanzee; fourth to seventh rib for gorilla and second to third for human

The conclusions that were drawn as to identify which rib each of the fragments of Sts 14 probably corresponds with are as follows:

Rib fragment of Sts 14	Rib that it probably corresponds to
Right proximal fragment	second or third
Left proximal fragment	second or third
Sts 14x	Left fourth
Superior of “set of 3”	Left 5 th
Inferior of “set of 3”	Left seventh

Table 5.3: The indices of the primates against which Sts 14 were compared

SPECIES		1SFHI	2SFHI	3SFHI	4SFHI	5SFHI	6SFHI	7SFHI
Baboon	Average	93.8	61.7	68.1	62.2	69.3	72.8	74.2
	Std Dev	9.5	13.1	5.1	6.2	6.2	8.3	11.5
Chimpanzee	Average	61.0	80.8	57.9	55.2	51.9	57.6	49.5
	Std Dev	3.0	1.8	1.6	9.8	14.8	20.4	3.0
Gorilla	Average	65.1	72.6	70.2	65.6	60.0	65.3	65.8
	Std Dev	21.0	7.6	1.3	4.7	3.5	5.5	9.4
Human	Average	90.8	64.7	59.9	55.8	60.6	63.0	71.5
	Std Dev	14.3	12.2	8.2	8.0	8.5	6.8	8.5
SPECIES		1IFHI	2IFHI	3IFHI	4IFHI	5IFHI	6IFHI	7IFHI
Baboon	Average		72.2	70.4	73.5	75.7	81.5	89.5
	Std Dev		10.0	5.3	10.3	10.3	12.2	15.1
Chimpanzee	Average	61.3	75.6	69.3	75.3	69.4	63.8	59.1
	Std Dev	13.9	3.1	0.1	18.7	21.7	0.2	0.8
Gorilla	Average	82.6	72.1	58.6	70.4	70.6	78.3	69.7
	Std Dev	20.2	5.9	2.3	3.0	4.0	14.8	9.6
Human	Average		76.2	72.3	71.8	78.2	80.7	85.0
	Std Dev		10.3	12.3	12.2	7.9	9.0	11.0
SPECIES		1NI	2NI	3NI	4NI	5NI	6NI	7NI
Baboon	Average	36.4	46.3	49.4	51.8	57.4	62.7	68.1
	Std Dev	5.1	3.8	5.6	5.9	6.7	9.5	11.2
Chimpanzee	Average	54.8	57.5	51.3	76.5	77.2	79.4	83.3
	Std Dev	2.0	12.2	3.3	7.4	15.7	6.9	5.6
Gorilla	Average	72.7	64.9	63.5	67.2	66.2	76.9	76.4
	Std Dev	18.0	13.8	14.0	16.0	10.6	12.6	10.8
Human	Average	47.3	45.0	50.9	54.4	59.7	63.1	66.1
	Std Dev	10.3	7.1	5.4	8.3	7.3	6.9	5.7

Table 5.4. (cont.) The indices of the primates against which Sts 14 were compared

SPECIES		1NHI	2NHI	3NHI	4NHI	5NHI	6NHI	7NHI
Baboon	Average	106.7	138.0	155.8	172.0	188.5	224.9	201.3
	Std Dev	21.1	24.8	23.9	18.8	42.1	46.1	35.9
Chimpanzee	Average	124.3	142.1	196.0	216.8	249.5	233.0	251.7
	Std Dev	15.6	17.7	30.3	3.3	7.8	11.7	25.8
Gorilla	Average	89.3	139.5	152.8	156.8	142.2	141.7	143.7
	Std Dev	20.1	19.1	25.6	33.0	29.0	19.0	14.1
Human	Average	85.2	114.8	154.0	168.0	170.5	181.4	192.0
	Std Dev	16.8	26.4	25.7	34.3	25.6	30.6	30.7

SPECIES		1NTI	2NTI	3NTI	4NTI	5NTI	6NTI	7NTI
Baboon	Average	44.0	67.8	118.0	138.2	149.1	152.5	168.5
	Std Dev	6.4	35.5	18.5	11.1	19.7	24.3	27.2
Chimpanzee	Average	58.1	109.3	113.8	167.4	181.3	173.4	161.1
	Std Dev	7.0	8.5	36.8	43.0	30.2	10.2	18.0
Gorilla	Average	64.9	123.9	168.8	158.9	138.4	140.0	128.1
	Std Dev	7.5	37.7	50.3	24.6	25.8	35.4	33.4
Human	Average	55.1	87.2	150.3	165.6	174.1	180.4	171.6
	Std Dev	7.8	15.1	27.7	26.7	23.3	27.7	23.6

SPECIES		1TFI	2TFI	3TFI	4TFI	5TFI	6TFI	7TFI
Baboon	Average	73.4	65.6	79.0	77.9	72.3	74.9	76.7
	Std Dev	22.5	15.6	21.1	14.4	9.1	9.2	16.4
Chimpanzee	Average	55.0	70.5	103.6	88.3	78.6	83.4	81.9
	Std Dev	0.3	10.5	10.4	30.1	23.5	19.0	22.9
Gorilla	Average	74.6	73.9	74.4	80.0	96.6	86.2	89.6
	Std Dev	9.9	7.6	2.5	14.1	10.8	3.1	18.5
Human	Average	66.7	75.5	83.8	87.9	93.0	87.5	84.5
	Std Dev	9.6	16.4	18.2	22.5	24.2	14.4	27.9

CHAPTER 6: THE COSTAL ELEMENTS OF *AUSTRALOPITHECUS*

SEDIBA

Since mid-2008, the Malapa site in the Cradle of Humankind, South Africa has yielded a large number of hominin fossil remains, the majority associated with two partial skeletons, namely a juvenile probable male (MH1) and an adult probable female (MH2) (Berger *et al.* 2010, Dirks *et al.* 2010). Both specimens have been ascribed to a new species of early hominin, *Australopithecus sediba* (Berger *et al.* 2010). Post-cranial remains of both individuals are well preserved, and elements of their skeletons have been recently described ((Berger (2012), Berger (2013), Berger *et al.* (2010), Carlson *et al.* (2011), De Ruiter *et al.* (2013), De Silva *et al.* (2013), Irish *et al.* (2013), Kibii *et al.* (2011), Kivell *et al.* (2011), Schmid *et al.* (2013), Williams *et al.* (2013) and Zipfel *et al.* (2011).

Both individuals preserve a number of thoracic remains that were found in near articulation and that possibly shed light on the form of the thorax in *Australopithecus sediba*. The preserved costal elements are in different states of completeness; ranging from being undamaged or largely complete ribs of both individuals to unidentifiable fragments of the shafts of lower ribs. In both skeletons, the cranial thoracic region is better preserved than the caudal end. Both individuals have complete first ribs whereas MH2 retains the proximal portions of the second and third ribs. In addition, MH2 preserves a nearly complete rib from the middle of the vertebrosteral series (likely Rib 5 or Rib 6), while MH1 preserves two partial ribs from the lower part of that series (Ribs 7-9). The general appearance of the thoracic region can be determined by looking at these elements from the different parts of the thoracic cage. In MH2, the preservation of a shaft

fragment from a 9th or 10th rib, along with its well preserved iliac regions of both individuals (Kibii *et al.* 2011), and enables the reconstruction of at least the general shape of the lower thoracic region.

6.1. Description of the Malapa costal elements

In this section, the morphologies of the Malapa fossils are described including measurement and metric analysis of the anatomical parts of the complete rib or rib fragments of each individual.

An inventory of the costal remains described in this section is provided in Table 6.1. and Table 6.2.

Table 6.1: Inventory of the Malapa Hominin 1 (MH 1) Ribs

Specimen Number	Initial anatomical position	Side	Anatomical part of rib					Notes
			Head	Neck	Tubercle	Shaft	Costal pit	
U.W. 13		R				P	C	Distal piece
U.W. 15/131	5 (or 6)	L		P	C	P		Proximal one fifth
U.W. 17		L				P		Distal piece
U.W. 41	7 (or 8)	R				P	C	Distal half
U.W. 74	6 (or 7)	L				P	C	Distal piece
U.W. 86	5 (or 6)	R		P	C	P		Proximal two thirds
U.W. 141		R				P		Fused Fragments
U.W. 148	1	R	P	C	C	C		2 fragments
U.W.88-154		L				P		

R = Right; L = Left; C = Complete; P = Partial

Table 6.2.: Inventory of the Malapa Hominin 2 (MH 2) Ribs

Specimen Number	Initial anatomical position	Side	Anatomical part of rib					Notes
			Head	Neck	Tubercle	Shaft	Costal Pit	
U.W. 58	2	R		P	C	C	P	almost complete
U.W. 60	9 (or 10)	R				P		Shaft fragment
U.W. 61	5 (or 4)	R		P	C	C	C	Almost complete/broken head
U.W. 154		R				P		3 fragments
U.W. 166	3	R	C	C	P	P		proximal end third/broken neck
U.W. 167	7 (or 8)	R		P	C	P		proximal end/ 1st quarter
U.W. 178	2	L	C	C	C	P		Proximal upto tubercle
U.W. 187	1	L	C	C	P			Proximal upto tubercle
U.W. 192						P		Shaft fragment
U.W. 193						P		Shaft fragment
U.W. 198	1	R	C	C	C	C	C	in Block/ Virtual reconstruction
U.W. 199						P		Distal shaft

R = Right; L = Left; C = Complete; P = Partial

6.1.1. Malapa hominin 1 (MH1) Costal elements

U.W. 88-13

U.W. 88-13 is rib fragment from the right side that preserves a distal part of the shaft and the sternal end with a costal pit. It is flattened producing two surfaces (internal and external) and two margins (cranial and caudal). The cranial margin is rounded and the caudal margin is sharp. The costal pit is oval in shape.

Measurements of the shaft (mm)	
Internal-external width (proximally)	3.7
Cranial-caudal height (proximally)	7.6
Internal-external width (distally)	4.9
Cranial-caudal height (distally)	10.7

U.W. 88-15 (conjoins with U.W. 88-131)

U.W. 88-15 is a proximal fragment of a left rib, most likely the 5th or 6th. This specimen preserves a partial neck, tubercle and proximal part of the shaft. U.W. 88-131 is the remaining part of the shaft up to a point just distal to the attachment of the *iliocostalis* muscle.

The neck is oval in cross-section with two surfaces (internal and external) and two margins (cranial and caudal). The internal surface is smooth, the external surface is rough. A part of the crest is visible on the cranial margin. The caudal margin of the neck blends into the caudal margin of the shaft. The tubercle is well developed and composed of an articular facet and a non-articular part for the attachment of the lateral costotransverse ligament. The facet is oval in shape and convex. It faces caudally and medially. The non-articular part is lateral to the facet. The proximal shaft has a rounded cranial surface and a flattened caudal surface. The internal surface is smooth compared to the roughened external surface. The proximal part of the *iliocostalis* line is visible on the external surface, caudally. A shallow and wide costal groove is visible and continuous between the two fragments.

Measurements of the neck (mm)	
Cranial-caudal height	10.1
Internal-external width	6.8
Measurements of the tubercle (mm)	
Cranial-caudal height	8.1
Medial-lateral width	12.8
Measurements of the shaft (mm)	
Internal-external width (at the tubercle)	8.8
Cranial-caudal height (at the tubercle)	7.9
Internal-external width (at the <i>iliocostalis</i> line)	10.4
Cranial-caudal height (at the <i>iliocostalis</i> line)	6.2
Internal-external width (distally)	11.5
Cranial-caudal height (distally)	9.6
Straight line distance between the tubercle and the <i>iliocostalis</i> line	21.4

U.W. 88-17

U.W. 88-17 is the rib fragment (29.8 mm in length) from the distal end of the 11th or 12th rib from the left side. The internal surface is smooth. The external surface is rough and irregular due to the preservation of the specimen. The cranial margin is smooth compared to the caudal margin which is irregular. The distal tip appears round and possesses a costal pit for the costal cartilage.

Measurements of the shaft (mm)	
Internal-external width (proximally)	3.8
Cranial-caudal height (proximally)	7.9
Internal-external width (distally)	3.5
Cranial-caudal height (distally)	4.5

U.W. 88-41 (conjoins with U.W. 88-86)

U.W. 88-41 is the distal end of a right rib fragment, possibly the 7th (or 8th) rib, which preserves a partial shaft and sternal end with a costal pit. The flattened shaft is composed of two surfaces (internal and external) and two margins (cranial and caudal). The internal surface is smooth and caudally has a shallow costal groove. The external surface is rough. The cranial margin is rounded and the caudal margin is sharp. Towards the distal sternal end the shaft narrows cranio-caudally. The shaft thickens interno-externally and widens cranio-caudally at the sternal end where it terminates as the costal pit. The shaft curves internally as the sternal end is approached.

Measurements of the shaft (mm)	
Internal-external width (proximally)	6.7
Cranial-caudal height (proximally)	10.8
Internal-external width (middle)	6.0
Cranial-caudal height (middle)	10.9
Internal-external width (distally)	9.4
Cranial-caudal height (distally)	18.7



Figure 6.1: Rib fragment of MH1 of U.W.88-41: Cranial (left) and caudal view (right) (scale = 50 mm). (Courtesy of Peter Schmid).

U.W. 88-74

U.W. 88-74 is a distal rib fragment from the 6th (or 7th) rib left side that preserves a distal shaft and a sternal end with a costal pit. It is flattened, producing two surfaces (internal and external) and two margins (cranial and caudal). Towards the sternal end, the shaft widens and produces a costal pit that is elliptical in shape. There is an internal curvature of the shaft as it approaches the sternal end at the costal pit.

Measurements of the shaft (mm)	
Internal-external width (proximally)	4.6
Cranial-caudal height (proximally)	9.5
Internal-external width (distally)	6.1
Cranial-caudal height (distally)	16.4

U.W. 88-86 (conjoins with U.W.88-41)

U.W. 88-86 is a proximal rib fragment from the right side representing most likely the 5th (or 6th) rib. It lacks a head but preserves a partial neck, tubercle and proximal shaft. The neck appears oval in cross-section. The tubercle is well developed and composed of an articular facet and a non-articular part for the attachment of the lateral costotransverse ligament. The facet is oval in shape and convex. It faces caudally and medially. The non-articular part is lateral to the facet. The shaft is thick. Its cross-sectional shape is cylindrical (proximally) and oval (distally) respectively) The *iliocostalis* attachment is present on the external-caudal margin of the rib. The curvature of the shaft is not pronounced. No torsion is visible in this proximal rib fragment. A costal groove is present on the internal aspect of the rib aspect of the rib.

Measurements of the neck (mm)	
Cranial-caudal height	9.9
Internal-external width	6.6
Measurements of the tubercle (mm)	
Cranial-caudal height	8.1
Medial-lateral width	9.8
Measurements of the shaft (mm)	
Internal-external width (at the tubercle)	8.2
Cranial-caudal height (at the tubercle)	7.9
Internal-external width (at the <i>iliocostalis</i> line)	10.4
Cranial-caudal height (at the <i>iliocostalis</i> line)	6.2
Internal-external width (distally)	11.5
Cranial-caudal height (distally)	9.2
Straight line distance between the tubercle and the <i>iliocostalis</i> line	29.3



Figure 6.2.: Rib fragment of MH1 of U.W.88-86: Cranial (left) and caudal view (right) (scale = 50 mm). (Courtesy of Peter Schmid).



Figure 6.3.: Rib fragments of MH1: (a) U.W. 88-13, (b) U.W. 88-15, (c) U.W. 88-17, (d) U.W. 88-74, (e) U.W. 88-141. Top: external view; second row: internal view; third row: caudal view; bottom: cranial view (scale = 50 mm). (Courtesy of Peter Schmid)

U.W. 88-141

U.W. 88-141 is a rib fragment from the right side. It is composed of multiple sub-fragments that are held together by the matrix of preservation. It appears to be a distal part of the shaft approaching the sternal end and costal pit of the rib. The fragmentary nature of this specimen makes it difficult to obtain accurate measurements due to the distortion of the elements.

U.W. 88-148

U.W. 88-148 is a 1st rib from the right side. Figure 6.4 shows different views of this rib.

This rib is composed of two fragments that articulate well with one another:

- i. a larger fragment that preserves the head, neck, tubercle and proximal three-fifths of the shaft and
- ii. a smaller fragment that preserves the distal two-fifths of the shaft

The head is devoid of the articular facet because the epiphysis has not yet fused with the head region. The neck is round and ascends external-laterally. The external aspect of the neck shows that presence of a pit medial to the tubercle. The external border is also slightly constricted.

The tubercle is complete and prominent. It coincides with the external angle. The tubercle lies at a higher plane as compared to the head due to the angle of the neck.

The shaft is flattened in a cranial-caudal plane producing two surfaces (cranial and caudal) and two margins (internal/medial and external/lateral). The shaft has an acute curvature at the external angle/tubercle. The cranial surface is roughened and shows the shallow grooves for the subclavian vessels. A small scalene tubercle is visible between the two grooves and close to the medial margin. The caudal surface is smooth. Both margins have edges that are rounded.

The sternal end of U.W. 88-148 does not preserve the costal pit. This indicates that a piece of the distal rib may be missing.

Measurements of the neck (mm)	
Internal-external width (at the head)	4.9
Cranial-caudal height (at the head)	5.4
Internal-external width (at the middle)	6.3
Cranial-caudal height (at the middle)	3.4
Internal-external width (at the tubercle)	7.5
Cranial-caudal height (at the tubercle)	3.6
Measurements of the tubercle (mm)	
Cranial-caudal height	4.1
Medial-lateral width	6.1
Measurements of the shaft (mm)	
Internal-external width (at the tubercle)	10.6
Cranial-caudal height (at the tubercle)	4.2
Internal-external width (at the scalene tubercle)	11.6
Cranial-caudal height (at the scalene tubercle)	3.1
Internal-external width (at the sternal end)	12.5
Cranial-caudal height (at the sternal end)	4.3

U.W. 88-154

U.W. 88-154 is a fragment of the proximal shaft immediately distal to the tubercle upto the midshaft part of a left rib. It appears to be from the more caudal part of the thoracic cage. Its incompleteness of features makes it difficult to sequence this fragment. The *iliocostalis* line is visible on the external surface. The internal surface is smooth and exhibits a wide but shallow costal groove.

Measurements of the shaft (mm)	
Internal-external width (at the <i>iliocostalis</i> line)	9.4
Cranial-caudal height (at the <i>iliocostalis</i> line)	6.4
Internal-external width (distally)	10.1
Cranial-caudal height (distally)	5.2



Figure 6.4.: The fossil right 1st rib (U.W. 88-148) of the Malapa hominin 1 individual (Courtesy of Peter Schmid).

6.1.2. Malapa hominin 2 (MH2) costal elements

U.W. 88-58

U.W. 88-58 is a 2nd rib from the right side that preserves approximately the entire neck, the tubercle and the shaft of the rib including a part of its sternal end.

The head has not been preserved.

The neck appears rounded on the cranial surface and flattened on the caudal surface. It is elongated, narrower proximally than distally. The external or dorsal margin of the neck is straight. The internal or ventral margin of the neck lies at an angle and blends into the internal/medial margin of the shaft. The angle between the neck and the shaft appears very similar to that observed in the chimpanzee and the modern human.

The tubercle is a prominent knob-like process projecting dorsally from the corresponding angle of the rib. It lies in a slightly more cranial plane than that of the head. Its articular facet is well preserved and faces dorso-medially. The non-articular ligamentous part is present dorso-lateral to the articular facet.

The shaft is flattened in a cranio-caudal plane and lies at an oblique angle relative to the cranio-caudal. The cranial surface of the shaft is roughened when compared to the smooth caudal surface. The lateral/external margin of the shaft is sharp whereas the internal/medial margin appears more rounded. There is a shallow costal groove visible on the caudal surface. It runs from the tubercle “line” and terminates on the external margin of the distal third of the shaft. The costal pit situated distally is partially broken.

Measurements of the neck (mm)	
Dorso-ventral width measured distal to the break	4.4
Dorso-ventral width (proximally at headend)	3.8
Cranio-caudal height (proximally at headend)	3.9
Dorso-ventral width (distally at tubercle)	6.0
Cranio-caudal height (distally at tubercle)	4.1
Straight line length measured from the proximal neck to tubercle	11.41
Measurements of the tubercle (mm)	
Medio-lateral width between the tubercle tip and the inner margin measured perpendicularly	11.1
Dorso-ventral width of the tubercle	4.5
Cranio-caudal height of the tubercle	4.1
Measurements of the shaft (mm)	
Internal-external width (proximally)	9.79
Internal-external (distally).	8.2
Mid shaft cranio-caudal height (thickness)	4.3
Mid-shaft internal-external width	8.8
Straight line length from the tip of the tubercle to the tip of the external margin (at the sternal end)	51.2
Circumferential length as measured from the tip of the tubercle to the tip of the external margin at the sternal end	53.7
Circumferential length as measured from head end to the tip of the inner margin	46.7



Figure 6.5.: Views of U.W. 88-58 Cranial view (left) and caudal view (right) (scale = 50 mm). (Courtesy of Peter Schmid).

U.W.88-60

U.W.88-60 is a distal fragment of a 9th (or 10th) right rib shaft. The internal/medial surface is smooth compared to the textured external/lateral surface. The cranial margin is rounded. The caudal margin is sharp due to the presence of a costal groove. On the caudal border the costal groove disappears and blends into the distal caudal margin. This rib fragment may be positioned in the lower part of the thorax because the corpus becomes more slender distally. The distal part is slightly deformed due to compression. A slight torsion within the corpus is observed.



Figure 6.6: Views of U.W.88-60, right rib fragment. From top to bottom: caudal, external, cranial and internal surface (scale = 50 mm). (Courtesy of Peter Schmid).

U.W. 88 – 61

U.W. 88-61 is a nearly complete right vertebrosteral rib that was recovered adjacent to (and overlapping) the right upper limb remains of MH2. The size of the rib, along with its torsion, position of the *iliocostalis* line, and shaft cross-sectional morphology all suggest that the rib derives from the middle of the vertebrosteral rib series, most likely representing a 5th (or 4th) rib.

It is composed of 2 rib fragments that articulate well to form an almost complete rib. It preserves a partial neck, tubercle, a shaft that is broken in approximately the middle and the costal pit.

The neck is broken and appears flattened dorso-ventrally producing two surfaces (internal and external) and two margins (cranial and caudal). The internal surface of the neck is orientated to face vento-caudally. The external surface is angled to face dorso-cranially and exhibits an oval depression due to taphonomic damage.

The cranial margin is sharp and exhibits a well-developed crest of the neck for the cranial costo-transverse ligament. This crest continues onto the internal or medial margin of the shaft of the rib. The caudal margin is also sharp blending in with the caudal surface proximally.

The tubercle has an oval and convex articular facet that faces dorso-cranially and medially. The non-articular part for the attachment of the lateral costotransverse ligament is situated dorso-lateral to the articular facet.

The proximal part of the shaft is triangular in cross-section with 3 surfaces (caudal, dorso-cranial and ventro-cranial). The dorso-cranial surface has the roughened elevation for the *iliocostalis* muscle that corresponds with the external angle of the rib. Progressing further distally along the shaft becomes flattened

producing 2 surfaces (internal and external) and 2 margins (cranial and caudal). The shaft lies at an oblique angle to cranio-caudal plane. The internal surface is smooth compared to the external surface.

A shallow costal groove is visible on the internal surface and runs parallel to the caudal margin. This costal groove is visible only on the proximal one quarter of the shaft. The cranial margin is rounded as compared to the caudal margin that appears more sharpened. Distally the 2nd angle of the rib is visible and the shaft bends medially as it approaches the sternal end/costal pit. The shaft exhibits no torsion along its length. The costal pit is elliptical in shape.

Measurement of the neck (mm)	
Ventro-external width	4.2
Cranio-caudal height	5.8
Measurement of the tubercle articular facet (mm)	
Ventro-external width	4.6
Cranio-caudal height	6.3
Measurements of the Shaft (mm)	
Straight line distance between the tubercle and the <i>iliocostalis</i> attachment (at the caudal margin)	26.9
Cranio-caudal height (proximally)	5.1
Internal –external width (proximally)	8.6
Cranio-caudal height (at <i>iliocostalis</i> line)	5.4
Internal –external width (at <i>iliocostalis</i> line)	9.7
Cranio-caudal height (distally)	11.1
Internal-external width (distally)	3.8
Straight line length of the shaft measured from the tip of the tubercle to the cranial edge of the costal pit	167.1
Straight line length of the distal shaft between the 2 nd angle and the sternal end	34.2

Given the completeness of the rib, and its association with a complete 1st and partial 2nd and 3rd ribs from the same individual, accurate identification of the anatomical position of this rib was important in understanding thoracic shape in *Australopithecus sediba*.

To refine this estimate the tubercle-*iliocostalis* line distance (TID) in the context of the comparative samples was examined. The *iliocostalis* muscle attaches on the borders of the ribs at the posterior angle, and thus the tubercle-*iliocostalis* line measures the lateral extent of the muscle insertion. In order to allow for the variation in body size between the different genera studied, TID measurements were standardised against humeral maximum length (HL). Although humeral length is variable relative to body size in the genera used here, tubercle-*iliocostalis* line distance standardised by humeral length (TID/HL) seems to be a reasonable indication of the serial position of a rib in an individual regardless of taxon (Schmid *et al.* 2013).

In this study it was noted that the standardised distance (TID/HL) increased steadily from rib one to twelve in all of the taxa examined (Figure 6.8.). In *Pongo pygmaeus*, the shape of the arc was less steep than that observed in the other species. *H. erectus* showed higher values than *H. sapiens*, except for rib seven, which had values similar to *Pan troglodytes*. The atypical second rib of *Australopithecus sediba* was close to the mean value of *Pongo pygmaeus*. The *Australopithecus sediba* U.W.88-61 rib was assessed three times, as a possible 4th, 5th or 6th rib (Figure 6.8). In terms of its relative TID, the rib is most consistent with the fourth or fifth ribs of the comparative sample. The observed TID/HL argues against this being a 6th rib, as it would have a value below that observed in the comparative samples. While its TID/HL value is consistent with U.W.88-61 being a 4th rib, the large size of the rib argues against this identification (incorporating it into the rib series in this position would demand an exaggerated

mediolateral widening in the thorax between the 3rd and 4th ribs). Accordingly this rib was identified as the 5th rib in all analyses and reconstructions.



Figure 6.7.: Rib specimen U.W. 88-61 Cranial view (left) and caudal view (right)
(Scale = 50 mm) (Courtesy of Peter Schmid).

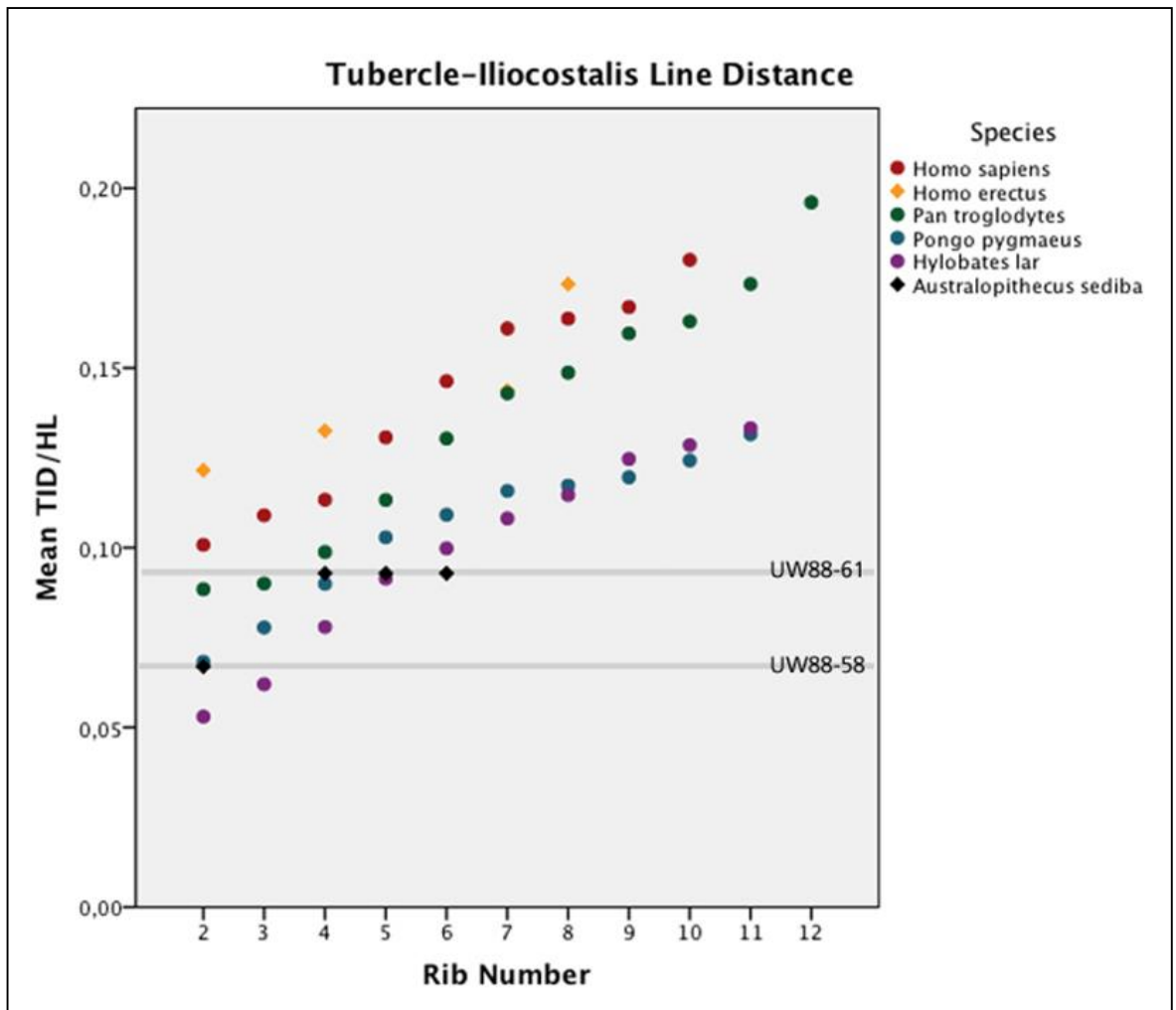


Figure 6.8. Scatterplot of the mean tubercle-*iliocostalis* line distance divided by humerus length vs. rib number. *Homo sapiens*, *Homo erectus* (N=4), *Pan troglodytes*, *Pongo pygmaeus* *Hylobates lar* and *Australopithecus sediba* (Schmid *et al.* 2013).

U.W. 88-154

U.W. 88-154 is the distal part of the shaft a right rib. It is composed of three fragments; a long fragment that is made up of two parts and a distal segment that was broken during the removal of the specimen from the surrounding matrix. A taphonomic break is visible in the middle of this specimen. Two surfaces (internal and external) and two margins (cranial and caudal) can be observed. The shaft is elliptical in cross-section, proximally appearing more rounded and becoming progressively flattened distally. The cranial margin is rounded as compared to the caudal margin which is sharp. A costal groove is present on the internal surface of the proximal fragment and it runs parallel to the caudal margin.

Measurements of the Shaft (mm)	
Internal-external width (proximally)	6.2
Cranial-caudal height (proximally)	10.1
Internal-external width (distally)	4.1
Cranial-caudal height (distally)	8.4



Figure 6.9: Rib fragment of U.W.88-154 of MH2: Cranial view (left) and caudal view (right) (Scale = 50 mm). (Courtesy of Peter Schmid).

U.W. 88 – 166

U.W. 88-166 is a 3rd rib fragment from the right hand side that preserves a head, the neck, the tubercle and approximately three-quarters of the shaft.

The head is oval in shape and exhibits 2 articular facets separated by a well-developed crest of the head. The cranial facet appears smaller than the caudal one.

The angle between the facets is obtuse producing a head that is very similar shaped to that observed in the ribs of extant primates inclusive of the modern human but not chimpanzee and gorilla. These latter non-human primates possess a head that is more pointed and “arrow-head” shaped.

The neck appears distorted in its middle part due to a break that occurred during the sedimentation process. It is flattened dorso-ventrally thus producing two surfaces (internal/ventral and external/dorsal) and two margins (cranial and caudal). A well-defined crest of the neck is observed on the cranial margin of the neck. The external surface has a deep and oval shaped depression similar to that observed on U.W.88-61. There is a taphonomic break where the neck meets the corpus of the rib.

The tubercle is prominent and well defined. The articular facet is not preserved.

The ligamentous part is well developed and situated dorso-laterally.

The shaft is proximally cranio-caudally flattened producing two surfaces (cranial and caudal) and two margins (internal and external). Distal to the tubercle is the roughened attachment point of the iliocostalis muscle. The distal shaft appears triangular in cross-section and exhibits three surfaces (caudal, dorso-cranial and ventro-cranial) and two margins (internal and external). Both margins appear sharp. The distal shaft is oriented in an oblique angle relative to the cranio-caudal

plane. There is a shallow costal groove visible on the caudal surface and runs parallel to the external margin of the rib.

Measurements of the head facets (mm)		
Cranial Facet	Ventro-external width	3.3
	Cranio-caudal height	4.9
Caudal Facet	Ventro-external width	4.6
	Cranio-caudal height	5.7
Measurements of the neck (mm)		
Maximum height		8.4
Ventro-external width at the head (thickness)		3.7
Ventro-external width at the tubercle (thickness)		5.7
Measurements of the shaft (mm)		
Shaft height proximal at the tubercle		5.2
Shaft height distally at sternal end		5.5
Internal-external width (proximal at the tubercle)		9.3
Internal-external width (distally)		8.8
Straight line length from the tip of the tubercle to the tip of the internal margin (towards the sternal end)		51.2
Straight line length measured from the tubercle to the <i>iliocostalis</i> attachment (external angle)		
Circumferential length as measured from the tip of the tubercle to the tip of the external margin at the sternal end		56.2
Circumferential length as measured from the head end to the tip of the inner margin		52.0



Figure 6.10: U.W.88-166 rib of MH2 Cranial view (left) and caudal view (right) scale = 50 mm). (Courtesy of Peter Schmid).

U.W. 88-167

U.W. 88-167 is the proximal part of a right rib, most likely the 7th (or 8th) rib based on the position of its *iliocostalis* line, lack of pronounced rib torsion, cross-sectional morphology at the external angle and shaft and its overall size. The specimen preserves a partial neck, tubercle and proximal shaft.

The neck is flattened producing two surfaces (internal/ventral and external/dorsal). The margins are not well preserved, the cranial exhibiting a part of the well-developed crest of the neck.

The tubercle has an oval and convex articular facet that faces caudally and medially. The non-articular attachment of the lateral costotransverse ligament is situated dorso-lateral to the articular facet.

The proximal part of the shaft is triangular in cross-section with three surfaces (caudal, dorso-cranial and ventro-cranial). The dorso-cranial surface has the pronounced roughened elevation for the attachment of the *iliocostalis* muscle. This corresponds with the external (posterior) angle of the rib. The internal surface is smooth compared to the external surface. A shallow costal groove is visible on the internal surface and runs parallel to the caudal margin.

Measurement of the Tubercle articular facet (mm)	
Ventro-external width	5.9
Cranio-caudal height	6.5
Measurements of the Shaft (mm)	
Straight line distance between the tubercle and the <i>iliocostalis</i> attachment (at the caudal margin)	34.8
Cranio-caudal height (proximally)	4.8
Internal –external width (proximally)	7.9
Cranio-caudal height (at <i>iliocostalis</i> line)	5.1
Internal –external width (at <i>iliocostalis</i> line)	9.7
Cranio-caudal height (distally)	5.4
Internal-external width (distally)	8.1
Straight line length of the shaft measured from the tip of the tubercle to the cranial edge of the costal pit	167.1
Straight line length of the distal shaft between the 2nd angle and the sternal end	34.2



Figure 6.11: Rib fragment U.W.88-167 of MH2: Cranial view (left) and caudal view (right) (Scale = 50 mm). (Courtesy of Peter Schmid).

U.W. 88 - 178

U.W. 88-178 is the proximal end of the 2nd rib from the left hand side. It preserves a head, neck, tubercle and proximal part of the shaft (length of 7 mm).

The head is composed of two facets separated by a well-defined crest of the head for the intra-articular ligament of the costovertebral joint. The neck appears rounded and is elongated. The cranial surface is convex compared to the caudal surface which is concave. The tubercle is complete and exhibits an oval convex articular facet as well as the non-articular part for the attachment of the lateral costotransverse ligament. The articular facet is orientated dorso-medially. The ligamentous attachment is situated dorso-lateral to the articular facet. The shaft is absent. It appears to be flattened in a cranio-caudal plane orientation when looking at the broken edge just distal to tubercle.

Measurement of the head facets (mm)		
Cranial Facet	Ventro-external width	5.4
	Cranio-caudal height	3.2
Caudal facet	Ventro-external width	5.4
	Cranio-caudal height	4.4
Measurement of the neck (mm)		
Ventro-external width (at head)		4.8
Cranio-caudal height (at head)		3.6
Ventro-external width (at tubercle)		4.1
Cranio-caudal height (at tubercle)		4.8
Measurement of the tubercle articular facet (mm)		
Ventro-external width		4.2
Cranio-caudal height		6.1

U.W. 88 – 187

U.W. 88-187 is the proximal end of the 1st rib from the left hand side. It preserves the head, neck and partial tubercle. The head has a single facet (“univertebral pattern”) that is oval in shape. It has a rim that is thickened for the attachment of the costovertebral ligament. The neck is flattened in the cranio-caudal plane and exhibits a “waisting” in its center. The cranial surface is smooth and exhibits a slight concavity. The caudal surface is smooth and exhibits a slight concavity. Due to its preservation, hair line cracks appear on both surfaces. The tubercle is broken distally. Only a proximal part of the articular facet is visible. The cranio-caudal height of the articular facet is 3.8 mm.

Although the shaft is absent, the break at the tubercle shows a cross-section of the shaft that appears to be flattened in a cranio-caudal plane.

Measurements of the head facet (mm)	
Internal-external width	6.9
Cranio-caudal height	5.1
Measurements of the neck (mm)	
Internal-external width (at head)	5.7
Cranio-caudal height (at head)	3.2
Internal-external width (at tubercle)	9.9
Cranio-caudal height (at tubercle)	4.4



Figure 6.12: Rib fragments of MH2: (a) U.W. 88-187, (b) U.W. 88-178. Top: cranial view; second row: caudal view; third row: dorsal view; bottom: ventral view (scale = 50 mm) (Courtesy of Peter Schmid).

U.W. 88-198

U.W. 88-198 is the complete 1st rib from the right hand side. It preserves the head, neck, tubercle and corpus of the rib. The specimen is embedded in matrix in contact with the dorsal surface of the manubrium, making its physical removal from the matrix impossible at this time. The description is from a virtually rendered model of the fossilised rib, courtesy of Dr. Kristian Carlson.

The head exhibits a single facet for the articulation with the complete costal facet of the first thoracic vertebra. This facet on the head is for articulation with the first thoracic but not the seventh cervical vertebra and is defined as the “uni-vertebral pattern” as found in *Australopithecus afarensis* and the genus *Homo* (Ohman 1983 and 1986) and some other primates (Stern and Jungers 1990).

The neck is narrow and rounded proximally and widens dorso-ventrally and is flattened cranio-caudally as it approaches the corpus. The tubercle is well-developed and exhibits an articular facet for the articulation with the transverse process. The shaft of the corpus is cranio-caudally flattened. The head is at an angle lower than the tubercle indicating its position relative to the associated thoracic vertebra.

The shaft exhibits two well defined margins (external/lateral and internal/medial) and two surfaces (cranial and caudal). The cranial surface has present the shallow grooves for the subclavian vasculature. Distally, the cranial surface thickens to form a part of the boundary of the costal pit. The caudal surface has a taphonomic break on the plate of compact bone but this does not affect the bone structure in terms of measurement or structure. The costal pit is present and shallow.

Measurements of this fossil were taken from the virtually rendered model obtained and printed.

Measurements of the head facet (mm)	
Internal-external width	7.96
Cranio-caudal height	7.31
Measurements of the neck (mm)	
Internal-external width (at head)	5.32
Cranio-caudal height (at head)	4.15
Internal-external width (at tubercle)	11.43
Cranio-caudal height (at tubercle)	4.56
Measurement of the tubercle articular facet (mm)	
Internal-external width	8.04
Cranio-caudal height	6.88
Measurements of the Shaft (mm)	
Straight line distance between the tubercle and the <i>iliocostalis</i> attachment (at the caudal margin)	71.88
Cranio-caudal height (proximally)	5.56
Internal –external width (proximally)	13.89
Cranio-caudal height (distally)	8.08
Internal-external width (distally)	11.93



Figure 6.13: Virtual model (obtained from micro-CT scanning) of the MH2 right first rib (U.W.88-198). From top to bottom: lateral, dorsal, cranial (left), caudal (right), ventral, and medial perspectives. (Courtesy Kris Carlson; Schmid *et al.* 2013).

6.2. Analysis of the descriptive and the determination of the probable thoracic shape of *Australopithecus sediba*

Thoracic shape has been considered important in the evolution of the hominins (Schultz 1950, Schmid 1983 and 1991, Ohman 1986, Jellema *et al.* 1993, Ward 2002, Kagaya *et al.* 2008 and 2009). With apes having conically-shaped rib cages and human thoraces being more barrel-shaped, changes in the overall form of the thorax have been considered as a potential critical marker of the transition of hominins to terrestrial bipedal locomotion (Schmid 1983 and 1991, Hunt 1991, Lovejoy *et al.* 2009, Haile-Selassie *et al.* 2010).

In order to determine the thoracic shape of *Australopithecus sediba*, a comparative analysis of the costal elements of extant hominin species needed to be done. The following features that influence the shape of the thorax were thus then further analysed:

- 1) posterior angle index;
- 2) total rib curvature;
- 3) shaft diameter and
- 4) neck index.

6.2.1. Results for the fossil hominin material

The results obtained for the costal elements of the fossil specimens are indicated in Tables 6.3 to 6.8.

Table 6.3.: Measurements of the left costal elements of *Homo erectus* (KNM-WT 15000) (Schmid *et al.* (2013) and Eveline Weissen, unpublished material).

Rib	TID (1)	PAC (2)	PAS (3)	PA- INDEX (4)	SMXD (5)	SMND (6)	SH- INDEX (7)	MMX D (8)	MMN D (9)	MS- INDEX (10)	NL (11)	NCK- INDEX (13)	TVC (14)	TVS (15)	TRC- INDEX (16)	HL (17)
1								18.4	12.6	68.5	20.4	17.6	79.0	18.0	22.8	
2	33.1	58.9	8.9	15.1	10.6	9.1	85.8	12.1	9.8	81.0	18.6	36.0	128.0	51.8	40.5	
3								11.2	8.6	76.8						
4								10.5	8.7	82.9						
5								11.1	8.6	77.5						
7	48.0	89.7	11.5	12.8	10.6	8.7	82.1	11.8	10.0	84.7			208.0	69.3	33.3	
8	51.8	93.6	18.4	19.7	10.6	8.5	80.2	10.3	9.4	91.3	21.5	27.9	170.0	50.5	29.7	
9	57.7	100.6	17.0	16.9	8.6	7.8	90.7	11.2	9.3	83.0			136.0	61.1	44.9	
10	48.3	87.8	14.9	17.0	8.9	7.4	83.1	9.9	8.5	85.9	13.8	52.2	144.0	43.6	30.3	
11								9.8	8.4	85.7						

Table 6.4.: Measurements of the right costal elements of *H. erectus* (KNM-WT 15000) (Schmid *et al.* (2013) and Eveline Weissen unpublished material).

Rib	TID (1)	PAC (2)	PAS (3)	PA- INDEX (4)	SMXD (5)	SMND (6)	SH- INDEX (7)	MMX D (8)	MMN D (9)	MS- INDEX (10)	NL (11)	NCK- INDEX (13)	TVC (14)	TVS (15)	TRC- INDEX (16)	HL (17)
1								20.2	14.0	69.3	23.1	13.9	79.0	15.9	20.1	311.0
2	37.8	68.1	11.4	16.7	9.2	8.3	90.2	16.7	9.0	53.9	15.7	28.7	115.0	55.8	48.5	311.0
4	41.2	74.4	15.0	20.2	9.8	8.0	81.6	10.2	9.7	95.1	18.9	35.4				311.0
5					10.3	9.6	93.2	10.9	7.2	66.1						311.0
6					10.0	8.5	85.0	10.2	9.0	88.2						311.0
7	44.7	83.6	12.0	14.4	11.8	10.0	84.7	10.9	9.4	86.2			210.0	65.6	31.2	311.0
8	53.9	97.6	18.5	19.0	11.8	10.6	89.8	12.0	9.7	80.8	19.6	36.2	202.0	61.6	30.5	311.0
9								11.9	9.7	81.5						311.0
10								10.7	9.0	84.1						311.0

Table 6.5.: Measurements of the costal elements of *Australopithecus afarensis* AL 288-1 (Schmid *et al.* (2013) and Eveline Weissen, unpublished material).

Rib	MMXD (8)	MMND (9)	MS-INDEX (10)	NL (11)	NCK-INDEX (13)
3	10.9	9.1	83.5		
5					
6	11.5	8.4	73.0		
7	11.2	9.0	80.4		
8	10.9	8.7	79.8	12.1	59.5
10				11.7	83.8
11	9.0	7.9	87.8		

Table 6.6.: Measurements of the left costal elements of *Australopithecus afarensis* AL 288-1 (Schmid *et al.* (2013) and Eveline Weissen, unpublished material).

Rib	TID (1)	SMXD (5)	SMND (6)	SH-INDEX (7)	MMXD (8)	MMND (9)	MS-INDEX (10)	NL (11)	NCK-INDEX (13)	TVC (14)	TVS (15)	TRC-INDEX (16)
1					13.1	9.7	74.0	13.0	38.5	55.0	9.3	16.9
3		10.5	9.8	93.3	11.6	9.0	77.6					
4					10.1	8.2	81.2					
5					10.5	8.5	81.0					
6		10.7	9.3	86.9	13.3	9.3	69.9					
7					11.5	9.1	79.1					
8						8.7						
9	39.5	9.5	8.9	93.7	11.2	9.0	80.4					
10					10.3	7.2	69.9					

Table 6.7.: Measurements of the right costal elements of *Australopithecus africanus* Sts 14 (Schmid *et al.* (2013) and Eveline Weissen, unpublished material).

Rib	TID (1)	PAC (2)	PAS (3)	PA-INDEX (4)	SMXD (5)	SMND (6)	SH-INDEX (7)	MMXD (8)	MMND (9)	MS-INDEX (10)
2	14.2	28.4	2.5	8.8	7.6	6.7	88.2	10.6	5.7	53.8
3	17.2	33.2	3.3	9.9	8.1	7.3	90.1			
4	10.6	21.0	2.1	10.0	6.8	6.2	91.2	12.8	6.4	50.0
d								8.9	6.1	68.5
e								8.1	7.3	90.1
f								9.6	5.8	60.4
g								7.2	6.3	87.5

Table 6.8.: Measurements of the costal elements of *Australopithecus sediba* (Schmid *et al.* (2013) and Eveline Weissen, unpublished material).

Species (U.W. 88-)	Rib	TID (1)	PAC (2)	PAS (3)	PA-INDEX (4)	SMX D (5)	SMN D (6)	SH-INDEX (7)	MMX D (8)	MMN D (9)	MS-INDEX (10)	NL (11)	NCK-INDEX (13)	TVC (14)	TVS (15)	TRC-INDEX (16)	HL (17)
148 MH1	1								12.9	10.0	77.5	14.8	29.7	56.0	7.7	13.8	
198 MH2	1								16.42	4.68	28.50	13.3 2	33.63	71.14	21.3	29.94	
58 MH2	2	17.8	35.2	2.4	6.8	9.6	9.0	93.8				19.4	26.3				266. 0
61 MH2	4-6	24.7	46.8	3.5	7.5	10.3	8.2	79.6	12.5	10.4	83.2			176.0	45.6	25.9	266. 0
86 MH1	4-6	24.5	47.2	3.3	7.0	9.5	7.6	80.0	12.3	10.3	83.7						
41 MH1	4-6								11.4	10.1	88.6						
15 MH1	5	24.9										16.0	43.8				
155 MH2	4-6					10.3	9.6	93.2	10.7	10.1	94.4						266. 0
143 MH2									12.3	12.1	98.4						266. 0
145 MH1									11.2	10.4	92.9						
59 MH2									13.2	11.7	88.6						266. 0

6.2.2. Analysis of the results

6.2.2.1. Posterior angle index

The morphology of the posterior angle of the rib reflects two functionally important aspects of thoracic shape:

- 1) mediolateral expansion of the rib cage and
- 2) degree of invagination of the vertebral column.

The posterior angle index (PA-Index) was used to quantify the amount of rib curvature expressed at the posterior angle. The PA-Index is derived from the posterior angle subtense and chord, such that higher values indicate a greater amount of curvature at the posterior angle. The mediolateral expansion of the thorax is associated with high index values in the ribs. The degree of invagination of the vertebral column is primarily determined by the angular relationship between the neck and the shaft, although curvature at the posterior angle is also likely to contribute to invagination. The posterior angle index values for *Homo sapiens* were uniformly larger than for *Homo erectus*. The value for rib number seven of *Homo erectus* was low (Figure 6.14). This was as a result of the condition of this fossil rib. A relatively larger value in this index depicts a less open curvature of this angle. However, *Australopithecus sediba* and *Australopithecus africanus* cluster together as a separate group (Figure 6.15).

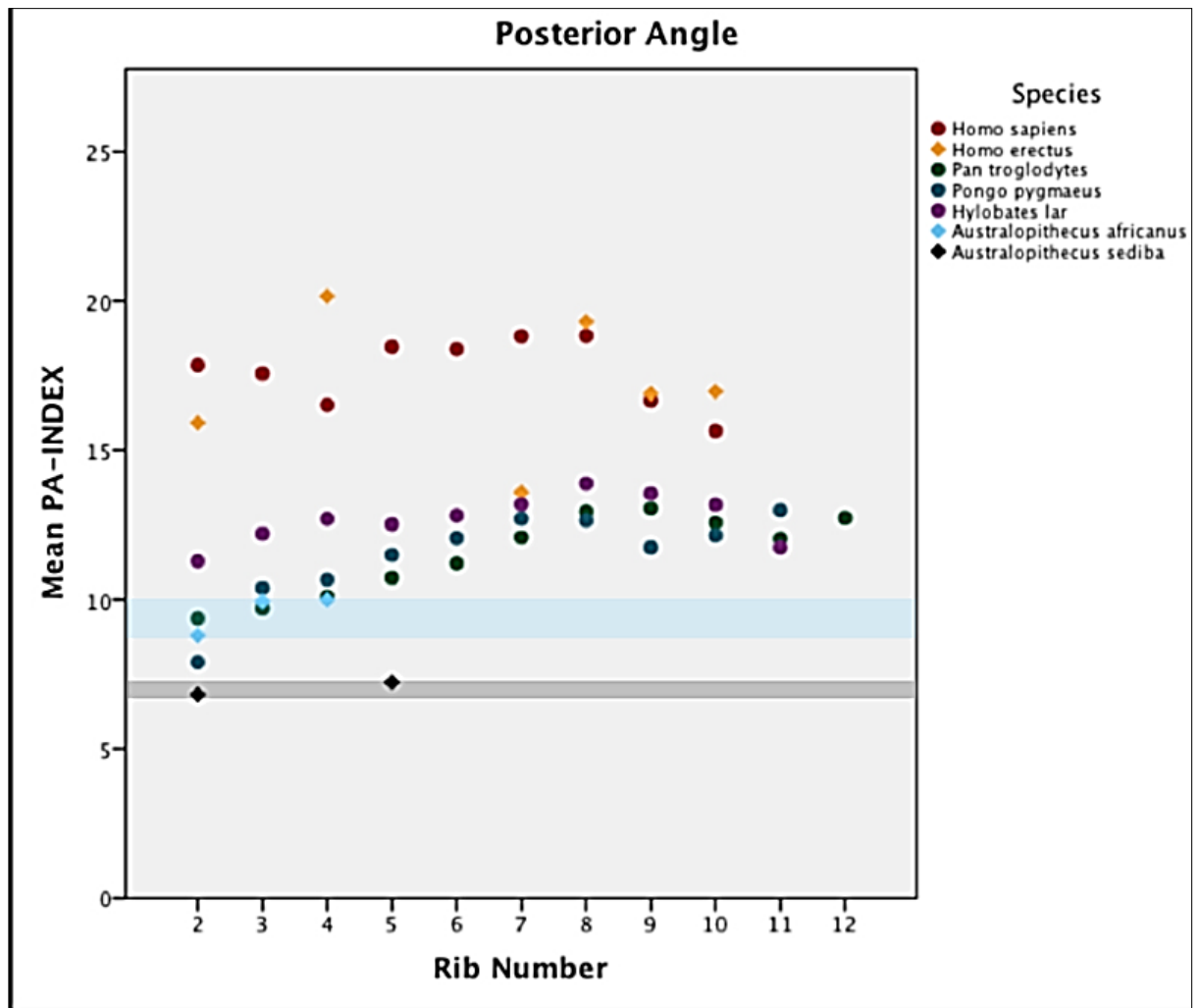


Figure 6.14.: Scatterplot of the mean posterior angle index vs. rib number. A

relatively larger value in this index depicts a less open curvature of this angle. *Homo sapiens*, *Homo erectus*, *Pan troglodytes*, *Pongo pygmaeus*, *Hylobates lar*, *Australopithecus africanus*, *Australopithecus sediba*..

(Schmid *et al.* 2013).

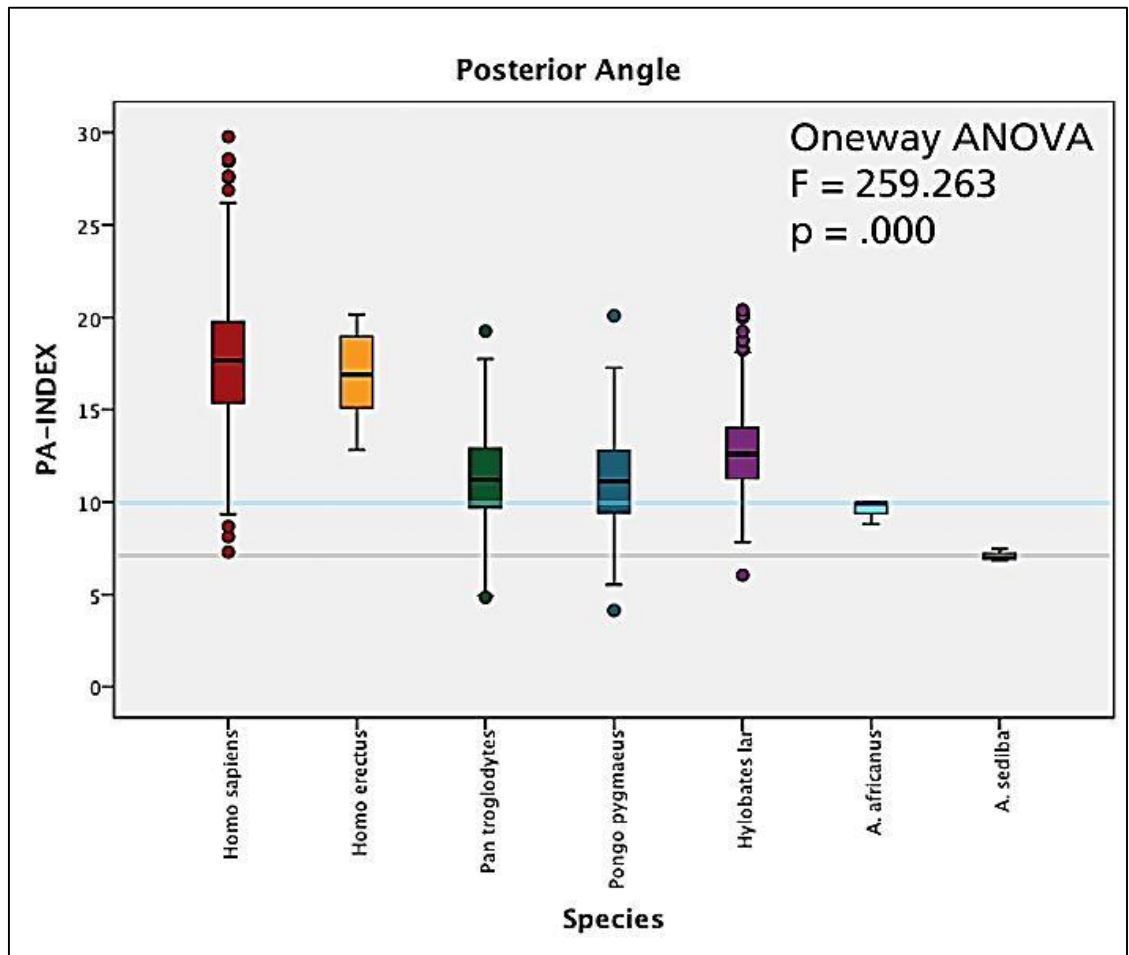


Figure 6.15. Box plot of the posterior angle index among the different species' ribs (lines indicate the medians, the box represents the interquartile range, and the whiskers the 95% CI, with circles as outliers). (Schmid *et al.* 2013).

6.2.2.2. Total rib curvature

The costal arc was analysed by the calculation of the total rib curvature index. The relatively larger values of this index indicate a less “open” curvature.

The scatterplot (Figure 6.16) shows the course of the arc from rib one to 12/13. The index values increased from rib two to three. This increase was greater in *Homo sapiens* and *Hylobates lar* than in *Pan troglodytes* and *Pongo pygmaeus*. The curvature of the ribs two, three and also four was closer and therefore the upper thorax is broader in *Homo sapiens* and *Hylobates lar*. The invagination of the vertebral column in the latter therefore is more pronounced than in the other hominoids. Halfway through, the costal arc became more open in all species, i.e. the values decreased. For the ribs eight to eleven, *Homo sapiens* showed again higher values of the total rib curvature index. The high value for the ninth rib of *Homo erectus* could be explained for the same reasons as mentioned above.

In a next step, ANOVA was performed for three sets of ribs and for the first rib to determine the differentiations and distinctions between the species in the upper, middle and lower thorax. There was no significant difference in the total rib curvature for the first rib (Figure 6.17).

The set of ribs analysed for the upper thorax consisted of the ribs two, three and four. As expected from the scatterplot, *Homo sapiens* and *Hylobates lar* were significantly different from the ape species *Pan troglodytes* and *Pongo pygmaeus*. *Homo erectus* clustered with *Hylobates lar*, which indicates a closer total rib curvature for this fossil (Figure 6.18).

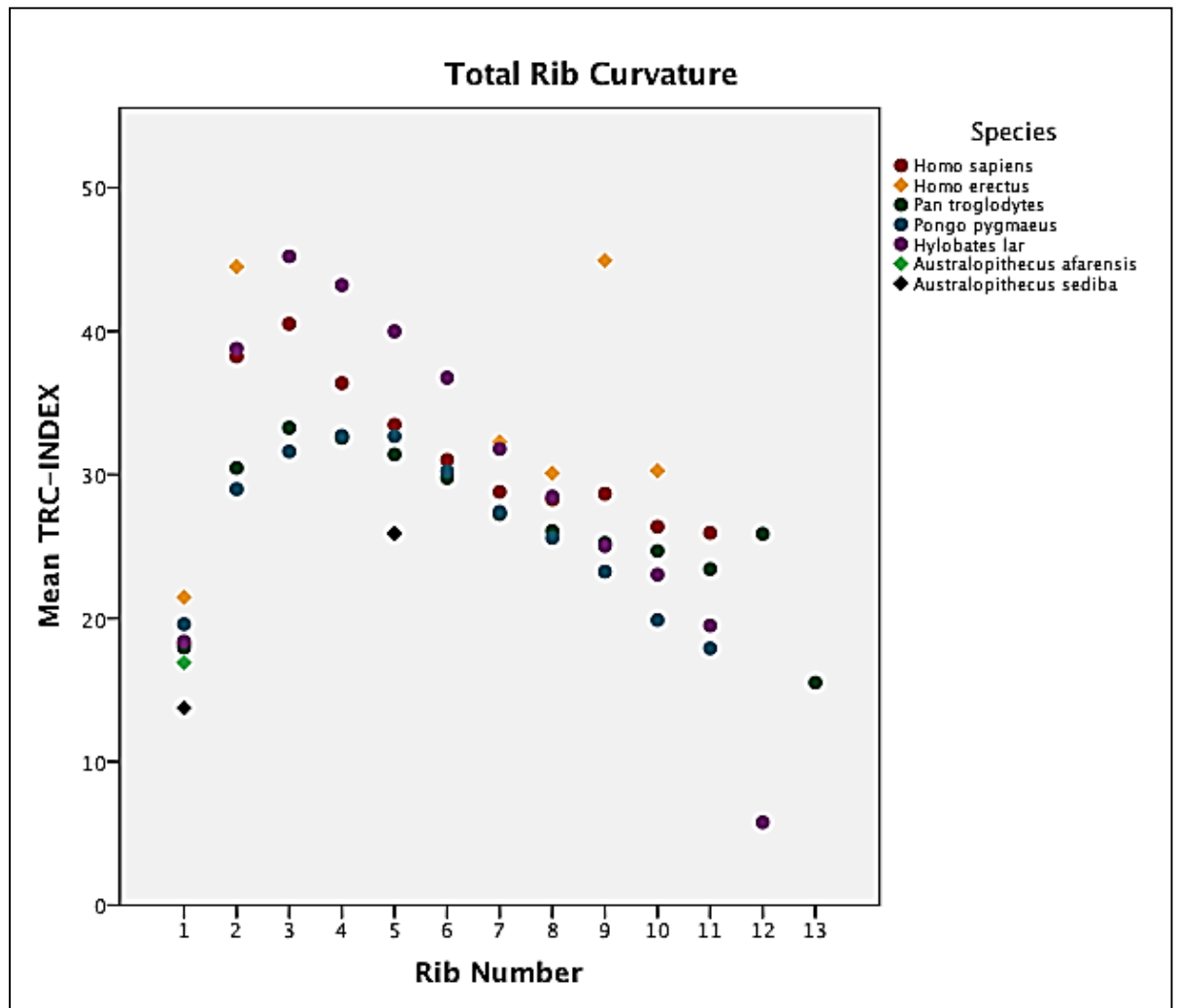


Figure 6.16.: Scatterplot of the mean total rib curvature index vs. rib number. *Homo sapiens*, *Homo erectus*, *Pan troglodytes*, *Pongo pygmaeus*, *Hylobates lar*, *Australopithecus afarensis* and *Australopithecus sediba*. Lower values indicate a more open curvature. (Schmid *et al.* 2013).

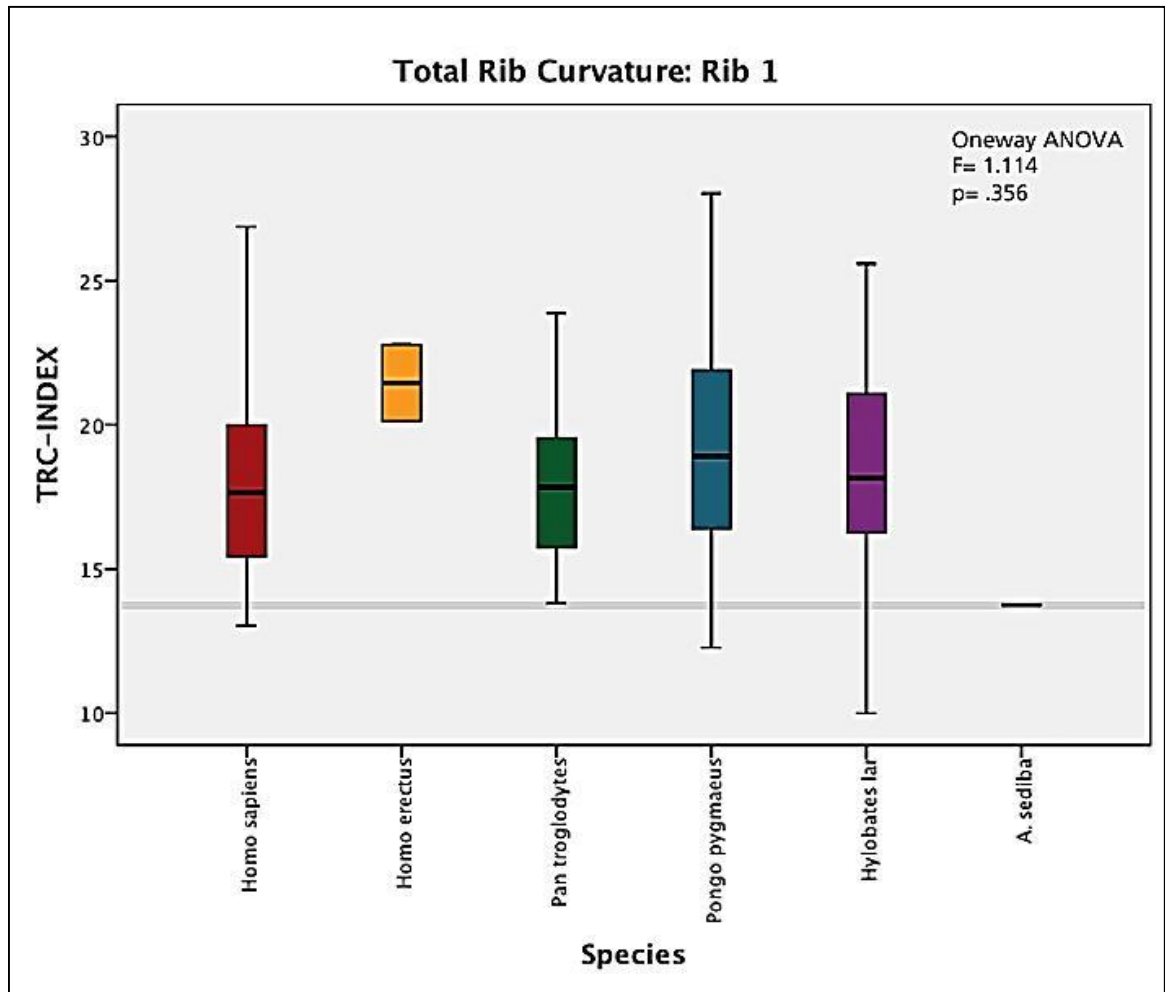


Figure 6.17.: Box plot of the total rib curvature index for the first rib among the different species (Weissen 2010).

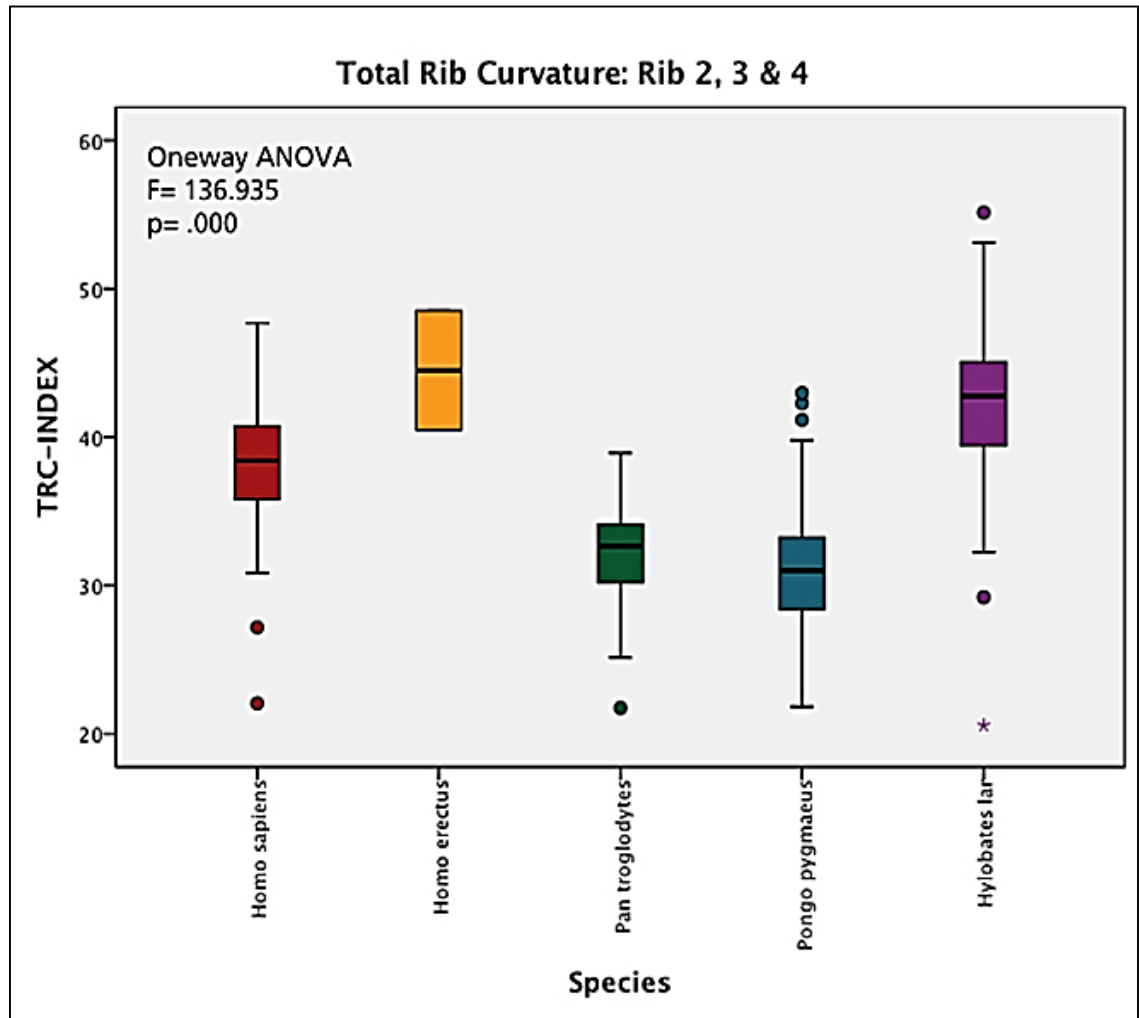


Figure 6.18.: Box plot of the total rib curvature for the upper thorax among the different species (Weissen 2010).

The second set included the ribs five, six and seven. Significantly higher index values were found for *Hylobates lar*, however the Tukey Post Hoc test showed that *Homo sapiens* and *Homo erectus* grouped with *Hylobates lar*, as did *Pan troglodytes* and *Pongo pygmaeus*. Because there was only one single rib in this set for *Australopithecus sediba*, no Post Hoc test including this species was possible. But with a noted mean of 25.909, it fell in the range of *Pan troglodytes* (see Figure 6.19). The last analysed set included the ribs eight, nine and ten. *Homo sapiens* showed significantly higher values in the total rib curvature index. For *Homo erectus*, even higher values were found; however, they are not representative as there were only the ribs of one individual in the sample (see Figure 6.20). For *Hylobates lar* as well as for *Pan troglodytes*, the Post Hoc test showed a grouping with *Homo sapiens* and *Pongo pygmaeus*, which has low values in this index in the lower thorax.

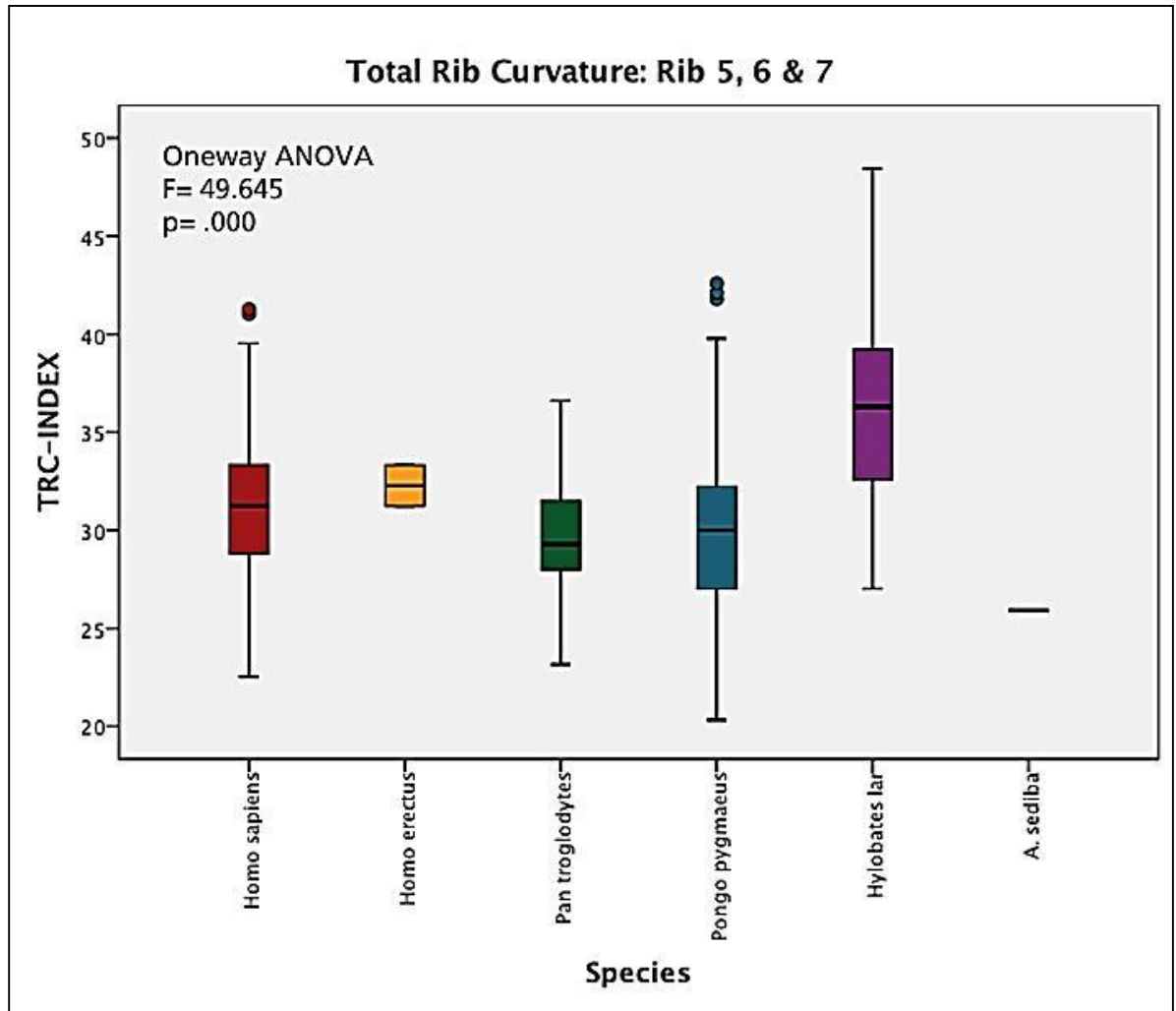


Figure 6.19.: Box plot of the total rib curvature index middle thorax among the different species. (Weissen 2010).

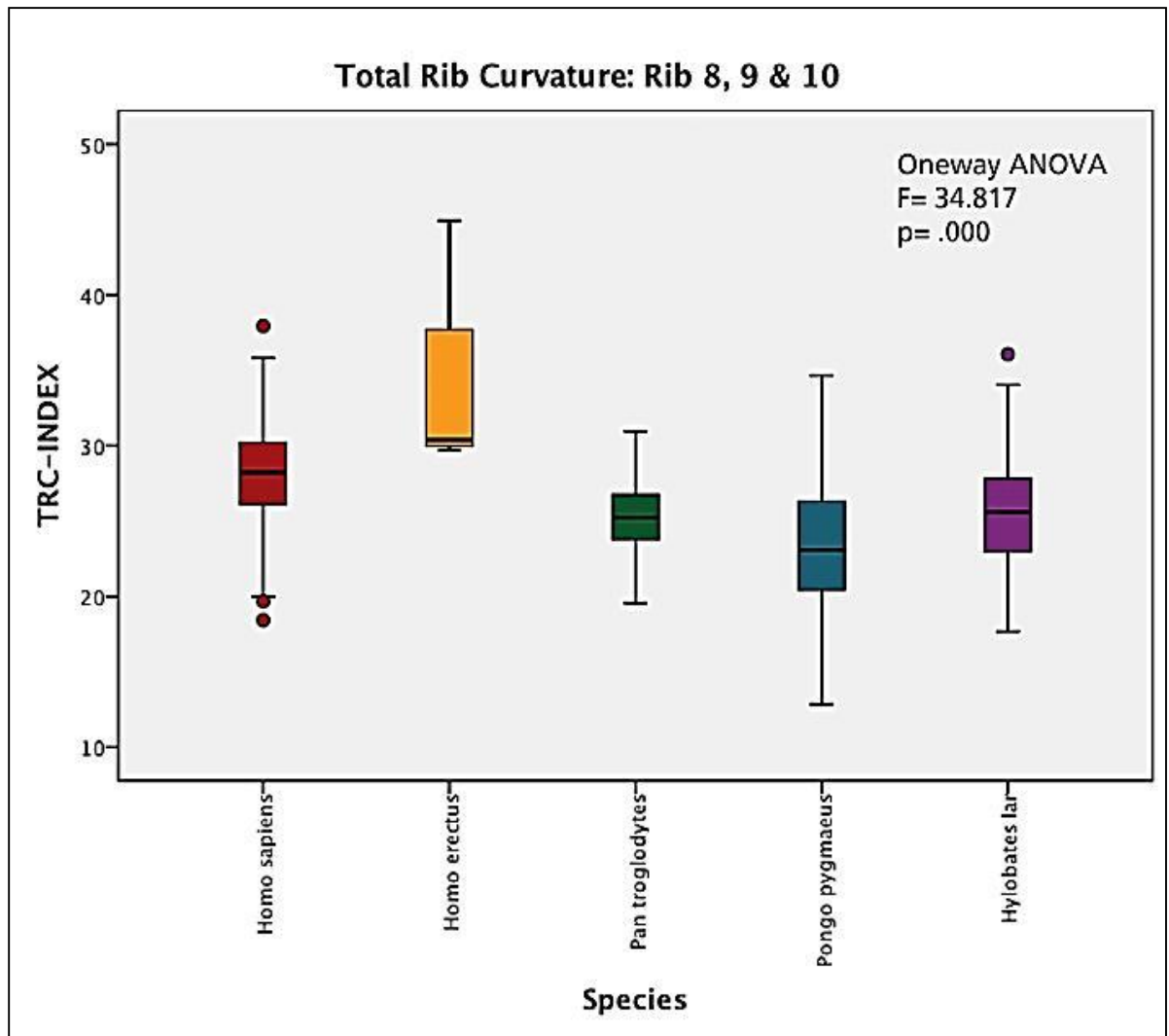


Figure 6.20.: Box plot of the total rib curvature index lower thorax among the different species (Weissen 2010).

6.2.2.3. Shaft diameters

A difference in the shape of the ribs seen between the human “barrel-shaped” and the ape inverted “funnel-shaped” thorax is said to be detected in the cross section of the ribs (Schmid 1983). Two indices were measured; one positioned at the posterior angle and the second at a mid-shaft position. The relative higher values for the index reflected a more “circular” shaft cross section. The main difference between the two thorax shapes is generally expressed in the mid-thorax region.

The scatterplot (Figure 6.21.) shows that the ribs two, three and four of *Homo sapiens* had higher shaft index values at the posterior angle than in the following ribs. Thus the cross section of the ribs in the upper thorax is rounder and changes subsequently into flatter ones at the posterior angle. *Pan troglodytes* and *Pongo pygmaeus* showed no such shift. The cross sections of the ribs at the posterior angle were round in all of the ribs. *Hylobates lar* showed the lowest index values. However, the course looked different; the values were low in the beginning and then became greater. This means that the cross sections were flat at the beginning and changed into rounded cross sections at the lower thorax.

ANOVAs were conducted for a total of three sets of ribs (one for the upper thorax, a second for the middle thorax and a third for the lower thorax), in order to reveal the differences described in the scatterplot.

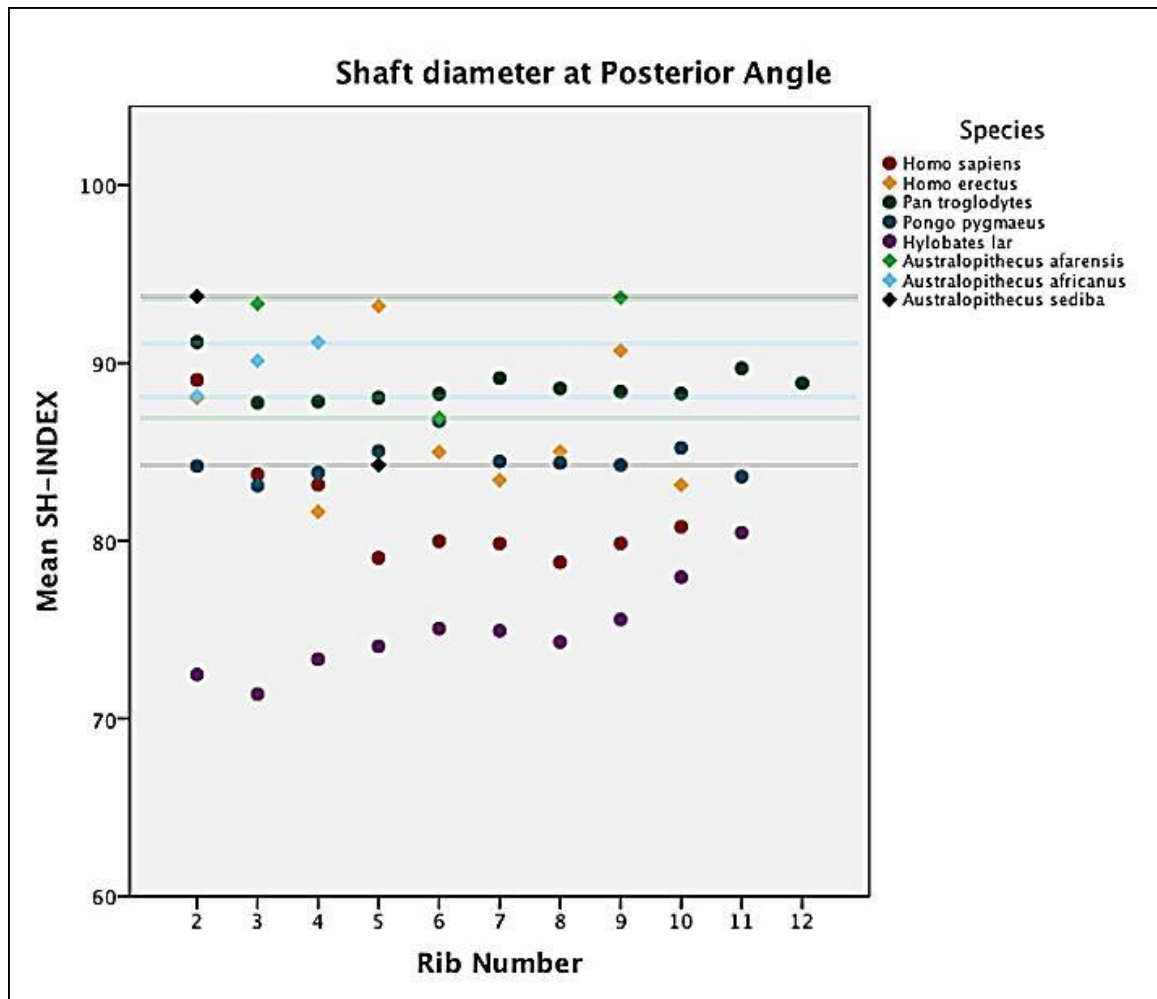


Figure 6.21. Scatterplot of mean Shaft index at angle vs. rib number. *Homo sapiens*, *Homo erectus*, *Pan troglodytes*, *Pongo pygmaeus*, *Hylobates lar*, *Australopithecus afarensis*, *Australopithecus africanus* and *Australopithecus sediba*. Lower values indicate a mediolaterally flatter cross section. (Weissen 2010).

The performed ANOVA and the following Post Hoc test of the first set of ribs showed that *Hylobates lar* had significantly mediolaterally flattened cross sections in the ribs of the upper thorax than the other species in the analysis (Figure 6.22).

The second set included the ribs five, six and seven (Figure 6.23). In the middle part of the thorax, *Homo sapiens* grouped with *Hylobates lar* as well as with the other species, except *Pan troglodytes*. Because there was only one rib of *Australopithecus afarensis* in the set, no Post Hoc test was possible including this species. With an index value of 86.9, it would have fallen in the *Pan troglodytes* group. *Homo erectus* is found in the great ape group with rounder cross sections at the posterior angle position.

The set of ribs analysed for the lower thorax consisted of the ribs eight, nine and ten (Figure 6.24). *Homo sapiens* and *Hylobates lar* built one subset. As before, *Homo sapiens* also grouped with *Pongo pygmaeus*. *Homo erectus* was found in the same group as *Pan troglodytes*. The value measured for *Australopithecus afarensis* was quite high, namely 93.7. The second shaft diameter taken into account was measured at a mid-shaft position. Here no differences were found at all. The scatterplot (Figure 6.25) did not detect any pattern and the ANOVA overall as well as for the sets including the thorax parts showed no differences.

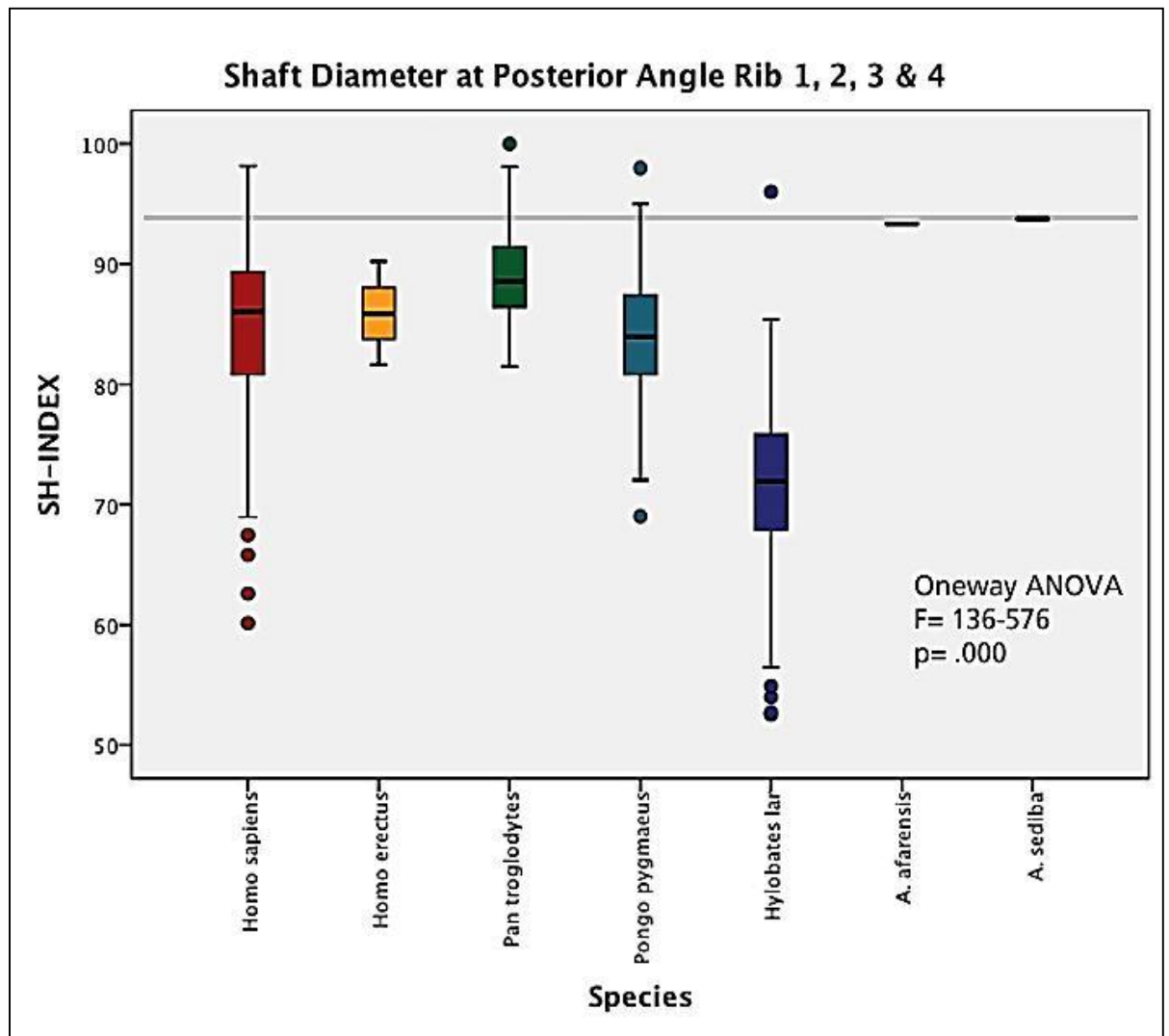


Figure 6.22.: Box plot of the shaft index at angle upper thorax among the different species (Weissen 2010).

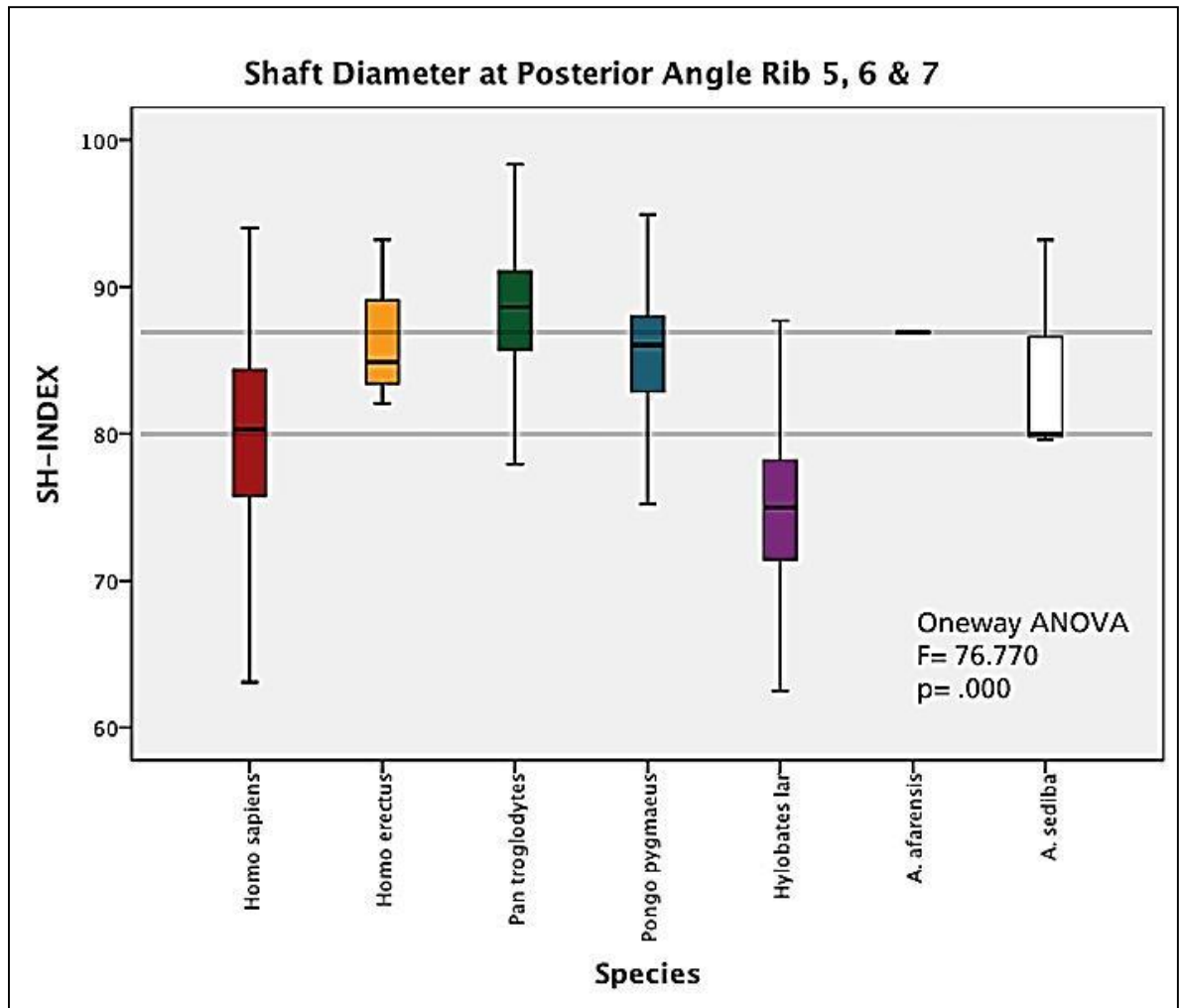


Figure 6.23.: Box plot of the shaft index at angle middle thorax among the different species. (Weissen 2010).

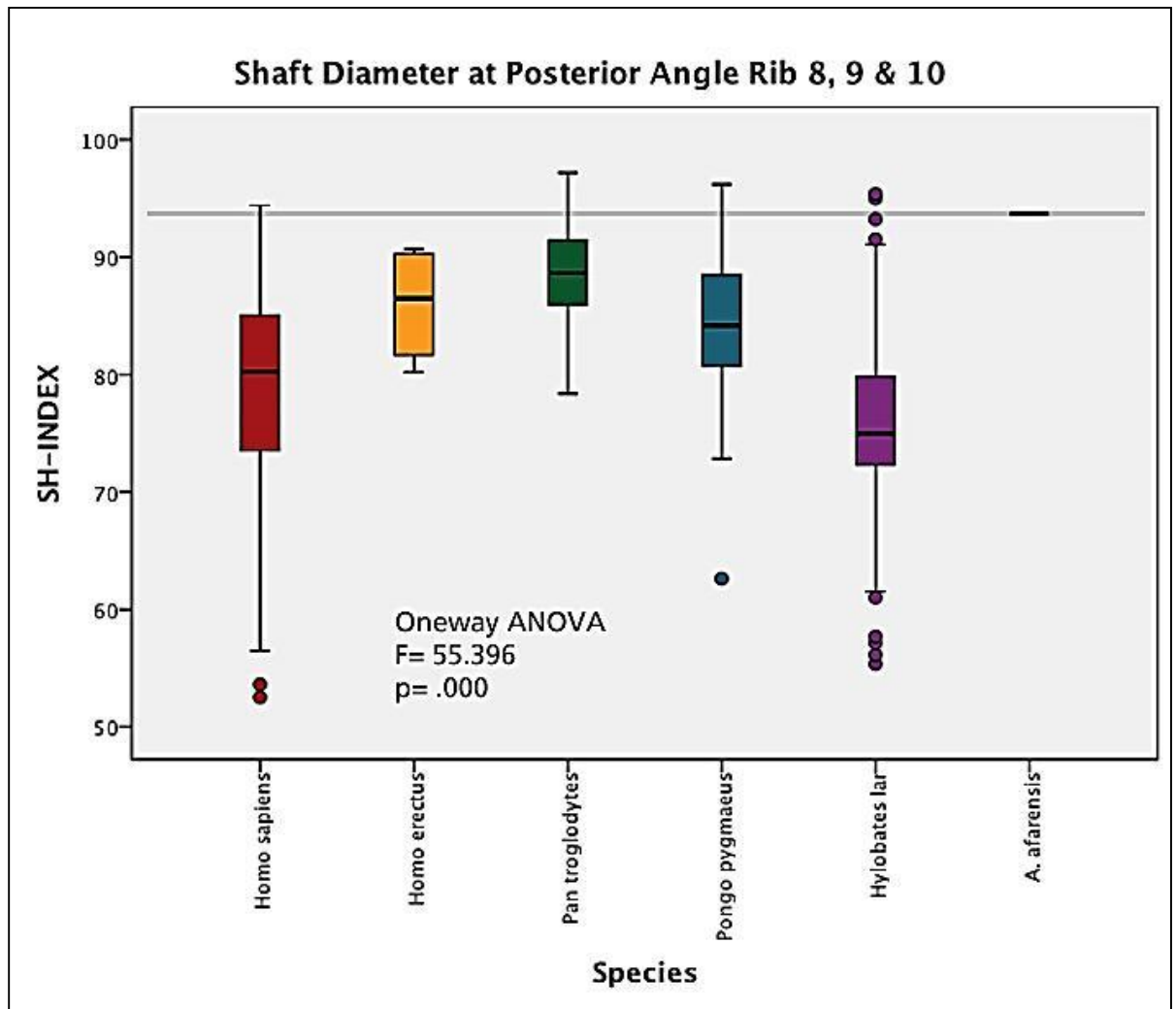


Figure 6.24. Box plot of the shaft index at angle lower thorax among the different species (Weissen 2010).

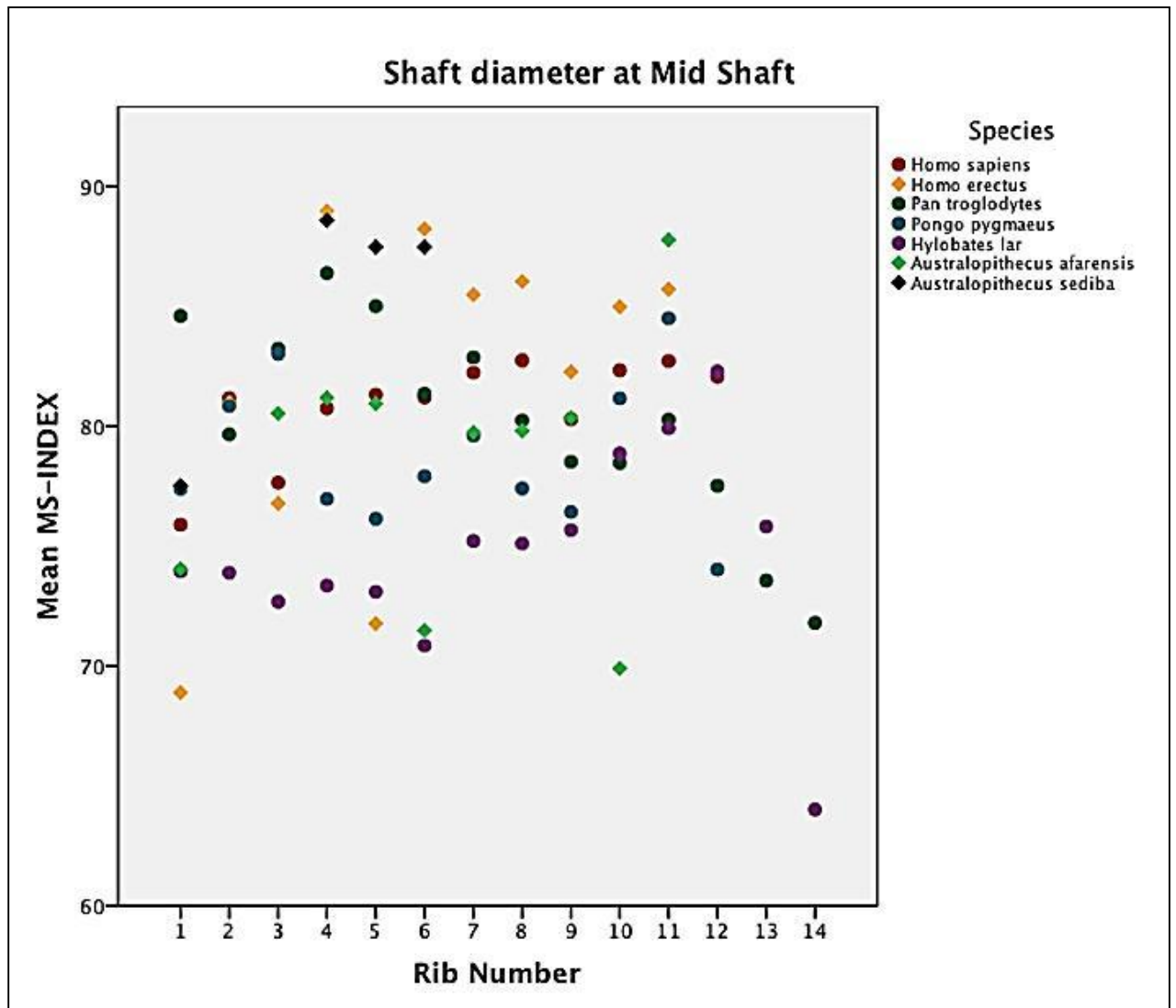


Figure 6.25.: Scatterplot of mean Mid-shaft index vs. rib number. *Homo sapiens*, *Homo erectus*, *Pan troglodytes*, *Pongo pygmaeus*, *Hylobates lar*, *Australopithecus afarensis*, *Australopithecus africanus* and *Australopithecus sediba*. Lower values indicate a mediolaterally flattened cross section (Weissen 2010).

6.2.2.4. Neck Index

Figure 6.26. shows the values of the *Australopithecus sediba* (U.W.88-15), which fit in the positions of rib four, five or six. The costal neck index was calculated by the neck S-I diameter divided by the neck length, with higher values indicating a superoinferiorly wider rib neck and/or shorter neck length. The values increased according to the rib number. For ribs that could not have been ordinarily sequenced, the neck index enabled an appreciation of the position of the rib.

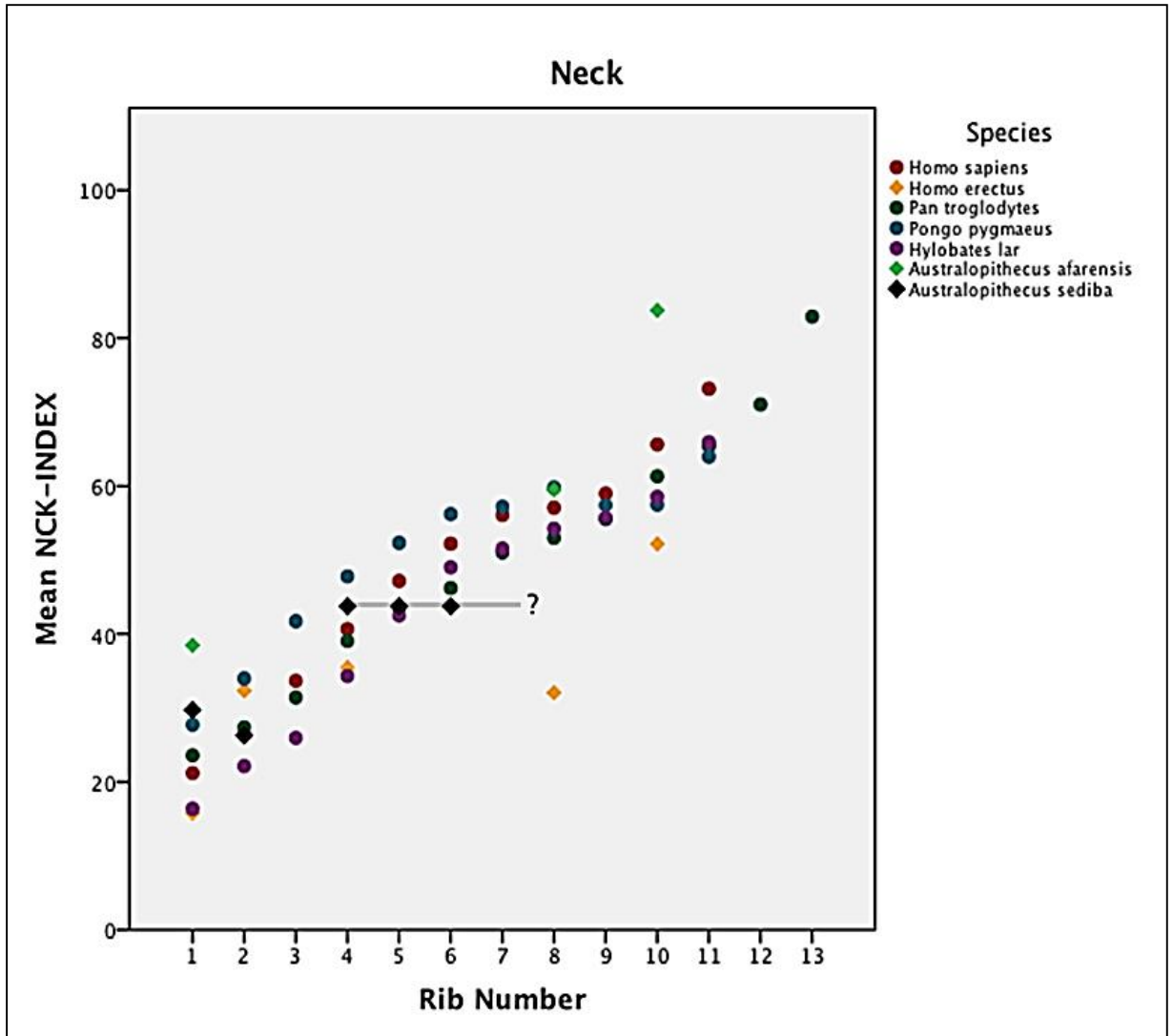


Figure 6.26: Scatterplot mean neck index vs. rib number. *Homo sapiens*, *Homo erectus*, *Pan troglodytes*, *Pongo pygmaeus*, *Hylobates lar*, *Australopithecus afarensis* and *Australopithecus sediba*. (Weissen 2010).

6.2.3. *Australopithecus sediba*: Thoracic shape determined and compared

In both the individual specimens of the *Australopithecus sediba* fossils, it is noted that the upper thoracic region is better preserved than the lower parts.

Analysis of the costal remains of MH1 and MH2 has indicated that the thoracic shape of *Australopithecus sediba* appears to be a combination of the following:

- 1) an upper thoracic region that is more primitive and ape-like in shape i.e. narrow and
- 2) a lower thoracic region that is derived and human-like in shape.

The thoracic region associated with the first three ribs is clearly ape-like, being narrow in the region of the first three ribs to form a typical ape-like cone for this region (Schmid *et al.* 2013). An ape-like, less acute posterior bending of the upper ribs (producing ribs that flare less laterally, and thus a mediolaterally-narrower rib cage) and possibly a less ventrally-positioned vertebral column (i.e. less invagination: see (Lovejoy 2005)) in *Australopithecus sediba* is indicated by its low posterior angle index (see. 6.2.2.1 above). This conclusion is also supported by the rib curvature index of the second rib (Haile-Selassie 2010), which in MH2 is estimated to be 75 (making a generous allowance for the missing head). This value is higher than and outside of the range of observed values in humans, within that of gorillas, and just below the observed range in chimpanzees as reported by (Haile-Selassie 2010). This value is also nine index units above that of the KSD-VP-1/1n second rib. The upper thorax of KSD-VP-1/1 (Woranso-Mille *Australopithecus afarensis*) has been described as been *Homo*-like (Haile-Selassie 2010).

Schmid *et al.* (2013) reconstructed the trunk of *Australopithecus sediba* by articulating ribs R₁₋₃ and R₅ using MH2's thoracic vertebrae T₃₋₆ and interpolating the morphology of the T₁ and T₂ from the preserved vertebrae plus that of the T₂ of MH1 (Williams *et al.* 2013). The shape of the thoracic inlet was obtained by articulating the right first rib and the manubrium in MH2, allowing an appropriate gap for the costal cartilage. This hemithorax was then mirror-imaged to obtain the upper portion of the complete rib cage. The thoracic inlet shape, as seen from the cranial aspect, appears typically hominoid, being broadly kidney-shaped with the vertebral column positioned ventrally (invaginated) within the thorax but less so than in modern humans. This reconstruction supported the narrow cone-like appearance of the apical thoracic region.

A fragment of a 9th or 10th rib belonging to the MH2 skeleton shows that it is slenderer than the more cranial fragments, a condition very different from that of the inferior ribs of apes (which are the largest and longest in the series). There also appears to be some degree of torsion along its body of the rib fragment, which is characteristic of the reduced last ribs of humans (but not apes). By looking at the lower rib fragments of *Australopithecus sediba*, together with the derived, human-like vertical reorientation and greater curvature of the iliac blades of *Australopithecus sediba* (Kibii *et al.* 2011), the lower thoracic region is thus found to be more human-like in its shape being wider. This correspondence between the shapes of the inferior rib cage and the false pelvis (formed by the iliac blades) is observed in both apes (Hill 1939; Ward 1993) and humans (Jellema *et al.* 1993).

According to Schmid *et al.* (2013) the thoracic cage morphology observed in *Australopithecus sediba* contrasts with that of *Homo erectus* the KNM-WT 15000 juvenile skeleton (Jellema *et al.* 1993; Hausler 2011). Jellema *et al.* (1993) deduced an essentially modern human-barrel shaped thorax in KNM-WT 15000, which is cranially and caudally narrow. This shape of the thorax is confirmed by the recent study of KNM-WT 15000 by Haeusler *et al.* (2011).

6.3. Application and Implications of thoracic Shape on posture, locomotion and physiological processes

The phylogenetic assessment of ape and human locomotor evolution was presented by Tuttle (1975), who likewise adhered to a climbing and suspensory model, excluding brachiation to explain the innovative upper limb and thorax characteristics of apes and humans (Gebo 1996). The study of the thoracic shape is closely related to the study of the morphology of the pectoral girdle and the adaptation of the shoulder joint. This is because the thorax forms an intrinsic part of the shoulder girdle (Chan 1997 a and b). Morphology of the thoracic cage thus affects the functioning of the forelimb during positional behavior (Ward 1993; Preuschoft *et al.* 2003; Chan 2007). Hunt (1991a) has argued that the biomechanical design of the ape thorax and forelimb are adaptive complexes related to arm suspension and vertical climbing. Due to a reduction in the dimensions of the lower rib cage, an expansion of the upper thoracic region in order to maintain a proper lung volume to body mass relationship (Gehr 1981).

The morphology of the upper thorax and elements of the pectoral girdle suggest that *Australopithecus sediba* had habitually elevated, “shrugged” shoulders like that of a chimpanzee (Churchill *et al.* 2013). The shape of the thorax and the positioning of the scapulae are critical in bipedal gait, as they affect the pendular mechanics of the upper limbs in their role as counter-balances to trunk rotation (Preuschoft 2004; Bramble and Lieberman 2004). Chan (1997) however, showed that the dorsoventral thoracic diameter is actually relatively longer in the hominoids than in most other primates, and may not lead to a more dorsally positioned scapula. In combination with features found in the foot (Zipfel *et al.* 2011) and lower limb (De Silva *et al.* 2013), the thoracic shape of *Australopithecus sediba* implies a gait unlike that predicted for any other early hominin species (Schmid *et al.* 2013).

The emergence of cylindrical thoraces in early *Homo* may have more to do with relative reduction in pelvic breadth (Jellema *et al.* 1993) than with upper limb pendular mechanics related to striding bipedalism or long distance running (Preuschoft 2004; Bramble and Lieberman 2004). Mediolateral expansion of the upper thorax in *Homo erectus* (and *Homo sapiens*) has been argued to be the necessary consequence of narrowing of the pelvis and lower rib cage relative to body size (Jellema *et al.* 1993) in early *Homo*. Schmid *et al.* (2013) concluded that the commitment to a fully terrestrial lifestyle in *Homo erectus* may have relaxed the functional constraints operating on early hominin shoulder and upper thoracic morphology, allowing for a reorganisation of the thorax and shoulder more conducive to the kinematic and respiratory demands of full striding bipedalism and endurance running. This

reorganisation established the basic *Homo* thoracic bauplan (as noted by Jellema *et al.* (1993) seen in all later species of Pleistocene *Homo* (Franciscus and Churchill 2002; Gomez-Oliventia *et al.* 2009 and 2010).

CHAPTER 7: DISCUSSION AND CONCLUSION

7.1. Non-metric study of the rib

Osteological features that differentiate the first and the second to the seventh ribs of the primate and non-primate species studied are summarised in Table 3.1 in chapter 3.

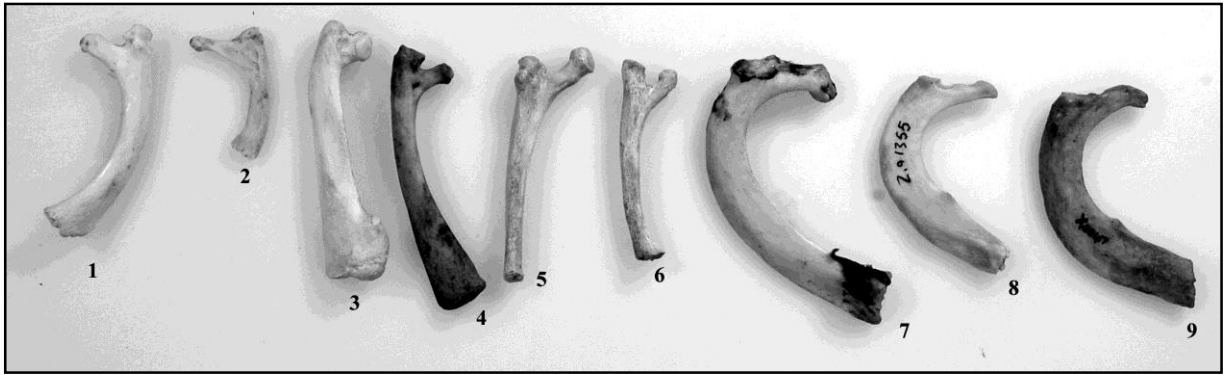
7.1.1. First rib

Figure 7.1. shows the superior/cranial and inferior/caudal views of the first rib.

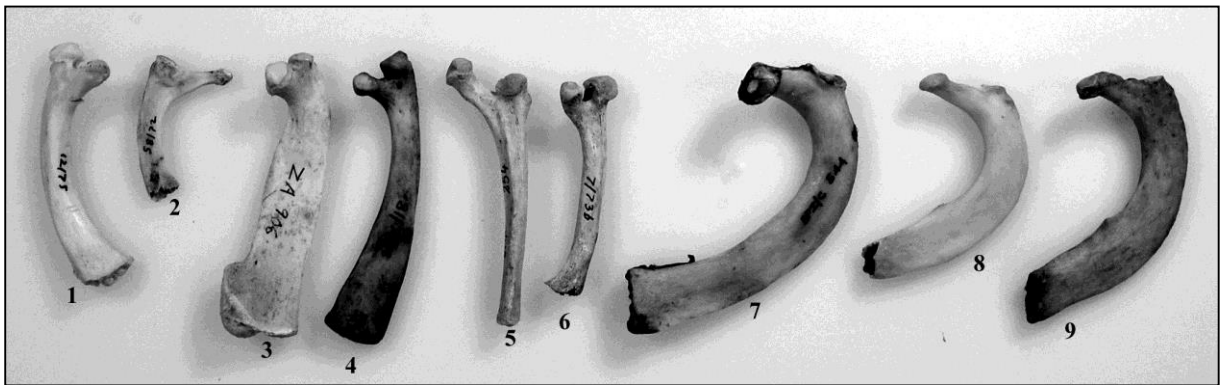
The first rib, because of its distinctive morphology, can be considered the most diagnostic in distinguishing the different taxa. Morphology of especially the proximal end of the first rib can be used for species identification of fossilised fragments found in the field as well as aid in the determination of thoracic shape.

Key characters of the first rib that show differences within and between the primate and non-primate species, i.e. inter- and intra-species differences, are the following:

- i. number of head facets;
- ii. presence of the crest of the head;
- iii. length of the neck;
- iv. size, position and prominence of the rib tubercle and its articular facet;
- v. orientation of the tubercular articular facet and
- vi. overall curvature of the shaft.



(a)



(b)

Figure 7.1. The first rib of the taxa studied (a) Superior/cranial view (b)

Inferior/caudal view.

1 – Leopard 2 – Baboon 3 - Domestic Pig 4 – Impala 5 – Spotted Hyena 6 –
Domestic Dog 7- Gorilla 8 – Chimpanzee 9 - Human

The single facet on the head of the human first rib confirms the same observation made by Ohman (1984). *Papio ursinus* is the only other species examined in this study that has a single facet on its head. All the other primates as well as the non-primate mammals in this study exhibited a double faceted head of the first rib.

The primate neck shape has less variability in shape than in length. The length of the neck is longer in humans and chimpanzees than the other primates and non-primate mammals. The structure and position of the tubercle of the rib provides an indication of the stability related to the rib elements relative to the vertebral column. These features point to anatomical sequelae that may be associated with the evolutionary transition to bipedality. The resultant formation of a wider muscular gutter, between the spinous processes of the vertebra and the transverse process (at which the rib tubercle articulates), that accommodates more strongly developed muscles of the back, especially the spinalis band of the erector spinae muscle group. This allows for a more supportive and stable vertical strut that stabilises the vertebral column during bipedal locomotion. Schmid (1991) came to a similar conclusion pertaining to the musculature associated with the vertebral column and thorax. As noted by Jellema *et al.* (1993), the position of the epaxial spinal musculature in the maintenance of the vertical position of the trunk during bipedalism resulted in an associated skeletal modification being observed in certain parts of the rib e.g. change in rib angulation and the position of the observed muscle insertions.

There is a probable association between the curvature of the first rib, the thoracic shape and position of the vertebral column relative to the thorax. Thoracic shape is determined by rib shape, especially the torsion of the rib, so differences in thoracic shape will be reflected in patterns of rib-shape variation (Barker and Ward 2008). The curvature of the first rib clearly influences the overall thoracic shape typical of the species under study. In the current study, it was observed that in the primate first rib, the curvature is most pronounced as compared to the much straighter shaft of the non-primate rib. The leopard exhibits a slight curvature of the shaft when compared to the other non-primate mammals but the curvature is not as pronounced as that observed in the primates.

McCown and Keith (1939) state that the greater curvature of modern human upper ribs indicated a derived, anteriorly (ventrally) positioned vertebral column as compared to the apelike configuration of a more posteriorly positioned vertebral column. Lovejoy (2005) also noted that in the chimpanzees and humans, the vertebral column has become invaginated into the thorax, greatly increasing its rigidity, and making it more elliptical in its shape as compared to the old world monkeys.

The observed supero-inferior/cranio-caudal flattening of the primate rib shaft is the anatomical feature that can best be utilised to differentiate the first rib from especially the second rib and the remaining rib sequence. This flattening creates a larger surface area for the attachment of the cupula pleural ligaments that isolate and insulate the upper parts of the thoracic cavity from the cervical region.

The variation in rib curvature in the atypical first and second ribs and its relationship to the variation in thoracic volume is to date still unclear as noted by Franciscus and Churchill (2002).

The presence of a scalene tubercle was a special feature that was noted only on the shaft of human and chimpanzee first ribs. A similar observation was also made by Bouvier (1967) in a study of the first rib. In this study he observed the scalene tubercle on the first rib of the gorilla as well. This was not found to be the case in this current study. The scalene tubercle is for the attachment for the *scalenus anterior* muscle. The function of this muscle is as follows: acting from inferiorly, *scalenus anterior* bends the cervical portion of the vertebral column forwards and laterally and rotates it towards the opposite side; acting from superiorly, this muscle assists in the elevation of the first rib. *Scalenus anterior* is thus also considered to be an accessory respiratory (inspiratory) muscle (Moore *et al.* (2009). The reason for this feature only being visible in these primate species may possibly indicate the similarity in the gait motion and subsequent impact of especially the neck and uppermost thoracic region of these primate species. The greater flexibility observed in the cervical region of the hominoid, and especially the modern human, may be as a result from the further development of this muscle and its attachment to the first rib.

Baboons are the only species that showed the presence of a costal groove on the first rib. The groove protects the neurovascular bundle that is present in the first intercostal space. The absence of a costal groove in the remainder of the species

under study implies that these neurological structures are sufficiently protected by the relative proximity of the thorax to the cervical associated neurovasculature.

7.1.2. The second to seventh ribs

The second rib (Figure 6.2) also shows features that allow for the differentiation between primate and non-primate species. These features include

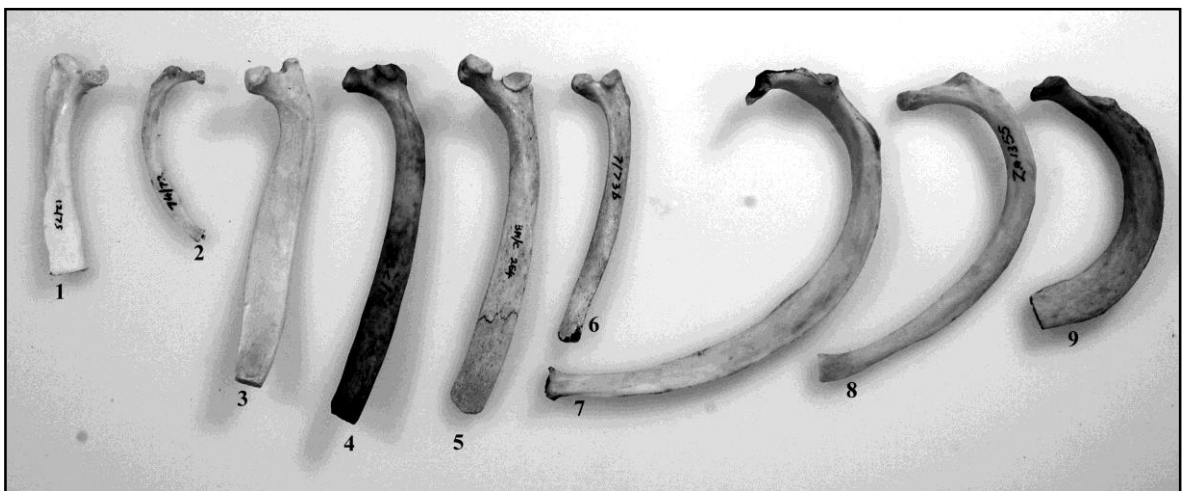
- i. Head shape;
- ii. Neck shape and length;
- iii. Angle of the neck to the shaft. Ankel-Simons (2000) observed that the ribs of all Hominoidea are more heavily bent near their articulation with the thoracic vertebrae than in other primates;
- iv. Shaft orientation relative to the long axis of the rib and
- v. Features of the shaft as one progresses along its length from the proximal end to distal end.

For example, cross-sectional variability in the shaft as also observed by Walker (1984). Schmid (1991) also states that most of the mid-thoracic ribs of the great apes have a rounded cross-section and are rather massive as compared to that observed in the modern human form where the ribs of the mid-thorax have a compressed cross-section. Jenkins (1970) also noted that rib cross-sections are variable amongst vertebrate taxa and that the adaptive reasons for the modifications of cross-sections are complex.

Individual primate and non-primate species differentiation and identification poses more of a greater challenge within the sequence of ribs caudal to the first rib.



(a)



(b)

Figure 7.2. The second rib of the taxa studied (a) Superior/cranial view (b) Inferior/caudal view.

1 – Leopard 2 – Baboon 3 - Domestic Pig 4 – Impala 5 – Spotted Hyena 6 – Domestic Dog 7- Gorilla 8 – Chimpanzee 9 - Human

7.2. The metric study of the rib

A summary of the correlations between the different measurements and indices of the first, second, fourth and seventh ribs in the various non-human and human primate groups is given in Tables 4.35 and 4.40.

Significant differences were observed between most of the measurements studied among the non-human primates. The following measurements showed non-significant differences between the different species:

- i. Neck dimensions of all the ribs for the chimpanzee versus the baboon and gorilla and
- ii. Tubercle and shaft dimensions between the baboon and chimpanzee

Among the non-human primates, significant differences are observed between the gorilla, baboon and vervet groups in the all indices (that reflect shape as compared to the measurement that reflect purely size) of all the ribs studied, except for the:

- i. (Superior) facet of the head of the first rib;
- ii. Tubercular facet of the second, fourth and seventh ribs;
- iii. Neck at tubercle for the fourth rib and
- iv. Tubercle-*iliocostalis* line for the fourth and seventh ribs

Chimpanzee, baboon and vervet differences were found to be not significantly different in the following:

- i. for all indices for ribs one and two;
- ii. shaft height at posterior angle for rib four; and
- iii. neck, neck at head and neck at tubercle of the seventh rib.

These results indicate that all the ribs, except for the first, of the non-human primates are generally variable and no specific defining measurements can be obtained that will allow for primate species differentiation. Differences between the different species of primates are all related to the associated soft tissue impacts and influences on the skeletal structure. These all correlate to the adaptative relationship that exists between structure and functionality.

The observations noted above could be associated with the natural size differences that are prevalent between the individual species as well as the gait and body position of these species. The gorilla is the largest of the extant primates and when compared to both baboons and chimpanzees, this size differentiation is amplified (also note that there is significant sexual dimorphism in gorillas). There are less significant differences observed in the calculated indices, and measurements, between the gorilla and chimpanzee than the gorilla and baboon. This possibly indicates a closer similarity in the posture, during foraging and gait. Both gorillas and chimpanzees are quadrupedal. Their food requirements take them long distances on the ground and into the trees. But whereas the gorilla is essentially terrestrial, climbing trees with

caution, chimpanzees are best characterised as arbo-terrestrial, being equally at home and skillful in the trees as on the ground (Reynolds 1965).

Non-significant differences were observed in many of the measurements as well as the indices of the human groups studied. This may be due to the closer relationship that exists between the Sotho and the Zulu, who represent the descendents of Bantu-speaking recent migrants from equatorial Africa and the Europeans.

The significant differences that were observed in some of the indices between the groups may be due to sexual dimorphism (see Bellemare 2006).

There are very few indices of the first, second and fourth ribs of the human that differ significantly from those indices of the gorilla and chimpanzee. The baboon shows more significantly different indices of the ribs when compare to humans. As one progresses distally towards the shaft on ribs four and seven, there appears to be significant differences in the indices calculated for the human ribs compared with the baboon. All the primate species differ significantly from each other in especially the seventh rib (see summary Table 4.40).

The metric study shows specific trends in some of the ribs of primate species but not in others. For example, the significant differences observed in baboon and chimpanzee first and second ribs when compared to those of humans with regards to shaft height at the posterior angle (SHI) could possibly also be associated with the surface area been created to accommodate erector spinae musculature development related to postural and gait influences. SHI may also indicate the cross-sectional

shape of the rib as a ratio between the diameters of the rib. There is a great deal of overlap in the comparisons of this feature of the ribs among the primates.

The greater significant differences that are observed in the indices of the seventh rib may be due to the fact that it is the “last” vertebra-sternal rib and also that it is at the interface between the thoracic and abdominal regions of the body. Thus this rib is more susceptible to the influences of the functions of these regions than the more mid-sequence ribs that are in an area of greater stability. Loring and Mead (1982) and Mead *et al.* (1995) emphasised the role of the rib cage in accommodating the displacements observed in thoracic and abdominal volume changes that occur during breathing.

Further investigation into the functional relationships that may exist between the indices of the different mammalian species is clearly required.

7.3. The comparison of the fossil ribs

A mosaic of primitive and derived features of the ribs is present in the different mammalian genera studied. These features are more prevalent on the first rib e.g. the single faceted head of the first rib is considered a derived human feature (Ohman 1984 and 1986) is also observed in the first rib of A.L. 288-1ax. The primitive features noted in A.L. 288 - 1ax is the cranio-caudal flattened rib shaft that is devoid of a scalene tubercle. Thus in the fossilised hominin rib both derived and primitive osteological features are observed.

7.4. Suggested future projects

It would be revealing to further study to what extent great apes and extinct hominins vary in terms of the epigenetic and the subtle phylogenetic traits found in humans. Unfortunately, due to the paucity of the hominin fossil record, this component of a future study cannot as yet be comprehensively dealt with; at least not until more complete hominin ribs are discovered. This study only included three groups of humans that were all from Southern Africa. It is suggested that any future study should include more geographically distantly related human groups, extant apes and hominin fossils.

The limitations of the first part of this study are reflected in the small sample sizes of the non-human primates and the basic linear measurements that were used in the measurement of the costal elements studied. The impact of these limitations could be reduced by future strategies being employed e.g. an increase in the number of non-human primate specimens for any future study will eliminate any inaccuracies encountered in the methodology and the results of this study.

Future studies are thus needed to assess the full extent or subtleness of variability of the osteological features of the ribs and associated thorax as exhibited by especially the pre-modern and modern human sample. A future morphometric study will provide greater insight into the more subtle species differences that may be prevalent on the proximal end of the hominin and hominin rib.

7.5. Concluding remarks

This project investigated whether the osteology of the rib, and especially the proximal end, could be utilised to differentiate mammalian species so as to assist in the identification of fossilised rib fragments.

This study also suggests that the primate rib is clearly differentiable from the non-primate rib, when looking at the detailed osteological non –metric features located proximally on a rib as well as the features of the shaft of the rib.

Some of the key observations made are that:

- i. the human proximal rib is clearly variable, both metrically and in terms of non-metric traits, but not to the extent that different populations can be clearly differentiated and discriminated;
- ii. the ribs, especially the first, second and the seventh, in that order of sequential priority, can be used to differentiate the different primate species from each other and from other mammalian species and
- iii. in order to discriminate between the mammalian species (both extant and extinct), there is a place for the utilisation of ribs which for a long time have been an ignored set of bones.

The principal objectives of this study are thus attained as the osteological elements that form the proximal end of the vertebra-sternal rib were comprehensively studied, both metrically and non-metrically. The methods employed in the current study were successfully utilised in providing an identification of the fossilised rib fragments of Stw 43, Sts 14 and MH 1 and MH 2.

Thus a template that could be used for the identification and differentiation of any future finds of fragmentary primate and non-primate fossilised ribs has been created. In the correct identification and positioning of fragmentary rib material, questions about the shape of the thorax are answered, as observed by the determination of the thoracic shape of *Australopithecus sediba*. This in turn facilitates a better understanding of not only the evolution of locomotion but also of the lineage of discovered fossilised members of the Homininae.

REFERENCES

Aiello, L.C. and Dean, C. (1996) *An Introduction to Human Evolutionary Anatomy* Academic Press, London, 1996.

Aiello, L.C. and Wheeler, P. (1995) The expensive Tissue Hypothesis: The brain and digestive system in human and primate evolution, *Current Anthropology* 36, pp. 199-221.

Allan, J.C. (1982) *Learning about statistics – A Primer in Simple Statistical Methods for Students of the Medical, Biological, Paramedical, Social and Behavioral Sciences* Macmillan South Africa, Johannesburg, 1982.

Ankel-Simons, F. (2000) *Primate Anatomy: an Introduction*. Academic Press, London, 2000.

Arensburg, B. (1991). The vertebral column, thoracic cage and hyoid bone. In *Le Squelette Mousté ´rien de Ke ´bara* (O. Bar Yosef & B. Vandermeersch, Eds) 2, pp. 113–146. Paris: Euditions du C.N.R.S.

Barker, K.B. and Ward, C.V. (2008) Patterns of upper rib morphology in hominoids, *American Journal of Physical Anthropology Supplement* 46, pp. 64-64.

Bellemare, F., Fuamba, T. and Bourgeault, A. (2006) Sexual dimorphism of human ribs, *Respiratory Physiology & Neurobiology* 150, pp. 233–239.

Berger, L.R. (2013). The mosaic nature of *Australopithecus sediba*. *Science* Vol 340 (Issue 6129 12 April 2013) pp. 163-165

Berger, L.R. (2012) *Australopithecus sediba* and the earliest origins of the genus *Homo*. *Journal of Anthropological Sciences* 90, pp. 1-16

Berger, L.R., de Ruiter, D.J., Churchill, S.E., Schmid, P., Carlson, K.J., Dirks, P.H.G.M. and Kibi, J.M. (2010) *Australopithecus sediba*: A New Species of Homo-Like Australopithec from South Africa, *Science*, 328, pp. 195-204.

Boule, M. (1911–1913) L’homme fossile de la Chapelle aux Saints, *Annals of Paleontology* 6, pp. 111–172; 7, pp. 21–56, pp. 85–192; 8, pp. 1–70.

Bouvier, J.C. (1967) Morphologic variations in the first rib of man and some other primates, *Archives Suisses D’Anthropologie Generale* 32, pp 1-136.

Boaz, N.T. (1980) A hominoid clavicle from the Mio-Pliocene of Shahabi Libya *American Journal of Physical Anthropology*, 53, pp. 46 – 54.

Brain, C.K. (1974) Some suggested procedures in the analysis of bone accumulations from southern African Quaternary sites. *Annals of the Transvaal Museum* 29 pp. 1 – 8.

Brain, C.K. (1981) *The Hunters or the Hunted? An Introduction to African Cave Taphonomy*. University of Chicago Press, 1981.

Bramble, D.M. and Lieberman, D.E. (2004) Endurance running and the evolution of *Homo*. *Nature*, 432, pp. 345 – 352.

Broom, R. and Robinson, J.T. (1947) Further remains of the Sterkfontein Ape-man, *Plesianthropus*, *Nature*, 160, pp. 430-431.

Cachel, S. and Harris, J.W.K. (1996) The paleobiology of *Homo erectus*: Implications for understanding the adaptive zone of this species, in *Aspects of African Archaeology*, G. Pwiti, R. Soper, Eds. University of Zimbabwe Publications, Harare, 1996.

Carlson, K.J., Stout, D., Jashashvili, T., de Ruiter, D.J., Tafforeau, P., Carlson, K. and Berger, L.R. (2011) The endocast of MH1, *Australopithecus sediba*., *Science* 333, pp. 1402

Carretero, J.M., Lorenzo, C. and Arsuaga, J.L. (1999) Axial and appendicular skeleton of *Homo antecessor*, *Journal of Human Evolution*, 37, pp. 459–499.

Chan, L.K. (1997a) Thoracic shape and shoulder biomechanics in primates. PhD thesis, Duke University, Durham, 1997.

Chan, L.K. (1997b) Variation of thoracic shape among primates, *American Journal of Physical Anthropology*, Supplement 24, p. 90.

Chan, L.K. (2007) Scapular position in primates, *Folia Primatologia*, 78, pp. 19 – 35.

Churchill, S.E. (1994) Medial clavicular length and upper thoracic shape in Neanderthals and Europeans early modern humans (abstract), *American Journal of Physical Anthropology*, Supplement 18, pp. 67–68.

Churchill, S.E., Holliday, T.W., Carlson, K.J., Jashashvili, T., Macias, M.E., Mathews, T., Sparling, T.L., Schmid, P., de Ruiter, D.J. and Berger, L.R. (2013) The upper limb of *Australopithecus sediba*, *Science* Vol 340 (Issue 6129 12 April 2013)

Coon, C.S. (1962) *The Origin of Races*. Knopf. New York, 1962.

Dawson, B. and Trapp, R. (2001) *Basic and Clinical Biostatistics*. New York: McGraw-Hill, 2001.

Dayal, M.R, Kegley, A.D.T., Štrkalj, G., Bidmos, M. A. and Kuykendall, K.L. (2009) The History and Composition of the Raymond A. Dart Collection of Human Skeletons at the University of the Witwatersrand, Johannesburg, South Africa. *American Journal Of Physical Anthropology* 140:324–335

De Palma, A.F. (1950) Origin and comparative anatomy of the pectoral limb. In: De Palma, A.F., *Surgery of the Shoulder*. Philadelphia, PA: Lippincott Williams & Wilkins. pp: 1–14.

De Ruiter, D.J., DeWitt, T.J., Carlson, K.B., Brophy, J.K., Schroeder, L., Ackermann, R.R., Churchill, S.E. and Berger, L.R. (2013) Mandibular remains support taxonomic validity of *Australopithecus sediba*, *Science* Vol 340 (Issue 6129 12 April 2013)

De Silva, J.M., Kenneth, G., Holt, K.G., Churchill, S.E., Carlson, K.J., Walker, C.S., Zipfel, B. and Berger, L.R. (2013) The lower limb and the mechanics of walking in *Australopithecus sediba*, *Science* Vol 340 (Issue 6129 12 April 2013)

Dirks, P.H.G.M Kibii, J.M., Kuhn, B.F., Steininger, C. Churchill, S.E., Karmers, J.D., Pickering, R., Farber, D.L., Meriaux, A-S., Herries, A.I.R., King, G.C.P. and Berger, L.R. (2010) Geological setting and age of *Australopithecus sediba* from Southern Africa, *Science*, vol.328, pp. 205–208.

Drake, R.L., Vogl, W. and Michell, A.W. (2009) *Gray's Anatomy for students*. Elsevier. Chicago, 2009.

Dudar, J.C. (1993) Identification of rib number and assessment of intercostal variation at the sternal rib end, *Journal of Forensic Sciences*, 38, pp. 788–797.

Endo, B. and Kimura, K. (1970) Postcranial skeleton of the Amud man. In: Endo, B., Kimura, K. (Eds.), *The Amud Man and His Cave Site*, The University of Tokyo, Tokyo, 1970.

Flower, W.H. (1885) *An Introduction to Osteology of Mammalia (3rd edition)*. Macmillan and Co., London, 1885.

Franciscus, R. G. (1989). Neanderthal mesosterna and noses: implications for activity and biogeographical patterning (abstract), *American Journal of Physical Anthropology*, 78, p. 223.

Franciscus, R.G. and Churchill, S.E. (2002) The costal skeleton of Shanidar 3 and a reappraisal of Neanderthal thoracic morphology, *Journal of Human Evolution*, 42, pp. 303–356.

Gea, J. (2008) The evolution of the human species: a long journey for the respiratory system, *Archives of Bronconeumology*, 44 (5), pp. 263-70.

Gebo, D.L. (1996). Climbing, brachiation, and terrestrial quadrupedalism: historical precursors of hominin bipedalism, *American Journal of Physical Anthropology*, 101, pp. 55–92.

Gegenbaur, C. (1878) *Elements of Comparative Anatomy*, Macmillan and Company. London, 1878.

Gehr, P., Deter, K., Mwangi, D.K., Ammann, A., Mailoiy, G.M.O., Taylor, C.R. and Weibel, E.R. (1981) Design of the mammalian respiratory system V. Scaling morphometric pulmonary diffusing capacity to body mass: wild and domestic mammals, *Respiratory Physiology*, 44, pp. 61 – 86.

Getty, R. (1975) *Sisson and Grossman's The Anatomy of the Domestic Animals (5th Edition) Volume 1 and Volume 2*, WB Saunders Company, Philadelphia, 1975.

Gloobe, H. and Nathan, H. (1970) Myocardial atrio-venous junctions and extensions (sleeves) over the pulmonary and caval veins, *Thorax*, 25, pp. 317-324.

Gommery, D. and Thackeray, J.F. (2006) Sts 14, a male sub-adult partial skeleton of *Australopithecus africanus?*, *South African Journal of Science*, 102, pp. 91-92.

Gomez-Olivencia, A., Eaves-Johnson, K.L., Franciscus, R.G., Carretero, J.M. and Arsuaga, J.L. (2009) Kebara 2: new insights regarding the most complete Neanderthal thorax, *Journal of Human Evolution*, 57, pp. 75–90.

Gómez-Olivencia, A., Carretero, J.M., Lorenzo, C., Arsuaga, J.L., de Castro, J.M.B. and Carbonell, E. (2010) The costal skeleton of *Homo antecessor*: preliminary results, *Journal of Human Evolution*, 59, pp. 620-640.

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

Haile-Selassie, Y., Latimer, B.M., Alene, M., Deino, A.L., Gibert, L., Melillo, S.M., Saylor, B.Z., Scott, G.R., Owen Lovejoy, C. (2010) An early *Australopithecus afarensis* postcranium from Woranso-Mille, Ethiopia, *Proceedings of National Academy of Sciences (PNAS)*, 107 (27), pp. 12121–12126.

Heim, J.L. (1976) *Les Hommes fossiles de la Ferrassie. I. Le gisement. Les squelettes adultes (craˆne et squelette du tronc)*, Masson, Paris, 1976.

Hill, W.C.O. (1939) Observations on a giant Sumatran orang, *American Journal of Physical Anthropology*, 24, p. 449.

Hillson, S. (1992) *Mammal Bones and Teeth: An introductory guide to methods of identification*, UCL Institute of Archaeology Publications, 1992.

Hoppa, R.D. and Saunders, S. (1998) Two quantitative methods of rib seriation in human skeletal remains, *Journal of Forensic Sciences*, 43, pp.185-191.

Hrdlicˆka, A. (1920) *Anthropometry*. Wistar Institute of Anatomy and Biology, Philadelphia, PA, 1920.

Hrdlička, A. (1930) The skeletal remains of early man. *Smithsonian Miscellaneous Collection*, 83, pp. 1–379.

Hunt, K.D. (1991a) Mechanical implications of chimpanzee positional behaviour, *American Journal of Physical Anthropology*, 86, pp. 521 – 536.

Hunt, K.D. (1991b) Positional behavior in the Hominoide, *International Journal of Primatology*, 12, pp. 95-118.

Irish, J.D., Guatelli-Steinberg, D., Legge, S.S., de Ruiter, D.J and Berger, L.R. (2013) Dental morphology and the phylogenetic “Place” of *Australopithecus sediba*. *Science* Vol 340 (Issue 6129 12 April 2013)

Jayne, H. (1898) *Mammalian Anatomy – a preparation for human and comparative anatomy*, JB Lippincott Company, Philadelphia, 1898.

Jellema, L.M., Latimer, B. and Walker, A. (1993) The rib cage. *The Nariokotome Homo erectus Skeleton*. (Eds. Walker, A.C. and Leakey, R.E.F.), Harvard University Press, Cambridge, pp. 294-325.

Jenkins, F.A. (1970) Anatomy and Function of Expanded Ribs in Certain Edentates and Primates, *Journal of Mammalogy*, 51(2), pp. 288-301.

Johanson, D.C. and Taieb, M. (1976) Plio-Pleistocene hominin discoveries in Hadar, Ethiopia, *Nature*, 260, pp. 293–297.

Johanson, D. and Edey, M. (1981) *Lucy: The Beginnings of Humankind*, Simon and Schuster, New York, 1981.

Johanson, D.C., Lovejoy, C.O., Kimbel, W.H., White, T.D., Ward, S.C., Bush, M.E., Latimer, B.M. and Coppens, Y. (1982) Morphology of the Pliocene partial hominin skeleton (A.L. 288-1) from the Hadar Formation, Ethiopia, *American Journal of Physical Anthropology*, 57, pp. 403–451.

Jungers, W.L. and Stern, J.T. Jr. (1983) Body proportions, skeletal allometry and locomotion in the Hadar hominins: a reply to Wolpoff, *Journal of Human Evolution*, 12, pp. 673–684.

Kagaya, M., Ogihara, N. and Nakatsukasa, M. (2008) Morphological study of the anthropoid thoracic cage: scaling of thoracic width and an analysis of rib curvature, *Primates*, 49, pp. 89–99.

Kagaya, M., Ogihara, N. and Nakatsukasa, M. (2009) Rib orientation and implications for orthograde positional behaviour in nonhuman anthropoids, *Primates*, 50(4), pp. 305-310.

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

- Kivell, T.L., Kibii, J.M., Churchill, S.E., Schmid, P. and Berger, L.R. (2011) *Australopithecus sediba* hand demonstrates mosaic evolution of locomotor and manipulative abilities, *Science*, 333, pp. 1411 – 1417.
- Kramer, P.A. and Sylvester, A.D. (2009) Bipedal form and locomotor function: Understanding the effects of size and shape on velocity and energetics, *PaleoAnthropology*, pp. 238 -251.
- Larson, S.G., Jungers, W.L., Morwood, M.J., Sutikna, T., Saptomo, J.E.W., Due, R.A. and Djubiantono, T. (2007) *Homo floresiensis* and the evolution of the hominin shoulder, *Journal of Human Evolution*, 53 pp. 718-731.
- Latimer, B. and Ward, C.V. (1993) *The Nariokotome Homo erectus Skeleton*. (Eds Walker, A.C. and Leakey, R.E.F.), pp: 266 - 293 Harvard University Press, Cambridge, 1993.
- Leakey, R.E. and Lewin, R. (1992): *Origins reconsidered: in search of what makes us human*, New York: Doubleday, 1992.
- Lordkipanidze, D., Jashashvili, T., Vekua, A., Ponce de León, M.S., Zollikofer, C.P.E., Rightmire, G.P., Pontzer, H., Ferring, R., Oms, O., Tappen, M., Bukhsianidze, M., Agusti, J., Kahlke, R., Kiladze, G., Martinez-Navarro, B., Mouskhelishvili, A., Nioradze, M. and Rook, L. (2007) Postcranial evidence from early *Homo* from Dmanisi, Georgia, *Nature*, 449, pp 305-310.

Loring, S. and Mead, J. (1982) Action of the diaphragm on the rib cage inferred from a force-balance analysis, *Journal of Applied Physiology*, 53, pp. 197–204.

Loth, E. (1938) Beitrage zur Kennis der Weichteilanatomie des Neanderthalers, *Zeit. Rass*, 7, pp. 13–35.

Lovejoy, C.O. (1988) Evolution of human walking, *Scientific American*, 259, pp.118-125.

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

Lovejoy, C.O., Johanson, D.C. and Coopens, W. (1982) Elements of the Axial Skeleton Recovered From the Hadar Formation: 1974 - 1977 Collections, *American Journal of Physical Anthropology*, 57, pp. 531-635.

Lovejoy, C.O., Suwa, G., Simpson, S.W., Matternes, J.H., White, T.D. (2009) The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestors with African apes, *Science*, 326 (73), pp. 100–106.

Lovejoy, C.O., Suwa, G., Spurlock, L., Asfaw, B. and White, T.D. (2009) The pelvis and femur of *Ardipithecus ramidus*: the emergence of upright walking, *Science*, 326, pp. 711 – 716.

- Mann, R.W. (1993) A method for siding and sequencing human ribs, *Journal of Forensic Sciences*, 38, pp. 151–155.
- May, E. and Martins, M. (1985) Differentiation of human and non-human primate ribs, *Anatomical Anziger*, 160(3), pp.179-202.
- McCown, T.D. and Keith, A. (1939) *The Stone Age of Mount Carmel II: The Fossil Human Remains from the Levallois-Mousterian*, Clarendon Press, Oxford, 1939.
- McHenry, H.M. and Berger, L.R. (1998) Body proportions in *Australopithecus afarensis* and *A. africanus* and the origin of the genus *Homo*, *Journal of Human Evolution*, 35, pp. 1–22.
- Mead, J., Loring, S. and Smith, J. (1995) Volume displacements of the chest wall and their mechanical significance. In: Roussos, C. (Ed.) *Lung Biology in Health and Disease: The Thorax, Part A*. 85, pp. 565–586 Marcel Dekker, New York, 1995.
- Moore, K.L., Dalley, A. and Agur, A.M. (2009) *Clinically Oriented Anatomy (6th Edition)* Lippincott Williams and Wilkins. Philadelphia, 2009.
- Napier, J.R. and Napier, P.H. (1967) *A Handbook of Living Primates*, Academic Press, New York, 1967.

Ohman, J.C. (1983) A change in morphology in the cervico-thoracic region of the vertebral column in hominin evolution, *American Journal of Physical Anthropology* 60, pp. 233 – 234.

Oettlè, A.C. and Steyn , M. (2000) Age estimation from sternal ends of ribs by phase analysis in South African Blacks, *Journal of Forensic Sciences* 45 (5): 1071 - 9

Ohman, J.C. (1984) *Morphological Variation in the Cervico-Thoracic Region of the Vertebral Column in Modern Humans, Extant Apes, Fossil Hominins and With Reference to Mammalia in General*. M.A. Thesis, Kent State University, Kent, Ohio, 1984.

Ohman, J.C. (1986) The first rib of hominoids, *American Journal of Physical Anthropology*,70(2), pp. 209-229.

O'Regan, H.J. and Kitchener, A. (2005) the effects of captivity on the morphology of the morphology of captive, domesticated and feral mammals.. *Mammal Review*34 pp 215 - 230

Owen, R. (1835) On the osteology of the chimpanzee and orang-utan, *Transactions of the Zoological Society of London* Volume 1, pp. 343 – 380.

Owen, R. (1854) *The Principal forms of the skeleton and of the teeth*, Blanchard and Lea. Philadelphia, 1854.

Pickering, R., Dirks P.H.G.M., Jinnah, Z., de Ruiter, D.J. Churchil, S.E., Herries, A.I.R., Woodhead, J.D., Hellstrom, J.C. and Berger, L.R. (2011). *Australopithecus sediba* at 1.977 Ma and implications for the origins of the genus Homo. *Science* 333, pp. 1421

Plug, I. (1988) *Hunters and herders: an archaeological study of some prehistoric communities in the Kruger National Park*. D Phil Thesis, Univeristy of Pretoria

Plug, I. (2001) Archaeozoology at the Transvaal Museum: From hominid times to history. In *Animals and Man in the Past Essays in honour of Dr. A.T. Clason emeritus professor of archaeology Rijkuniversiteit Groningen, the Netherlands*, eds. H. Buitenhuis and Prummel, W. pages 371- 379. Groningen ARC-Pulicatie 41

Pontzer, H., Rolian, C., Rightmire, G.P., Jashashvili, T., Ponce de León, M.S., Lordkipanidze, D. and Zollikofer, C.P.E. (2010) Locomotor anatomy and biomechanics of the Dmanisi hominins, *Journal of Human Evolution*, 58, pp. 492-504.

Preuschoft, H. (2004) Mechanisms for the acquisition of habitual bipedality: are there biomechanical reasons for the acquisition of upright bipedal posture, *Journal of Anatomy*, 204, pp. 363-384.

Reynolds, V. (1965) Some Behavioural Comparisons between the Chimpanzee and the Mountain Gorilla in the Wild America, *Anthropologist*, 67, pp. 691- 706.

Robinson, J.T. (1972) *Early Hominin Posture and Locomotion*, The University of Chicago Press, Chicago and London, 1972.

Ruff, C. and Walker, A.C. (1993) Body size and shape, in *The Nariokotome Skeleton*, AC. Walker, R.E. Leakey, Eds., Harvard University Press, Cambridge, pp. 234-265.

Schaafhausen, D. (1858) Zur Kenntnis der ältesten Rassenstraße, *Archives of Anatomy and Physiology*, 25, pp. 453–478.

Schultz, A.H. (1950) The specialization of man and his place among the catarrhine primates, *Quaternary. Biology*, 15 pp. 37-53.

Schultz, A.H. (1961) Vertebral column and thorax. In *Primatologia, Handbuch der Primatenkunde*, IV (Eds Hofer H, Schultz AH, Starck D), S. Karger, Basel. pp. 1– 66.

Schultz, A.H. (1969a) *The Life of Primates*, Universe Books, New York, 1969.

Schultz, A.H. (1969b) The Skeleton of the Chimpanzee. In: Bourne, G.H. (Ed.), *The Chimpanzee: Anatomy, Behaviour, and Diseases of Chimpanzees*. Vol. 1 pp. 50-103. Basel: Karger, 1969.

Schmid, P. (1983) Eine Rekonstruktion des Skelettes von A.L. 288-1 (Hadar) und deren Konsequenzen/A reconstruction of the skeleton of A.L. 288-1 (Hadar) and its consequences, *Folia Primatologia*, 40, pp. 283–306.

Schmid, P. (1991) The trunk of the australopithecines. In: Coppens Y, Senut B, editors. *Origine(s) de la bipédie chez les hominines*. Cahier de Paléanthropologie, Y. Coppens, B. Senut, Eds. (Editions du CNRS, Paris, pp. 225–234.

Schmid, P. (2004) Functional interpretation of the Laetoli footprints, in *From Biped to Strider: The Emergence of Modern Human Walking, Running, and Resource Transport.*, D. J. Meldrum, C. E. Hilton, Eds. (Kluwer Academic/Plenum Publishers, New York, pp. 49-62.

Schmid, P., Churchill, S.E., Nalla, S., Weissen, E., Carlson, K.J., de Ruiter, D.J. and Berger, L.R. (2013) Mosaic Morphology in the Thorax of *Australopithecus sediba*. *Science* Vol 340 (Issue 6129 12 April 2013) pp.109 - 236

Shaw, C.N. and Stock, J.T. (2011). The influence of body proportions on femoral and tibial midshaft shape in hunter-gatherers, *American Journal of Physical Anthropology*, 144, pp. 22 -29.

Slijper, E.J. (1946) Comparative biologic-anatomical investigations on the vertebral column and spinal musculature of mammals, *Verl. K. Ned. Akad. Wet. Tweedie Sectie* 42 (5), pp. 1-128.

Smith, F.H. (1976) The Neanderthal remains from Krapina: a descriptive and comparative study, *University of Tennessee Department of Anthropology Report Invest.*, 15, pp. 1–359.

Solecki, R.S. (1960) Three adult Neanderthal skeletons from Shanidar Cave, northern Iraq, *Smithsonian Report for 1959*, pp. 603–635.

Steele, D.G. and Bramblett, C.A. (1988) *The Anatomy and Biology of the Human Skeleton*. College Station: Texas A&M Press, 1988.

Stern, J.T. and Jungers, W.L. (1990) The capitular joint of the first rib in primates: a re-evaluation of the proposed link to locomotion, *American Journal of Physical Anthropology*, 82, pp. 431–439.

Stringer, C.B. and Gamble, C. (1993) *In Search of the Neanderthals*. New York: Thames and Hudson, 1993.

Struthers, J. (1875) On variations of the vertebrae and ribs in man, *Journal of Anatomy and Physiology*, 9, pp. 17-96.

Struthers, J. (1893) On the articular processes of the vertebra in the gorilla compared to those in man and on the costo-vertebral variation in the gorilla, *Journal of Anatomy and Physiology*, 27, pp. 131-138.

Thackeray, J.F., Braga, J., Treil, J., Nicksch, N. and Labuschagne, J.H. (2002) ‘Mrs. Ples’ (Sts 5) from Sterkfontein: an adolescent male?, *South African Journal of Science*, 98, pp. 21-22.

Toussaint, M., Macho, G.A. , Tobias, P.V., Partridge, T.C. and Hughes, A.R. (2003)
The third partial skeleton of a late Pliocene hominin (Stw 431) from Sterkfontein,
South Africa, *South African Journal of Science*, 9, pp. 215- 223.

Tredgold, A.F. (1897) Variations of ribs in the Primates with special reference to the
number of sternal ribs in man, *Journal of Anatomy and Physiology*, 31 (2), pp. 288-
302.

Trinkaus, E. (1986) The Neanderthals and modern human origins, *Annual Review of
Anthropology*, 15, pp. 193-218.

Vallois, H.V. (1965) Le sternum ne'anderthalien du Re'gourdou, *Anthropology
Anzeiger*, 29, pp. 273–289.

Voigt, E. (1983). *Mapungubwe: an archaeozoological interpretation of an Iron age
community*. Pretoria: Transvaal Museum (Monograph No. 1)

Walker, A. and Leakey, R. (Eds) (1993) The Nariokotome *Homo erectus* Skeleton,
Harvard University Press, Cambridge, 1993.

Walker, R. (1984) A guide to postcranial bones of East African mammals,
Hylochoerus Press. Norfolk, UK, 1984.

- Ward, C.V. (1993) Torso morphology and locomotion in *Proconsul nyanzae*, *American Journal of Physical Anthropology*, 92, pp. 291- 328.
- Ward, C.V. (2002) Interpreting the posture and locomotion of *Australopithecus afarensis*: where do we stand? *Yearbook of Physical Anthropology*, 45, pp. 185-215.
- Weissen, E. (2010) *Rib Morphology in Hominoids*, Masters Dissertation. Anthropological Institute and Museum, Universitaat Zurich, 2010.
- Weinstein, K.J. (2008) Thoracic morphology in Near Eastern Neanderthals and early modern humans compared with recent modern humans from high and low altitudes, *Journal of Human Evolution*, 54, pp. 287-295.
- White, T.D., Suwa, G., Richards, G., Watters, J.P. and Barnes, L.G. (1983) “Hominoid clavicle” from Sahabi is actually a fragment of cetacean rib, *American Journal of Physical Anthropology*, 61, pp. 239 – 244.
- White, T.D. (1991) *Human Osteology*, Academic Press, San Diego, 1991.
- White, T.D. and Arend Folkens, P. (1999) *Human Osteology (2nd edition)*, Elsevier Science & Technology Books, 1999.
- Williams PL (1995) *Gray’s Anatomy*, Churchill-Livingstone, London.

Williams, S.A., Ostrofsky, K.R., Frater, N., Churchill, S.E., Schmid, P. and Berger, L.R. (2013) Numerical composition and hyperlordosis in the vertebral column of *Australopithecus sediba*, *Science*, Vol 340 (12 April 2013)

Wolsan, M.1982 A comparative analysis of the ribs of ungulates for archaeozoological purposes. *Acta Zool. Cracov.* 26(6):167-228

Zihlman, A.L. (1984): Pygmy chimps, people, and the pundits. *New Scientist*, 104 (1430) November , pp. 39-40

Zipfel, B. (2004) *Morphological variation in the metatarsal bones of selected recent and pre-pastoral humans from South Africa*, Unpublished Ph.D. Thesis, University of the Witwatersrand, 2004.

Zipfel, B., DeSilva, J.M., Kidd, R.S., Carlson, K.J., Churchill, S.E. and Berger, L.R. (2011) The foot and ankle of *Australopithecus sediba*, *Science*, 333, pp. 1417 – 1420.

APPENDIX 1: Details of primate specimens utilised from South African

Collections (BPI = Bernard Price Institute; TM = Transvaal Museum)

	SPECIMEN NO.	SEX	AGE	SPECIES	REPOSITORY
1	74/73	Female		BABOON	BPI
2	AZ767		TM		
3	BPI/C 260		BPI		
4	Za 1363		Wits Comparative Lab		
5	Za 1364				
6	Za 1365				
7	Za 1454				
8	Za 1462				
9	Za 1463				
10	Za 1472				
11	58/72	Male			BPI
12	AZ191				TM
13	Za 107				Wits Comparative Lab
14	Za 113				
15	Za 1457				
16	Za 1458				
17	Za 1469				
18	Za 156				
19	Za 159				
20	Za 160				

	SPECIMEN NO.	SEX	AGE	SPECIES	REPOSITORY
21	BPI/4/1288	U		BONOBO	BPI
22	Za 1475	Female		CER AETHIOPS	Wits Comparative Lab
23	Za 1355			CHIMPANZEE	
24	Za 1354	Male			
25	Za 1071				
26	Za 1513				
27	AZ3004				
28	AZ1152	Female		GORILLA	
29	AZ1162				
30	BPI/C 544				BPI
31	Za 1311	Male			Wits Comparative Lab
32	Za 1312			Wits Fossil Lab	
33	Za 95			Wits Comparative Lab	
34	AZ1153		Female		ORANGUTAN
35	AZ1153				
36	Za 1334	M			
37	Za 106	Female		VERVET	Wits Comparative Lab
38	Za 128				
39	Za 788				
40	Za 798				

	SPECIMEN NO.	SEX	AGE	SPECIES	REPOSITORY
41	Za 799	Female		VERVET	Wits Comparative Lab
42	Za 821				
43	Za 823				
44	Za 880				
45	BP4 979	Male			BPI
46	Za 103				Wits Comparative Lab
47	Za 120				
48	Za 129				
49	Za 658				
50	Za 822				
51	Za 824				
52	Za 862				
53	Za 864				
54	Za 865				
55	Za 866				
56	Za 878				
57	A19342558	Female	50	EUROPEAN	Dart Collection
58	A23583319		50		
59	A24093275		21		
60	A24533300		47		

	SPECIMEN NO.	SEX	AGE	SPECIES	REPOSITORY	
61	A29304047	Female	49	EUROPEAN	Dart Collection	
62	A29464231		50			
63	A29574247		21			
64	A31294678		29			
65	A36036166		46			
66	A36836090		57			
67	A15572117		28	SOTHO		
68	A23543196		28			
69	A30574503		30			
70	A34595779		33			
71	A34985801		32			
72	A458527		24			
73	A866957		30			
74	A883985		27			
75	A923909		25			
76	A9531028		33			
77	A13021514		35			ZULU
78	A24043301		38			
79	A30624521		37			
80	A31244694		23			

	SPECIMEN NO.	SEX	AGE	SPECIES	REPOSITORY	
81	A31464712	Female	39	ZULU	Dart Collection	
82	A31574771		43			
83	A31624700		36			
84	A31964844		38			
85	A32444928		38			
86	A34505728		33			
87	A22213134		44			
88	A20312656	Male	45	EUROPEAN		
89	A21873106		31			
90	A24213142		44			
91	A24563567		49			
92	A24943441		43			
93	A27193632		44			
94	A29514296		40			
95	A30464485		32			
96	A36486675		42			
97	A39337176		48			
98	A14591934		29			SOTHO
99	A17852355		35			
100	A24313302		26			

	SPECIMEN NO.	SEX	AGE	SPECIES	REPOSITORY
101	A29334232	Male	29	SOTHO	Dart Collection
102	A31434530		30		
103	A33105385		37		
104	A33955591		39		
105	A33965592		44		
106	A34185556		30		
107	A34585765		40		
108	A20182659		30	ZULU	
109	A21672844		50		
110	A21732815		27		
111	A22813083		40		
112	A23033130		45		
113	A23193131		40		
114	A23223145		32		
115	A23233150		45		
116	A24993452		45		
117	A26533536		36		

APPENDIX 2: Details of non-primate specimens utilised from South African Collections (BPI = Bernard Price Institute; TM = Transvaal Museum)

	SPECIMEN NO.	SEX	AGE	SPECIES	REPOSITORY
1	212	M	Adult	Domestic Dog	BPI
2	213				
3	214				
4	215				
5	217	F			
6	218				
7	219				
8	220				
9	730	M			
10	936				
11	1042	F			
12	1181				
13	1465				
14	1466	M		Wits Comparative Lab	
15	1158				
16	4	M		Domestic Pig	BPI
17	10				
18	292				
19	294	F			
20	565	M			

	SPECIMEN NO.	SEX	AGE	SPECIES	REPOSITORY
21	685	F		Domestic Pig	BPI
22	88				Wits Comparative Lab
23	906				
24	907	M			
25	203				
26	254				
27	649	F		Spotted Hyena	
28	656				
29	732				
30	253	F		Leopard	
31	258	M			
32	101			M	Impala
33	102	F			
34	105				
35	389				
36	638				
37	711				
38	712	F		Wits Comparative Lab	
39	389	M			
40	1030	F			
41	1033				
42	1327	M			