A COMPARATIVE FUNCTIONAL ANALYSIS OF SPINOUS PROCESS, TRANSVERSE PROCESS AND ARTICULAR FACET MORPHOLOGY OF THE UPPER THORACIC SPINE IN EXTANT HOMINIDS AND FOSSIL HOMININS

by

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DECLARATION

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

C. Yelverton

14/12/2022

ABSTRACT

This study utilized three focus areas to evaluate and compare the variation in morphology of the spinous processes and articular facets of the upper thoracic spine (T1-T6) in African apes, contemporary humans, Later Stone Age (LSA) humans, baboons and fossil hominins, with the goal of finding and explaining potential functional differences. Further questions included if the spinous process deviations observed were specific to the structure or included changes to articular surface orientation and size (i.e., were changes noted only structural, or were there additional functional changes that occurred simultaneously).

A skeletal sample consisting of hominines—chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla*), LSA humans and contemporary humans—and baboons (*Papio ursinus*) were compared to each other (as examples of varying locomotor propensity or lifestyle) and to relevant fossil hominins including *Australopithecus africanus* (Sts 14), *Australopithecus sediba* (MH1 and MH2), *Australopithecus afarensis* (A.L. 288-1) and *Australopithecus prometheus* (StW 573). A novel process for photography of samples was established and demonstrated to be reproducible. Specimens were photographed and linear and angular measurements taken utilizing ImageJ software and non-metric visual observations.

Comparisons of hominines and baboons demonstrated statistically significant differences between species and sex. Spinous process deviations demonstrated a lower than anticipated overall incidence when evaluating the entire vertebrae sample, although the presence within an individual's sequence of T1-T6 was significantly higher and was more prevalent in males in all groups. Morphological presentations of spinous

process deviations were classified into five patterns based on the region of deviation identified. Age in the contemporary humans, and locomotor propensity when all selected primates were compared did not appear to have an impact on frequency of occurrence of this feature.

In relation to the comparison to fossil hominins, there did not appear to be sufficient consistency in presentation to allow for this feature to be proposed as a developmental feature in the upper thoracic vertebrae related to bipedalism. The LSA humans sample group demonstrated an increased likelihood of spinous process deviations in the upper thoracic vertebrae and may be related to lifestyle and activity levels that were significantly different to contemporary humans.

In summary, the study found morphometric measurements and spinous process deviation to relate more to species differences and sexual dimorphism than to locomotor differences, with lifestyle and activity levels in humans potentially increasing the frequency of spinous process deviations. It may be concluded that spinous process deviations are a consequence of various related factors that may interact in their development, or in many cases may be the result of random normal variations between individuals. Spinous process deviation in the upper thoracic vertebrae is therefore not a reliable indicator of postural or locomotor behavior in the extant comparative sample or in fossil hominins but may be an indicator of lifestyle and activity levels in humans.

DEDICATION

This research is dedicated to Caroline Yelverton. As my wife, partner for life and best friend, you are the one I shared this journey with. You have given me support, an ear to listen, an extra reader and a “kick in the butt” when I needed it. Being married to you has made me a better person, and I love you.

This is also dedicated to God, who has endowed me with so many gifts and talents that I probably don’t deserve. I will continue to use them to His purpose and glory.

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When thinking of embarking on the PhD journey, I was invited by Bernhard Zipfel to visit the Evolutionary Studies Institute (ESI) to see if any fossil vertebrae would be of interest to study as a chiropractor. I was privileged to meet with Scott Williams and Patrick Randolph-Quinney, and over coffee we discussed the spinous process deviations in U.W. 88-37 (which was recently discovered) and in other fossil hominins, and my interpretation from a clinical contemporary human perspective. And so, this research was conceptualized.

The following people contributed to this research and thesis, who I wish to acknowledge:

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

1.1 Background

The vertebral column plays a central role in posture, locomotion, and overall trunk stability, especially in hominins where the distinct role in force transmission and weight bearing is required to allow the upright torso to be balanced over two legs. The vertebral columns of hominoids are unusual among primates, as they have reduced numbers of lumbar vertebrae and an overall reduction in the thoracolumbar region (Schultz, 1961; Haeusler, 2002; Whitcome, 2012; Williams and Russo, 2015).

The human spine therefore has several specialized traits not seen in other mammals, including a sigmoid curvature, pyramidal configuration of articular facets that descend through the lower lumbar column and a wide curved sacrum (Latimer and Ward, 1993; Lovejoy, 2005; Ward and Latimer, 2005). These changes are also seen in extinct hominins to various degrees (Latimer and Ward, 1993; Lovejoy, 2005; Been et al., 2012; Williams et al., 2013; Williams et al., 2021). The upright posture required for bipedal locomotion in humans has been discussed as one of the causes of mechanical low back pain (Filler, 2007) and other pathologies such as spondylolysis (Ward and Latimer, 2005; Plomp et al., 2020) and scoliosis (Machida et al., 1999; Naique et al., 2003; Adam et al., 2008) which are not seen in the great apes. Non-specific low back pain in modern humans is reported to have a lifetime prevalence of 84%, and chronic low back pain 23% (Balague et al., 2012).

The morphology of thoracic vertebrae is proposed as an important aspect to determine the interrelationships between locomotor behaviour and trunk morphology (Kikuchi and Ogihara, 2021). Spinous process deviation is a morphological feature under consideration in the current study and may be the result of rotation of the entire vertebra or developmental asymmetry of the neural arch (Mellado et al., 2011). As presented by Plomp et al. (2019) paleontologists have attempted to reduce the amount of uncertainty in the evolution of bipedalism by determining potential adaptations for bipedalism in the skeleton of *Homo sapiens* compared to other primates through comparative analysis and enable easier recognition of bipedal taxa in the fossil records. Williams and Russo (2015) point out that the spine has been neglected in many of these studies, especially the upper thoracic region (Kikuchi and Ogihara, 2021).

The thoracic spine is considered a common site for normal skeletal and joint morphological variations (Edmonston and Singer,1997) and in a clinical setting, static palpation of the human spinous processes is utilized in manual therapy as a means of assessment and determination of where treatment interventions should be focused (Holmgren and Waling, 2008; Gross et al., 1996). The current study will therefore allow for additional information in this regard, in terms of frequency of spinous process deviations in contemporary human populations as a variant.

The study of pathological conditions in recent samples and the more distant past (paleopathology) is an important approach in determining how evolutionary changes may occur (Gilmour and Plomp, 2021), and spinous process deviations may be an example of a common occurrence in certain contemporary modern human pathologies. Plomp et al.’s (2015, 2019, 2020) work indicates that the evolution of bipedalism

predisposed humans to acquired spine pathologies, although research into the thoracic spine is limited. Ravichandran (1983) proposed that spinous process deviation may be seen in patients with lumbar spine disc protrusion, although Tang et al. (2015) found that spinous process deviation of the lumbosacral segments were common, but found no correlation to disc degeneration. In the cervical spine, MacPherson and Campbell (1991) evaluated C2 spinous process deviation (or asymmetrical prominence) in relation to the patient presenting with a migraine type headache and found the control and symptomatic groups had similar incidences, concluding that any association was incidental.

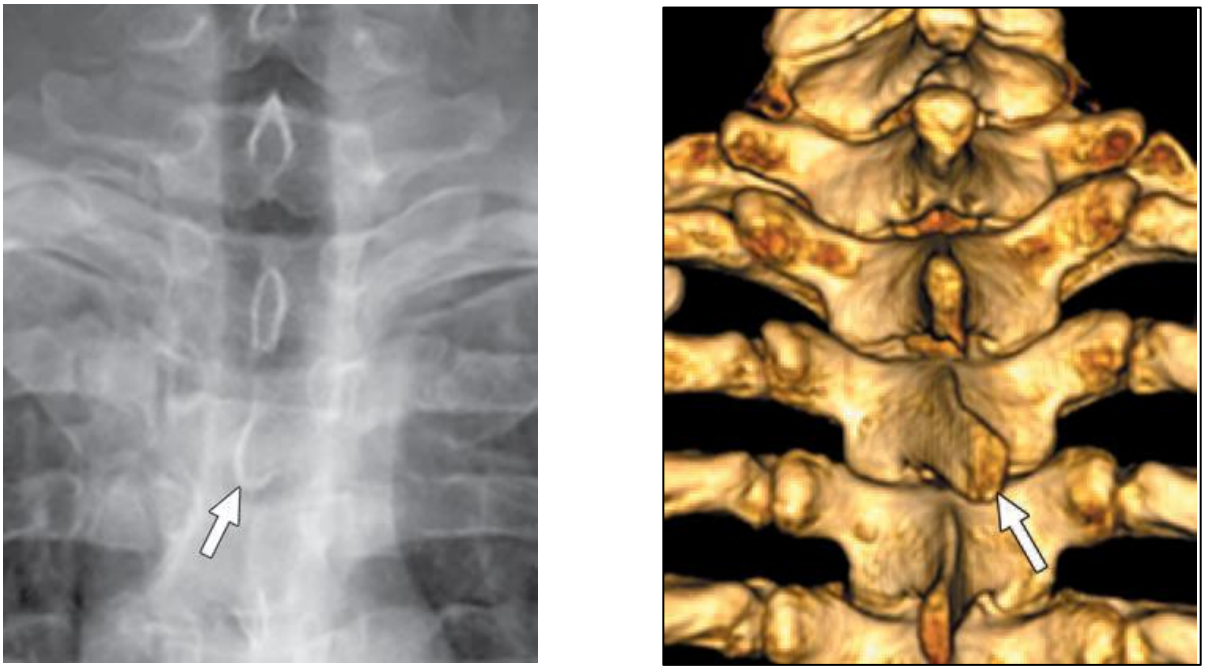
Lewit (1957) found that 80% of young adults presented with spinous process deviation and proposed that the deviations were a result of asymmetrical muscle pull, if one considers that they are muscle insertion points and the bone has plastic properties to load (Wolff, 1870). Four possible changes were noted:

a. Simple deviation as an anomaly in an individual (especially if multiple levels indifferent directions),
b. Deviation of the center of the spinous arch (i.e., root of the spinous process),
c. Deviation of spinous process with associated or combined signs of vertebral rotation (altered pedicle),
d. Change in axis of spinous process (i.e., deviation of several or all spinous processes from a certain point).

Van Schaik et al. (1989) describe spinous process deviation as the result of one or more of several possible causes; namely, rotation of the entire vertebrae (as in scoliosis), developmental asymmetry of the neural arch, or isolated deviation. Van

Schaik et al. (1989) concluded that the oval shadow seen on anterior-posterior radiographs is the tip of the spinous process (not the base) and was therefore not a reliable method of differentiating the three types.

Mellado et al. (2011) utilized multidetector computed tomography (MDCT) to identify variations in spinous process presentation and demonstrate isolated developmental spinous process deviation radiographically and on MDCT (Figure 1.1).



(A) (B)

Figure 1.1: Isolated deviation of dorsal spinous process in a 27-year-old man who was involved in a motor vehicle accident. A and B**,** anteroposterior radiograph: (A) and posterior coronal volume-rendered MDCT image: (B) shows developmental deviation of D3 spinous process (*arrow*). From Mellado et al. (2011).

Similarly, in the context of fossil hominins, variations in the morphology of the spinous processes have been observed and presented as a component of vertebral pathology (Randolph Quinney et al., 2016). Schiess et al. (2014) demonstrated that

previously described vertebral asymmetries thought to represent idiopathic scoliosis of the KNM-WT 15000 *Homo erectus* skeleton (Ohman et al., 2002) were normal vertebral variations.

Spinous process deviations have been reported in archaeologic and modern domestic dogs, and have been attributed to abnormal spine morphology, infection, taphonomic or post-depositional origin or life history (Lawler et al., 2016). Mechanisms such as these are relevant to the current study as plastic changes, those occurring during one's lifetime, may have an effect on morphology when evaluating Later Stone Age and contemporary humans as a result of different lifestyle activities.

The significance of these findings in relation to the evolution of bipedalism and the considerations of dexterity of the upper limb are proposed areas for investigation. They are proposed in the current study as a consequence of upright posture and functional dexterity while having comparative anatomy. A determination of the effects of functional changes and resultant muscular directional action on the development of spinous process and articular facet morphology (as found by Nalley et al., 2018) is considered.

Changes relating to the morphology of vertebrae are proposed to be a result of mechanical force changes due to bipedal locomotion. Muscles attaching to the upper thoracic vertebrae may alter force patterns on vertebrae and ultimately change the morphology of attachment sites (enthesis). In addition, muscles that attach these vertebrae to the scapula may have a similar effect, as the scapular form and position are adapted to different locomotor and postural (positional) behaviors (Schultz, 1961; Ashton and Oxnard, 1964; Lovejoy, 2005; Selby and Lovejoy, 2017). Specifically,

muscles attaching from the upper thoracic spine spinous processes of T1-T6 and to the upper limb or cervical spine such as trapezius, splenius cervicis, rhomboid major and minor, may have an influence.

1.2 Effects of muscle activity and function on bone morphology

Bone remodeling has been shown to create changes which are mechanically appropriate according to loading, known as Wolff's law, which states that natural healthy bones will adapt and change to the stress that it is subjected to and therefore the primary mechanism for bone adaptation is mechanical loading (Wolff, 1870; Enlow, 1962). This mechanical loading may also stimulate periosteal growth (Pearson and Lieberman, 2004).

Sharpey's fibers are responsible for anchoring of muscles to bone by passing through the periosteum (Benjamin et al., 2002). Mechanical stresses in the form of muscle force, may create changes in bony attachment points in more active muscles. The enthesis are regions in which tendons, ligaments and joint capsules attach to bone, with two types being identified, namely fibrous and fibrocartilaginous (Benjamin et al., 2002). When muscles' entheses are subjected to increased force of contracting muscles, blood flow to the periosteum increases, which can stimulate bone growth and increase size of attachments sites to strengthen them (Montgomery et al., 2005). Anthropologists have presumed that morphologic variations in long bones entheses result from frequent, strenuous, habitual activity, where muscle contractions are frequently recruited for limb movements (Schlecht, 2012). Karakostis et al. (2019) found that to have this effect on the enthesis, it requires repetitive muscle contraction with

rapid (high rate) and regularly repeated contraction, over a long period of time (although acknowledging that animal studies do not necessarily simulate real life function such as locomotor pattern).

Entheses are often used to infer cultural behaviour, technology use, labour difference or locomotion patterns (Molnar, 2010). Changes in muscle attachment morphology have been proposed to reflect differences in behavior and functional links to bony landmarks (hypertrophy of bone, in the form of a robust muscle attachment) may be the direct result of increased stress, and continual stress of a muscle in daily, repetitive tasks (Hawkey and Merbs, 1995; Mosley and Lanyon, 2002). Karakostis et al. (2019) identified patterns (in turkeys) involving three different entheses (associated with the gluteus primus, medial gastrocnemius, vastus medialis and adductor magnus muscles) and showed differences between controls from runners. They indicated that the differences were not seen when comparing groups within each of the three entheseal structures separately (although body mass was not correlated).

Karakostis et al. (2017) utilized the contemporary human Basel-Spitalfieldhoff collection, that has detailed occupational documentation such as jobs and position and life history such as genealogical medical and socioeconomic details and found a clear separation across individuals with distinct occupational characteristics.

Rabey et al. (2015) found predictors for changes in attachment site did not change significantly in mice with increased exercise and that gross morphology of entheses is less reliable than internal bone structure for inferring individual's past behaviour, but acknowledged that they only utilized voluntary activity levels for physiologically normal variations in the levels, and type of activity, age, body size and

muscle force on enthesis morphology with in primates and non-primate mammals would need to be considered. Wallace et al. (2017) also proposes that diaphyseal and trabecular structure may be more reliable as an indicator than entheseal morphology for inferring physical activity levels in humans, and Foster et al. (2014) indicate that other factors such as age, sex and genetics may also affect enthesis robusticity expression.

1.3 Forms of locomotion

Bipedal locomotion as an exclusive adaptation is unique to humans and other fossil hominins among primates (Prost, 1980; Schmitt, 2003; Lovejoy, 2004), and extant apes are commonly used as analog models of early hominin bipedalism (Pilbeam, 1996; Williams and Russo, 2015). When humans walk, the center of mass is at its lowest point at heel strike and rises to its highest point at midstance, and it is plausible that modern human gait may have developed from a stiff quadrupedal walking style, and the subsequent inverted pendulum like gait is considered an effective exchange of gravitational potential and kinetic energy (Lee and Farley,1998; Schmitt, 2003).

The majority of characteristics of gait have been associated directly or indirectly with the mechanical requirements for arboreal locomotion on thin flexible branches (Schmitt, 2003). The biomechanics of arboreal gait are considered by Preuschoft (2002) to differ little from those of terrestrial locomotion on horizontal substrates. This however changes with inclination of the substrate, where a body posture with the head upwards and tail downwards, results in increased body weight consistently acting on the hindlimbs. This may result in a functional division of labour, where the hindlimbs carry more body mass; while the forelimbs provide balance, and may be freed for other tasks,

such as investigating and manipulating objects, food intake and social behaviour. Structural strengthening of the hindlimbs may therefore be observed when comparing more terrestrial primates to arboreal primates (Kimura, 2002). Schmitt (2003) discussed various primate locomotor pattens, with apes (gibbons, orangutans, chimpanzees and gorillas) showing a wide range of locomotor modes such as acrobatic arm-swinging, quadrumanous climbing, quadrupedal knuckle- or fist-walking, and regular periods bipedal locomotion. The great apes (orangutans, chimpanzees and gorillas) show a wide variety of positional behaviors, with the most common being quadrupedalism when on the ground (Hunt, 2016). African apes (gorillas and chimpanzees) are considered plantigrade (placing the whole length of the foot, from heel to toe, on the ground); however, in human walking, the heel hits the ground before any other part of the foot while chimpanzees place the lateral midfoot on the ground at the same time as the heel (Vereecke et al., 2003).

Many factors such as body size, morphology, growth rates, neurological and neuromuscular development (including physical features and metabolic rates), as well as social, ecological and life history variables may influence the development of locomotor skills (Rasmussen and Tan, 1992). The great apes (orangutans, chimpanzees and gorillas) show a wide variety of positional behaviors, with the most common being quadrupedalism when on the ground (Hunt, 2016). Most characteristics of gait have been associated directly or indirectly with the mechanical requirements for arboreal locomotion on thin flexible branches (Schmitt, 2003). Doran (1997) found the ontogeny of locomotion in chimpanzee and gorillas differ in timing but was generally associated with increasing age and body size, with an increase in quadrupedalism

(leading to approximately 86% of locomotion being terrestrial knuckle walking quadrupedalism in gorillas) and a decrease in suspensory behavior, climbing, and bipedalism. As a result, chimpanzees utilize a wider range of habitual locomotor gaits, which would include bipedal and quadrupedal walking in trees and on the ground (Doran 1997; Pontzer, 2014).

The earliest hominins are speculated to have evolved between five and six million years ago in Africa (Ward et al., 1999) and include purported early hominins (*Incertae sedis*) such as *Ardipithecus ramidus* (White et al., 2015), *Ardipithecus kadabba* (Haile-Sellasie et al., 2004) and *Orrorin tugenensis* (Senut et al., 2001), with *Sahelanthropus tchadensis* (Brunet, 2002) potentially being older. These early hominins had primitive ape-like features such as small lower limbs (Richmond and Jungers, 2008) and vertebral joints (McHenry, 1991), curved fingers and toes (Stern and Susman, 1983) and relatively long upper limbs (McHenry and Berger, 1998). They also had derived human like features for bipedalism such as valgus knees and short and broad, laterally facing iliac blades (Schmitt, 2003; Lovejoy, 2005). It is proposed by Schmitt (2003) that early hominin bipedalism evolved in an arboreal, climbing primate, and the shift to a more robust modern skeleton in the genus *Homo* reflects an adaptation of the upright bipedal gait. Gebo (1996) and Richmond (2001) include a terrestrial quadrupedal (i.e., knuckle-walking) phase as part of hominoid evolution, prior to the adoption of bipedalism. Niemitz (2010) presented a review and synthesis evolution of upright gait and includes hypothesis such as watching out, freeing of the hands, throwing, infant carrying, reaching for food, carrying food, display, orthograde scrambling, scavenging, aquatic ancestor and thermoregulation as functional causes for

upright posture, but not necessarily for why this posture was maintained, and may be considered more ecological and behavioral than biomechanical hypotheses.

1.4 Spinal regions and vertebral formulae

The vertebral column in contemporary humans is divided into the cervical (7 vertebrae), thoracic (12), lumbar (5), sacral (5) and coccygeal regions (modally 4, sometimes 5) (Moore, 1992). In contrast most primates are described as having a formulation of 7:13:6 or 7:12:7 for the pre-sacral segments (Williams, 2011).

Quadrupedal mammals have spines that actively contribute to locomotion through sagittal plane flexion and extension during running and leaping (like many primates) and possess cranially positioned transitional vertebrae, and long post-transitional spines, that extend the region where sagittal movements can occur (Slijper, 1946; Hildebrand, 1959; Hurav, 1987). Great apes typically have 4 lumbar vertebrae (less commonly 3), resulting in dorsoventrally stiff vertebral columns adapted to suspension and other forelimb-dominated activities in large bodied primates (Schultz, 1961). Humans have a longer lumbar region as a result of increased flexion and extension ranges of motion, which allows for achieving an increased lumbar lordosis which is important for bipedalism (Lovejoy, 2005; Williams, 2012). Numerical variations exist between and within species due to selection—directional, relaxed, or stabilizing—and possibly other evolutionary forces like genetic drift, with western gorilla, humans and chimpanzees usually having 17 thoracolumbar vertebrae (Williams et al., 2019).

Table 1.1 below indicates the mean number of vertebrae and the common vertebral formulae for hominoid species specifically used within this study.

Table 1.1: Mean number of vertebrae (top row) and most common vertebral formulae (subsequent rows) observed for relevant species (adapted from Williams 2011; 2012).

Taxon	Cervical	Thoracic	Lumbar	Sacral	Frequency
H. sapiens	7	12	4.98	5.22	
	7	12	5	5	63.3%
	7	12	5	6	15.5%
P. troglodytes	7	13.1	3.66	5.71	
	7	13	4	6	32%
	7	13	4	5	21.3%
	7	13	3	6	14.4%
G. gorilla	7	13.04	3.55	5.60	
	7	13	4	5	24.5%
	7	13	3	6	21.9%
	7	13	4	6	16.6%

1.5 Normal spinal curvature

As an adaptation to upright posture and bipedal locomotion (and the need for altered weight bearing), the spine in hominins has developed secondary curves, namely the cervical and lumbar, as opposed to the singular kyphotic curve seen in most primates (Latimer and Ward, 2003; Lovejoy, 2005; Williams et al., 2013). While the center of gravity is shifted posteriorly to be over the pelvis and hips with this adaptation, it does alter the loading pattern on the vertebrae, specifically the dorsal components (zygapophyses, laminae and pedicles) as they are required to function in a weight bearing capacity (Davis, 1961; Pal and Routal, 1986; 1987; Shapiro, 1993; Whitcome et al., 2007). Been et al. (2017) identify three proposed spinal alignments for hominins, the sinusoidal alignment with moderate to high spinal curvatures and pelvic incidence found in *Homo erectus* and *Homo sapiens*, the straight alignment with small spinal curvatures and small pelvic incidence found in Neanderthal lineage hominins (NLH), and the compound alignment found in *Australopithecus* with moderate pelvic incidence and lumbar lordosis and a nearly straight cervical spine. This is illustrated in Figure 1.2.

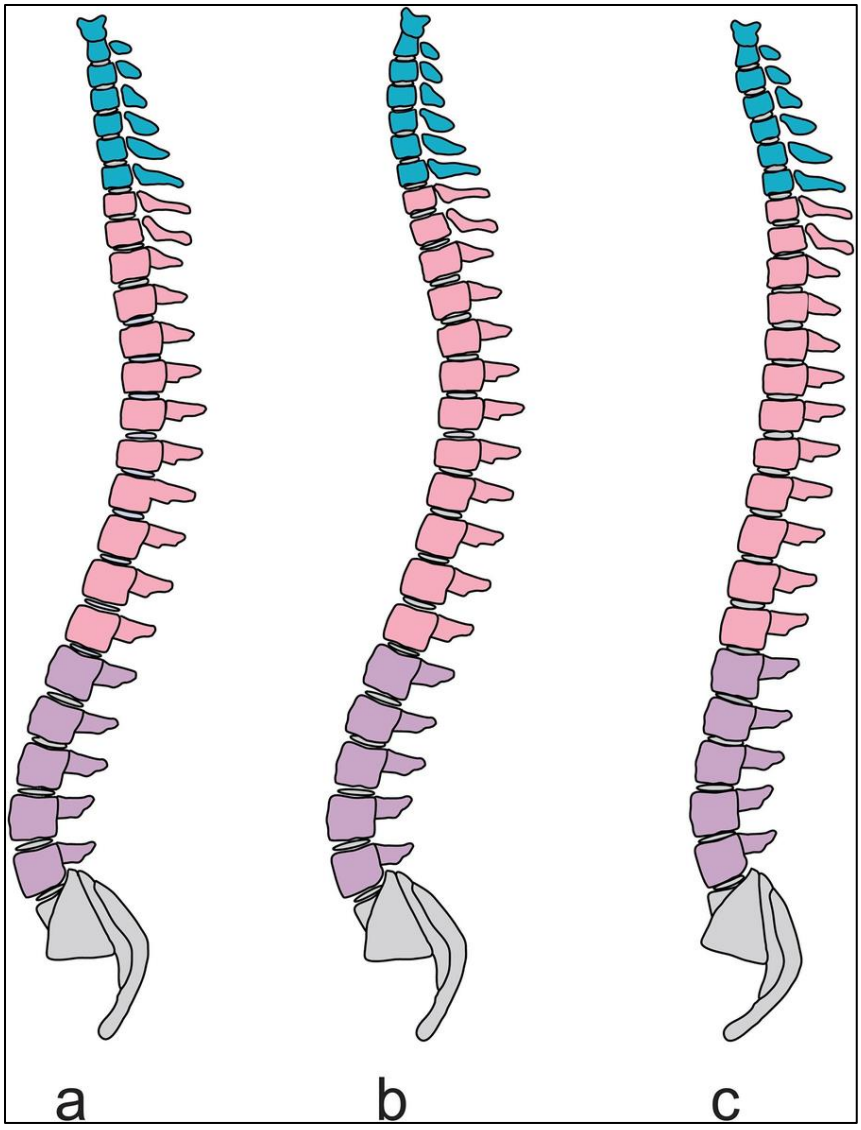


Figure 1.2: Schematic configuration of spinal curvatures in hominins. The compound alignment with moderate pelvic incidence and lumbar lordosis, and a nearly straight cervical spine (**a**). The sinusoidal alignment with moderate to high spinal curvatures and pelvic incidence (center, **b**). The straight alignment with small spinal curvatures and small pelvic incidence (**c**). Blue, cervical vertebrae; Pink, thoracic vertebrae; Purple, lumbar vertebrae; Grey, sacrum. From Been et al., (2017).

1.6 Thoracic vertebral anatomy

Moore (1993) describes the typical vertebrae as have the following anatomical regions and structures:

a. Vertebral body: this is the anterior component of the vertebra and is the main support for weight onto the vertebrae. The bodies increase is size from approximately T4, in order to support progressive weight.
b. Vertebral arch: this encloses the vertebral foramen and is formed by left and right pedicles (arising from the superior part of the posterior body) that join the laminae (extending posteromedially and slightly inferiorly) which combine in the median plane to form the spinous processes. The spinous process provides attachment to muscles and ligaments.
c. Transverse processes: these project from the junction of the pedicles and laminae (posterolaterally) and function as “levers” for the attachments of deep back muscles.
d. Articular processes (zygapophyses): arise for the junction of the pedicles and laminae, with superior and inferior processes projecting. Each process has an articular facet which articulates to form the facet or zygapophyseal joint, which restricts anterior movement of the superior vertebra relative to the inferior vertebra, and allows for some flexion, extension, lateral flexion and rotation, dependent on the facet orientation.

The thoracic vertebrae are characterized by the presence of costal facets (one or more on each side of the body) for articulation to the head of the ribs. The middle 4 thoracic vertebrae (T4-T8) are considered typical, with the T1-T4 being atypical as they

have some features of cervical vertebrae, and T9-T12 having some features of lumbar vertebrae. T1 has a complete facet for articulation to the first rib, with a demi-facet for articulation to the second rib, and a long almost horizontal spinous process. Figure 1.3 represents the features of typical *Homo sapiens* thoracic vertebrae.

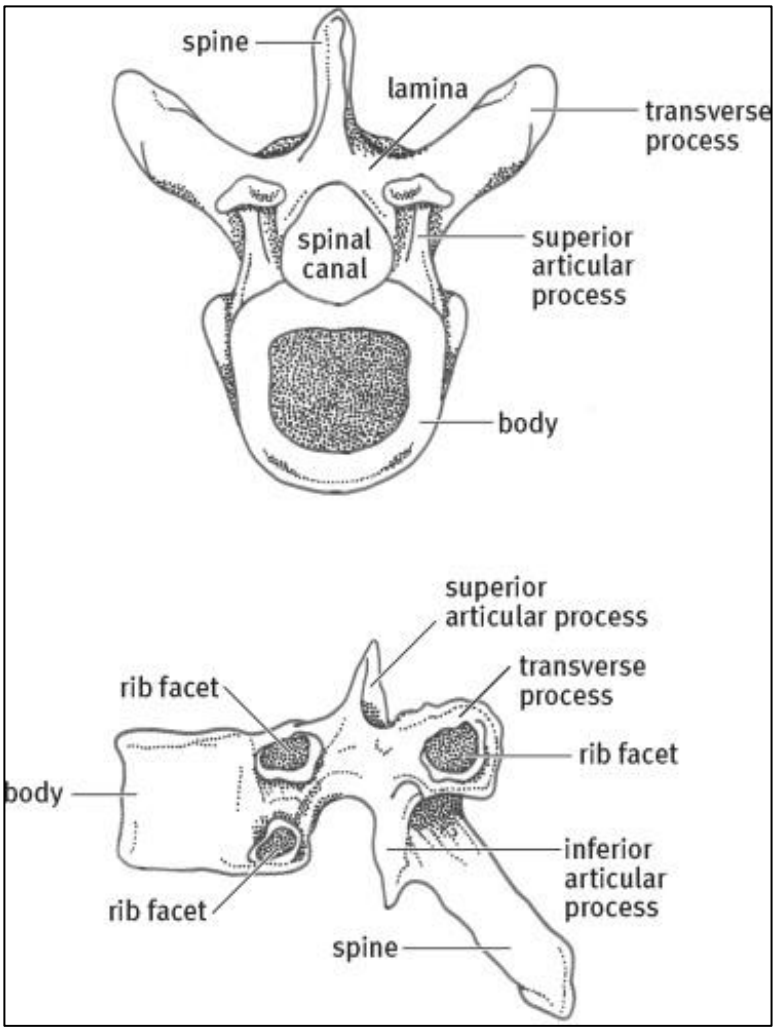


Figure 1.3: Typical *Homo sapiens* thoracic vertebrae. From Kayalioglu (2009).

1.7 Muscles of the back

The muscles of the back are divided into three groups, namely the superficial, intermediate (both considered extrinsic) and deep muscles (considered intrinsic).

1.7.1 Intrinsic muscles of the back

These are concerned with the maintenance of posture and movement of the vertebral column and head. These muscles are further subdivided into the superficial layer (splenius cervicis and capitis) an intermediate layer (erector spinae – composed or iliocostalis, longissimus and spinalis) and deep layer (semispinalis, multifidus and rotatores). Table 1.2 summarizes the individual intrinsic muscles. Actions are described based on human attachments, and comparison to relevant primates will also be presented.

1.7.2 Extrinsic muscles of the back

These muscles connect the upper limb to the trunk and are associated with movement of the limbs. They are further subdivided (in terms of muscles of the shoulder) into the superficial (trapezius and latissimus dorsi), deep (levator scapulae, rhomboids, and serratus anterior) and intrinsic (deltoid, supraspinatus, infraspinatus, subscapularis, teres major and teres minor). Table 1.3 summarizes the superficial and deep layers of the extrinsic muscles of the back, which have relevance to this study as they attach between the thoracic vertebrae and the upper limb and may therefore have an influence on the morphology of the vertebrae (Aiello and Dean, 2019). Actions described are based on human attachments, comparison to relevant primates are also presented.

Table 1.2: Intrinsic muscles of the back. From Moore (1993).

Muscle	Origin	Insertion	Innervation	Action
Splenius	Inferior half of ligamentum nuchae and spinous process of T1 to T6	Capitis: lateral aspect of mastoid process and lateral 1/3 of superior nuchal line Cervicis: posterior tubercle of transverse process of C1 to C4	Dorsal rami of inferior cervical nerves	Alone: laterally flex and rotate head and neck to same side. Together: extension of head and neck
Erector spinae	Common origin inferiorly to iliac crest, posterior sacrum, sacroiliac ligament, sacral and inferior lumbar spinous processes	Iliocostalis: angle of the ribs Longissimus: transverse processes of thoracic and cervical vertebrae, mastoid process of temporal bone Spinalis: spinous process of superior lumbar and inferior thoracic vertebrae		Together: extend the head and part or all of the vertebral column Alone: laterally flexes the head or part of the vertebral column
Semispinalis	Cervicis and thoracic: thoracic and cervical transverse processes Capitis: transverse processes of T1 to T6	Thoracic and cervical spinous processes superiorly Between superior and inferior nuchal lines on occiput	Dorsal rami of cervical nerves	Together: extend cervical and thoracic regions of the vertebral column Alone: rotate region to opposite side
Multifidus	Vertebral arch	Spinous process (spanning 1 to 3 vertebrae)	Dorsal rami of spinal nerves	Alone: lateral trunk flexion and rotation to opposite side Together: extend trunk and stabilize vertebral column
Rotatores	Transverse process of vertebra	Base of spinous process of vertebra superior to it	Dorsal rami of spinal nerves	Rotate superior vertebra to opposite side, stabilization

Table 1.3: Superficial and deep extrinsic muscles of the back. From Moore (1993).

Muscle	Medial attachment	Lateral attachment	Innervation	Action
Trapezius	Medial 1/3 of superior nuchal line, external occipital protuberance, ligamentum nuchae, spinous process of C7 to T12.	Lateral 1/3 of clavicle, acromion and spine of scapula	Spinal accessory nerve, C3 and C4	Elevates (superior fibers), retracts (middle fibers) and depress (lower fibers) scapula, superior and inferior fibers together rotate scapula.
Latissimus dorsi	Spinous process of inferior 6 vertebrae, thoracolumbar fascia, iliac crest, inferior 3 or 4 ribs	Floor of intertubercular groove of humerus	Thoracodorsal nerve (C6, C7)	Extend, adduct and medially rotate humerus, raises body towards arm in climbing
Levator scapulae	Posterior tubercle of transverse process of C1 to C4 vertebrae	Superior part of medial border of scapula	Dorsal scapula nerve (C5) and C3, C4	Elevates scapula and tilts the glenoid cavity inferiorly by rotating scapula
Rhomboid major and minor	Minor: Ligamentum nuchae and spinous process of C7 and T1 Major: spinous process of T2 to T5	Medial border of scapula from level of spine to inferior angle	Dorsal scapula nerve (C5)	Retracts scapula and rotates it to depress glenoid cavity; fixes scapula to thoracic wall

1.7.3 Comparative anatomy of muscles of the back

Direct comparisons of non-human to human primate muscles are not frequently presented (Benton, 1967; Swindler and Wood, 1982), and Diogo et al. (2017) present the variations in bonobos (*Pan paniscus*) with reference to chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*). Relative to the muscles presented, Table 1.4 is a summary of variations indicated by Diogo et al. (2017) with *Homo sapiens* comparisons from Moore (1993).

Table 1.4: Summary of variations in muscles between *Pan paniscus*, *Pan troglodytes* and *Homo sapiens* (adapted from Diogo et al., 2017; Moore, 1993).

Muscle	*Pan Paniscus*	*Pan Troglodytes*	*Homo sapiens*
Trapezius	Distal insertion to T9 spinous process	Distal insertion to variation from T8 to T13	Distal insertion to T12
Rhomboid	Medial insertion to spinous process of C3-T7 Additional rhombodius occipitalis may be present	Medial insertion to spinous process of C3-T8	Medial insertion from C7-T5 (if combined rhomboid minor and major, as they are not distinct in *Pan*.)
Levator scapulae	Posterior tubercle of transverse process of C1-C5	Posterior tubercle of transverse process of C1-C5	Posterior tubercle of transverse process of C1 to C4 vertebrae
Splenius capitis	Mastoid process of occipital bone to spinous process of lower cervical and first thoracic vertebrae	Mastoid process of occipital bone to spinous process of C5 to T4	Mastoid process to inferior half of ligamentum nuchae and spinous process of T1 to T6
Splenius cervicis	Transverse process of C1-C2 to T5-T7 spinous process	Similar to *P. paniscus*	C1-C4 posterior tubercle to T1-T6 spinous process
Semispinalis cervicis	Transverse process of T1-T4 to spinous process of C1-C6	Transverse process of T1-T4 to spinous process of C1-C6	Transverse processes on thoracic region to spinous processes in cervical region
Multifidus	Extending to C2 from sacrum (from lamina and spinous process)	Extending from C2 to sacrum (from lamina and spinous process)	Vertebral arch to spinous process

1.8 Regional factors that may influence thoracic vertebrae morphology

The following factors are proposed to have a potential effect on spine morphology in this study:

1. Thoracic shape related to bipedal posture
2. Musculature relating to the upper thoracic region
3. Basicranium and nuchal musculature

4. Shoulder girdle structure in humans and primates
5. Vertebral morphology related to bipedal posture

1.8.1 Thorax shape related to bipedal posture

Lovejoy (2005) proposes that one of the effects of upright posture was a decrease in erector spinae mass, with simultaneous “rigidification” or passive spinal immobilization to prevent buckling of the column. In addition, Schultz (1961) proposed when comparing invagination of the vertebral column into the thorax, that the position of the scapular axis is more mediolaterally orientated (than the anteroposterior oriented position in comparative Old-World monkeys), with a posterolateral repositioning of the scapula potentially resulting in muscular adaptation of the shoulder girdle. This is demonstrated diagrammatically in Figure 1.4.

1.8.2 Musculature relating to upper thoracic region

The erector spinae is a large muscle mass that is situated lateral to the multifidus. In the thoracic region specifically, it is known as iliocostalis thoracis (Bogduk, 1980). A significant decrease in the mass of these muscles in hominoids relative to Old-World monkeys is seen as a result of the rigid thoracic spine (Lovejoy, 2005) and is considered as result of invagination of the spine ventrally into the thorax (Figure 1.4), although some authors (Ward et al., 2018; Middleton et al.,2017; Shapiro & Russo, 2019) propose this to be due to selection against running and leaping and for forelimb-dominated locomotor behaviors such as suspensory behaviour and ape-like vertical climbing, where a long, flexible back would be susceptible to injury due to buckling.

Spinal invagination seems to have evolved in concert with rigidity and possibly also with dorsally-placed scapulae and wide iliac blades of the pelvis (see Ward et al., 2018; Middleton et al. (2017); Shapiro & Russo, 2019).

One of the effects of this rigidity is a resultant change in the vertebral morphology, specifically relating to muscle insertion regions. For example, the transverse processes in the lumbar spine are shifted dorsally in hominoids, and especially hominids, and provides enhanced leverage of epaxial muscles, while accommodating the decrease in muscle mass (Latimer and Ward, 1993; Shapiro, 1993).

In the current study the upper thoracic vertebrae (T1-T6) were selected as the functional relationship to muscle attachments of the cervical spine and shoulder girdle are important aspects that may alter loading of the vertebrae to their insertion sites.

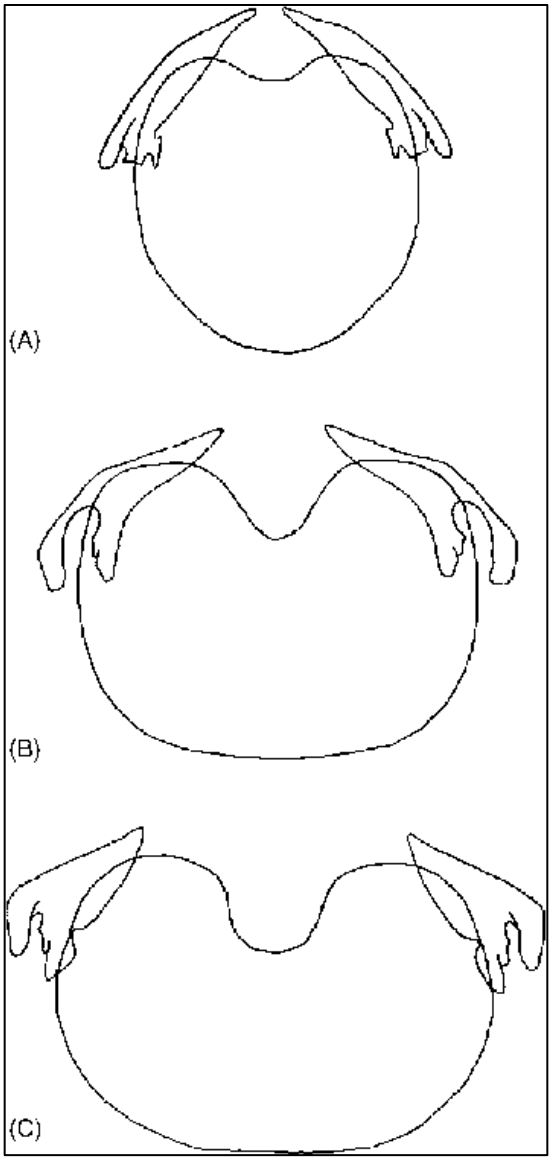


Figure 1.4: Invagination of the vertebral column into the thorax and its effect on both structural integrity and scapular position. (A) Old World monkey (OWM) (macaque); (B) chimpanzee; (C) human. The primary axis of the scapular blade in the monkey is nearly anteroposterior. In the two hominoids, the vertebral column has become invaginated into the thorax, greatly increasing its rigidity, and making it more elliptical. This has also caused the scapular axis to become more mediolaterally oriented. The invagination is more dramatic in the human because of lumbar lordosis. Thoraces redrawn from Schultz who traced plaster casts of eviscerated thoracic cavities. From Lovejoy (2005).

1.8.3 Basicranium and nuchal musculature

The cervical spine functions to allow for upper limb musculature attachments, transmission of mechanical load from head to trunk, maintaining visual field and natural head position, and a flexible platform for head mobility (Nalley and Gridder-Potter, 2019). As has been presented previously, posterior cervical musculature share connection between the cervical and upper thoracic spines, and as such, a consequent load on the thoracic spine exists to allow for cervical spine function.

Slijper (1946) investigated the presacral vertebral column in various species and developed several body-axis models. He also noted positive scaling of body size and spinous process size and proposed differences in spinous process length in humans, great apes and monkeys existed based on head posture and maintenance of head position. Schultz (1961) focused mainly on the thoracic and lumbar regions and noted the long spinous processes of great apes contrasted with the short processes of monkeys and humans, and were found to be highly variable across primates, especially in length and angle.

The head balancing model proposes that a first-class lever exists between the skull and cervical spine, with the fulcrum at the atlantoaxial joint. The downward force of gravity acts on the load arm (precondylar weight of the anterior skull), which are counteracted by the effort arm of the inferiorly directed forces of the nuchal muscles (Slijper, 1946; Jaanuson, 1987; Smit, 2002). This model proposes that a relationship exists between cranial shape and the cervical spine. An expectation is that an increase in anterior cranial length would correspond to an increased mass of the nuchal muscles, and attachment sites on cervical vertebrae (Nalley and Gridder-Potter, 2019). This is

demonstrated in Figure 1.5, with comparison to *Homo sapiens, Australopithecus afarensis*, and *Pan troglodytes*.

Axial movements have been shown to vary between locomotor mode (Dunbar, 2004; Dunbar et al., 2004; Hirasaki and Kumakura, 2004; Xiang et al., 2008; Dunbar et al., 2008). When humans and other primates walk slowly, the trunk remains stabilized (<20 degrees), but the head rotates more than 20 degrees, and in faster movements (such as quadrupedal gallop, and bipedal running), the trunk becomes less stabilized (Dunbar et al., 2004). Trunk movements therefore differ depending on locomotor mode and the position of the head depending on substrate orientation and the neck therefore provides compensatory movement between the two regions when transitioning from rest to various locomotor behaviours (Dunbar, 2004; Hirasaki and Kumakura, 2004; Xiang et al., 2008).

Humans are considered outliers in terms of orthograde neck position (Strait and Ross, 1999). Primates with pronograde head and necks exhibit increased mechanical advantage of deep nuchal muscles, along with craniocaudally long cervical vertebral bodies and coronally orientated facets, to facilitate lordosis curve formation (Slijper, 1946; Schultz, 1961; Arlegi et al., 2017; Meyer, 2016; Meyer et al., 2018). Associated research regarding this model has focused on the cervical spine but given the biomechanical linkage to the upper thoracic region, a compensatory loading change would be expected to be exhibited as the posterior neck musculature attaching to the spinous processes would alter potential load, and impact on the morphometric measurements both in terms of spinous process directly and indirectly to the articular facets.

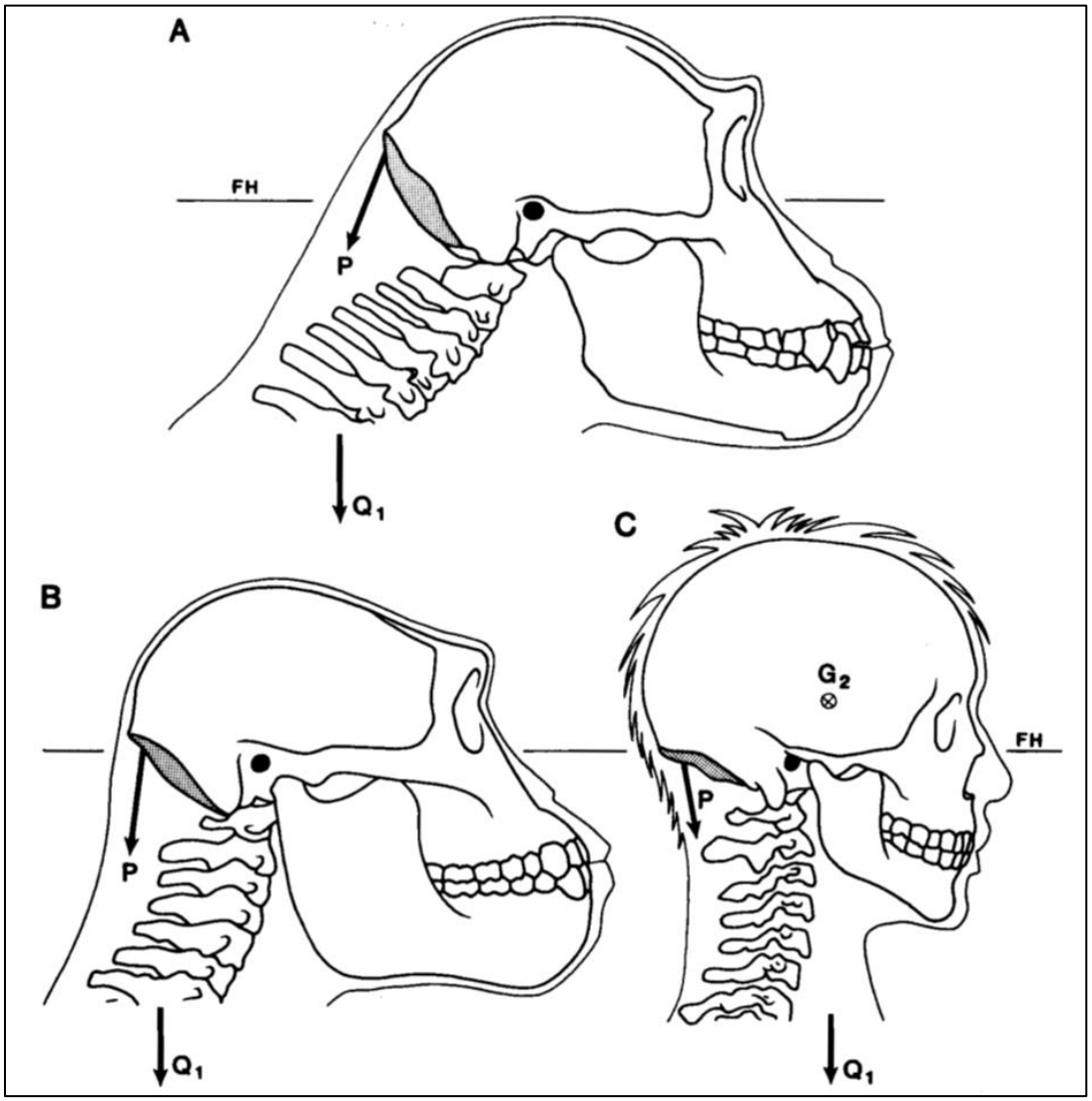


Figure 1.5: Diagrammatic drawings of the head and neck of (A) *Pan troglodytes;* (B) *Australopithecus afarensis*; based on the reconstruction of the skull by Kimbel *et al.* (1984); and (C) *Homo sapiens.* Not to scale. G2, centre of gravity of the head; Q1, gravity vertical of the whole body; P, approximate direction of the line of action of nuchal muscles. FH, Frankfurt Horizontal. The nuchal plane is stippled. The degree of forward inclination of the neck in *Australopithecus* is uncertain; in some reconstructions (e.g., Matternes in Johanson and Edey, 1981) a somewhat greater inclination is suggested. From Jaanusson (1987).

1.8.4 The shoulder girdle structure in humans and primates

Relative to the current study, the musculature attaching the scapula (as part of the shoulder girdle) to the upper thoracic spine is an important consideration. Scapular morphology corresponds closely with locomotor habits (Green and Alemseged, 2012; Green et al., 2012) varying in primates to the extent that the trunk is suspended by the arms during locomotion (Oxnard, 1967).

Hominoids share a shoulder girdle that is positioned on the back of the rib cage as opposed to its sides, allowing for greater range of motion (Schultz, 1961; Latimer and Ward, 1993; Lovejoy, 2005). Variations in human and ape shoulder girdles reflect their use during locomotion. A comparison of ape and human musculoskeletal structure of the shoulder girdle shows the same muscles are present. Due to the lever arm advantages producing upper limb movement, additional upper limb morphological differences are seen between humans and apes (Aiello and Dean, 1990).

Miller (1932) described the muscular anatomy of the pectoral girdle and correlated these to osteologic features related to mode of locomotion. Brachiating primates were found to show enhanced development of the muscles associated with upper limb elevation such as trapezius, levator scapulae, deltoid and supraspinatus, but also noted role in suspending the trunk below the supporting arm of muscles like pectoralis, latissimus dorsi, infraspinatus, and teres major.

Scapular shape varies in primates, dependent on locomotor behavior with aspects such as infraspinous fossa shape and breadth, glenoid size and angle, and overall blade characteristics, being utilized in comparative research, when determining locomotor adaptations in primates and fossil hominins (Green and Alemseged, 2012).

Larson (2007) discusses hominin shoulders, with changes in structure potentially being related to increased use of tools, and a change from the use of trees for refuge. It is also postulated that these may have facilitated the ability to throw and run, considered a factor in the survival and success of human lineage (Roach et al., 2013). A comparison of these lever arm forces between apes and humans, specifically on the spinous and transverse processes and articular facets, will be an aspect for consideration in the current study. As indicated below, loading patterns on bone may affect morphology.

1.8.5 Vertebral morphology related to bipedal posture

The morphology of vertebrae is proposed to be affected by function within primates. Slijper (1946) highlighted positive scaling of body size and spinous process length and proposed that differences existed based on head posture and maintenance of head position, as supported in the head balancing model (Slijper, 1946; Jaanuson, 1987; Smit, 2002). Schultz (1961) focused mainly on the thoracic and lumbar regions and noted that the long spinous processes of great apes contrasted with the short processes of monkeys and humans.

Shapiro and Simons (2002) found in *strepsirrhine* lumbar vertebral bodies and spinous processes that these morphologic differences are a complex result of the influences of primary locomotor behavior, habitual posture, body size, and phylogenetic history. Russo and Williams (2015) found similarities in lumbar vertebral morphology between Ailuropoda (giant pandas) and hominoids and suggest this provides evidence for morphological convergence on lumbar vertebral adaptations for their respective

positional behavioral repertoires that they share. They conclude that vertebral morphologies may have evolved for generalized orthograde behaviour. Similarly, it would be expected that the thoracic spine would demonstrate morphological changes with function, and as discussed, the shape of the thorax is different in primate species due to different positional behaviours (Schultz, 1961; Aiello and Dean, 1990; Lovejoy, 2005). Kikuchi and Ogihara (2021) found that in a comparison of hominoids, cercopithecoids, and platyrrhines the morphology of the upper thoracic vertebral appear to reflect functional adaptation to locomotor and postural modes and several morphology traits in vertebrae have been identified as being adaptations for bipedalism humans (compared to apes) and are summarized in Table 1.5.

In addition, Plomp et al. (2019) found that contemporary human thoracic and lumbar vertebrae (compared to the great apes) have the following proposed traits related to adaptations to bipedalism:

- vertebral bodies that are relatively tall and wide
- transverse processes that are relatively long and project more cranially and laterally
- vertebral foramina that are relatively wide
- pedicles that are relatively shallow (i.e., small in the dorsoventral direction)
- articular facets that are more coronally oriented
- laminae that are relatively deep (i.e., relatively large in the dorsoventral direction)
- spinous processes that are relatively short, more caudally directed, and more craniocaudally "pinched" at the tip.

Table 1.5: Identified traits in human vertebrae compared to apes as adaptation for bipedal posture (after Plomp et al., 2019).

Vertebral structure	Trait	Reference
Body	Ventrally wedged; the bodies of the lower lumbar vertebrae are dorsally wedged	Keith, 1923; Schultz, 1961; Shapiro, 1993; Abitbol, 1995; Ward and Latimer, 2005.
	Greater height in the craniocaudal direction	Latimer and Ward, 1993; Hernandez et al., 2009.
	Greater depth in the dorsoventral direction	Robinson, 1972; Latimer and Ward, 1993; Hernandez et al., 2009; Plomp et al., 2015; Meyer and Williams, 2019.
	Gradually increasing mediolateral width as one moves down the spine	Schultz, 1961; Rose, 1975.
Neural arch	Dorsoventrally longer, mediolaterally narrower, and craniocaudally shorter pedicles in the lower thoracic and upper lumbar vertebrae	Shapiro, 1993; Plomp et al., 2015; Williams et al., 2017.
	Mediolaterally wider pedicles in the penultimate and final lumbar vertebrae	Panjabi et al., 1993; Shapiro, 1993; Sanders and Bodenbender, 1994; Whyne et al., 1998; Briggs et al., 2004; Been et al., 2010.
Vertebral foramina	Mediolaterally wider than those of the great apes	Schultz,1930; MacLarnon, 1987; Sanders and Bodenbender, 1994; MacLarnon and Hewitt, 1999; Meyer and Haeusler, 2015.
Articular facets	Superior and inferior articular facets are coronally oriented in thoracic vertebrae (except the last one), while in apes these articular facets are obliquely oriented	Latimer and Ward, 1993; Shapiro, 1993a; Williams and Russo, 2015; Meyer et al., 2017.
	Superior and inferior articular facets of the final thoracic vertebrae of humans are coronally and sagittally oriented. The great apes are coronally and obliquely oriented	Latimer and Ward, 1993; Shapiro, 1993; Russo, 2010; Williams and Russo, 2015; Meyer et al., 2017.
	Superior and inferior articular facets of the lumbar vertebrae of humans are sagittally oriented, while those of the great apes are more obliquely oriented	Latimer and Ward, 1993; Shapiro, 1993; Russo, 2010; Williams and Russo, 2015; Meyer et al., 2017.
Transverse process	In the upper thoracic vertebrae of humans project cranially and laterally, in the apes project more dorsally	Jellema et al., 1993; Latimer and Ward, 1993; Been et al., 2012; Bastir et al., 2014, 2017.
	In the lower thoracic and lumbar vertebrae, transverse processes of humans are shorter and project more dorsally than those of apes	Jellema et al., 1993; Latimer and Ward, 1993; Been et al., 2012.
Spinous process	All the vertebrae are shorter from base to tip in humans than in apes	Schultz, 1961; Latimer and Ward, 1993; Gomez-Olivencia et al., 2013; Meyer, 2016; Meyer et al., 2017.
	Upper thoracic vertebrae of humans projects more caudally than those of apes	Latimer and Ward, 1993; Gomez-Olivencia et al., 2013.

The current study, which is supported by the research presented, assumes that locomotor behaviour repertoire in the species utilized influences the morphology of the structures being measured, namely the articular facets, and the spinous process.

1.8.6 Asymmetrical loading and degenerative changes of articular facets

Vertebral articular facets are associated with load transfer in the spinal column and restriction of motion (Shirazi-Adl, 1994). Constant increased mechanical load has the ability to alter the morphology of vertebral articular facets, as this load may result in degenerative changes (Adams and Hutton, 1980). Brown et al. (2008), specifically investigated if degenerative changes in human thoracic and lumbar facet joints are directly related to high levels of compressive load bearing. Their findings suggest that load transmission is mainly between the tips of the inferior articular facet and the laminae, and may result in bone change such as pitting, marginal osteophytes, bony contour change and eburnation, which are indicators of soft tissue change and indicate degenerative change.

Yong-Hing and Kirkaldy-Willis (1983) propose a three joint complex exists at a vertebral level, where the intervertebral disc (as a joint) and two facet joints have a biomechanical relationship and degeneration in one joint will progress to the other two joints. Conceptually this is supported by Zheng et al. (2022) in their systematic review which concluded that a link exists between lumbar facet tropism, degenerative disc disease and degenerative spondylolisthesis.

Lewit (1957) proposed that spinous process deviations may be a result of asymmetrical muscle pull, which would imply biomechanical differences in loading pattern on the articular facets as a structurally linked feature, with Van Schaik et al. (1989) considering SPD in the lumbar spine as a feature of degenerative arthritis. In the current study this may have an implication for the articular facets, as degenerative changes as described may be visible associated with SPD.

1.9 Summary and aims

In the current study, changes seen relating to the morphology of vertebrae, namely deviations in the spinous process and articular facet angle and width were proposed to be as a result of mechanical force alterations required for bipedal locomotion patterns. As presented, muscles attaching to the upper thoracic vertebrae, as the main anchor for the scapula and likely influenced by limb movement, may alter force patterns on vertebrae and ultimately change the morphology of attachment sites (namely the spinous process) or articular facets. In addition, muscles that attach these vertebrae to the scapula may have a similar effect, as scapula position is thought to be an adaptation to locomotor behavior. These factors may therefore allow for a discussion in terms of bipedalism and the presence of spinous process deviations and articular facet morphology relative to morphology changes previously described in primate vertebrae.

The overarching aim of the study was therefore to evaluate and compare the variations in the morphology of the spinous processes and articular facets of the upper thoracic spine in selected primates and fossil hominins, with the goal of determining if differences existed, and if they are result of locomotor behavior. Further questions included if the spinous process deviations seen were specific to the spinous process or include articular surface orientation and size changes (i.e., were changes noted only structural or were there additional indicators of functional changes that occurred simultaneously).

The study focused on three main areas:

a. Focus area one

A comparative analysis of contemporary human, selected African apes (*Pan troglodytes, Gorilla gorilla*) and baboons (*Papio ursinus*). This allowed for a determination of differences and variability of morphology measurements, subject to locomotor strategies.

b. Focus area two

A comparative analysis of fossil hominins, which allowed for a determination if differences and variability in the measured morphology existed when compared to contemporary humans and other selected primates.

c. Focus area three

To determine if differences in morphology and variability in measurements are noted in Later Stone Age compared to contemporary modern humans. This allowed for a determination of the potential effect of lifestyle and activity function on the morphometric measurements obtained.

The research questions proposed were:

1. Do locomotor strategy differences between contemporary humans and great apes have an impact on frequency and direction of upper thoracic vertebrae spinous process deviations?
2. Is the incidence and direction of upper thoracic vertebrae spinous process deviations linked to asymmetrical loading or age-related degenerative changes of the articular facets?

3. Is spinous process deviation in the upper thoracic vertebrae a potential indicator of bipedal posture and locomotor function, and is there a correlation between the selected primates and fossil hominins?
4. Do lifestyle and activity function differences between LSA and contemporary humans have an impact on the frequency and direction of upper thoracic spinous process deviations?

CHAPTER 2

MATERIALS AND METHODS

2.1 Introduction

This chapter outlines the process for the selection of groups under study, the specific methods utilized to obtain the morphometric measurements, and the statistical analysis applied. In broad terms, the study had three focus areas:

1. Comparison of features and measurements of T1 to T6 vertebrae in extant African great apes (gorillas and chimpanzees), an obligate quadrupedal taxon (chacma baboon) and contemporary humans.
2. Comparison of features and measurements of T1 to T6 vertebrae between Later Stone Age humans and contemporary human populations.
3. Comparison of select fossil hominin T1 to T6 vertebrae between other species and to contemporary humans.

2.2 Materials

2.2.1 Selection of sample groups

Several factors were used to determine which sample groups and specimens were suitable for inclusion in the study which are expanded on below.

a. Predominant locomotion strategy

As indicated in the literature review, spinous process deviations are noted in contemporary humans, and in limited hominin fossils. One of the concepts explored in

this research was to determine if this is a function of upright posture and the biomechanical adaptations required for this, in terms of altered muscle dynamics and potential changes to morphology that may occur.

For the purposes of the current study and to demonstrate locomotor propensity, African great apes, namely chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*) were used for comparison with the addition of chacma baboons (*Papio ursinus*) included as a pronograde Old-World monkey outgroup. Chimpanzees (*Pan troglodytes*) were utilized as an example of semi-terrestrial or mixed locomotion (Doran, 1992; Doran, 1993; Doran and Hunt, 1994; Doran, 1997; Sockol et al., 2007, Pontzer, 2014), gorillas (*Gorilla gorilla*) included as an example of predominant terrestrial locomotion (Doran, 1995; Doran, 1997; Doran and McNeilage, 1998) and baboons (*Papio ursinus*) as terrestrial quadrupeded comparison (Fleagle, 2013).

Relevant sample size and collection repositories utilized are indicated in Table 2.1. Only wild-collected animals were included in the chimpanzee, gorilla and baboon samples, as the restrictions of captive activity may alter behavioral patterns and may not be a true reflection of the species, which may in turn have an impact on morphological measurements (O'Regan and Kitchener, 2005; Courtney Jones et al., 2018).

A list of the chimpanzee, gorilla and baboon specimen numbers (including sex) are indicated in Appendix 1.

Table 2.1: Selected ape and pronograde obligate quadrupedal group size and collection repositories utilized.

Species	Sample size	Collection/Institution
Chimpanzee (*Pan troglodytes*)	n=45 (15 male/30female)	Powell-Cotton Museum, Quex Gardens, UK.
Gorilla (*Gorilla gorilla*)	n=60 (31 male/29female)	
Obligate pronograde quadrupedal comparison		
Chacma baboon (*Papio ursinus*)	n=51 (23 male/28 female)	Comparative Fauna Collection, School of Anatomical Sciences, University of Witwatersrand, South Africa.

b. Regions of the thoracic spine

As discussed in the literature review, comparative anatomy of the human and ape groups indicates a corresponding anatomy of the shoulder girdle and muscular articulation to the spine. The vertebrae selected for measurement and comparison in all groups were therefore T1 to T6, as these spinous processes have insertion areas for the associated shoulder girdle as the main anchor for the scapula and likely influenced by limb movement and cervical spine extension muscles (Slijper, 1942; Aiello and Dean, 1990; Kikuchi and Ogihara, 2021).

c. Human comparison

As presented in Chapter 1, the discussion related to deviations in the morphology of contemporary humans versus Later Stone Age (LSA) humans is important to determine if lifestyle has a potential impact on changes noted in morphometric measurements. For the purposes of this study, the LSA sample group utilized was from

Matjies River excavation, which is housed in the Florisbad Research Station, Human Remains, National Museum Bloemfontein, and is considered to be from the early Holocene period 9000 to 2000 BP (Sealy et al., 2006; L'abbe et al., 2008). As indicated by Sealy and Pfeiffer (2000), Stock and Pfeiffer (2003) and Sealy et al. (2006) the site is considered an important indicator of lifestyle and habits of early Holocene foragers. The sample size and collections utilized are indicated in Table 2.2.

Table 2.2: Human sample group size and collection repositories utilized.

Sample	Sample size	Collection/Institution
Later Stone Age Human (L' abbe et al., 2008)	n=8	Florisbad Research Station, Human Remains, National Museum, Bloemfontein, South Africa [data related to sex and age was not available]
Contemporary Human (Dayal et al., 2009)	n=58 (30 male/28 female)	Department of Human Anatomy and Physiology, Human osteology laboratory, University of Johannesburg, South Africa. Raymond A. Dart Collection of Human Skeletons, School of Anatomical Sciences, University of Witwatersrand, South Africa. [Data relating to sex and age was recorded].

Details of the contemporary human sample group are indicated in Appendix 2.

d. Fossil hominin

The impact of upright posture and the consequent potential for changes in morphologies measured (as a potential predictor for this locomotor pattern), required comparison with fossil hominins. Vertebrae from the upper thoracic region are not

common in the fossil records, and the following hominins were selected as they presented some preserved upper thoracic vertebrae. Table 2.3 summarizes the sample and collections utilized with referenced vertebral level confirmation.

Table 2.3: Fossil hominin sample group, specimen number, vertebral level and collection repositories utilized.

Fossil hominins				
Species	**Specimen number**	**Original Fossil material/cast**	**Vertebral level**	**Collection/Institution**
Australopithecus africanus	Sts 14m Sts 14i	Original fossil material	T5 T6 (Haeusler et al. 2002)	Ditsong National Museum, South Africa
Australopithecus sediba (MH1)	U.W. 88-11 U.W. 88-37	Cast	Upper thoracic Mid thoracic (Williams et al. 2018)	Evolutionary Studies Institute (ESI), University of Witwatersrand, South Africa.
Australopithecus sediba (MH2)	U.W. 88-188 U.W. 88-189	Original fossil material and 3D printed reconstructions from CT scan	Upper thoracic Mid thoracic (Williams et al. 2018)	Evolutionary Studies Institute (ESI), University of Witwatersrand, South Africa.
Australopithecus afarensis	A.L. 288-1ae	Cast	T6 (Cook et al. 1983)	Evolutionary Studies Institute (ESI), University of Witwatersrand, South Africa.
Australopithecus prometheus	StW 573	Original fossil material	Upper thoracic Mid Thoracic (Williams and Zipfel, from observation)	Evolutionary Studies Institute (ESI), University of Witwatersrand, South Africa.

e. Inclusion and exclusion criteria

The following inclusion criteria were applied to the selected specimens:

- All vertebrae of the T1-T6 sequence were intact, with no damage to the entire sequence. This was not applied to hominin fossil or LSA human specimens.
- For the contemporary human remains, information regarding sex were available. This was based on collection catalogue information as provided by related curators.
- In the case of contemporary humans and baboons (where specimens were readily available) skeletally mature samples were used. This was not applied to chimpanzee, gorilla, LSA human or fossil hominin samples due to limited available samples.
- Pathology demonstrated was not considered an exclusion criterion but was noted for discussion as applicable.
- If original fossil material was not accessible, suitable high-quality casts demonstrating sufficient attributes of fossils hominins were utilized, as presented in Table 2.4.
- Available fossil material was evaluated and excluded if they were not considered to be from the upper or mid thoracic region. This was based on current literature and analysis by the researcher and supervisors should this information not have been available. Table 2.5 indicates the fossil hominin specimens evaluated and excluded from the study based on this criteria.

Table 2.4: Excluded fossil hominin specimens.

Hominin fossils			
Species	**Specimen number**	**Original Fossil material/cast**	**Reason for exclusion**
Australopithecus africanus	Sts 14p Sts 14n	Original fossil material	Only vertebral body present. Only posterior arch noted, with right TVP broken, left inferior facet not full.
Homo naledi	U.W. 101-855	Cast	T10 vertebra (Williams et al, 2017).
Australopithecus sediba (MH2)	U.W. 88-190 (MH2) U.W. 88-191 (MH2)	Original fossil material and 3D printed reconstructions	Mid-low thoracic. Mid-low thoracic (Williams et al, 2018).
Australopithecus africanus	StW 431	Original fossil material	Levels below T6 (Haeusler, 2002).
Australopithecus africanus	StW H8/H41	Original fossil material	Lumbar vertebrae (Sanders, 1998).

f. Permission and ethical considerations

Permission was applied for and granted for access to the relevant collection repositories as summarized in Table 2.6.

Table 2.5: Summary of access granted to relevant collection repositories.

Collection	**Contact person**	**Ethical approval**
Powell-Cotton Museum	Dr Inban Livne, Head of Collections, Powell-Cotton Museum, United Kingdom	N/A
Comparative Faunal Collection	Dr Brendon Billings, Curator RA Dart Collection of Human Skeletons, University of Witwatersrand, South Africa	N/A

Raymond A. Dart collection of human skeletons	Dr Brendon Billings, Curator RA Dart Collection of Human Skeletons, University of Witwatersrand, South Africa	Ethics waiver approved by School of Anatomical Sciences (W-CBP-220504-01)
Human anatomy osteology collection, University of Johannesburg	Prof Shahed Nalla, Head of Department of Human Anatomy and Physiology, University of Johannesburg	Ethical approval from Faculty Research Ethics Committee (REC-01-14-2020)
Evolutionary Studies Institute, Hominin Collection, University of Witwatersrand	Dr Bernhard Zipfel, Curator, ESI	ESI fossil access advisory panel approval
Florisbad human remains	Dr Daryl Codron, Specialist Museum Scientist, Florisbad Quaternary Research Department, South Africa	Approved by Department

2.3 Methods

The following specified methodologies were applied to all specimens to ensure consistency of images and measurements. Subsequent analysis was performed on each photograph.

2.3.1 Photographic Methodology

Each specimen was photographed utilizing the same parameters to ensure consistency of images and measurements.

a. Process

For the purposes of the current study, each vertebra was required to be photographed from a lateral view (Figure 2.2), inferior view (Figure 2.3) and superior view (Figure 2.4).

b. Light box and foam block system

To accommodate the various bony processes emanating from the vertebra, and allow for reproducible images, each specimen was required to be placed perpendicular to the camera lens and a custom-made foam block system was therefore created and utilized (Figure 2.1).

Figure 2.1: Foam block system utilized to photograph specimens. a: information tag; b: incision to accommodate articular/transverse process; c: scale bar; d: cutout to accommodate spinous process; e: spirit level.

The foam block had incisions (Figure 2.1, point “b”) made to accommodate the transverse processes or articular processes of the vertebrae and allowed for true lateral images to be obtained. The same incision was utilized for inferior views, where the superior articular processes were placed in the incision. This allowed for a method of stabilizing the specimen in a reproducible manner, with minimal pressure to avoid any damage to specimens utilized.

Similarly, for the superior views a cutout in the foam was made to accommodate the spinous process (and angle), allowing the vertebral body to rest supported on the foam itself (Figure 2.1, point “d”).

A scale bar was included for all images, as was an information tag that included date, image, specimen, sex, and specimen number (Figure 2.1, point “a” and “c”).

A custom fashioned light box with LED lighting that surrounded each specimen was utilized to ensure uniformity of light and avoid shadowing that could obscure are alter morphology and measurements. This system was designed to be collapsible and portable to allow for reproduction of the photographic techniques at the various locations required. An illustration of this lightbox and camera combination is included in Figure 2.2.

c. Camera settings

A Nikon D3200 digital single reflex camera was used with a 55mm focal length, shutter speed of 1/100s and f stop 5. The camera was set on a tripod over the light box, with a spirit level used to ensure the camera was horizontal for all images. The camera was not moved for the image sequences; only the foam block was adjusted as required.

Figure 2.2: Example of light box and camera utilized, illustrating photography of specimens.

d. Specific image description

Image 1 and 2 (lateral view)

Each vertebral specimen had a left and right lateral image taken. To place the vertebrae in the foam block and ensure no damage would occur to the specimen, the incision was opened by hand, and the transverse process gently inserted into the incision and the foam released to support the vertebra. While observing the image

through the camera view finder, the vertebra was adjusted until the intervertebral foramen of the left and right sides were visualized equally. This ensured a true lateral view of the vertebrae, perpendicular to the camera lens and sensor. The focal point was on the proximal part of the inferior articular process.

An example of a lateral image is indicated in Figure 2.3.

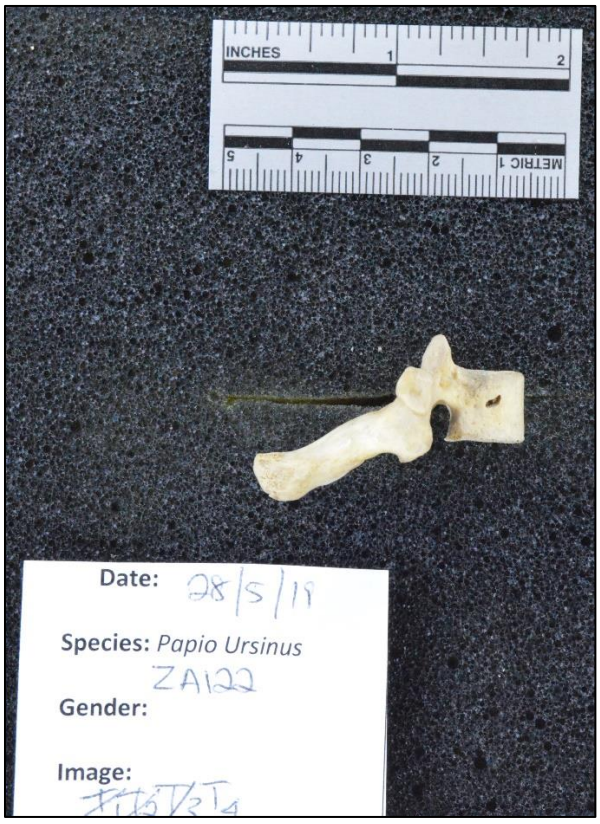


Figure 2.3: Example of lateral view image of *Papio ursinus* 4th thoracic vertebra.

Image 3 (inferior view)

Each vertebral specimen had an inferior view image taken. The superior articular processes were inserted into the opened incision in the foam block and then released to support the vertebra. A spirit level was placed on the inferior surface of the vertebral body and the specimen adjusted until horizontal (and therefore aligned to the leveled

camera sensor). The focal point was on the convergence point of the lamina closest to the camera.

An example of an inferior view image is indicated in Figure 2.4.

Figure 2.4: Example of inferior view image of *Papio ursinus* 4th thoracic vertebra.

Image 4 (superior view)

Each vertebral specimen had a superior view image taken. The spinous process was placed in the cutout of the foam block with the articular processes below the top of the foam. A spirit level was placed in the superior surface of the vertebral body, and the specimen adjusted until horizontal, and therefore aligned to the leveled camera sensor. The focal point was on the convergence point of the lamina.

An example of the superior view image is indicated in Figure 2.5.

Figure 2.5: Example of superior view image of *Papio ursinus* 4th thoracic vertebra.

2.3.2 Measurement methodology

ImageJ (version 1.53e, NIH, USA) was utilized to measure various morphometric measurements as indicated below. This is an open-source image programme designed for image processing and analysis. ImageJ was found to be a valid and reliable tool when compared to goniometric analysis with an Interclass Correlation Co-efficient of 0.89 (Roush, Bustillo and Low, 2008).

The following morphometric measurements were taken for each view:

- Superior view:
    - Central spinous process deviation (this is a component of spinous process deviation, region and direction: SPDRD)

- Region of spinous process deviation (this is a component of spinous process deviation, region and direction: SPDRD)
- Dorsoventral superior articular facet width (SAFW)
- Dorsoventral superior articular facet orientation (SAFO)

- Inferior view:
  - Dorsoventral inferior articular facet width (IAFW)
  - Dorsoventral inferior articular facet orientation (IAFO)
- Lateral view:
  - Spinous process length (SPL)
  - Craniocaudal spinous process angle (SPA)

a. Superior view measurements definitions and methods

Specific definitions and descriptions of morphometric measurements from the superior view image are visually represented in Figure 2.6 and defined in the description to follow.

Central spinous process deviation

This measurement was a non-metric visual determination of spinous process deviation noted, relative to the sagittal midline of the vertebra (represented in Figure 2.6 by the green line). This is a component of the spinous process deviation, region and direction (SPDRD) as presented in the results and discussion.

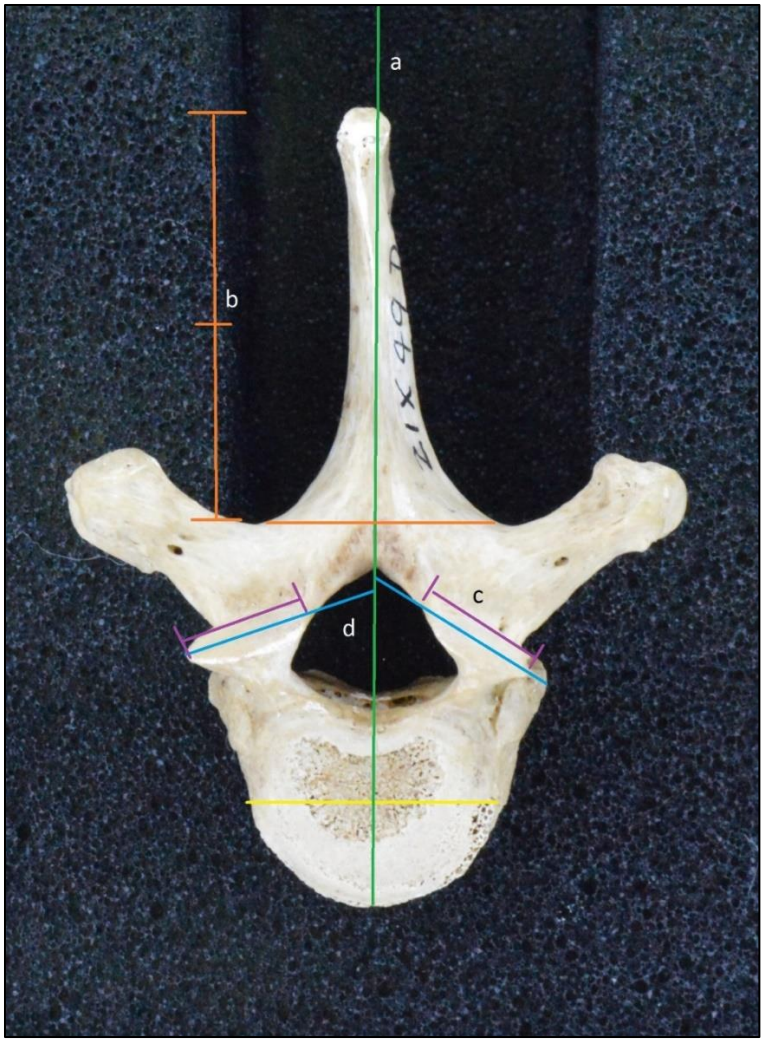


Figure 2.6: Morphologic measurements taken from superior view image. a: central spinous process deviation (green line: sagittal midline of vertebra); b: region of spinous process deviation (red line); c: dorsoventral superior articular facet width (purple line); d: dorsoventral superior articular facet orientation.

Region and direction of spinous process deviation

This is a non-metric visual determination of the region and direction of deviation (when these were identified). The line (based on the sagittal midline of the vertebra and represented in Figure 2.6 by the red line) extended from the dorsal end/tip to the base of the spinous process (where the lamina converged). The midpoint of this line was utilized to visually determine if the occurrence of deviation was either at the proximal or

distal components of the spinous process, and either right or left. This was used in conjunction with central spinous process deviation, to determine SPDRD, where a visual allocated was made of “1” for no deviation, “2” for distal left deviation, “3” for distal right deviation, “4” for proximal left deviation and “5” for proximal right deviation was determined.

Dorsoventral superior articular facet width (superior facet width – SFW)

This was a metric measure (in mm) of the superior articular facet dorsoventral width (represented in Figure 2.6 as point “c” and the purple line). The image was calibrated in ImageJ to the measurement key and measured from the most medial to most lateral border of the articular process (Williams et al. 2018).

Dorsoventral superior articular facet orientation (superior facet orientation – SFO)

This measurement was defined as the ventral angle, in the transverse plane, between the lines parallel to superior articular facet surface (medial and lateral edges), and the sagittal mid plane of the vertebral body (Williams et al. 2018) and is depicted in Figure 2.6 (angle “d”). The central spinous process deviation line as described, was utilized again as the reference for the articular angle. The line drawn from the dorsal surface of the superior articular facet (represented by the blue line) was extended to intersect the central spinous process deviation line (represented by the green line) with the ventral angle produced measured in degrees with ImageJ.

Measurements of the left and right angles were recorded for comparison purposes.

b. Inferior view image definitions and measurements

Specific definitions and descriptions of morphometric measurements from the inferior view image are visually represented in Figure 2.7 and defined in the descriptions to follow.

Dorsoventral inferior articular facet width (inferior facet width – IFW)

This was a metric measure (in mm) of the inferior articular facet dorsoventral length (as indicated in Figure 2.7, represented by the purple line). This image was calibrated to the key in ImageJ, and the measurement taken from the most medial to most lateral end of the articular process (Williams et al. 2018).

Dorsoventral inferior articular facet orientation (inferior facet orientation – IFO)

This measurement was defined as the angle, in the transverse plane, between the lines parallel to inferior articular facet surface (medial and lateral edges), and the sagittal mid plane of the vertebral body (Williams et al. 2018) and is depicted in Figure 2.7. The central line spinous process deviation line (represented by the green line) was utilized again as the reference for the articular angle. The line drawn from the ventral surface of the inferior articular facet was extended to intersect the central vertebral line and the ventral angle (represented by the blue line and angle “a” in Figure 2.7) produced measured in degrees with ImageJ.

Measurements of the left and right angles were recorded for comparison purposes.

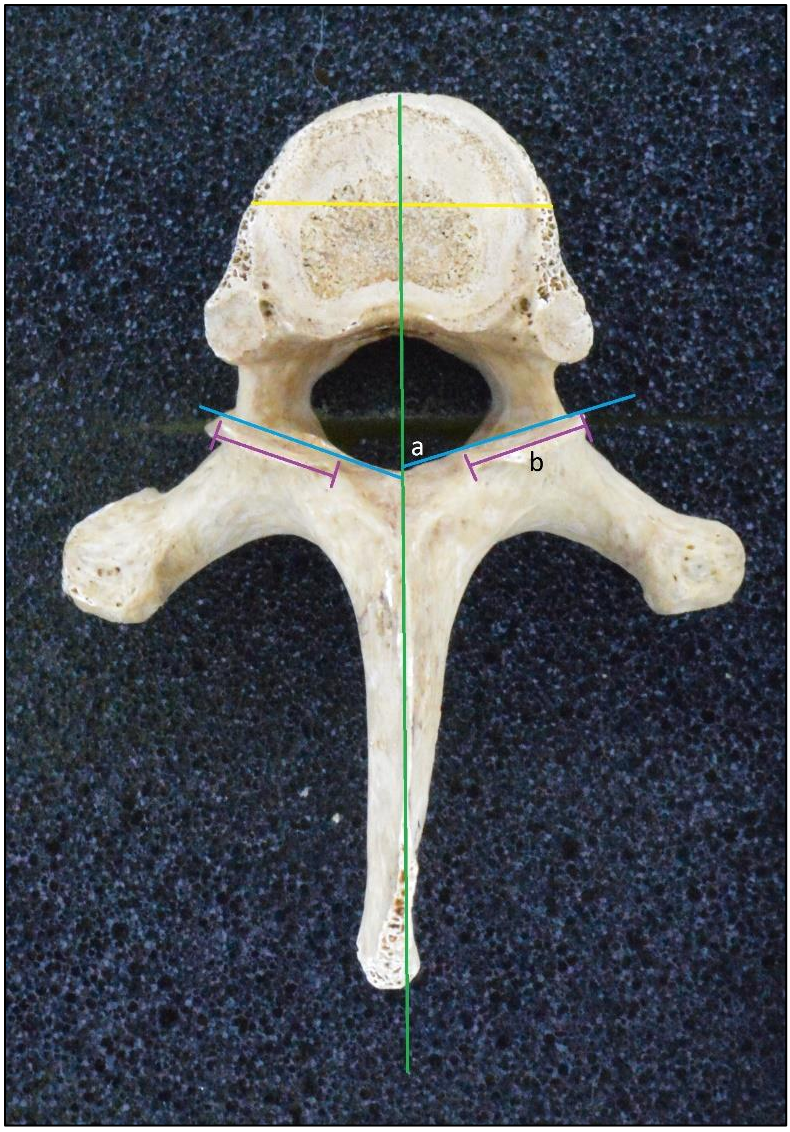


Figure 2.7: Morphologic measurements from inferior view image. a: dorsoventral inferior articular facet orientation; b: dorsoventral inferior articular facet width.

c. Lateral view image definitions and measurements

Specific definitions and descriptions of morphometric measurements from the lateral view image are visually represented in Figure 2.8 and defined in the descriptions to follow.

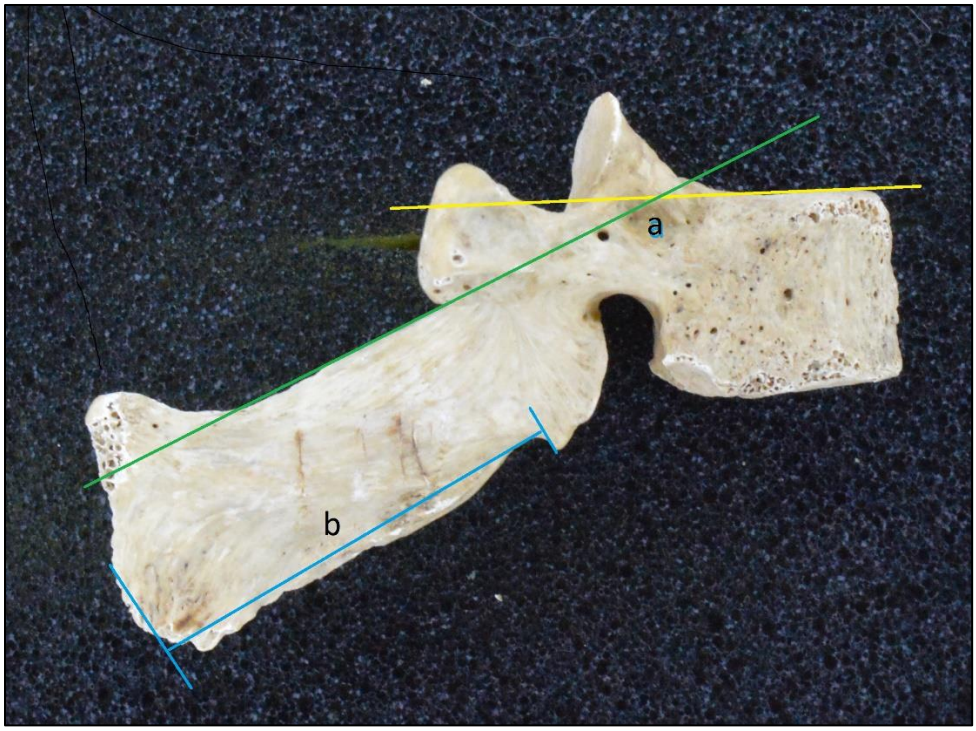


Figure 2.8: Morphologic measurements from lateral view image. a: craniocaudal spinous process angle; b: spinous process length.

Craniocaudal spinous process angle (spinous process angle – SPA)

As indicated in Figure 2.8, this was defined by Bräuer (1998), as the inferior angle (point “a") created between the extended line from the superior border of the spinous process (represented by green line), and the superior surface of the vertebral body (represented by the yellow line) and measured utilizing ImageJ. The superior border of the spinous process was determined by selecting a point on the origin of the spinous process superior surface and extending this to follow the superior border of the structure. The superior border of the vertebral body was determined by selecting the anterior point of the vertebral body, and the continuing the line along the body border, and then extending this to intersect with the extended line of the spinous process.

Spinous process length (SPL)

This was the physical measurement of the spinous process length (in mm), from the posterior aspect of the inferior articular process to the end of the spinous process, following the inferior margin of the process (represented in Figure 2.8 by the blue line). The image was calibrated to the key in ImageJ prior to measurement.

2.3.3 Reproducibility of measurements

Reproducibility testing was performed on the measurements to facilitate confidence in values obtained, by analysis of repeated measures, similar to the methods proposed by Neubauer (2009). The researcher took photographs of a single T3 specimen on 10 separate occasions, with multiple measures taken from each image. In addition, the researcher used a single sample, and measured these on 3 separate occasions, followed by the measurements as indicated being conducted. These were then compared utilizing the T-test. Metric measurements were compared to corresponding caliper measurement of the physical specimen. All values indicate $p>0.05$, indicating good confidence in measurement reproducibility, and low intra-observer error. Table 2.7 summarizes the results for each measurement.

Table 2.6: Summary of T-test results for reproducibility of measurements.

View	Measurement	p value for photographic measurements comparison	p value of caliper measurement comparison
Right lateral	Spinous process length	0.49	0.23
	Craniocaudal spinous process angle	0.33	N/A
Inferior	Right dorsoventral inferior articular facet width	0.21	0.35
	Left dorsoventral inferior articular facet width	0.37	0.07
	Right dorsoventral inferior articular facet orientation	0.2	N/A
	Left dorsoventral inferior articular facet orientation	0.18	N/A
Superior	Right dorsoventral superior articular facet width	0.47	0.25
	Left dorsoventral superior articular facet width	0.14	0.15
	Right dorsoventral superior articular facet orientation	0.44	N/A
	Left dorsoventral superior articular facet orientation	0.1	N/A

2.3.4 Analysis of data

a. Descriptive statistics and frequencies

Descriptive statistics and frequencies were utilised for all measurements to explore the nature of the variables measured and describe the characteristics of the sample groups (Pallant, 2007). These included analysis and presentation of:

- Frequencies of spinous process deviation (counts and percentages) within each sample group per species separately and then also per species and split by sex.
- Morphometric measurements and SPDRD frequencies, means, maximum/minimum, standard deviations. These were conducted initially within each species and per vertebral level, followed by within each species per vertebral level with a split per sex.
- Any relevant pathologies or anatomical variations identified for descriptive analysis or comparison.

b. Tests for normality

Normality was tested using the Kolmogorov-Smirnov (if the sample size was 50 or greater) and the Shapiro-Wilk (if the sample was less than 50) tests (Mishra et al. 2019). If $p \geq 0.05$ (a non-significant result), data were considered normally distributed and if $p < 0.05$ (a significant result) not normally distributed (Mishra et al., 2019). Testing was performed (with histogram presentation and analysis of kurtosis /skewness) on morphometric measurements and SPDRD per species and vertebral level, followed by per sex, and finally per sex within species (Tabachnick et al., 2007; Mishra et al. 2019).

c. Independent-samples T-test and analysis of variance (ANOVA)

As the results of normality testing were predominantly normally distributed ($p \geq 0.05$) and because parametric tests are quite robust against deviations from normality (Mishra et al., 2019), parametric analysis utilising the T-test for differences between two groups and analysis of variance (ANOVA) testing for differences between three or more groups were performed. In the case of ANOVA, the Robust Tests of Equality of Means were used where the homogeneity of variance assumption was violated (Pallant, 2007).

d. Post-hoc comparisons

Post-hoc testing was performed on the ANOVA results with a Bonferroni adjustment/test and a refined p-value against a significance level of 0.0125 (0.05/4), as there were four species that were compared (Lee and Lee, 2018). Homogeneity of variances was analysed using Levene's test for equality of variances, for determination of which post-hoc statistical test was applicable (Pallant, 2007; Lee and Lee, 2018). Scheffe's test was utilized if $p \geq 0.05$ (equal variance) and Dunnett T3 if $p < 0.05$ (not equal variances) (Pallant, 2007; Lee and Lee, 2018).

e. Cross tabulations

In addition, Chi-squared tests (a non-parametric test designed to analyse group differences when the dependent variable is measured) were performed (Raudenbush, 2004; Pallant, 2007) specifically for frequency of SPDRD. This was initially performed comparing each species per vertebral level, followed by between species per sex per

vertebral level and finally between sex per species separately per vertebral level. These results did not comply with the required assumptions regarding minimum expected cell frequency of 5 or greater, or at least 80% of cells having expected frequencies of 5 or more (McHugh, 2013), with the exception of the baboon T2, and a descriptive analysis was therefore conducted. Due to the low overall incidence of deviations, statistical comparisons to measured parameters could not be performed, and a descriptive comparison to overall means is presented.

f. Overall analysis

The data obtained were compared within and between groups as described in the aims which allowed for. Differences within and between groups allowed for testing associations between morphological differences, activity and locomotor behaviour. The following differences were tested between species, within species between sex, and within sex between species using the previously mentioned morphometric measurements:

- Potential sex differences
- SPDRD relative to the proximal or distal portion of the spinous process, length of spinous process and craniocaudal spinous process angle
- SPDRD relative to dorsoventral articular facet angle and width (for superior and inferior articular facet measurements).

The following were also tested between groups:

- Comparative analysis of morphometric measurements in relation to locomotor pattern

- Comparative analysis of morphometric measurements between Later Stone Age (LSA) and contemporary human samples
- Comparative analysis of morphometric measurements to various species of fossil hominins, including extant hominins.

CHAPTER 3

EXTANT PRIMATE MORPHOMETRIC COMPARISON

3.1 Introduction

To facilitate the presentation of the results and discussion, each focus area of the study will be presented as a separate chapter.

The current chapter will present a comparative analysis of contemporary humans, selected great apes (*Pan troglodytes, Gorilla gorilla*) and obligate pronograde quadrupedal primates (*Papio ursinus*), with an emphasis on locomotor differences among taxa. This comparison and the descriptive statistics of measurements are presented per species, vertebral level and sex. Appendices of full data are available in the supplemental material to the graphical comparisons.

As indicated in the Materials and Methods in Chapter 2, the following measures were taken and presented as comparison for each sample ("_R"=right; "_L"=left):

1. Spinous process angle (SPA)
2. Spinous process length (SPL)
3. Right inferior articular facet width (IAFW_R)
4. Left inferior articular facet width (IAFW_R)
5. Right inferior articular facet orientation (IAFO_R)
6. Left inferior articular facet orientation (IAFO_L)
7. Right superior articular facet width (SAFW_R)
8. Left superior articular facet width (SAFW_L)
9. Right superior articular facet orientation (SAFO_R)

10. Left superior articular facet orientation (SAFO_L)

Spinous process deviation (SPD), region (distal or proximal) and direction (SPDRD) will be presented separately.

Statistical analysis conducted is described in Chapter 2. Appendix 3 presents the ANOVA comparisons for all groups and demonstrated statistically significantly differences ($p<0.0001$) for all measurements between groups. Homogeneity of variances was analyzed using Levene's test for equality of variances, for determination of which post-hoc statistical test was applicable (Pallant, 2007; Lee and Lee, 2018). Scheffe's test was utilized if $p\geq0.05$ (equal variance) and Dunnett T3 if $p<0.05$ (not equal variances) (Pallant, 2007; Lee and Lee, 2018). These post-hoc p values were tabulated in a comparison matrix and are presented in Appendices 4 and 5.

Morphometric measurements relating to sex, species and vertebral level are presented in Appendix 6 for males and Appendix 7 for females. Chi-squared tests were performed specifically for SPDRD and these did not comply with the required assumptions regarding minimum expected cell frequency of 5 or greater, or at least 80% of cells having expected frequencies of 5 or more (McHugh, 2013), with the exception of the baboons T2, and a descriptive analysis was therefore conducted.

3.2 Spinous process angle and length

Measurements for spinous process angles and lengths per species and sex are presented for males in Appendix 6 and females in Appendix 7. ANOVA comparisons (Appendix 3) were conducted on both of these measures and indicated statistically significant differences ($p<0.0001$) between each of the species. Post-hoc analysis was

performed with a Bonferroni adjustment and p-value against a significance level of $p<0.0125$ (0.05/4).

For ease of presentation, each vertebral level is presented per species and sex.

Table 3.1 indicates the cross tabulation of post-hoc results for spinous process angle and length per vertebral level and species in males with statistically significant differences between all species.

Table 3.2 represents the cross tabulated post-hoc results for spinous process angle and length per vertebral level in females and indicated statistically significant values for between species.

Table 3.1: Cross tabulation of post-hoc results for male spinous process angle and length per species and vertebral level.

Measure		Gorillas	Chimpanzees	Baboons
SPA T1	Chimpanzees	**0.001**		
	Baboons	**0.006**	0.084	
	Humans (contemporary)	**0.001**	**0.001**	**0.001**
SPL_T1	Chimpanzees	**0.001**		
	Baboons	**0.001**	0.024	
	Humans (contemporary)	**0.001**	0.556	0.118
SPA_T2	Chimpanzees	0.026		
	Baboons	0.093	0.883	
	Humans (contemporary)	**0.001**	**0.001**	**0.001**
SPL_T2	Chimpanzees	**0.001**		
	Baboons	**0.001**	0.874	
	Humans (contemporary)	**0.001**	0.988	0.976
SPA_T3	Chimpanzees	0.656		
	Baboons	1.000	0.360	
	Humans (contemporary)	**0.001**	**0.001**	**0.001**
SPL_T3	Chimpanzees	**0.001**		
	Baboons	**0.001**	0.996	

	Humans (contemporary)	**0.001**	0.999	1.000
SPA_T4	Chimpanzees	0.875		
	Baboons	**0.001**	**0.002**	
	Humans (contemporary)	**0.001**	**0.001**	**0.001**
SPL_T4	Chimpanzees	**0.001**		
	Baboons	**0.001**	0.847	
	Humans (contemporary)	**0.001**	0.201	0.965
SPA_T5	Chimpanzees	0.172		
	Baboons	**0.001**	0.040	
	Humans (contemporary)	**0.001**	**0.001**	**0.001**
SPL_T5	Chimpanzees	**0.001**		
	Baboons	**0.001**	0.696	
	Humans (contemporary)	**0.001**	0.285	0.998
SPA_T6	Chimpanzees	0.024		
	Baboons	**0.001**	**0.004**	
	Humans (contemporary)	**0.001**	**0.001**	**0.001**
SPL_T6	Chimpanzees	0.042		
	Baboons	**0.002**	0.923	
	Humans (contemporary)	**0.001**	0.628	1.000

Table 3.2: Cross tabulation of post-hoc results for female spinous process angle and length per species and vertebral level.

Measure		**Gorillas**	**Chimpanzees**	**Baboons**
SPA_T1	Chimpanzees	**0.001**		
	Baboons	0.970	**0.001**	
	Humans (contemporary)	**0.001**	0.079	**0.001**
SPL_T1	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.259	**0.001**
SPA_T2	Chimpanzee	0.049		
	Baboons	0.969	0.014	
	Humans (contemporary)	**0.001**	**0.001**	**0.001**
SPL_T2	Chimpanzees	**0.001**		
	Baboons	**0.001**	0.024	

	Humans (contemporary)	**0.001**	0.804	0.227
SPA_T3	Chimpanzees	0.997		
	Baboons	**0.005**	**0.002**	
	Humans (contemporary)	**0.001**	**0.001**	**0.001**
SPL_T3	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.048	0.753
SPA_T4	Chimpanzees	0.031		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.064	**0.001**	**0.001**
SPL_T4	Chimpanzees	0.232		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.002**	0.313	**0.002**
SPA_T5	Chimpanzees	**0.002**		
	Baboons	**0.001**	**0.003**	
	Humans (contemporary)	**0.002**	**0.001**	**0.001**
SPL_T5	Chimpanzees	1.000		
	Baboons	0.049	**0.009**	
	Humans (contemporary)	0.342	0.090	0.891
SPA_T6	Chimpanzees	**0.003**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	**0.001**	**0.001**
SPL_T6	Chimpanzees	0.359		
	Baboons	0.318	**0.005**	
	Humans (contemporary)	0.997	0.266	0.436

3.2.1 T1 spinous process angle and length per species and sex

In the male sample groups comparison for T1, SPA differences were statistically significantly different in gorillas compared to chimpanzees (p=0.001) and to baboons (p=0.006), and contemporary humans compared to gorillas, chimpanzees, and baboons (p=0.001). SPL differences were statistically significantly different between gorillas and to all other groups (p=0.001).

In the female sample groups comparison for T1, SPA differences were statistically significantly different in gorillas compared to chimpanzees (p=0.001), baboons compared to chimpanzees (p=0.001), and contemporary humans compared to gorillas and baboons (p=0.001). SPL differences were statistically significantly different between gorillas and chimpanzees, baboons to contemporary humans (p=0.001), and baboons compared to chimpanzees (p=0.024) and contemporary humans (p=0.001).

3.2.2 T2 spinous process angle and length per species and sex

In the male sample groups comparison for T2, SPA differences were statistically significantly different in contemporary humans compared to gorillas, chimpanzees and baboons (p=0.001). SPL differences were statistically significantly different between gorillas and chimpanzees (p=0.001), and baboons and gorillas (p=0.001).

In the female sample groups comparison for T2, SPA differences were statistically significantly different in contemporary humans compared to gorillas, chimpanzees and baboons (p=0.001). SPL differences were statistically significantly different between gorillas and chimpanzees, baboons, and contemporary humans (p=0.001).

3.2.3 T3 spinous process angle and length per species and sex

In the male sample groups comparison for T3, SPA differences were statistically significantly different in gorillas compared to contemporary humans (p=0.001), and in contemporary humans compared to gorillas, chimpanzees and baboons (p=0.001). SPL

differences were statistically significantly different between gorillas and all other groups (p=0.001).

In the female sample groups comparison for T3, SPA differences were statistically significantly different in baboons compared to gorillas (p=0.005) and chimpanzees (p=0.002), and in contemporary humans compared to all other groups (p=0.001). SPL differences were found to be statistically significantly different between gorillas and all other groups (p=0.001), and between baboons and chimpanzees (p=0.001).

3.2.4 T4 spinous process angle and length per species and sex

In the male sample groups comparison for T4, SPA differences were statistically significantly different in gorillas compared to baboons and contemporary humans (p=0.001), and in contemporary humans compared to gorillas, chimpanzees and baboons (p=0.001). SPL differences were statistically significantly different between gorillas and all other groups (p=0.001).

In the female sample groups comparison for T4, SPA differences were statistically significantly different in baboons compared to gorillas and chimpanzees (p=0.001), and in contemporary humans compared to chimpanzees and baboons (p=0.001). SPL differences were statistically significantly different between gorillas and baboons (p=0.001) and contemporary humans (p=0.002) and between baboons and chimpanzees (p=0.001) and between contemporary humans and baboons (p=0.002).

3.2.5 T5 spinous process angle and length per species and sex

In the male sample groups comparison for T5, SPA differences were statistically significantly different in gorillas compared to baboons and contemporary humans (p=0.001), and in contemporary humans to all other groups (p=0.001). SPL differences were statistically significantly different between gorillas and all other groups (p=0.001).

In the female sample groups comparison for T5, SPA differences were statistically significantly different in gorillas compared to chimpanzees (p=0.002), baboons (p=0.001) and contemporary humans (p=0.002), and baboons compared to chimpanzees (p=0.003), and in contemporary humans compared to gorillas (p=0.002), chimpanzees (p=0.001) and baboons (p=0.001). SPL differences were statistically significantly different between baboons and chimpanzees (p=0.009).

3.2.6 T6 spinous process angle and length per species and sex

In the male sample groups comparison for T6, SPA differences were statistically significantly different in gorillas compared to baboons and to contemporary humans (p=0.001), and in baboons and chimpanzees (p=0.004), and in contemporary humans compared to gorillas, chimpanzees and baboons (p=0.001). SPL differences were statistically significantly different between gorillas and baboons (p=0.002) and to contemporary humans (p=0.001).

In the female sample groups comparison for T6, SPA differences were statistically significantly different in gorillas compared to chimpanzees (p=0.003), baboons (p=0.001) and contemporary humans (p=0.001), and in baboons compared to chimpanzees (p=0.001), and in contemporary humans to all other groups (p=0.001).

SPL differences were statistically significantly different between baboons and chimpanzees (p=0.005).

3.3 Articular facet width and orientation

Measurements for articular facet width and orientation (left, right, superior and inferior) per species and sex are presented for males in Appendix 6 and females in Appendix 7. ANOVA comparisons (Appendix 3) were conducted on both of these measures and indicated statistically significant differences (p<0.0001) between each of the species. Post-hoc analysis was performed with a Bonferroni adjustment and p-value against a significance level of p<0.0125 (0.05/4).

Table 3.3 indicates the cross tabulation of post-hoc results for articular facet width and orientation per vertebral level and species for males with statistically significant differences (p<0.0125) noted between species.

Table 3.4 indicates the cross tabulated post-hoc results for female articular facet width and orientation per vertebral level with statistically significant differences (p<0.0125) noted between species.

Table 3.3: Cross tabulation of male post-hoc results for articular facet orientation and width per species and vertebral level.

Measure		Gorillas	Chimpanzees	Baboons
IAFWR_T1	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.076	**0.001**
IAFWL_T1	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.005**	0.013	**0.001**

IAFO_R.T1	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.968	**0.001**
IAFO_L.T1	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	1.000	**0.001**
SAFW_R.T1	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	**0.001**	**0.001**
SAFW_L.T1	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	**0.001**	**0.001**
SAFO_R.T1	Chimpanzees	**0.001**		
	Baboons	**0.001**	0.689	
	Humans (contemporary)	**0.001**	0.483	0.018
SAFO_L.T1	Chimpanzees	**0.001**		
	Baboons	**0.001**	1.000	
	Humans (contemporary)	**0.001**	0.041	**0.008**
IAFW_R.T2	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.234	**0.001**	**0.001**
IAFW_L.T2	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.009**	
	Humans (contemporary)	0.245	0.070	**0.001**
IAFO_R.T2	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.849	**0.001**
IAFO_L.T2	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.994	**0.001**
SAFW_R.T2	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.010**	0.023	**0.001**
SAFW_L.T2	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.002**	0.030	**0.001**
SAFO_R.T2	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	

	Humans (contemporary)	**0.001**	0.995	**0.001**
SAFO_L.T2	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	1.000	**0.001**
IAFW_R.T3	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.003**	
	Humans (contemporary)	0.857	**0.001**	**0.001**
IAFW_L.T3	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.004**	0.114	**0.001**
IAFO_R.T3	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.071	**0.001**
IAFO_L.T3	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.944	**0.001**
SAFW_R.T3	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.077	**0.001**	**0.001**
SAFW_L.T3	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.116	**0.001**
SAFO_R.T3	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.999	**0.001**
SAFO_L.T3	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.691	**0.001**
IAFW_R.T4	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.965	**0.001**	**0.001**
IAFW_L.T4	Chimpanzees	**0.001**		
	Baboons	**0.001**	0.024	
	Humans (contemporary)	0.337	0.015	**0.001**
IAFO_R.T4	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.437	**0.001**
IAFO_L.T4	Chimpanzees	**0.001**		

	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.004**	0.424	**0.001**
SAFW_R.T4	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.007**	
	Humans (contemporary)	0.965	**0.001**	**0.001**
SAFW_L.T4	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.046	0.038	**0.001**
SAFO_R.T4	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	1.000	**0.001**
SAFO_L.T4	Chimpanzees	0.018		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.029	0.911	**0.001**
IAFW_R.T5	Chimpanzees	**0.002**		
	Baboons	**0.001**	0.031	
	Humans (contemporary)	0.808	0.019	**0.001**
IAFW_L.T5	Chimpanzees	0.021		
	Baboons	**0.001**	0.014	
	Humans (contemporary)	0.553	0.262	**0.001**
IAFO_R.T5	Chimpanzees	0.036		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.366	0.511	**0.001**
IAFO_L.T5	Chimpanzees	0.443		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.984	0.629	**0.001**
SAFW_R.T	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.005**	
	Humans (contemporary)	0.891	**0.003**	**0.001**
SAFW_L.T5*	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.003**	
	Humans (contemporary)	0.196	**0.007**	**0.001**
SAFO_R.T5	Chimpanzees	0.064		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.758	**0.001**
SAFO_L.T5	Chimpanzees	0.017		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.238	0.478	**0.001**

IAFW_R.T6	Chimpanzees	0.057		
	Baboons	**0.001**	0.065	
	Humans (contemporary)	0.940	0.016	**0.001**
IAFW_L.T6	Chimpanzees	0.054		
	Baboons	**0.001**	0.026	
	Humans (contemporary)	0.994	0.091	0.026
IAFO_R.T6	Chimpanzees	**0.008**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.140	0.873	**0.001**
IAFO_L.T6	Chimpanzees	0.910		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.669	0.218	**0.001**
SAFW_R.T6	Chimpanzees	0.017		
	Baboons	0.001	0.017	
	Humans (contemporary)	0.956	0.058	**0.001**
SAFW_L.T6	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.177	0.170	**0.001**
SAFO_R.T6	Chimpanzees	0.357		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.005**	0.704	**0.001**
SAFO_L.T6	Chimpanzees	0.817		
	Baboonss	**0.001**	**0.001**	
	Human (contemporary)	0.997	0.891	**0.001**

Table 3.4: Cross tabulation of female post-hoc results for articular facet orientation and width per species and vertebral level.

Measure		**Gorillas**	**Chimpanzees**	**Baboons**
IAFW_R.T1	Chimpanzees	0.075		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.847	**0.001**	**0.001**
IAFW_L.T1	Chimpanzees	**0.006**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.941	**0.001**	**0.001**
IAFO_R.T1	Chimpanzees	**0.001**		

	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.980	**0.001**
IAFO_L.T1	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.950	**0.001**
SAFW_R.T1	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.835	**0.001**	**0.001**
SAFW_L.T1	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	1.000	**0.001**	**0.001**
SAFO_R.T1	Chimpanzees	**0.001**		
	Baboons	**0.001**	0.100	
	Humans (contemporary)	**0.001**	**0.010**	**0.001**
SAFO_L.T1	Chimpanzees	**0.001**		
	Baboons	**0.001**	0.158	
	Humans (contemporary)	**0.001**	**0.001**	**0.001**
IAFW_R.T2	Chimpanzees	0.198		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.014**	**0.001**	**0.001**
IAFW_L.T2	Chimpanzees	0.370		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.455	**0.001**	**0.001**
IAFO_R.T	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.433	**0.001**
IAFO_L.T2	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.749	**0.001**
SAFW_R.T2	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.999	**0.001**	**0.001**
SAFW_L.T2	Chimpanzees	**0.003**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.969	**0.001**	**0.001**
SAFO_R.T2	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	1.000	**0.001**

SAFO_L.T2	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.659	**0.001**
IAFW_R.T3	Chimpanzees	0.394		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.017	**0.001**	**0.001**
IAFW_L.T3	Chimpanzees	0.255		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.581	**0.011**	**0.001**
IAFO_R.T3	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.015	0.449	**0.001**
IAFO_L.T3	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.914	**0.001**
SAFW_R.T3	Chimpanzees	0.199		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.151	**0.001**	**0.001**
SAFW_L.T3	Chimpanzees	0.056		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.819	**0.002**	**0.001**
SAFO_R.T3	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.999	**0.001**
SAFO_L.T3	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.003**	0.089	**0.001**
IAFW_R.T4	Chimpanzees	0.012		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.696	**0.001**	**0.001**
IAFW_L.T4	Chimpanzees	0.228		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.769	**0.003**	**0.001**
IAFO_R.T4	Chimpanzees	0.012		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.498	0.360	**0.001**
IAFO_L.T4	Chimpanzees	**0.002**		
	Baboons	**0.001**	**0.001**	

	Humans (contemporary)	1.000	**0.001**	**0.001**
SAFW_R.T4	Chimpanzees	0.079		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.130	**0.001**	**0.001**
SAFW_L.T4	Chimpanzees	0.528		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.403	0.019	**0.001**
SAFO_R.T4	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	**0.001**	0.980	**0.001**
SAFO_L.T4	Chimpanzees	**0.001**		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.196	0.137	**0.001**
IAFW_R.T5	Chimpanzees	0.464		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.783	0.079	**0.001**
IAFW_L.T5	Chimpanzees	0.356		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	1.000	0.078	**0.001**
IAFO_R.T5	Chimpanzees	0.020		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.591	0.374	**0.001**
IAFO_L.T5	Chimpanzees	0.122		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.992	**0.002**	**0.001**
SAFW_R.T5	Chimpanzees	0.247		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.066	**0.001**	**0.001**
SAFW_L.T5	Chimpanzees	0.232		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.942	0.014	**0.001**
SAFO_R.T5	Chimpanzees	0.181		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.566	0.899	**0.001**
SAFO_L.T5	Chimpanzees	0.471		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.329	**0.001**	**0.001**
IAFW_R.T6	Chimpanzees	0.991		

	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.444	0.273	**0.001**
IAFW_L.T6	Chimpanzees	0.849		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.355	0.067	**0.001**
IAFO_R.T6	Chimpanzees	0.121		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.620	**0.004**	**0.001**
IAFO_L.T6	Chimpanzees	0.493		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.016	**0.001**	**0.001**
SAFW_R.T6	Chimpanzees	0.891		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.389	0.098	**0.001**
SAFW_L.T6	Chimpanzees	0.833		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.341	0.058	**0.001**
SAFO_R.T6	Chimpanzees	0.246		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.543	0.959	**0.001**
SAFO_L.T6	Chimpanzees	1.000		
	Baboons	**0.001**	**0.001**	
	Humans (contemporary)	0.070	0.045	**0.001**

As indicated in Table 3.3 and 3.4, the majority of results were statistically significantly different ($p<0.0125$), and a presentation of the results that were not significantly different (i.e., similar) are presented per vertebral level.

3.3.1 T1 articular facet width and orientation per species and sex

In the male sample groups comparison for T1, differences between species were not significantly different between chimpanzees compared to contemporary humans for IAFW_R ($p=0.076$), IAFW_L ($p=0.013$), IAFO_R ($p=0.968$), IAFO_L ($p=1.000$),

SAFO_R (p=0.483) and SAFO_L (p=0.041) and between chimpanzees and baboons for SAFO_R (p=0.689) and SAFO_L (p=1.000). Baboons were not statistically significant compared to contemporary humans for SAFO_R (p=.0689).

In the female sample groups comparison for T1, differences between species were not significantly different between gorillas compared to contemporary humans for IAFW_R (p=0.847), IAFW_L (p=0.941), SAFW_R (p=0.835) and SAFW_L (p=1.000), and between chimpanzees and contemporary humans for IAFO_R (p=0.980) and IAFO_L (p=0.950) and baboons for SAFO_R (p=0.100) and SAFO_L (p=0.158).

3.3.2 T2 articular facet width and orientation per species and sex

In the male sample groups comparison for T2, differences between species were not significantly different between contemporary humans compared to chimpanzees for IAFW_L (p=0.070), IAFO_R (p=0.849), IAFO_L (p=0.994), SAFW_R (p=0.023), SAFW_L (p=0.030), SAFO_R (p=0.995) and SAFO_L (p=1.000) and between gorillas and contemporary humans for IAFW_R (p=0.234) and IAFW_L (p=0.245).

In the female sample groups comparison for T2, differences between species were not significantly different between gorillas compared to contemporary humans for IAFW_L (p=0.455), SAFW_R (p=0.999) and SAWF_L (p=0.969). Chimpanzees were not significantly different to gorillas for IAFW_R (p=0.198) and IAFW_L (p=0.370), and for contemporary humans for IAFO_R (p=0.433), IAFO_L (p=0.749), SAFO_R (p=0.100) and SAFO_L (p=0.659).

3.3.3 T3 articular facet width and orientation per species and sex

In the male sample groups comparison for T3, differences between species were not significantly different between contemporary humans compared to chimpanzees for IAFW_L (p=0.071), IAFO_R (p=0.071), IAFO_L (p=0.994), SAFW_L (p=0.116), SAFO_R (p=0.999) and SAFO_L (p=0.691) and between gorillas and contemporary humans for IAFW_R (p=0.857) and SAFW_R (p=0.077).

In the female sample groups comparison for T3, differences between species were not significantly different between gorillas compared to contemporary humans for IAFW_L (p=0.581), IAFO_R (p=0.015), SAFW_R (p=0.151) and SAWF_L (p=0.819). Chimpanzees were not significantly different to gorillas for IAFW_R (p=0.394), IAFW_L (p=0.255), SAFW_R (p=0.199), SAFW_L (p=0.056), and contemporary humans for IAFO_R (p=0.449), IAFO_L (p=0.914), SAFO_R (p=0.999) and SAFO_L (p=0.089).

3.3.4 T4 articular facet width and orientation per species and sex

In the male sample groups comparison for T4, differences between species were not significantly different between contemporary humans compared to gorillas for IAFW_R (p=0.965), IAFW_L (p=0.337), SAFW_R (p=0.965), SAFW_L(p=0.046), and SAFO_L (p=0.029) and between chimpanzees IAFW_L (p=0.015), IAFO_R (p=0.437), IAFO_L (p=0.424), SAFW_L (p=0.038), SAFO_R (p=1.000) and SAFO_L (p=0.911). Chimpanzees also showed no significant differences to baboons for IAFW_L (p=0.024).

In the female sample groups comparison for T4, differences between species were not significantly different between gorillas compared to contemporary humans for IAFW_R (p=0.696), IAFW_L (p=0.769), IAFO_R (p=0.498), IAFO_L (p=1.000),

SAFW_R (p=0.130), SAFW_L (p=0.403) and SAFO_R (p=0.196). Chimpanzees were not significantly different to gorillas for IAFW_R (p=0.012), IAFW_L (p=0.228), IAFO_R (p=0.012), SAFW_R (p=0.079), SAFW_L (p=0.528), and contemporary humans for IAFO_R (p=0.360), SAFW_L (p=0.019), SAFO_R (p=0.980) and SAFO_L (p=0.137).

3.3.5 T5 articular facet width and orientation per species and sex

In the male sample groups comparison for T5, differences between species were not statistically significantly different between contemporary humans compared to gorillas for IAFW_R (p=0.808), IAFW_L (p=0.553), IAFO_R (p=0.366), IAFO_L (p=0.984), SAFW_R (p=0.891), SAFW_L(p=0.196) and SAFO_L (p=0.238) and between chimpanzees IAFW_R (p=0.019), IAFW_L (p=0.262), IAFO_R (p=0.511), IAFO_L (p=0.629), SAFO_R (p=0.758) and SAFO_L (p=0.478). Chimpanzees also showed no significant differences gorillas for IAFW_L (p=0.021), IAFO_R (p=0.036) IAFO_L (p=0.443), SAFO_R (p=0.064) and SAFO_L (p=0.017) and to baboons for IAFW_R (p=0.031 and IAFW_L (p=0.014).

In the female sample groups comparison for T5, differences between species were not significantly different between gorillas compared to contemporary humans for IAFW_R (p=0.783), IAFW_L (p=1.000), IAFO_R (p=0.591), IAFO_L (p=0.992), SAFW_R (p=0.066), SAFW_L (p=0.942), SAFO_R (p=0.566) and SAFO_L (p=0.329). Chimpanzees were not significantly different to gorilla for IAFW_R (p=0.464), IAFW_L (p=0.356), IAFO_R (p=0.020), IAFO_L (p=0.122), SAFW_R (p=0.247), SAFW_L (p=0.232), SAFO_R (p=0.181) and SAFO_L (p=0.471) and contemporary humans for

IAFW_R (p=0.079), IAFW_L (p=0.078), IAFO_R (p=0.374), SAFW_L (p=0.014) and SAFO_R (p=0.899).

3.3.6 T6 articular facet width and orientation per species and sex

In the male sample groups comparison for T6, differences between species were not statistically significantly different between contemporary humans compared to gorillas for IAFW_R (p=0.940), IAFW_L (p=0.994), IAFO_R (p=0.140, IAFO_L (p=0.669), SAFW_R (p=0.956), SAFW_L(p=0.177) and SAFO_L (p=0.997) and between chimpanzees IAFW_R (p=0.016), IAFW_L (p=0.091), IAFO_R (p=0.873), IAFO_L (p=0.218), SAFW_R (p=0.058), SAFW_L (p=0.170, SAFO_R (p=0.704) and SAFO_L (p=0.891). Chimpanzees also showed no significant differences gorillas for IAFW_R (p=0.057), IAFW_L (p=0.054), IAFO_L (p=0.910), SAFW_R (p=0.017), SAFO_R (p=0.357) and SAFO_L (p=0.817) and to baboons for IAFW_R (p=0.065), IAFW_L (p=0.026) and SAFW_R (p=0.017).

In the female sample groups comparison for T6, differences between species were not significantly different between gorillas compared to contemporary humans for IAFW_R (p=0.444), IAFW_L (p=0.355), IAFO_R (p=0.620), IAFO_L (p=0.016), SAFW_R (p=0.389), SAFW_L (p=0.314), SAFO_R (p=0.543) and SAFO_L (p=0.070). Chimpanzees were not significantly different to gorillas for IAFW_R (p=0.991), IAFW_L (p=0.849), IAFO_R (p=0.121), IAFO_L (p=0.493), SAFW_R (p=0.891), SAFW_L (p=0.833), SAFO_R (p=0.246) and SAFO_L (p=1.000) and contemporary humans for IAFW_R (p=0.273), IAFW_L (p=0.067), SAFW_R (p=0.098), SAFW_L (p=0.058), SAFO_R (p=0.959) and SAFO_L (p=0/045).

3.4 Spinous process deviation, region and direction (SPDRD)

Spinous process deviation in terms of direction and region (proximal or distal) are presented per sex per species, and as total values per species. As indicated, Chi-squared tests were performed, but these did not comply with the required assumptions regarding minimum expected cell frequency of 5 or greater (or at least 80% of cells having expected frequencies of 5 or more), except for the baboons T2. Therefore, a descriptive analysis is presented. Due to the low overall incidence of deviations, statistical comparisons to measured parameters could not be conducted, and a descriptive comparison to overall means is presented.

3.4.1 T1 SPDRD per sex and species

Table 3.5 summarizes the T1 spinous process deviations (in terms of being present, direction and region) for sex per species, and total per species. In the male sample groups comparison for T1, the gorilla group showed the highest overall incidence of 35.5% (n=11), with baboons showing the lowest incidence of 17.4% (n=3). Of the deviations noted, the distal right deviations had the highest incidence in the gorilla group with 29% (n=9), with proximal right deviations being absent in all groups (n=0). This is depicted visually in Figure 3.1.

Table 3.5: Cross tabulation and frequency of T1 spinous process deviation per sex and species.

Species				DRD_T1 None	DRD_T1 Distal Left	DRD_T1 Distal Right	DRD_T1 Proximal Left	Total
Gorillas	**Sex**	**Male**	**Count**	20	2	9	0	31
			% within sex	64.5%	6.5%	29.0%	0%	100.0%
		Female	**Count**	25	3	1	0	29
			% within sex	86.2%	10.3%	3.4%	0%	100.0%
	Total		**Count**	45	5	10	0	60
			% total	75.0%	8.3%	16.7%	0%	100.0%
Chimpanzees	**Sex**	**Male**	**Count**	12	2	1	0	15
			% within sex	80.0%	13.3%	6.7%	0%	100.0%
		Female	**Count**	19	4	6	1	30
			% within sex	63.3%	13.3%	20.0%	3.3%	100.0%
	Total		**Count**	31	6	7	1	45
			% total	68.9%	13.3%	15.6%	2.2%	100.0%
Baboons	**Sex**	**Male**	**Count**	19	2	2	0	23
			% within sex	82.6%	8.7%	8.7%	0%	100.0%
		Female	**Count**	28	0	0	0	28
			% within sex	100.0%	0 %	0%	0%	100.0%
	Total		**Count**	47	2	2	0	51
			% total	92.2%	3.9%	3.9%	0%	100.0%
Contemporary humans	**Sex**	**Male**	**Count**	24	2	4	0	30
			% within sex	80.0%	6.7%	13.3%	0%	100.0%
		Female	**Count**	23	1	4	0	28
			% within sex	82.1%	3.6%	14.3%	0%	100.0%
	Total		**Count**	47	3	8	0	58
			% total	81.0%	5.2%	13.8%	0%	100.0%

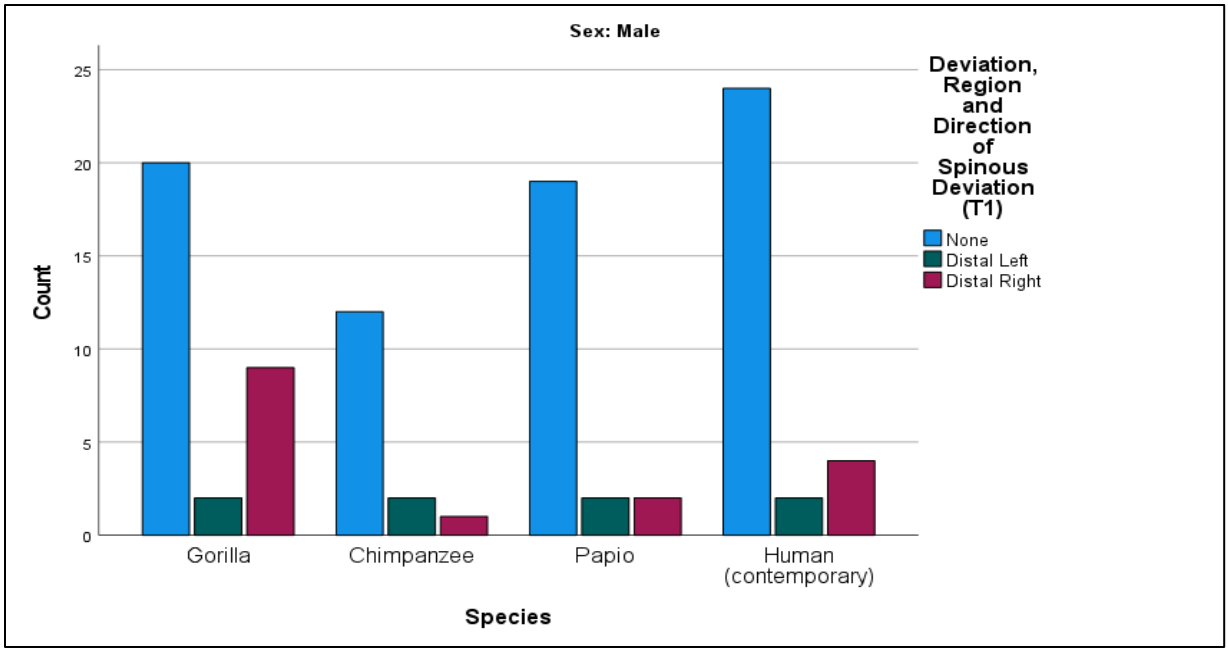


Figure 3.1: Bar graph of male T1 spinous process deviation per species.

In the female sample groups comparison for T1, the chimpanzee groups showed the highest overall incidence with 36.7% (n=19), with baboons not showing this trait (n=0). Of the deviations noted, the distal right deviations were highest in the chimpanzee group with 20%, (n=6), with proximal right deviations being absent in all groups (n=0). This is depicted visually in Figure 3.2.

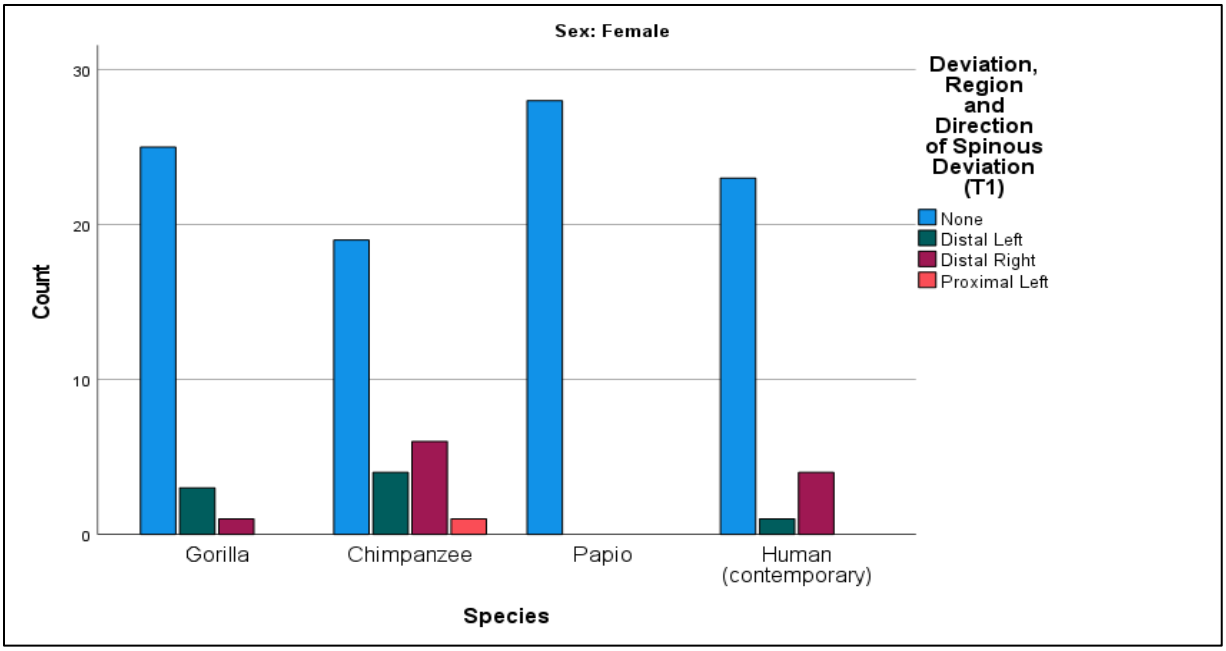


Figure 3.2: Bar graph of female T1 spinous process deviation per species.

In the overall species comparison (male and female combined) for T1 (as indicated in Table 3.5), the chimpanzee groups showed the highest overall incidence of 31.1% (n=31), with baboons showing the lowest incidence of 7.8% (n=4). Of the deviations noted, the distal right deviations were highest in the gorilla group with 16.7% (n=10), with proximal right deviations being absent for all species at T1 (n=0). This is depicted visually in Figure 3.3.

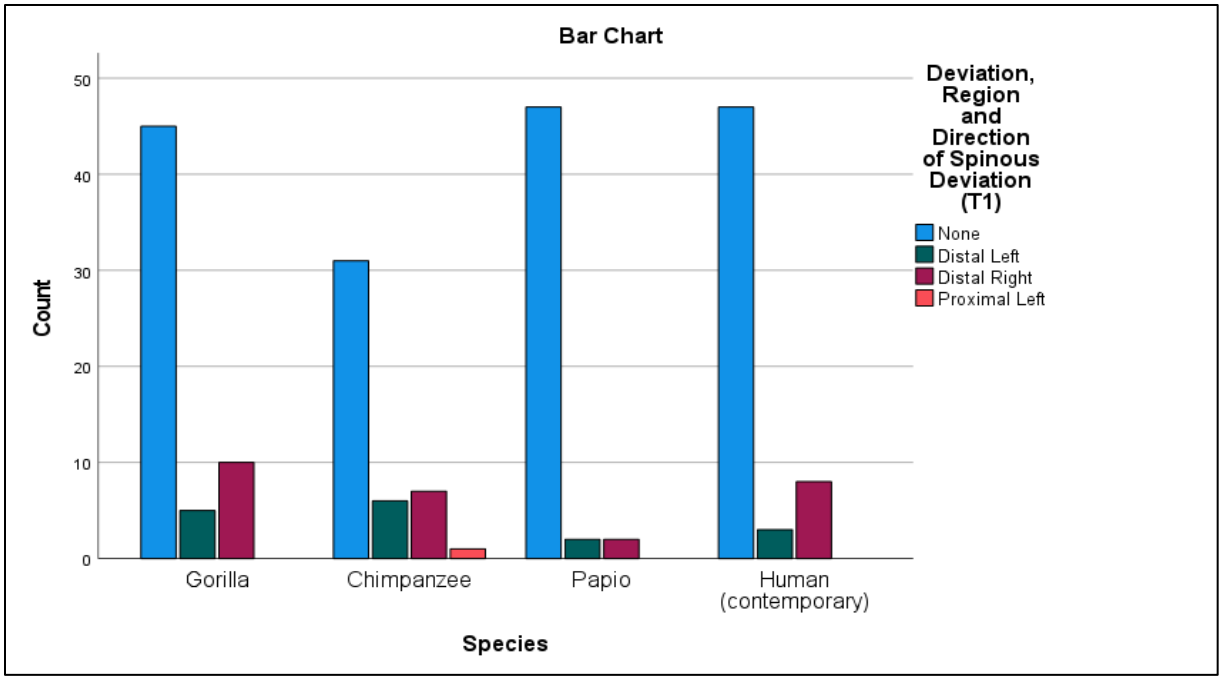


Figure 3.3: Bar graph of overall species T1 spinous process deviation.

Mean values of facet width (right and left superior and inferior) were calculated for T1 specimens with deviations and were compared to overall sample group measurements means for T1 specimens (Appendix 8). On comparison, all measurements were within the standard deviations, indicating no differences between specimens with or without SPD (Appendices 6 and 7).

3.4.2 T2 SPDRD per sex and species

Table 3.6 summarizes the T2 spinous process deviations (in terms of being present, direction and region) for sex per species, and total per species. In the male sample groups comparison for T2, the contemporary human groups showed the highest overall incidence of 46.7% (n=14) and was absent in baboons (n=0). Of the deviations noted, the distal right deviations showed the highest incidence in the contemporary

human and chimpanzee groups with 26.7% (n=8 and n=4), with proximal right deviations being absent in all groups (n=0). This is depicted visually in Figure 3.4.

Table 3.6: Cross tabulation and frequency of T2 spinous process deviation per sex and species.

Species				DRD_T2 None	DRD_T2 Distal Left	DRD_T2 Distal Right	DRD_T2 Proximal Left	Total
Gorillas	**Sex**	**Male**	**Count**	23	3	4	1	31
			% within sex	74.2%	9.7%	12.9%	3.2%	100.0%
		Female	**Count**	19	6	4	0	29
			% within sex	65.5%	20.7%	13.8%	0%	100.0%
	Total		**Count**	42	9	8	1	60
			% total	70.0%	15.0%	13.3%	1.7%	100.0%
Chimpanzees	**Sex**	**Male**	**Count**	8	3	4	0	15
			% within sex	53.3%	20.0%	26.7%	0%	100.0%
		Female	**Count**	14	5	10	1	30
			% within sex	46.7%	16.7%	33.3%	3.3%	100.0%
	Total		**Count**	22	8	14	1	45
			% total	48.9%	17.8%	31.1%	2.2%	100.0%
Baboons	**Sex**	**Male**	**Count**	23	0	0	0	23
			% within sex	100.0%	0%	0%	0%	100.0%
		Female	**Count**	26	0	2	0	28
			% within sex	92.9%	0%	7.1%	0%	100.0%
	Total		**Count**	49	0	2	0	51
			% total	96.1%	0%	3.9%	0%	100.0%
Contemporary humans	**Sex**	**Male**	**Count**	16	6	8	0	30
			% within sex	53.3%	20.0%	26.7%	0%	100.0%
		Female	**Count**	24	3	1	0	28
			% within sex	85.7%	10.7%	3.6%	0%	100.0%
	Total		**Count**	40	9	9	0	58
			% total	69.0%	15.5%	15.5%	0%	100.0%

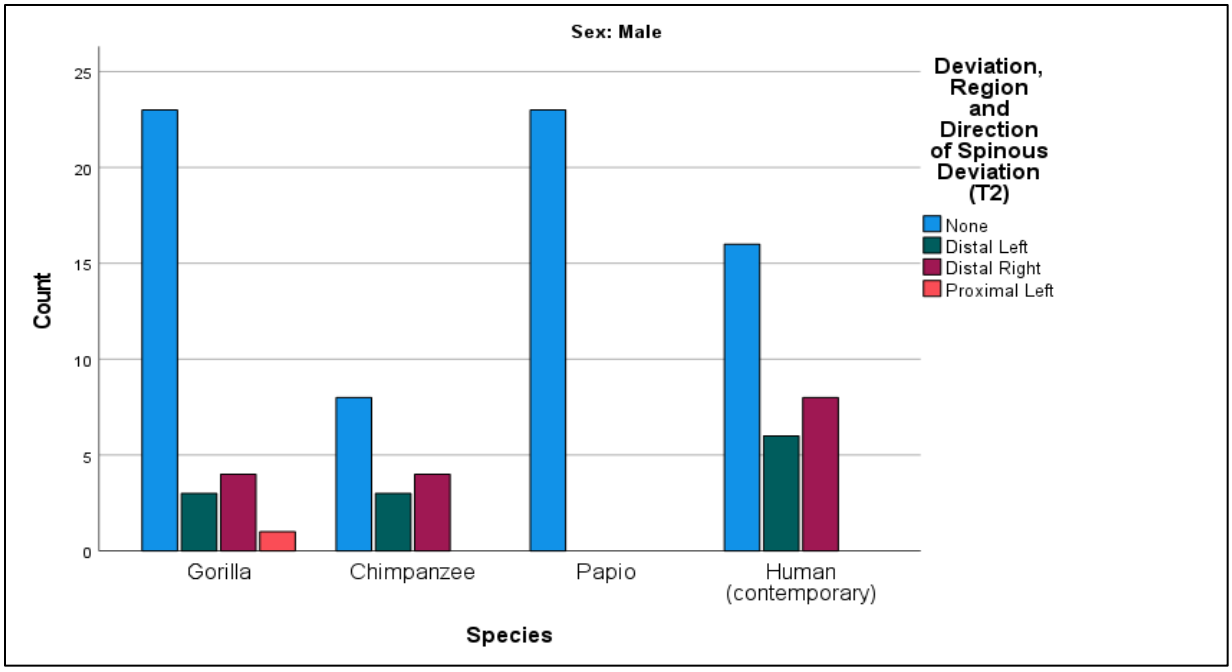


Figure 3.4: Bar graph of male T2 spinous process deviation per species.

In the female sample groups comparison for T2, the chimpanzees showed the highest overall incidence of deviations with 53.3% (n=16), with baboons showing the lowest incidence of 7.1% (n=2). Of the deviations noted, the distal right deviations were highest in the chimpanzee groups with 33.3% (n=10), with proximal right deviations being absent in all groups (n=0). This is depicted visually in Figure 3.5.

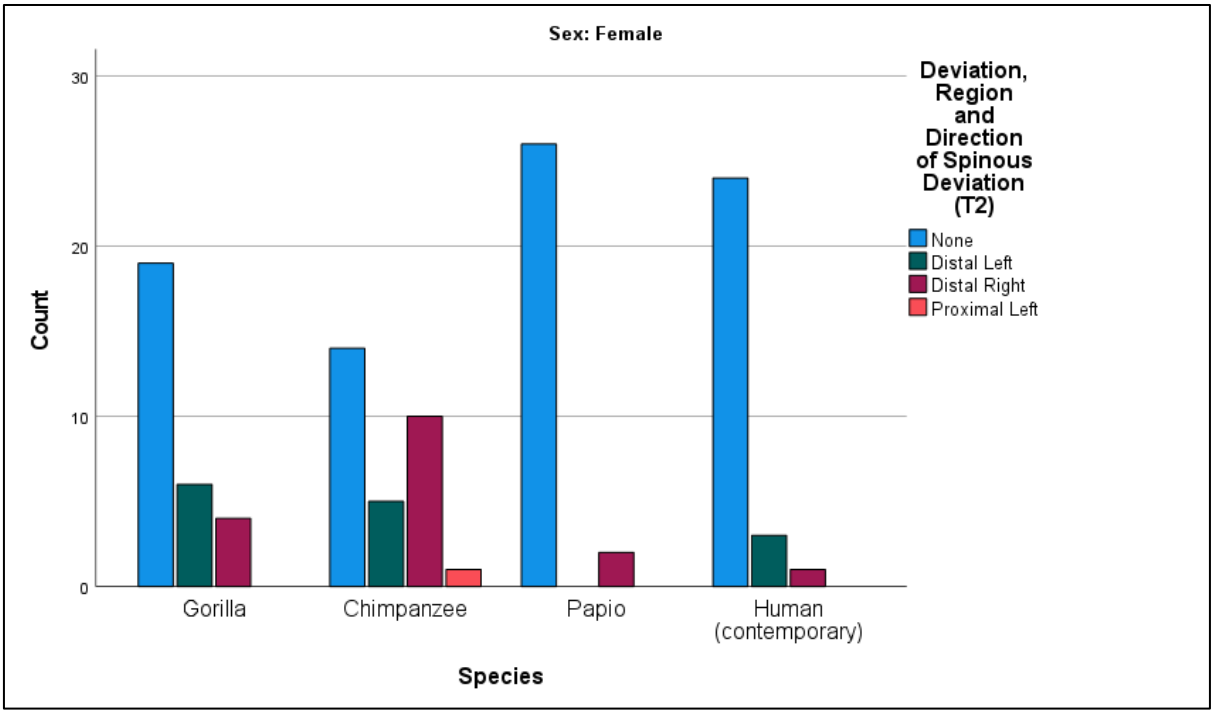


Figure 3.5: Bar graph of female T2 spinous process deviation per species.

In the overall species comparison (male and female combined) for T2 (as indicated in Table 3.6), the chimpanzee group showed the highest overall incidence of 51.1% (n=23), with baboons showing the lowest incidence of 3.9% (n=2). Of the deviations noted, the distal right deviations were highest in the chimpanzee group with 31.1% (n=14), with proximal right deviations being absent for all and species at T2 (n=0). This is depicted visually in Figure 3.6.

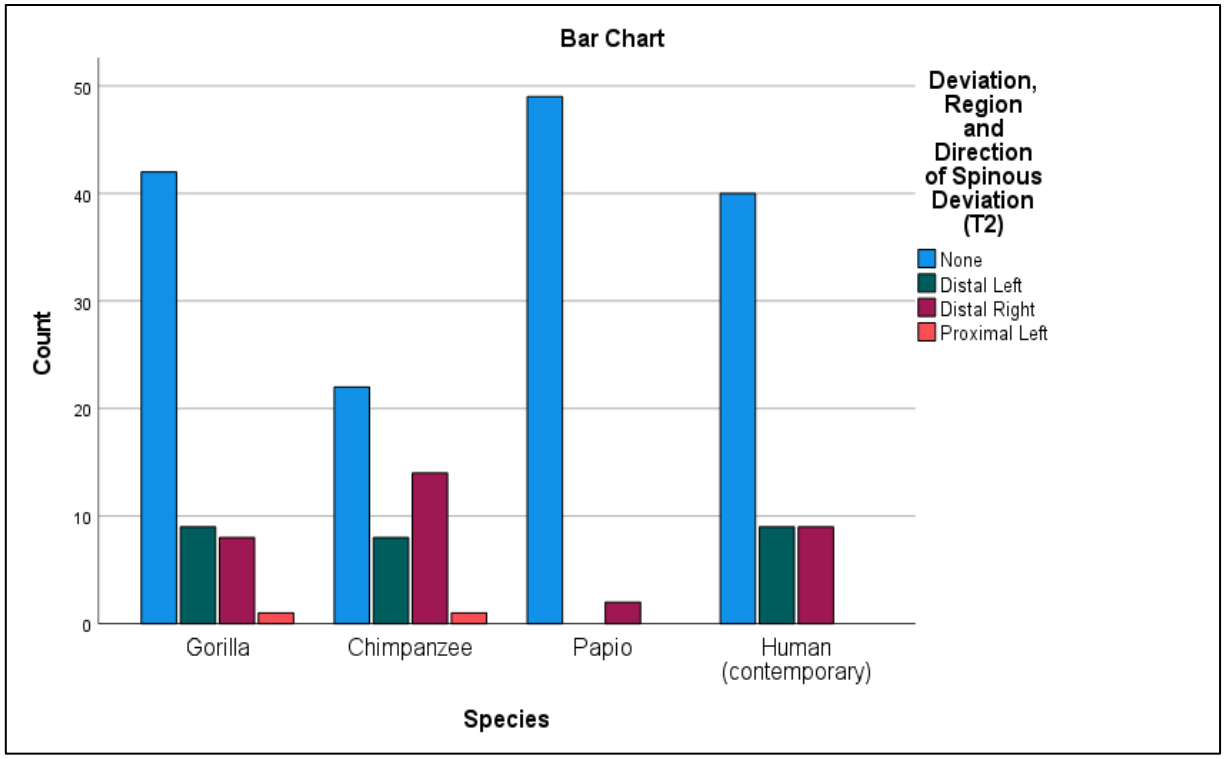


Figure 3.6: Bar graph of overall species T2 spinous process deviation.

Mean values of facet width (right and left superior and inferior) were calculated for T2 specimens with deviations and were compared to the overall sample group measurements means for T2 specimens (Appendix 8). On comparison, all measurements were within the standard deviations, indicating no differences between specimens with or without SPD (Appendices 6 and 7).

3.4.3 T3 SPDRD per sex and species

Table 3.7 summarizes the T3 spinous process deviations (in terms of being present, direction and region) for sex per species, and total per species. In the male sample groups comparison for T3, the contemporary human group showed the highest overall incidence of 50% (n=15) and was absent in baboons (n=0). Of the deviations

noted, the distal right deviations had the highest incidence in the contemporary humans of 30% (n=9), with proximal right deviations being absent in all groups (n=0). This is depicted visually in Figure 3.7.

Table 3.7: Cross tabulation and frequency of T3 spinous process deviation per sex and species.

				DRD_T3					Total
Species				**None**	**Distal Left**	**Distal Right**	**Proximal Left**	**Proximal Right**	
Gorillas	**Sex**	**Male**	**Count**	20	7	3	1	0	31
			% within sex	64.5%	22.6%	9.7%	3.2%	0%	100.0%
		Female	**Count**	19	4	4	2	0	29
			% within sex	65.5%	13.8%	13.8%	6.9%	0%	100.0%
	Total		**Count**	39	11	7	3	0	60
			% total	65.0%	18.3%	11.7%	5.0%	0%	100.0%
Chimpanzees	**Sex**	**Male**	**Count**	9	4	1	1	0	15
			% within sex	60.0%	26.7%	6.7%	6.7%	0%	100.0%
		Female	**Count**	18	7	4	0	1	30
			% within sex	60.0%	23.3%	13.3%	0%	3.3%	100.0%
	Total		**Count**	27	11	5	1	1	45
			% total	60.0%	24.4%	11.1%	2.2%	2.2%	100.0%
Baboons	**Sex**	**Male**	**Count**	23	0	0	0	0	23
			% within sex	100.0 %	0%	0%	0%	0%	100.0%
		Female	**Count**	26	0	2	0	0	28
			% within sex	92.9%	0%	7.1%	0%	0%	100.0%
	Total		**Count**	49	0	2	0	0	51
			% total	96.1%	0%	3.9%	0%	0%	100.0%
Contemporary humans	**Sex**	**Male**	**Count**	15	6	9	0	0	30
			% within sex	50.0%	20.0%	30.0%	0%	0%	100.0%
		Female	**Count**	19	7	2	0	0	28
			% within sex	67.9%	25.0%	7.1%	0%	0%	100.0%
	Total		**Count**	34	13	11	0	0	58
			% total	58.6%	22.4%	19.0%	0%	0%	100.0%

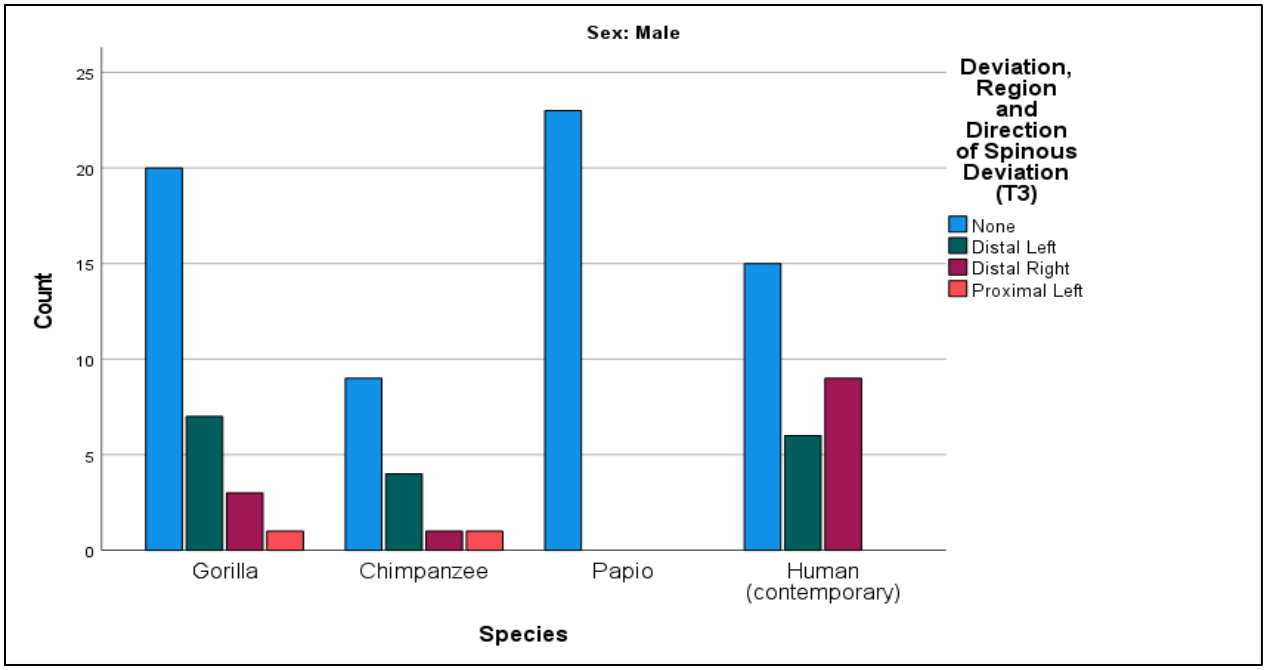


Figure 3.7: Bar graph of male T3 spinous process deviation per species.

In the female sample groups comparison for T3 (Table 3.3), the chimpanzee group showed the highest overall incidence with 40% (n=13), with baboons showing the lowest incidence of 7.1% (n=2). Of the deviations noted, the distal right deviations were highest in the chimpanzee group with 13.8% (n=4), with proximal right deviations being absent in gorillas, baboons, and contemporary humans (n=0). This is depicted visually in Figure 3.8.

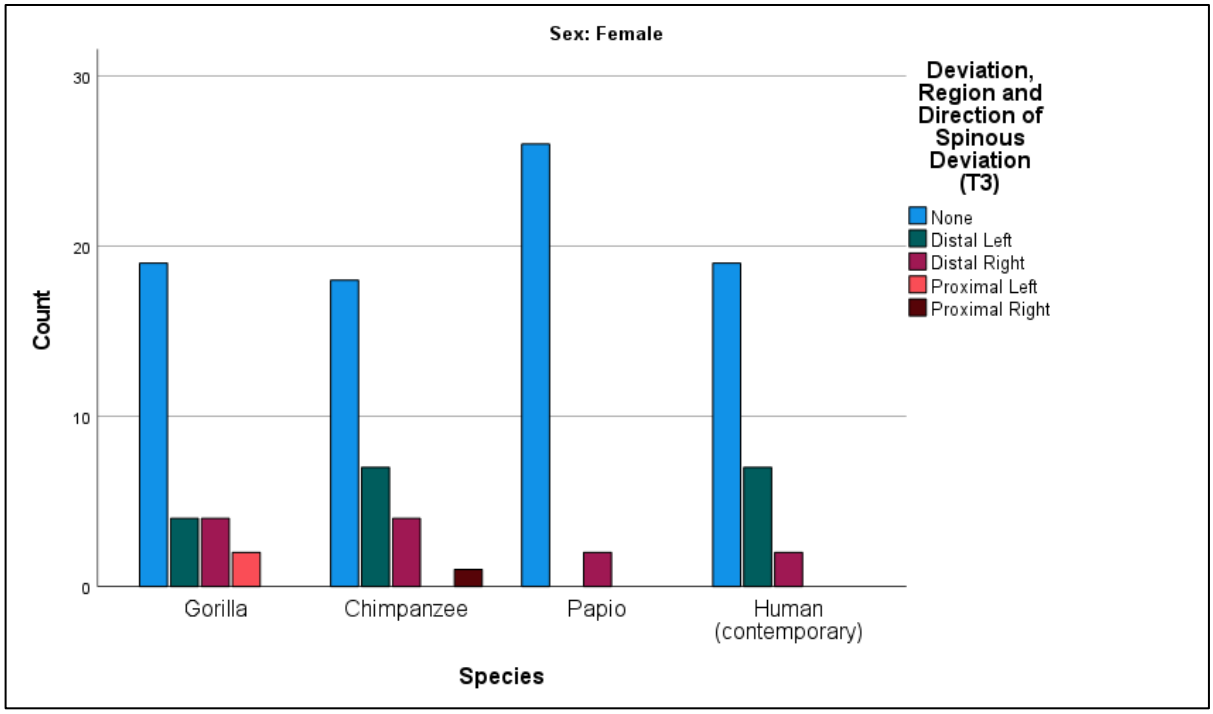


Figure 3.8: Bar graph of female T3 spinous process deviation per species.

In the overall species comparison (male and female combined) for T3 (as indicated in Table 3.7), the contemporary human group showed the highest overall incidence of 41.4% (n=24), with baboons showing the lowest incidence of 3.9% (n=2). Of the deviations noted, the distal left deviations were highest in the chimpanzee group with 24.4% (n=11), with proximal right deviations being absent for gorilla, baboon, and contemporary human groups at T3 (n=0). This is depicted visually in Figure 3.9.

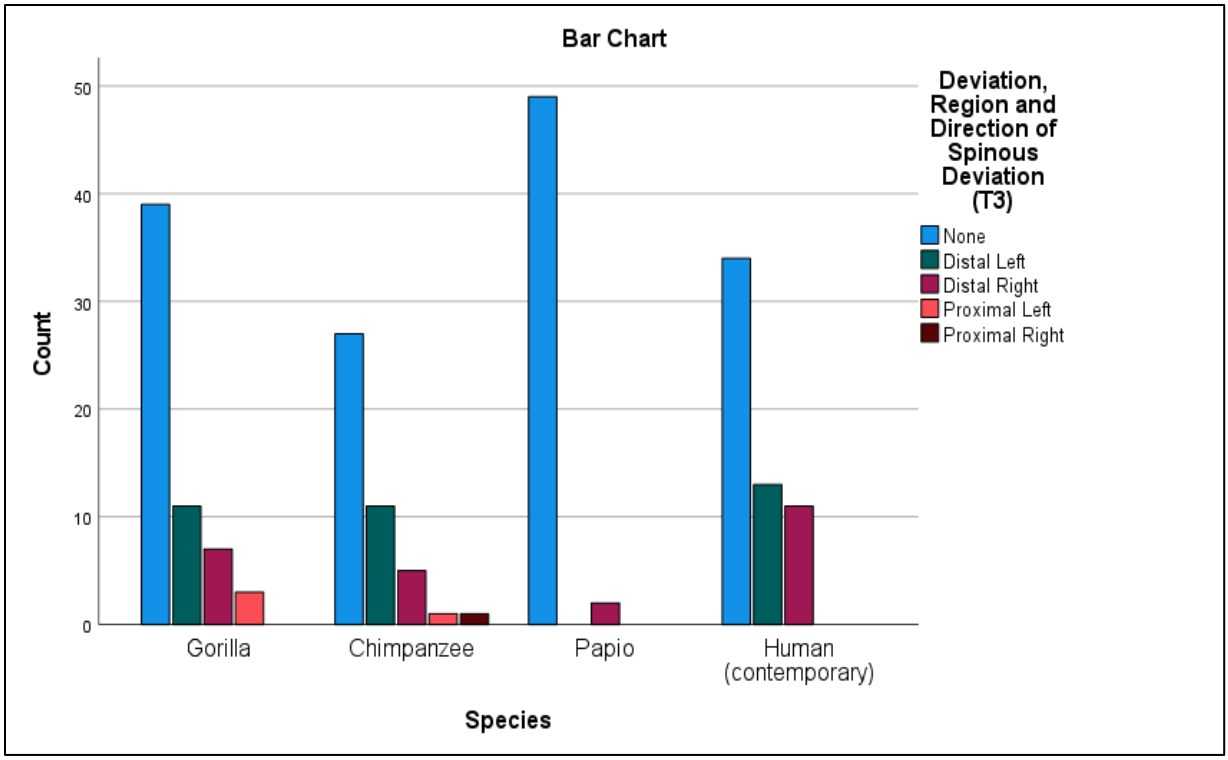


Figure 3.9: Bar graph of overall species T3 spinous process deviation.

Mean values of facet width (right and left superior and inferior) were calculated for T3 specimens with deviations and were compared to overall sample group measurements means for T3 specimens (Appendix 8). On comparison, all measurements were within the standard deviations, indicating no differences between specimens with or without SPD (Appendices 6 and 7).

3.4.4 T4 SPDRD per sex and species

Table 3.8 summarizes the T4 spinous process deviations (in terms of being present, direction and region) for sex per species, and total per species. In the male sample groups comparison for T4, the gorilla groups showed the highest overall incidence of 45.2% (n=14), with baboons showing the lowest incidence of 13% (n=3). Of

the deviations noted, the distal left deviations had the highest incidence in gorillas 19.4% (n=6), with proximal deviations to the left being absent in baboons and contemporary humans (n=0), and proximal deviations to the right being absent in chimpanzees and baboons (n=0). This is depicted visually in Figure 3.10.

Table 3.8: Cross tabulation and frequency of T4 spinous process deviation per sex and species.

Species				DRD_T4					Total
				None	Distal Left	Distal Right	Proximal Left	Proximal Right	
Gorillas	**Sex**	**Male**	**Count**	17	6	4	3	1	31
			% within sex	54.8%	19.4%	12.9%	9.7%	3.2%	100.0%
		Female	**Count**	14	5	9	1	0	29
			% within sex	48.3%	17.2%	31.0%	3.4%	0%	100.0%
	Total		**Count**	31	11	13	4	1	60
			% total	51.7%	18.3%	21.7%	6.7%	1.7%	100.0%
Chimpanzees	**Sex**	**Male**	**Count**	12	2	1	0	0	15
			% within sex	80.0%	13.3%	6.7%	0%	0%	100.0%
		Female	**Count**	16	8	4	2	0	30
			% within sex	53.3%	26.7%	13.3%	6.7%	0%	100.0%
	Total		**Count**	28	10	5	2	0	45
			% total	62.2%	22.2%	11.1%	4.4%	0%	100.0%
Baboons	**Sex**	**Male**	**Count**	20	1	2	0	0	23
			% within sex	87.0%	4.3%	8.7%	0%	0%	100.0%
		Female	**Count**	27	1	0	0	0	28
			% within sex	96.4%	3.6%	0.0%	0%	0%	100.0%
	Total		**Count**	47	2	2	0	0	51
			% total	92.2%	3.9%	3.9%	0%	0%	100.0%
Contemporary humans	**Sex**	**Male**	**Count**	22	3	4	0	1	30
			% within sex	73.3%	10.0%	13.3%	0%	3.3%	100.0%
		Female	**Count**	24	2	2	0	0	28
			% within sex	85.7%	7.1%	7.1%	0%	0.0%	100.0%
	Total		**Count**	46	5	6	0	1	58
			% total	79.3%	8.6%	10.3%	0%	1.7%	100.0%

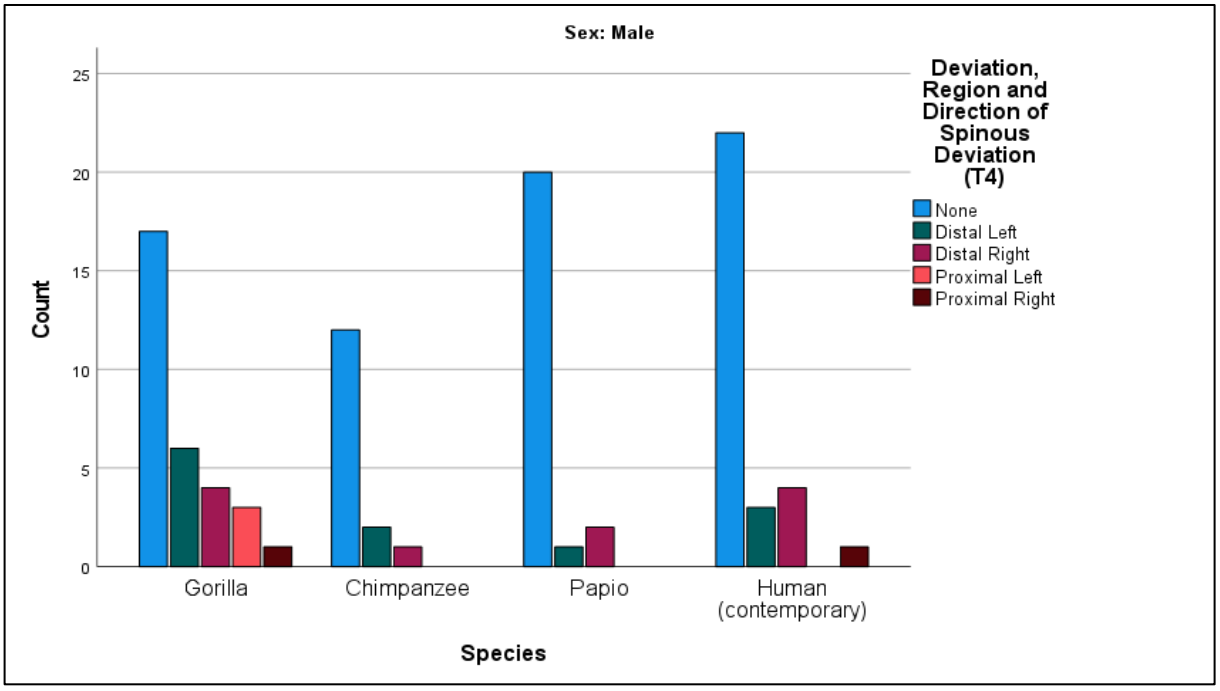


Figure 3.10: Bar graph of male T4 spinous process deviation per species.

In the female sample groups comparison for T4 (Table 3.8), the gorilla group showed the highest overall incidence with 51.7% (n=15), with baboons showing the lowest incidence of 3.6% (n=1). Of the deviations noted, the distal right deviations had the highest incidence in the gorilla group with 31% (n=9), with proximal deviations to the right being absent in chimpanzees and baboons (n=0) and proximal deviations to the left being absent in baboons and contemporary humans (n=0). This is depicted visually in Figure 3.11.

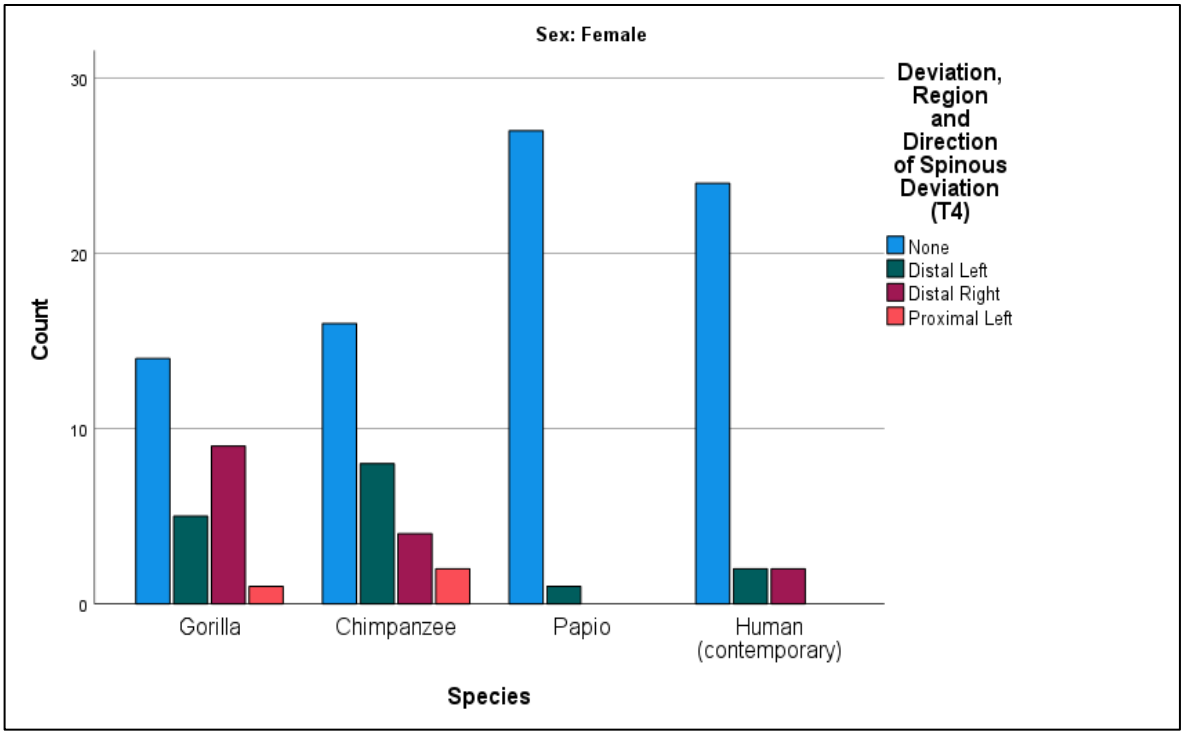


Figure 3.11: Bar graph of female T4 spinous process deviation per species.

In the overall species comparison (male and female combined) for T4 (as indicated in Table 3.8), the gorilla groups showed the highest overall incidence of 48.3% (n=29), with baboons showing the lowest incidence of 7.8% (n=4). Of the deviations noted, the distal left deviations had the highest incidence in the chimpanzee group with 22.2% (n=10), with proximal deviations to the right being absent in chimpanzees and baboons (n=0) and proximal deviations to the left being absent in baboons and contemporary humans (n=0). This is depicted visually in Figure 3.12.

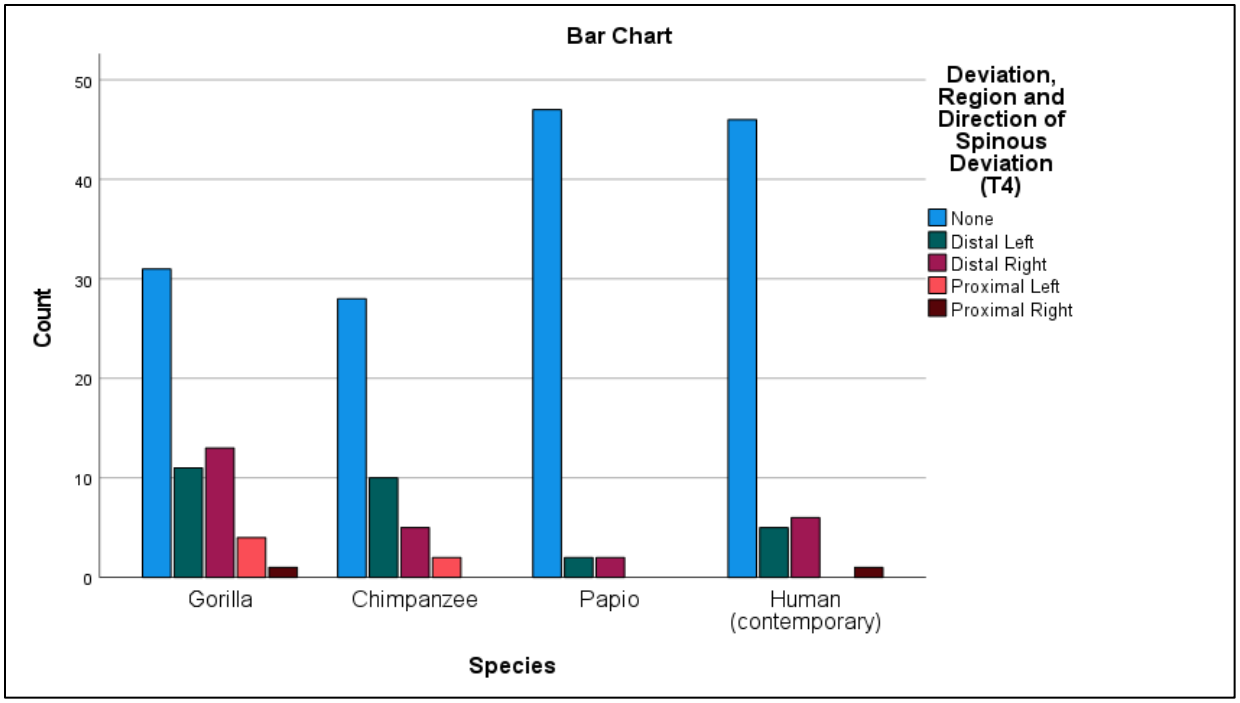


Figure 3.12: Bar graph of overall species T4 spinous process deviation.

Mean values of facet width (right and left superior and inferior) were calculated for T4 specimens with deviations and were compared to overall sample group measurements means for T4 specimens (Appendix 8). On comparison, all measurements were within the standard deviations, indicating no differences between specimens with or without SPD (Appendices 6 and 7).

3.4.5 T5 SPDRD per sex and species

Table 3.9 summarizes the T5 spinous process deviations (in terms of being present, direction and region) for sex per species, and total per species. In the male sample groups comparison for T5, the gorilla group showed the highest overall incidence of 43.3% (n=13), with baboons showing the lowest incidence of 13% (n=3). Of the deviations noted, the distal left and right deviations had the highest incidence in

chimpanzees with 20% (n=3), with proximal deviations to the left being absent in baboons and contemporary humans (n=0), and proximal right deviations being absent in baboons (n=0). This is depicted visually in Figure 3.13.

Table 3.9: Cross tabulation and frequency of T5 spinous process deviation per sex and species.

				DRD_T5					Total
Species				**None**	**Distal Left**	**Distal Right**	**Proximal Left**	**Proximal Right**	
Gorillas	**Sex**	**Male**	**Count**	17	4	4	3	2	30
			% within sex	56.7%	13.3%	13.3%	10.0%	6.7%	100.0%
		Female	**Count**	15	3	8	3	0	29
			% within sex	51.7%	10.3%	27.6%	10.3%	0%	100.0%
	Total		**Count**	32	7	12	6	2	59
			% total	54.2%	11.9%	20.3%	10.2%	3.4%	100.0%
Chimpanzees	**Sex**	**Male**	**Count**	9	3	3	0	0	15
			% within sex	60.0%	20.0%	20.0%	0%	0%	100.0%
		Female	**Count**	13	8	4	3	2	30
			% within sex	43.3%	26.7%	13.3%	10.0%	6.7%	100.0%
	Total		**Count**	22	11	7	3	2	45
			% total	48.9%	24.4%	15.6%	6.7%	4.4%	100.0%
Baboons	**Sex**	**Male**	**Count**	20	2	1	0	0	23
			% within sex	87.0%	8.7%	4.3%	0%	0%	100.0%
		Female	**Count**	25	1	2	0	0	28
			% within sex	89.3%	3.6%	7.1%	0%	0%	100.0%
	Total		**Count**	45	3	3	0	0	51
			% total	88.2%	5.9%	5.9%	0%	0%	100.0%
Contemporary humans	**Sex**	**Male**	**Count**	21	4	3	0	2	30
			% within sex	70.0%	13.3%	10.0%	0%	6.7%	100.0%
		Female	**Count**	24	2	2	0	0	28
			% within sex	85.7%	7.1%	7.1%	0%	0%	100.0%
	Total		**Count**	45	6	5	0	2	58
			% total	77.6%	10.3%	8.6%	0%	3.4%	100.0%

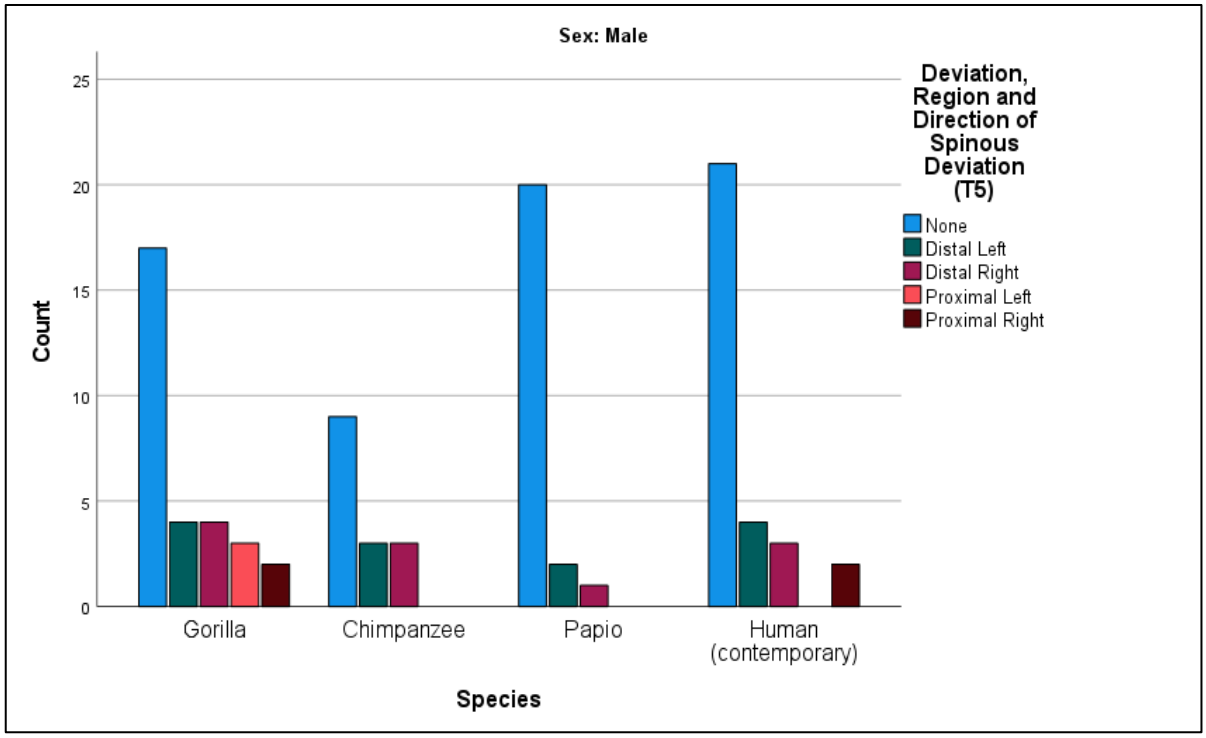


Figure 3.13: Bar graph of male T5 spinous process deviation per species.

In the female sample groups comparison for T5 (Table 3.9), the chimpanzee group showed the highest overall incidence with 56.7% (n=17), with baboons showing the lowest incidence of 11.7% (n=3). Of the deviations noted, the distal left deviations had the highest incidence in the chimpanzee group with 26.7% (n=8), with proximal deviations to the right being absent in baboons (n=0) and proximal deviations to the left being absent in baboons and contemporary humans (n=0). This is depicted visually in Figure 3.14.

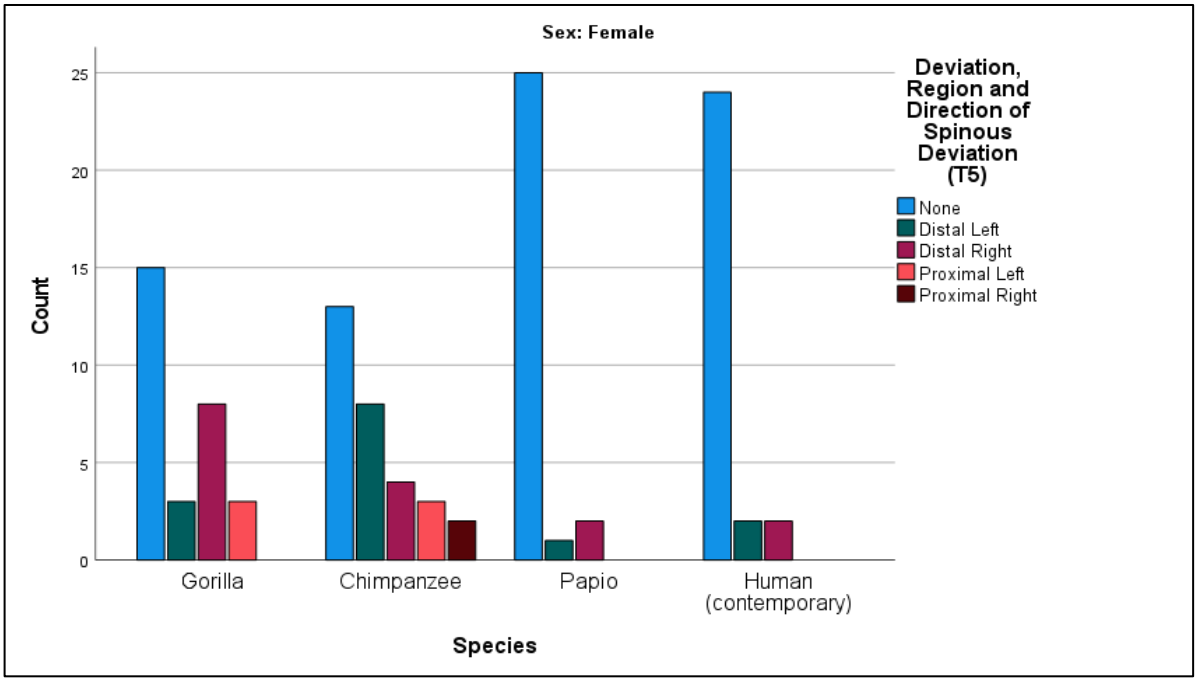


Figure 3.14: Bar graph of female T5 spinous process deviation per species.

In the overall species comparison (male and female combined) for T5 (as indicated in Table 3.9), the chimpanzee groups showed the highest overall incidence of 51.1% (n=23), with baboons showing the lowest incidence of 11.8% (n=6). Of the deviations noted, the distal left deviations had the highest incidence in the chimpanzee groups with 24.4% (n=11), with proximal deviations to the right being absent in baboons (n=0) and left proximal deviations being absent in baboons and contemporary humans (n=0). This is depicted visually in Figure 3.15.

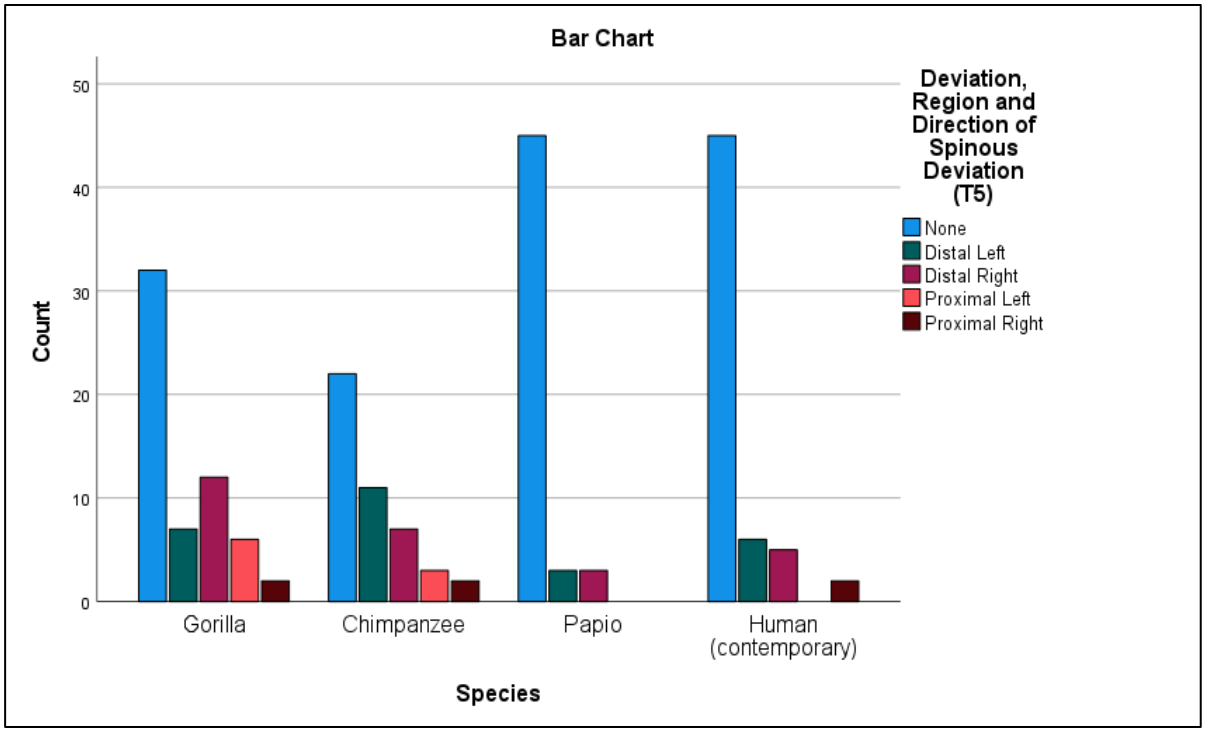


Figure 3.15: Bar graph of overall species T5 spinous process deviation.

Mean values of facet width (right and left superior and inferior) were calculated for T5 specimens with deviations and were compared to overall sample group measurements means for T5 specimens (Appendix 8). On comparison, all measurements were within the standard deviations, indicating no differences between specimens with or without SPD (Appendices 6 and 7).

3.4.6 T6 SPDRD per sex and species

Table 3.10 summarizes the T6 spinous process deviations (in terms of being present, direction and region) for sex per species, and total per species. In the male sample groups comparison for T6, the gorilla group showed the highest overall incidence of 54.8% (n=17), with baboons showing the lowest incidence of 17.4% (n=4). Of the deviations noted, the distal left had the highest incidence in chimpanzees with

26.7% (n=4), with proximal deviations to the left being absent in baboons and contemporary humans (n=0), and right proximal deviations being absent in baboons (n=0). This is depicted visually in Figure 3.16.

Table 3.10: Cross tabulation and frequency of T6 spinous process deviation per sex and species.

Species				DRD_T6					Total
				None	Distal Left	Distal Right	Proximal Left	Proximal Right	
Gorillas	**Sex**	**Male**	**Count**	14	5	5	4	3	31
			% within sex	45.2%	16.1%	16.1%	12.9%	9.7%	100.0%
		Female	**Count**	21	2	4	1	1	29
			% within sex	72.4%	6.9%	13.8%	3.4%	3.4%	100.0%
	Total		**Count**	35	7	9	5	4	60
			% total	58.3%	11.7%	15.0%	8.3%	6.7%	100.0%
Chimpanzees	**Sex**	**Male**	**Count**	9	4	1	0	1	15
			% within sex	60.0%	26.7%	6.7%	0.0%	6.7%	100.0%
		Female	**Count**	13	7	6	4	0	30
			% within sex	43.3%	23.3%	20.0%	13.3%	0.0%	100.0%
	Total		**Count**	22	11	7	4	1	45
			% total	48.9%	24.4%	15.6%	8.9%	2.2%	100.0%
Baboons	**Sex**	**Male**	**Count**	19	2	2	0	0	23
			% within sex	82.6%	8.7%	8.7%	0%	0%	100.0%
		Female	**Count**	27	0	1	0	0	28
			% within sex	96.4%	0.0%	3.6%	0%	0%	100.0%
	Total		**Count**	46	2	3	0	0	51
			% total	90.2%	3.9%	5.9%	0%	0%	100.0%
Contemporary humans	**Sex**	**Male**	**Count**	21	4	4	0	1	30
			% within sex	70.0%	13.3%	13.3%	0%	3.3%	100.0%
		Female	**Count**	25	1	2	0	0	28
			% within sex	89.3%	3.6%	7.1%	0%	0.0%	100.0%
	Total		**Count**	46	5	6	0	1	58
			% total	79.3%	8.6%	10.3%	0%	1.7%	100.0%

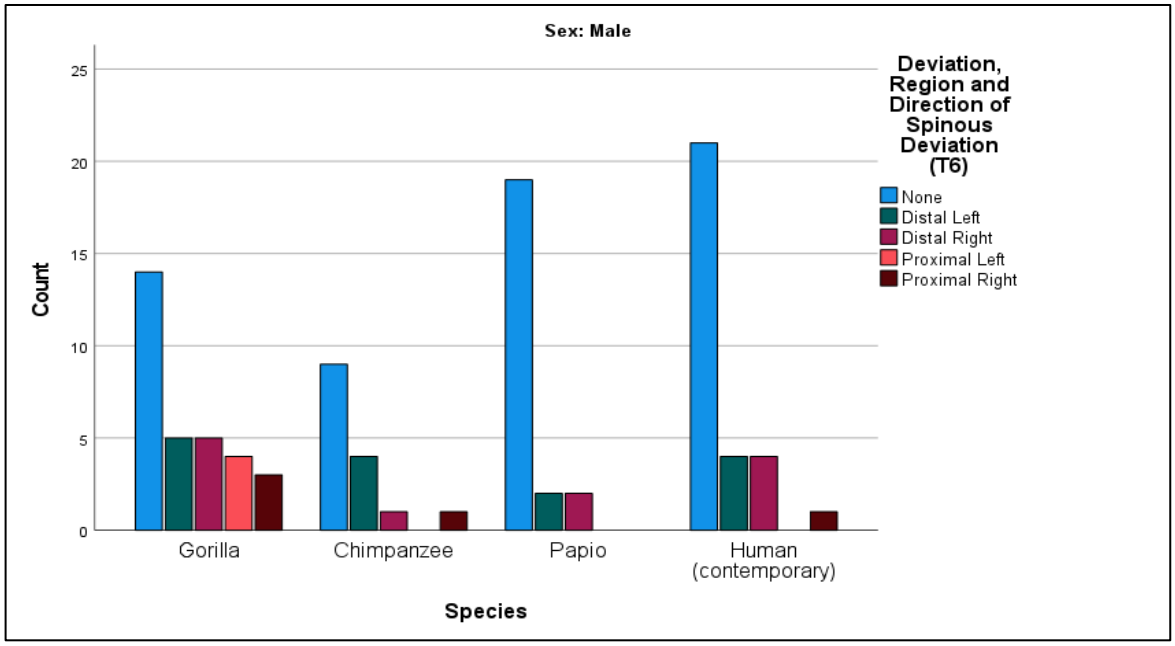


Figure 3.16: Bar graph of male T6 spinous process deviation per species.

In the female sample groups comparison for T6 (Table 3.10), the chimpanzee group showed the highest overall incidence with 56.7% (n=13), with baboons showing the lowest incidence of 3.6% (n=1). Of the deviations noted, the distal left deviations had the highest incidence in the chimpanzee group with 23.3% (n=7), with proximal deviations to the right being absent in baboons (n=0) and proximal deviations to the left being absent in baboons and contemporary humans (n=0). This is depicted visually in Figure 3.17.

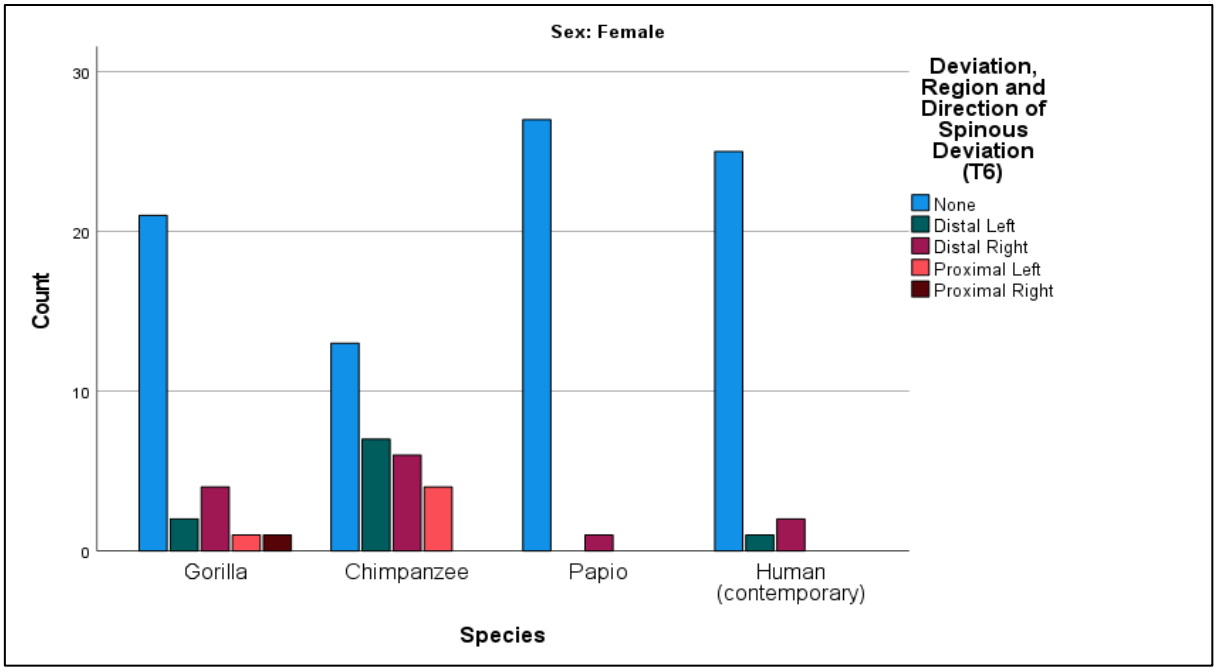


Figure 3.17: Bar graph of female T6 spinous process deviation per species.

In the overall species comparison (male and female combined) for T6 (as indicated in Table 3.10), the chimpanzee groups showed the highest overall incidence of 51.1% (n=23), with baboons showing the lowest incidence of 9.8% (n=5). Of the deviations noted, the distal left deviations had the highest incidence in the chimpanzee groups with 24.4% (n=11), with proximal deviations to the right being absent in baboons (n=0) and left proximal deviations being absent in baboons and contemporary humans (n=0). This is depicted visually in Figure 3.18.

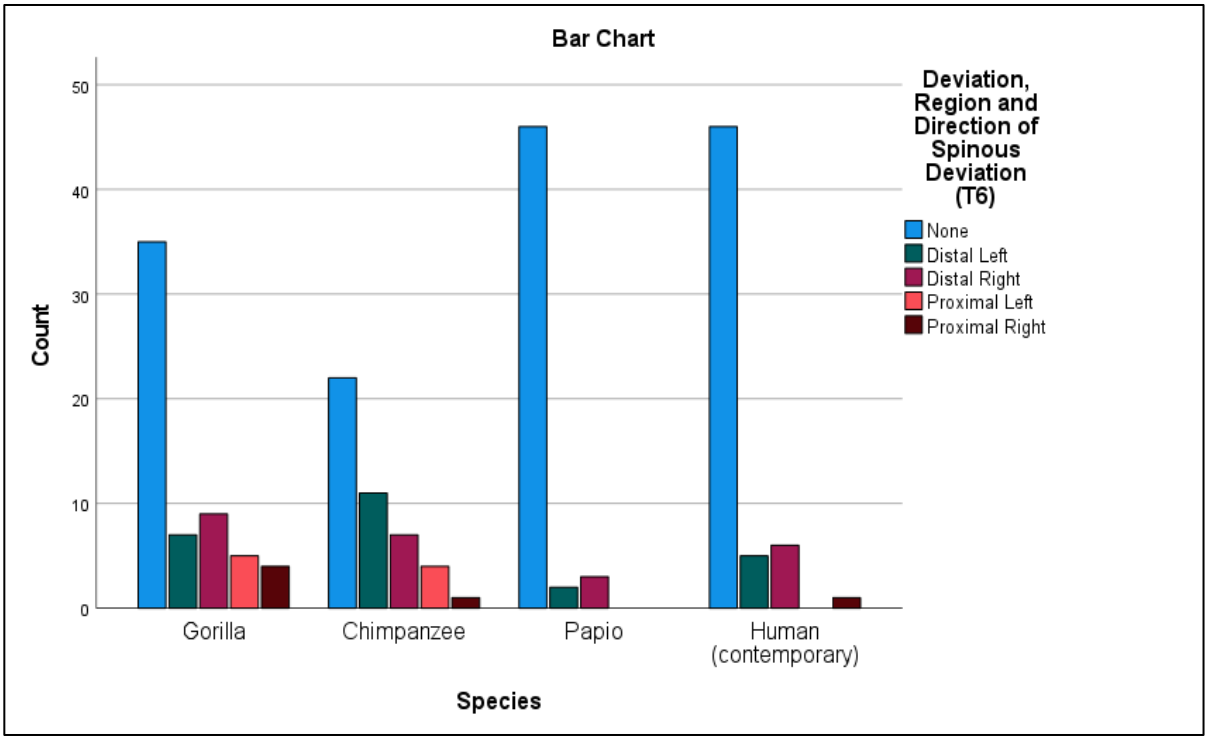


Figure 3.18: Bar graph of overall species T6 spinous process deviation.

Mean values of facet width (right and left superior and inferior) were calculated for T6 specimens with deviations and were compared to overall sample group measurements means for T6 specimens (Appendix 8). On comparison, all measurements were within the standard deviations, indicating no differences between specimens with or without SPD (Appendices 6 and 7).

3.4.7 Frequency of SPDRD presentation per sex and species

Table 3.11 is a representation of the overall frequency of SPDRD in all species and vertebral levels combined. T1 demonstrated the lowest incidence of SPD with 79.4% (n=170) showing no SPD. T5 showed the highest incidence of SPD with 67.6% (n=144) showing no SPD. Overall, 71.5% (n=917) of the specimens did not demonstrate SPD with the majority of the SPD's being distal left (12.2%, n=157) or distal right

(12.7%, n=163), with proximal deviations being 2.4%(n=31) for the left and 1.2%(n=15) for the right.

Table 3.11: SPDRD frequencies in all species and levels combined.

Level		None	Distal left	Distal right	Proximal left	Proximal right	Total
T1	**Count**	170	16	27	1	0	214
	%	79.4%	7.5%	12.6%	0.5%	0.0%	100.0%
T2	**Count**	153	26	33	2	0	214
	%	71.5%	12.1%	15.4%	0.9%	0.0%	100.0%
T3	**Count**	149	35	25	4	1	214
	%	69.6%	16.4%	11.7%	1.9%	0.5%	100.0%
T4	**Count**	152	28	26	6	2	214
	%	71.0%	13.1%	12.1%	2.8%	0.9%	100.0%
T5	**Count**	144	27	27	9	6	213
	%	67.6%	12.7%	12.7%	4.2%	2.8%	100.0%
T6	**Count**	149	25	25	9	6	214
	%	69.6%	11.7%	11.7%	4.2%	2.8%	100.0%
Total	**Count**	917	157	163	31	15	1283
	%	71.5%	12.2%	12.7%	2.4%	1.2%	100.0%

Table 3.12 summarizes the percentage of individuals per sex and species that presented with at least 1 SPD in the sequence of T1-T6 evaluated. Chimpanzees demonstrated the highest frequency of SPD with 91.11% (n=41) and baboons the lowest with 39.24% (n=20). In the comparison for male sex the gorillas demonstrated the highest frequency of 93.56% (n=29) with baboons the lowest with 56.52% (n=13). In the comparison for female sex the chimpanzees demonstrated the highest frequency of 90% (n=27) and baboons the lowest with 25% (n=7).

Table 3.12: SPD frequency per individual spinal series per species and sex.

				SPD within T1-T6
Gorillas (n=60)	**Sex**	**Male (n=31)**	**Count**	29
			% within sex	93.56%
		Female (n=29)	**Count**	21
			% within sex	72.41%
	Total		**Count**	50
			% total	83.33%
Chimpanzees (n=45)	**Sex**	**Male (n=15)**	**Count**	14
			% within sex	93.33%
		Female (n=30)	**Count**	27
			% within sex	90%
	Total		**Count**	41
			% total	91.11%
Baboons (n=51)	**Sex**	**Male (n=23)**	**Count**	13
			% within sex	56.52%
		Female (n=28)	**Count**	7
			% within sex	25%
	Total		**Count**	20
			% total	39.24%
Contemporary humans (n=58)	**Sex**	**Male (n=30)**	**Count**	25
			% within sex	83.33%
		Female (n=28)	**Count**	19
			% within sex	67.86%
	Total		**Count**	45
			% total	77.59%

3.4.8 Frequency of SPD in age and sex in contemporary human

In the contemporary human groups, age was available for interpretation related to SPD. As indicated in Table 3.13, 9% (n=5) of the specimens did not have an age indicated, with a total usable number of specimens 91% (n=53) indicating age. The age ranged from 18 years to 86 years, with a mean of 47 (SD±15.52) years.

Table 3.13: Age related information for the contemporary human group

Total sample size (n)	58
Specimens with known age indicated (%)	53 (91%)
Minimum age	18 years
Maximum age	86 years
Mean age (SD)	47 (±15.52) years

The specimens within the groups were compared to determine the frequency of SPD within age ranges as indicated in Table 3.14.

In the 18-30 years age range (15.09%, n=8) overall frequency of SPD (in the sample group of 53) was 15.09% (n=5), with males demonstrating 100% (n=2) and females 50% (n=3), representing a total frequency of 62.5% (n=5) demonstrating SPD within this age range. In the 31-40 years age range (24.53%, n=13) overall frequency of SPD (in the sample group of 53) was 22.65% (n=12). Males had 90% (n=9) and females 100% (n=3), representing a total frequency of 93.33% (n=12) demonstrating SPD within this age range. In the 41-50 years age range (20.75%, n=11) overall frequency of SPD (in the sample group of 53) was 15.09% (n=8). Males had 87.5% (n=7) and females 33.33% (n=1), representing a total frequency of 72.72% (n=8) demonstrating SPD within this age range. In the 51-60 years age range (18.87%, n=10) overall frequency of SPD (in the sample group of 53) was 11.32% (n=6). Males had 100% (n=3) and females 42.85% (n=3), representing a total frequency of 93.33% (n=12) demonstrating SPD within this age range. In the over 60 years age range (20.75%,

n=11) overall frequency of SPD (in the sample group of 53) was 16.98% (n=9). Males had 100% (n=4) and females 71.43% (n=5), representing a total frequency of 81.81% (n=9) demonstrating SPD within this age range.

Table 3.14: Contemporary humans SPD frequency per age range and sex.

Age range (years)			
19-30 (n=8)	**Male (n=2)**	**Count with SPD**	2
		% with SPD	100%
	Female (n=6)	**Count**	3
		% with SPD	50%
Total		**Count with SPD**	5
		% total SPD	62.5%
		% total with SPD for entire group (n=53)	15.09%
31-40 (n=13)	**Male (n=10)**	**Count with SPD**	9
		% with SPD	90%
	Female (n=3)	**Count with SPD**	3
		% with SPD	100%
Total		**Count with SPD**	12
		% total SPD	93.3%
		% total with SPD for entire group (n=53)	22.65%
41-50 (n=11)	**Male (n=8)**	**Count with SPD**	7
		% with SPD	87.5%
	Female (n=3)	**Count with SPD**	1
		% with SPD	33.33%
Total		**Count with SPD**	8
		% total	72.72%
		% total with SPD for entire group (n=53)	15.09%
51-60 (n=10)	**Male (n=3)**	**Count with SPD**	3
		% with SPD	100%
	Female (n=7)	**Count with SPD**	3
		% with SPD	42.85%
Total		**Count with SPD**	6

		% total with SPD	60%
		% total with SPD for entire group (n=53)	11.32%
>60 (n=11)	**Male (n=4)**	**Count with SPD**	4
		% with SPD	100%
	Female (n=7)	**Count with SPD**	5
		% with SPD	71.43%
Total		**Count with SPD**	9
		% total with SPD	81.81%
		% total with SPD for entire group (n=53)	16.98%

3.5 Discussion

3.5.1 Morphometric measurements

This section will discuss the results relating to spinous process angle and length, and the articular facets width and orientations measured within the study.

a. Spinous process angle and length

In the current study, spinous process angle and length were measured as indicated in the preceding chapter. As presented in Table 1.5, vertebrae in contemporary humans compared to apes have developed traits as adaptations to bipedalism. Previous research indicated that all spinous processes are shorter from base to tip in contemporary humans (Schultz, 1961; Latmier and Ward, 1993; Gomez-Olivencia et al., 2013, Meyer, 2016; Meyer et al., 2017; Plomp et al., 2019), and that human upper thoracic (T1 and T2) spinous processes project more caudally than other apes (Latimer and Ward, 1993; Gomes-Olivencia et al., 2013; Plomp et al., 2019).

In terms of spinous process lengths, the current study supports the previous findings, with the contemporary humans sample showing shorter SPL in male and female sample groups compared to other primates. According to Shapiro and Simons (2002) this may be explained in relation to body mass, however this is not supported in the current study. The chimpanzees may have an average body mass of 53kg (Smith and Jungers, 1997) which is considered similar to contemporary humans and although shorter, did not show statistically significantly differences in SPL compared to contemporary humans. In addition, the baboons (as the quadrupedal primate) with an average body mass of 29.8kg in males and 14.8kg in females (Smith and Junger, 1997; Kingdon et al., 2013) demonstrated similar and in some cases longer spinous process lengths, with no statistically significant differences with contemporary humans. It would therefore support the concept that these changes are related more to biomechanical requirements of upright posture and bipedalism, with a proposed mechanism being the altered requirements of multifidus to control spinal function (Shapiro and Jungers, 1994; Panjabi et al., 1993; Shapiro 1995) and that it may limit sagittal plane mobility in contemporary humans and combined with changes in vertebral body height is an adaptation for dorsal mobility (Plomp et al., 2019).

The relative length of the spinous process may be proposed as a contributing factor to SPD, as a longer spinous processes may be expected to demonstrate more deviations due to higher torque as a result of increased lever arms from the tip of the process to the pedicle (Kotwicki and Napiontek, 2008). This increased load on the distal region of the spinous process as a muscle attachment site, is proposed to have a subsequent impact on bone remodeling (Wolff, 1870; Enlow, 1962).

Montgomery et al. (2005) proposed that mechanical stresses in the form of muscle force, may create changes in bony attachment points in more active muscles. When these muscles' entheses are subjected to increased force of contracting muscles, blood flow to the periosteum increases, which can stimulate bone growth and increase size of attachments sites to strengthen them. Mellado et al. (2011) indicated that the neural arch and its processes may present with multiple anatomic variations and congenital anomalies that result from alterations in the ossification process. This would support the concept that the increased torque on the distal aspect of the spinous process (where the muscles attach), may impact on SPD.

As indicated, the thoracic region in the great apes have long spinous processes compared with the short processes of baboons and humans (Schultz, 1961). As an example, the male gorilla samples showed the longest SP length, and the highest incidences (per sex) of SPD in all groups, and most frequent SPD at the majority of vertebral levels. When one considers the relative size of the male gorilla, this again supports the proposal, as at many vertebral levels the mean SPL of male gorilla was almost double the length of other species. Figure 3.19 illustrates the relative lengths of the T1 male samples utilized.

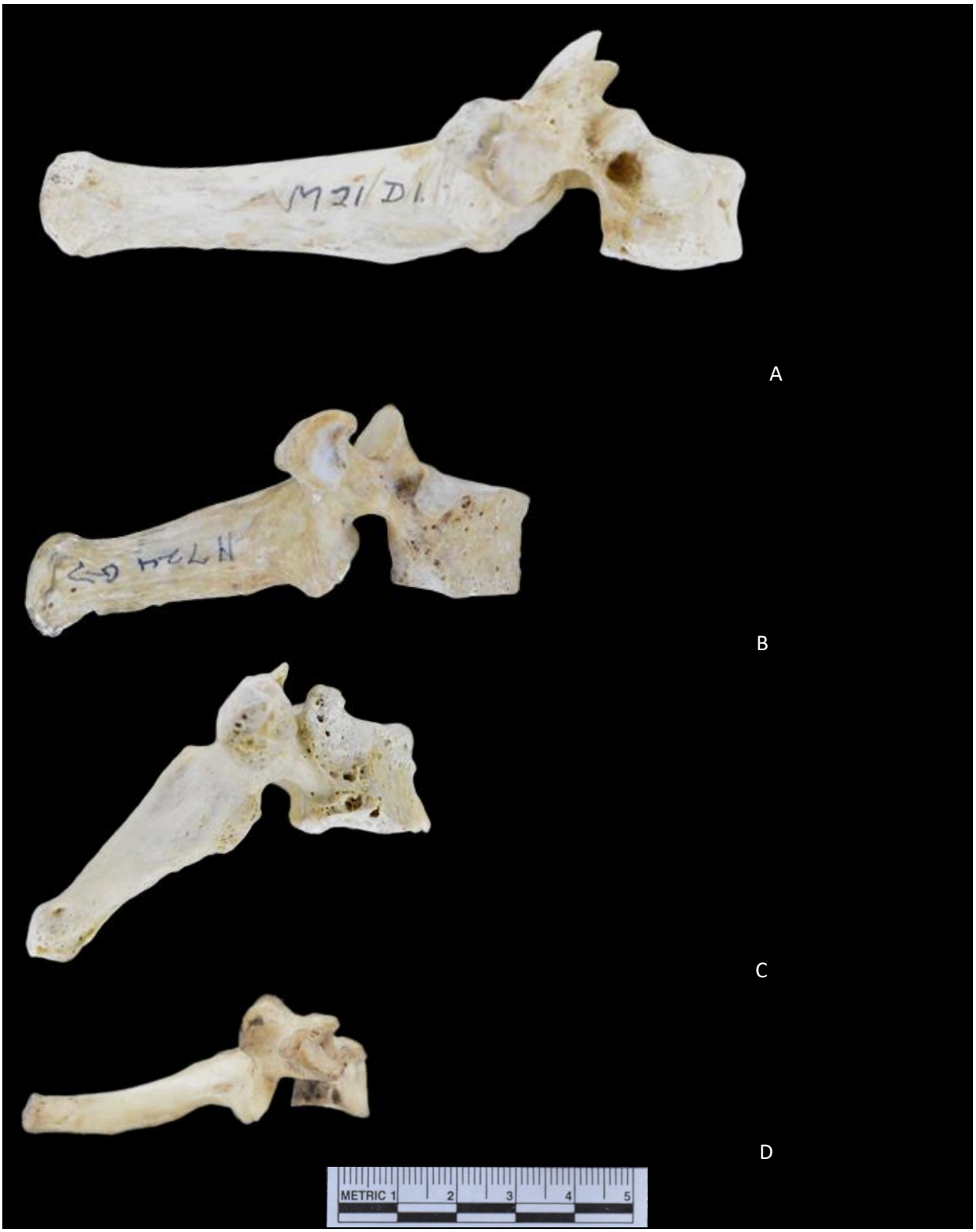


Figure 3.19: Comparative representation of size differences of T1 vertebrae (right lateral view) in male selected primates illustrating relative size. A: Gorilla; B: Chimpanzee; C: Contemporary Human; D: Baboon.

Spinous process angles demonstrated a more caudal direction in both male and female contemporary humans, and at all levels were statistically significantly different compared to the other primates. Latimer and Ward (1993) consider this an adaptation for bipedal posture where the spinous processes are less likely to impinge on one another in the lordotic curve and a create a more uniform spacing of the processes.

b. Articular facet width and orientation

Articular facet width was compared between species, and differences appear to be related to the size of species, and sexual dimorphism within the species. Sexual skeletal size dimorphism is proposed in contemporary humans to be in the region of 15% (Reno et al., 2003; Plavcan et al., 2005; Plavcan, 2018) although Richmond and Jungers (1995), Harmon (2006) and Gordon et al. (2008) indicate a similar postcranial dimorphic pattern to gorillas and orangutans, with males being significantly larger than females. The male comparisons result in general showed no statistically significant differences between contemporary humans and chimpanzees in superior articular facets width, with inferior articular facet widths additionally not showing statistically significantly differences in the contemporary humans compared to gorillas for T2-T6. In the female comparison, this morphology was more similar between the contemporary humans, chimpanzees and gorillas, and would be expected given lower levels of sexual dimorphism.

Latimer and Ward (1993), Shapiro (1993), Williams and Russo (2015), Meyer et al. (2017) and Plomp et al. (2019) indicate that the thoracic spine superior and inferior articular facets are coronally orientated in contemporary humans, while in apes they are

more obliquely orientated. This is supported in the current study when evaluating the contemporary humans, although in the majority of levels were not statistically significantly different from chimpanzees. Shapiro (1993) and Been et al. (2010) consider this an adaptation to stop forward slippage of vertebrae in upright posture.

3.5.2 Frequency of spinous process deviations

The overall incidence of identified SPD was relatively low with 366 (28.53%) of the 1283 vertebrae demonstrating SPD (Table 3.11). This figure represents a frequency of SPD within all the vertebrae utilized in the study and does not give a reflection of each individuals frequency or likelihood of having a spinous process deviation within their T1-T6 sequence. This may have implications in future studies in terms of palpation of spinous process deviations in manual therapies. In the current study, there also did not appear to be any association between thoracic spine level and incidence of SPD.

Lewit (1957) found 80% of young adult humans show SPD, compared to the overall incidence in the current study of 25.67% in the contemporary human group when evaluating the entire sample of vertebrae utilized. However, an important factor to consider is the incidence of SPD within an individuals' sequence of T1-T6. This was additionally calculated (Table 3.12) and when evaluating the frequency of deviations per individual, the figure proposed by Lewit (1957) is similar to the contemporary humans frequency of 77.59%. In comparison to the other species, gorillas (83.3%) and chimpanzees (91.1%) had a higher frequency than humans. Baboons had by far the lowest occurrence with 39.24% of individuals with asymmetry. In all species, males were more likely to show asymmetry.

In terms of previous studies on contemporary humans, Lewit (1957) based his study on radiologic evidence from antero-posterior thoracic radiographs, however Van Schaik et al. (1989) stated the use of x-rays is not reliable for determining SPD, as the impression of the deviation is from the tip of the spinous process, rather than the base, and that CT should be utilized. Tang et al. (2015) found the incidence (as calculated from their sample size) to be 41.53%. What is not stated by Tang et al. (2015) was if this was a frequency within individuals or as a total figure and may be considered a low estimate based on the current study's findings. In addition, this percentage was calculated based on the data as presented by Tang et al. (2015) which was not a study directly on a frequency of SPD, and participants had degenerative changes which may have affected the figure. This is an important consideration when interpreting results presented by Lewit (1957), Ravichandrin (1983) and Van Schaik et al., (1989) who specifically discuss SPD as a component of degenerative changes. However, when evaluating their data, it should be considered that they were focused on the lumbar spine and that the mechanical forces associated with the different regions of the spine may have a direct impact on SPD.

Lawler et al. (2016) determined an incidence of SPD in archeological and modern domestic dogs vertebrae of 36% in the thoracic spine. While the overall incidence of SPD in the vertebrae is in contrast to the baboon (obligate terrestrial quadrupedalism) in the current study which demonstrated an overall incidence of 7.5%, when compared to the incidence per individuals' frequency within the T1-T6 series of 39.24%, the finding is similar to that reported by Lawler et al. (2016). Lawler et al. (2016) points out that pack burdens may have affected these samples, however, the

similarity in frequency between the dogs and baboons in this study may simply indicate that obligate quadrupedalism rather than plastic changes from work would have had this impact on the vertebrae. Alternatively, Janssens et al. (2019) suggest that these features can be normal variants in dogs, expressing fluctuating asymmetry, which is supported in the current study.

A further consideration is that the current study utilized direct morphological measurements of the vertebrae, and as such would not have been influenced by radiographic positioning errors, functional rotations or anatomical superimpositions which may exist. All primate samples were “wild collected” specimens and would not have been affected by potential change in lifestyle related to captivity (O’Regan and Kitchener, 2005; Courtney Jones et al., 2018). An additional consideration is that this was not a direct incidence analysis of each group and randomization was therefore not a factor when selecting specimens, which should be performed to accurately calculate a true incidence of SPD over the species groups.

3.5.3 Spinous process deviations in relation to age and articular facet width

Age related factors have been considered in the contemporary human group, as age was available for the majority of individuals in the sample group. By coincidence, each of the age ranges indicated had similar numbers within each range (Table 3.14). The contemporary human group can be considered a fair representation of the overall Raymond A. Dart Collection of Human Skeletons as the current studies age range of 18 to 86 years is similar to that presented by Dayal et al. (2009) of the collection majority being within 20 and 70 years of age based on the original age at death data in the Dart

Collection database. In this study, although the sample size is small, age did not appear to be a determining factor for the presentation of this feature in both males and females. It may have been anticipated that age related degenerative changes in the spine would have the potential to alter vertebral morphology (Adams and Hutton, 1980; Brown et al., 2008) and studies related to SPD in contemporary humans, have generally focused on the lumbar spine, with the implication of SPD being associated with disc degeneration (Lewit, 1957; Ravichandrin,1983; Van Schaik et al.,1989) or ageing (Aylott, 2012)

In addition to spinous process deviations frequency related to age, spinous process deviations and articular width were compared in the various species, as mechanical changes in the facet joints have been associated with degeneration and osteoarthritis (Panjabi et al.,1993; Du et al., 2016) with facet joint hypertrophy being a recognized component of the degenerative changes associated with spondylosis of the spine (Weishaupt et al., 1999; Kalichman and Hunter, 2007). Wilde et al. (1988) observed that degenerative changes of the intervertebral disc can cause an abnormal burden in the moving segment accompanied by unilateral facet joint osteoarthrosis as a result of imbalance of the muscle attachments due to the SPD (Lewit, 1957; Tang et al., 2015). Yong-Hing and Kirkaldy-Willis (1983) proposed the 3 joint complex, made up of the 2 facet joints and the intervertebral disc at an intervertebral level, whereby a biomechanical relationship exists and degenerative changes in one of the 3 joints, will ultimately result in all joints being affected.

Given these observations, the current study proposed that should spinous process deviations may be associated with altered/asymmetrical loading of the spinous process, a commensurate change in size (hypertrophy) of the associated articular facet

width (as an indicator of degenerative change) may be seen. For example, if the SPD was to the right, was there an indication of right or left hypertrophy in the related articular facet. In all species and both sexes, the mean values of facet width with SPD were compared to overall sample group measurements facet width means (Appendix 6). In addition, all measurements were within the standard deviations (Appendices 4 and 5), indicating they were potentially within the normal variation range if compared to variances. When evaluating the specimens visually, the presentation was not consistent; where articular facet degenerative and an increase in width were noted, SPD was not necessarily present. In other specimens, degenerative changes of the vertebral body did not result in facet degenerative changes, and in some specimens unilateral articular facet degeneration and width change occurred without SPD (Figure 3.20).

This would suggest that articular facet degeneration and ageing in the upper thoracic spine are not associated with SPD (as proposed in the lumbar spine) or alternatively that loading of the spinous process as a mechanism of SPD development is not significant enough to have an effect on the articular facet joint. Similarly, although in the lumbosacral region, Tang et al. (2015) concluded that no correlation was found between degeneration of the disc and SPD.

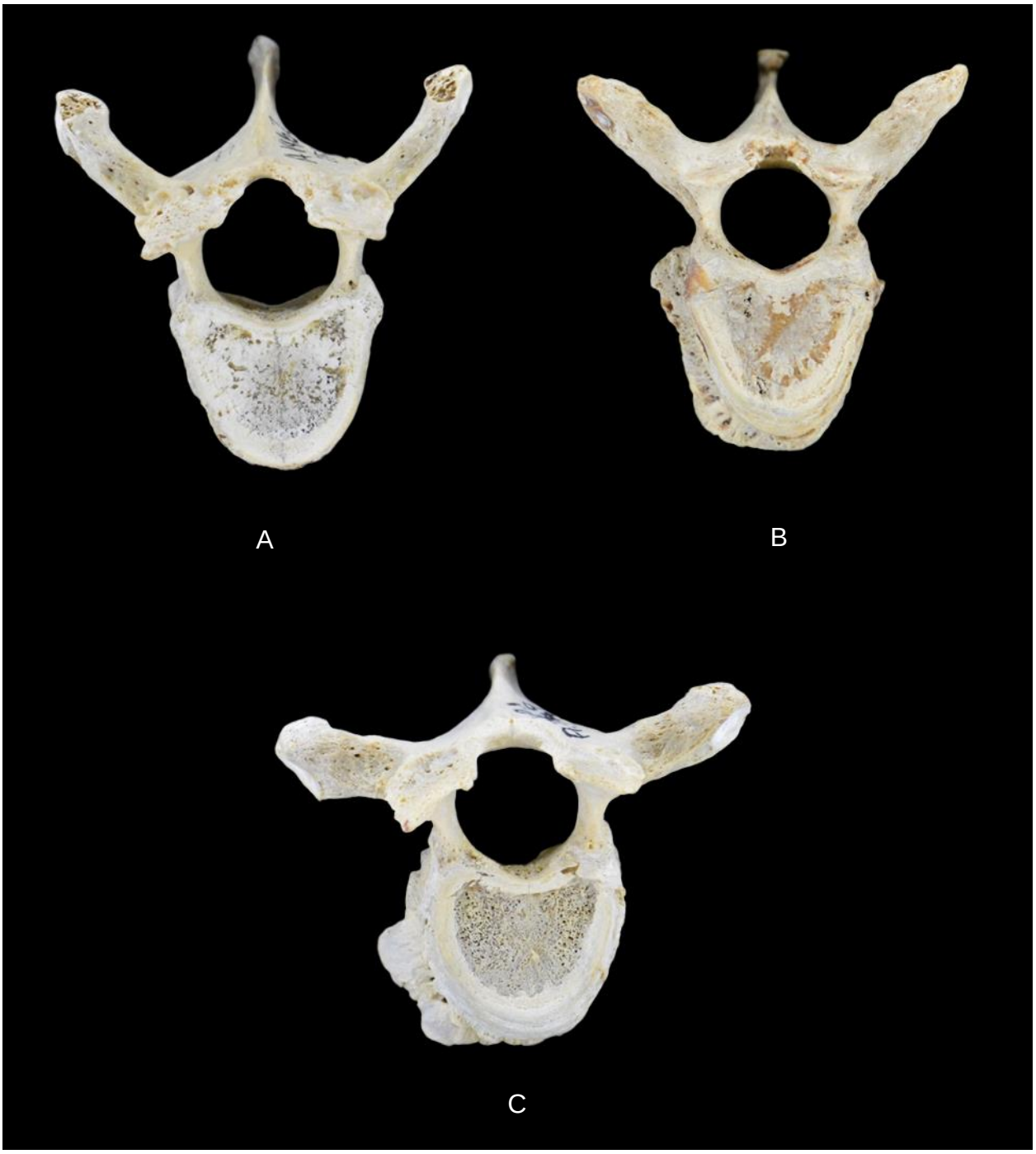


Figure 3.20: Selected variations of degenerative changes noted in facet and intervertebral disc related to SPD. A: bilateral facet degeneration, limited IVD degeneration, no SPD; B: IVD degeneration, normal facet, no SPD; C: unilateral facet and IVD degeneration, no SPD.

3.5.4 Region of spinous process deviations

On visual evaluation of SPD, it was noted that their presentation was not uniform. For the purposes of description, five variations were noted, and are described by angulation and region (distal or proximal), as presented in Figure 3.21.

These variations are:

1. Distal angular: the deviation is noted in the distal region and has a rapid deviation from a point.
2. Proximal angular: the deviation is noted in the proximal region and has a rapid deviation from that point.
3. Proximal gradual: the deviation is noted from the proximal region and has a gradual deviation from the base of the SP.
4. Distal gradual: this was the most common presentation and was a gradual deviation in the distal region.
5. Proximal gradual, returning to midline: this was the least common presentation, with a proximal gradual deviation, that returned to the SP midline.

Lawler et al. (2016) described four types of spinous process deviations in archaeological dog vertebral specimens: (a) lateral leaning from the base but not otherwise deviated (possibly similar to distal gradual presented in the current study); (b) lateral curving at some point above the base (possibly a combination of what is presented in the current study); (c) bowing because of multiple curves; and (d) torsion along the vertical axis, which are inconsistent with the current study presentations.

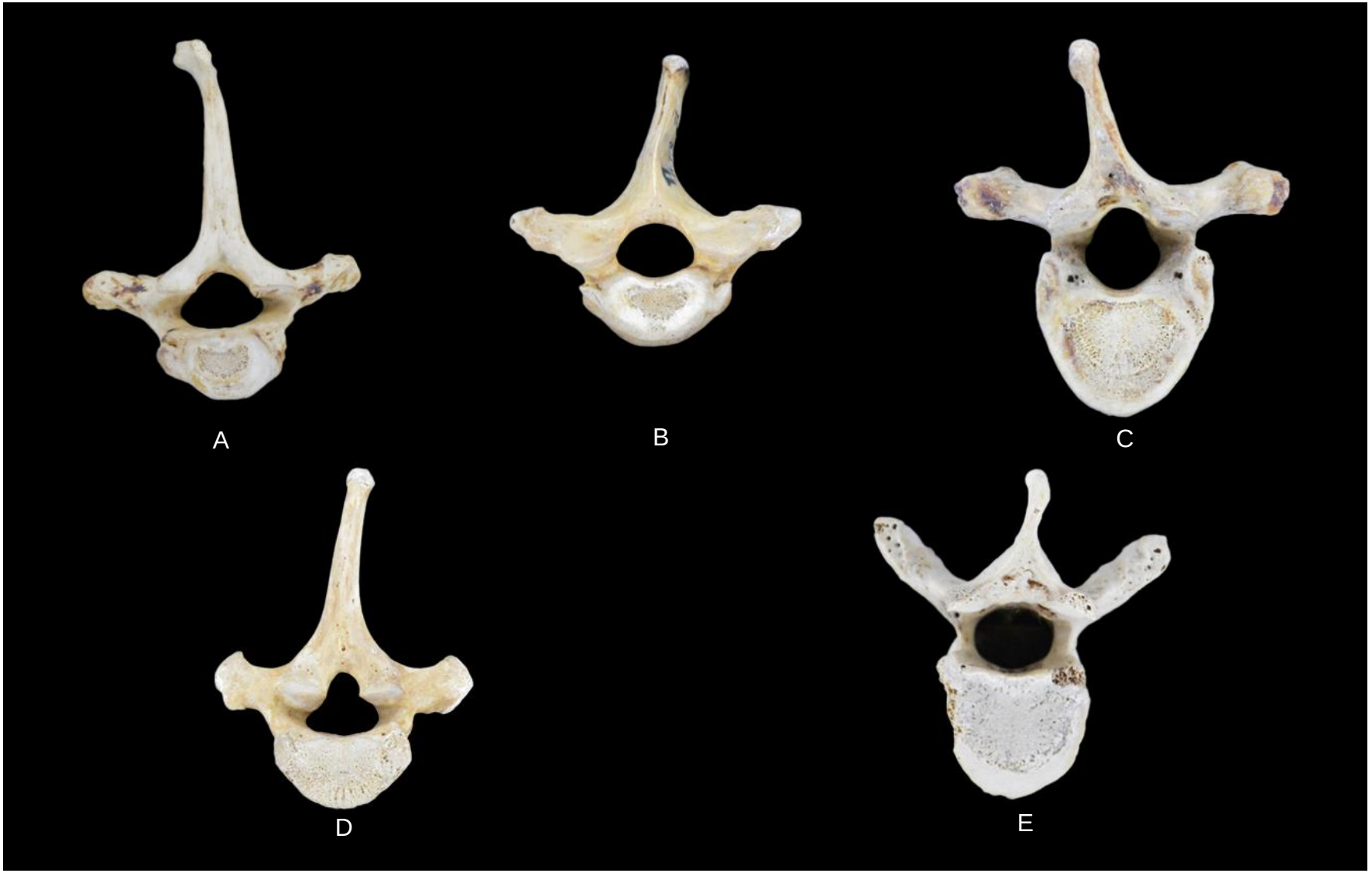


Figure 3.21: Variations in spinous process deviations based on all taxa utilized. A: distal angular; B: proximal angular; C: proximal gradual; D: distal gradual; E: proximal gradual returning to midline.

Previous research has not presented SPD in primates, in terms of categorizing the type of deviations that may occur, or the region of the SP that is deviated.

The overall frequency of deviations in all groups, is presented in Table 3.11. Of the deviations noted, distal deviations were the most frequent, with 87.43% (n=320), and an almost equal distribution between left (12.2%) and right (12.7%). Proximal deviations are the least common, with 3.59% (n=46), with left being almost twice as frequent as right.

A proposed mechanism for the direction of SPD, could be handedness of individuals, which may result in asymmetrical patterns of loading on the SP due to the increased motion or muscular loading toward the dominant hand side. Raymond et al. (1996) estimates that 10-13% of the human population are left-handed. Considering the current study, SPD direction in the contemporary human overall group was almost equal (11.7% left distal, and 12.9% right distal), this may suggest that handedness was not a significant factor in SPD development. Hopkins (2013) states that extant findings on handedness in nonhuman primates, have revealed inconsistent evidence for population level handedness within and between species. The symmetrical incidence of SPD in the current study, does not therefore suggest this would have a great effect as it would be anticipated to see an incidence similar to handedness (i.e., more right deviations).

Distal SPD are significantly more frequent than proximal. It stands to reason that considering the distance of the tip of the spinous process to the body, it would be more sensitive to any dynamic or functional stresses imposed on it.

The gorilla sample demonstrated a particular sequence in many cases (that was not observed in other species), where proximal deviations were preceded by two

consecutive vertebra demonstrating distal deviation in the same direction (Figure 3.22). This would potentially support a proposed mechanism that proximal deviations are as a result of progressive asymmetrical loading, and the cephalad vertebrae demonstrate progressively increased change which ultimately results in a proximal deviation occurring, this was only seen in the *gorilla* sample and it may be speculated that this is a result of body mass. However, more distal vertebrae did not necessarily demonstrate this change, and proximal deviations are in many cases followed by no deviation, as opposed to continuous proximal deviations, or reverting to distal deviation, which may therefore implicate more factors influencing this phenomenon.

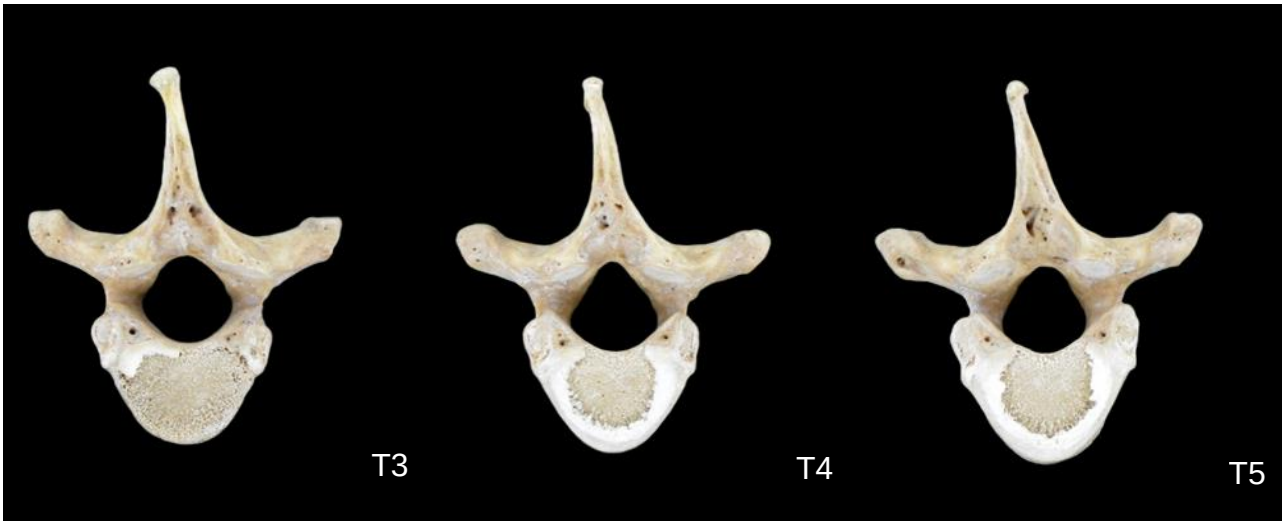


Figure 3.22: Sequential increase in SPD representing two consecutive distal followed by proximal deviation [in female gorilla – MC696].

3.5.5 Locomotor propensity and spinous process deviation

The impact of locomotor propensity is an important consideration in the current study. As discussed, adaptations for upright posture and bipedalism are associated with spinal changes such as sigmoid curvature, pyramidal configuration of articular facets that descend through the lower lumbar column and a wide curved sacrum (Latimer and Ward, 1993; Lovejoy, 2005; Ward and Latimer, 2005). In addition, specific vertebral morphometric or trait changes as adaptation for bipedal posture are proposed as presented in Table 1.5.

The current study's findings concur with previous work in relation to upper thoracic vertebral morphology adaptations for bipedalism namely spinous processes being shorter in humans than in apes (Schultz, 1961; Latimer and Ward, 1993; Gomez-Olivencia et al., 2013; Meyer 2016; Meyer et al., 2017 and Plomp et al. 2019), human spinous processes having a more caudal angulation than in apes (Latimer and Ward, 1993; Gomez-Olivencia et al., 2013 and Plomp et al. 2019) and human articular facets (superior and inferior) being more coronally orientated than in apes (Latimer and Ward, 1993; Shapiro, 1993; Williams and Russo, 2015; Meyer et al., 2017 and Plomp et al. 2019). Plomp et al. (2019) additionally presented tapering of the spinous processes as a trait, but this was not evaluated in the current study.

The frequency of spinous process deviations within an individual's series of T1-T6 in terms species, is presented in Table 3.12, and indicates the distinctions between each of the locomotor pattern. When considering sex related differences in groups, males were more likely to have SPD's than females in all groups. Chimpanzees, as semi-terrestrial/mixed locomotor climbers (Doran, 1992; Doran, 1993; Doran and Hunt,

1994; Sockol et al., 2007) demonstrated the highest frequency within an individual T1-T6 sequence (91.11%) and gorillas, which are predominantly terrestrial but also engage in climbing (Doran, 1995; Doran and McNeilage, 1998), demonstrated a high frequency (83.33%), specifically in the male group (93.56%). The contemporary human group (habitual bipeds) showed a lower incidence of 77.59%, and baboons, the pronograde terrestrial quadruped (Fleagle, 2013), demonstrated the lowest incidence of SPD (39.34% frequency within the T1-T6 series within an individual). Bipedalism does not therefore appear to make SPD more frequent as was proposed in the current study with terrestrial quadrupedalism alone not demonstrating a direct link given the large difference between gorillas and baboons. The predominant locomotor pattern does not therefore appear to have a direct impact on this feature, although the fact that hominoids are orthograde (upright) may play a role.

Two aspects that may be considered in terms of locomotor pattern in relation to development of SPD are the head balancing model, and differences in the thoracic shape between species. In the proposed head balancing model by Slijper (1946), Jaanuson (1987) and Smit (2002), the cranial shape (increased cranial length) has an impact on the cervical spine. Similarly, the nuchal muscles demonstrate an increased mass and larger attachment sites on cervical vertebrae (Nalley and Gridder-Potter, 2019).

If one considers that intrinsic muscles of the cervical spine such as splenius and semispinalis cervicis and capitis are a component of these nuchal muscles and have attachments to the upper thoracic vertebrae spinous processes (Moore, 1993; Diogo et al., 2017) increases in muscle mass would relate to more force applied to the insertion

site of the spinous process. The previously presented bone modeling effect may also be considered, where species with larger muscle mass would be more likely to demonstrate these increased forces on the insertion sites. These muscles are also responsible for extension of the cervical spine (Moore, 1983), as is required for upright posture. The current study findings support this proposition in terms of nuchal muscle mass, as gorillas (with the greatest nuchal mass) demonstrated the highest likelihood of change, followed by chimpanzees, contemporary humans and then baboons.

Another consideration may be that upright posture requires either shortening of the nuchal muscles or decreased mass. Lovejoy (2005) proposed that decreased muscle mass in hominoids relative to Old-World monkeys is seen as a result of the rigid thoracic spine. This appears to be supported within the primates utilized (namely gorillas, chimpanzees, humans and baboons), with the predominant terrestrial pattern showing the highest incidence of SPD, the mixed less and the bipedal the least incidence. However, this is contradicted by the pronograde obligate quadrupedal primate, that showed the least likelihood of SPD (if correlating SPD to posture and muscle mass). If the locomotor pattern was the primary factor, similarities would be expected between gorillas and the chimpanzees and as indicated this was not the case. As presented by Rabey et al. (2011) and Rabey (2014) no clear relationship between muscle fiber architecture, size of muscle and shape of forelimb muscle attachment sites (between species that differ in frequency of daily locomotor and postural behaviours) has been demonstrated in primates. This suggests that more than one factor may contribute to the development of SPD.

Schultz (1961) and Lovejoy (2005) discussed the impact of upright posture on the rigidification of the spine, the scapular axis is repositioned posterolaterally and potential muscular adaptation of the shoulder girdle. The rhomboid major and minor, and trapezius (transverse component) muscles attach to the scapula and the spinous processes of the upper thoracic vertebrae (Moore, 1993; Diogo et al., 2017). This change in position of the scapular axis, would result in elongation of the muscles in the more posterolaterally situated scapula, as represented in Figure 3.23.

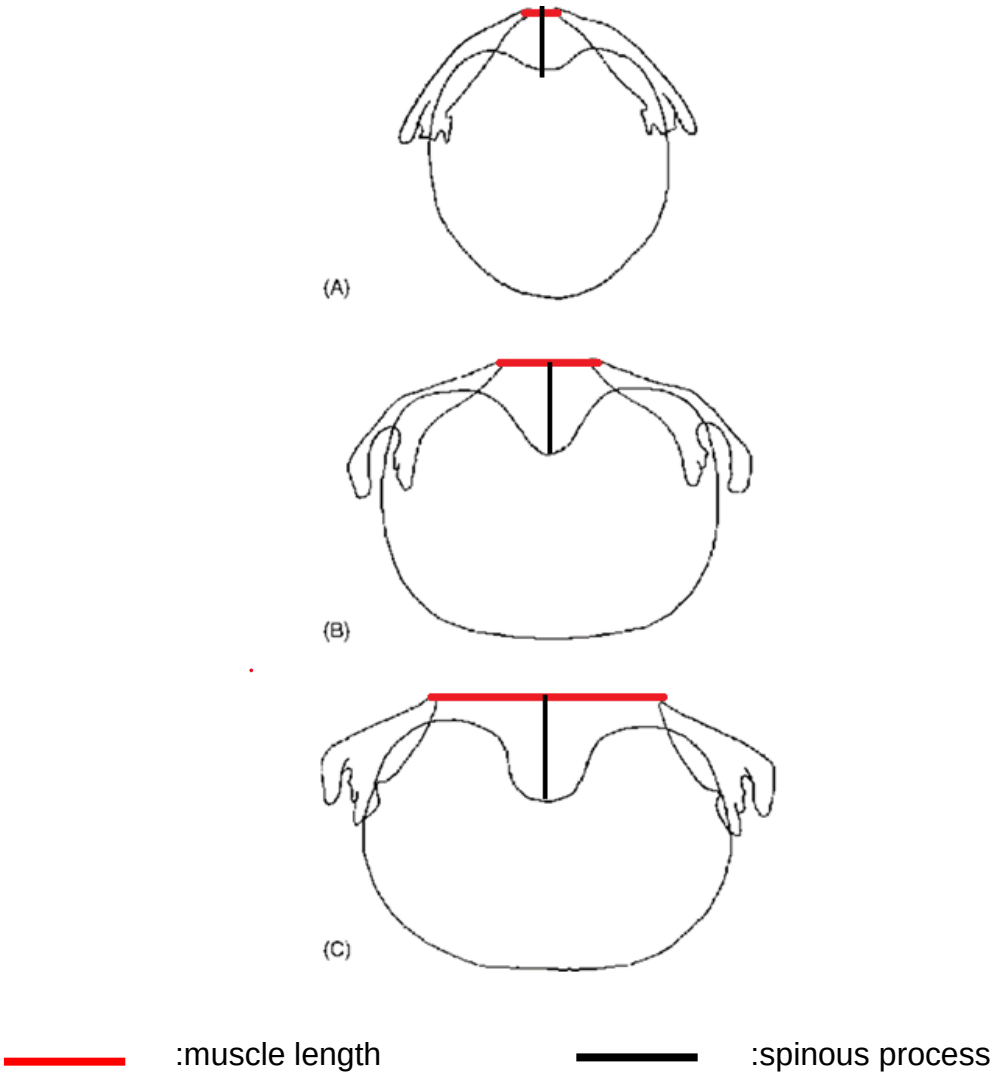


Figure 3.23: Illustration of the effect of invagination of the vertebral column and scapula position on length of medial scapular musculature (adapted from Lovejoy, 2005).

The fact that the arm is also free to move in bipedal posture, may increase the load on the spinous process, and increase the potential for SPD to occur. This is to some degree supported by the baboons results, which demonstrated very little SPD. However, this is not consistent in the other species, and would suggest a limited effect related to the muscles, and the scapula position in regard to SPD.

The models proposed allow for some degree of understanding of the potential influence of bipedal locomotion on vertebrae and spinous processes, however locomotor pattern in isolation does not appear to influence the frequency of SPD which was proposed as a factor in the current study, as no pattern could be identified within the comparison of groups.

Ultimately, the results and discussion in this chapter do not support any specific correlation relating to the incidence of SPD to locomotor propensity. Multiple factors may affect the development of SPD such as a congenital anomaly from altered ossification centers or developmental asymmetry of the neural arch (Van Schaik et al., 1989; Mellado et al., 2011), rotation of the entire vertebra (as in scoliosis or degenerative arthritis) or isolated deviation without rotation or asymmetry of the vertebral body or arch (Van Schaik et al., 1989). Ultimately, as proposed by Lawler et al. (2016), numerous factors may overlap within an individual that may result in presentation of SPD.

.

CHAPTER 4

COMPARATIVE MORPHOLOGY OF FOSSIL HOMININ UPPER THORACIC VERTEBRAE

4.1 Introduction

Thoracic vertebrae morphology has been proposed as an important aspect to determine the interrelationships between locomotor behaviour and trunk morphology (Kikuchi and Ogihara, 2021). One of the research questions posed in this study, was the relationship between spinous process deviation in the upper thoracic vertebrae and bipedal posture and locomotion, and if SPD could be an indicator for this adaptation. Plomp et al. (2019) discussed that comparative analysis of contemporary humans to primates allows for potential recognition of bipedal taxa by palaeontologists, and this chapter will present the hominin fossil measurements and morphology in comparison to the selected primates to determine if correlations could be found.

4.2 Fossil hominin morphometric measurements and spinous process deviation, region and direction results

Due to the limited number of fossil hominin specimens available, no statistical analyses were conducted, and descriptive analysis and comparison is presented. The morphometric measurement, including spinous process deviation, region and direction (SPDRD), of each identified species and sample are presented in Table 4.1. Each species identified will be presented individually, with comparison to selected primates where possible.

4.2.1 *Australopithecus africanus*

a. Background

Australopithecus africanus is represented in the current study by Sts 14m and Sts 14i, which are described as consecutive T5 and T6 vertebrae respectively (Haeusler et al., 2002; Ward et al., 2020), and is considered a very young adult or sub-adult female (Williams and Meyer, 2019). These vertebrae have been extensively described by Robinson (1972) and Ward et al. (2020) and formalized descriptions of specimens will therefore not be presented.

b. Results

Sts 14m (Figure 4.1), demonstrated a SPA of 121.21º, with a SPL of 19.32mm. IAFW measured 5.94mm (right) and 5.80mm (left), with inferior articular facet orientation (IAFO) being 77.39º (right) and 72.08º (left). Superior articular facet width (SAFW) measured 4.50mm (right) and 5.18mm (left), with superior articular facet orientation (SAFO) being 67.83º (right) and 75.08º (left). No spinous process deviation was noted.

Table 4.1: Fossil hominin sample morphometric measurements per species and level, including spinous process deviation.

Specimen	Species	Sex ****	Comments	Level	SPA**	SPL***	IAFW_R***	IAFW_L***	IAFO_R**	IAFO_L**	SAFW_R***	SAFW_L***	SAFO_R**	SAFO_L**	DRD*
Sts 14m	*A. africanus*	2	Right TVP broken	T5	121.21	19.32	5.94	5.80	77.39	72.08	4.50	5.18	67.83	75.08	1
Sts 14i	*A. africanus*	2	Almost full, right TVP tip damage	T6	121.56	15.96	6.19	5.64	74.96	76.1	6.66	5.97	72.18	72.33	1
U.W. 88-11	*A. sediba (cast) MH1*	1	No left transverse process, left lateral body damage	Upper thoracic	157.03	26.07	7.22	6.59	83.7	72.15	10.21	7.92	74.67	85.43	2
U.W. 88-37	*A. sediba (cast) MH1*	1	Right foramen on spinous process, osteoid osteoma,	Mid thoracic	131.25	23.24	5.74	7.45	77.9	70.18	6.52	6.87	71.59	76.64	3
U.W. 88-188	*A. sediba (3D print) MH2*	2	Reconstructed right neural arch	Upper thoracic	Not present	Not present	Not present	9.59	Not present	68.64	Not present	7.85	Not present	70.20	Not present
U.W. 88-189	*A.sediba (3D print) MH2*	2		Mid thoracic	123.46	Not present	7.76	7.61	73.07	67.11	4.92	5.49	82.44	72.64	Not present
A.L. 288-1ae	*A. afarensis (cast)*	2	Broken left superior articular process, spinous process only starting,	T6	121.22	Not present	6.39	5.60	73.07	63.68	6.05	Not present	65.68	Not present	Not present
StW 573	*A. prometheus*	3	3rd in sequence	single vert	145.64	24.80	9.28	7.701	65.72	61.65	7.55	8.93	79.53	65.24	3
StW 573	*A. prometheus*	3	4th in sequence	single vert	127.05	25.11	6.18	6.42	76.52	48.49	Not present	8.73	Not present	63.86	1

*Deviation, region, direction (DRD): 1=none; 2=distal left; 3=distal right; 4=proximal left; 5=proximal right
**Spinous process angle (SPA), inferior articular facet orientation (IAFO), superior articular facet orientation (SAFO) measured in degrees
***Spinous process length (SPL), inferior articular facet width (IAFW), superior articular facet width (SAFW) measured in mm
**** sex: 1=male; 2=female; 3=unknown

Sts 14i (Figure 4.2), demonstrated a SPA of 121.56º, with a SPL of 15.96mm. IAFW measured 6.19mm (right) and 5.64mm (left), with IAFO being 74.96º (right) and 76.1º (left). SAFW measured 6.66mm (right) and 5.97mm (left), with SAFO being 72.18º (right) and 72.33º (left). No spinous process deviation was noted.

Sts14m is compared to female T5 vertebrae of African apes, contemporary humans and baboons in Table 4.2. SPA and SPL was most similar to contemporary humans (125.15º and 27.8mm respectively). IAFW and SAFW on both sides was most similar to baboons, with IAFO being most similar to gorillas (R=75.07º; L=73.56º), and SAFO to chimpanzees (69.67º) on the right and contemporary humans (74.9º) on the left.

Sts 14i is compared to female T6 vertebrae of African apes, contemporary humans and baboons in Table 4.3. SPA was most similar to contemporary humans (121.21º), and SPL to baboons (26.93mm). IAFW was most similar to baboons (R=6.62mm; L=6.43mm), with IAFO similar to gorillas on the right (74.45º) and contemporary humans on the left (75.5º). The SAFW on both sides was most similar to baboons (R=6.64mm; L=6.40mm), with SAFO being most similar to gorillas on the right (72.18º), and chimpanzees on the left (71.04º).

Sts 14i is compared to female T6 vertebrae of African apes, contemporary humans and baboons in Table 4.3. SPA was most similar to contemporary humans (121.21º), and SPL to baboons (26.93mm). IAFW was most similar to baboons (R=6.62mm; L=6.43mm), with IAFO similar to gorillas on the right (74.45º) and contemporary humans on the left (75.5º). The SAFW on both sides was most similar to

baboons (R=6.64mm; L=6.40mm), with SAFO being most similar to gorillas on the right (72.18º), and chimpanzees on the left (71.04º).

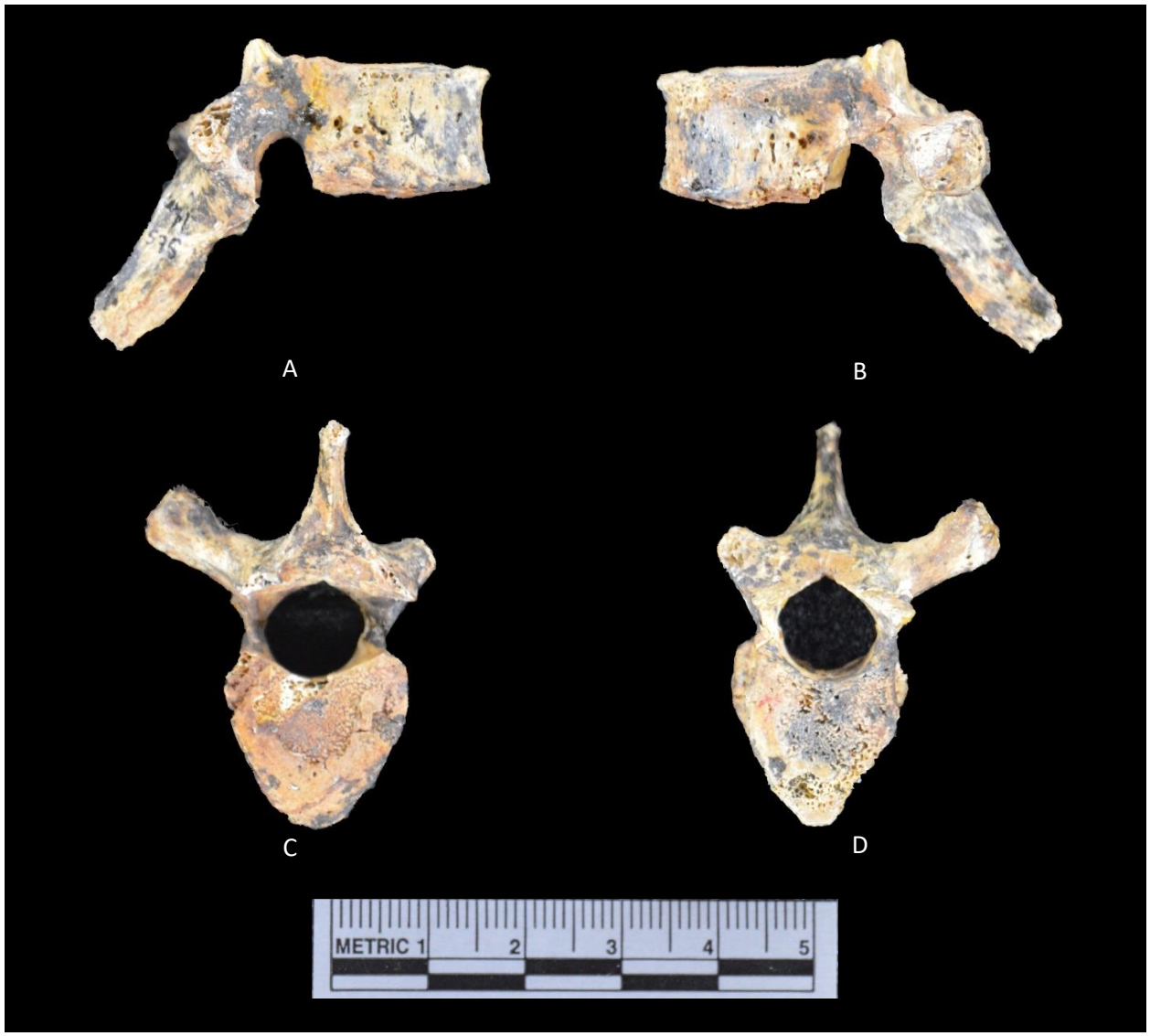


Figure 4.1: *Australopithecus africanus* (Sts 14m) T5 vertebra. A: right lateral view; B: left lateral view; C: inferior view; D: superior view.

Figure 4.2: *Australopithecus africanus* (Sts 14i) T6 vertebra. A: right lateral view; B: left lateral view; C: inferior view; D: superior view.

Sts 14i is compared to female T6 vertebrae of African apes, contemporary humans and baboons in Table 4.3. SPA was most similar to contemporary humans (121.21º), and SPL to baboons (26.93mm). IAFW was most similar to baboons (R=6.62mm; L=6.43mm), with IAFO similar to gorillas on the right (74.45º) and contemporary humans on the left (75.5º). The SAFW on both sides was most similar to

baboons (R=6.64mm; L=6.40mm), with SAFO being most similar to gorillas on the right (72.18º), and chimpanzees on the left (71.04º).

4.2.2 *Australopithecus sediba*

Australopithecus sediba is represented in this study by U.W. 88-11 and U.W. 88-37 (male, MH1), with upper thoracic and mid thoracic vertebrae respectively, and U.W. 88-188 and U.W. 88-189 (female, MH2), with upper thoracic and mid thoracic vertebrae respectively (Berger et al, 2010; Williams et al., 2018). These vertebrae have been extensively described by Williams et al. (2018).

a. U.W. 88-11 and U.W. 88-37

U.W. 88-11 (Figure 4.3), demonstrated a SPA of 157.03º, with a SPL of 26.07mm. IAFW measured 7.22mm (right) and 6.59mm (left), with IAFO being 83.7º (right) and 72.15º (left). SAFW measured 10.21mm (right) and 7.92mm (left), with SAFO being 74.67º (right) and 85.43º (left). The spinous process was deviated distally to the left.

U.W. 88-37 (Figure 4.4), demonstrated a SPA of 131.25º, with a SPL of 23.24mm. The IAFW measured 5.74mm (right) and 7.45mm (left), with the IAFO being 77.9º (right) and 70.18º (left). The SAFW measured 6.52mm (right) and 6.87mm (left), with the SAFO being 71.59º (right) and 76.64º (left). The spinous process was deviated distally to the right, with evidence of a fossa attributed to an osteoid osteoma on the right-side lamina (Randolph-Quinney et al., 2016).

Table 4.2: Comparison of female T5 mean morphometric measurements of Sts 14m to African apes, contemporary humans and baboons.

Specimen	Species	Level	N	SPA (SD)**	SPL (SD)***	IAFW_R (SD)***	IAFW_L (SD) ***	IAFO_R (SD)**	IAFO_L (SD)**	SAFW_R (SD)***	SAFW_L (SD)***	SAFO_R (SD)**	SAFO_L (SD)**
Sts 14m	*A. africanus*	T5	1	121.21	19.32	5.94	5.80	77.39	72.08	4.50	5.18	67.83	75.08
	Gorillas	T5	29	133.60 (9.39)	30.03 (4.44)	8.76 (1.18)	8.82 (1.19)	75.07 (3.98)	73.56 (7.7)	9.34 (1.14)	9.23 (1.28)	72.67 (5.89)	72.28 (6.73)
	Chimpanzees	T5	30	141.91 (7.25)	30.33 (2.7)	8.35 (0.71)	8.35 (0.74)	71.40 (4.8)	69.55 (4.98)	8.80 (0.84)	8.60 (1.07)	69.67 (5.5)	69.74 (4.83)
	Baboons	T5	28	150.15 (4.78)	26.43 (5.4)	6.46 (0.86)	6.38 (0.69)	61.01 (4.12)	61.68 (3.89)	6.53 (0.82)	6.31 (0.74)	56.85 (3.82)	60.87 (4.31)
	Contemporary humans	T5	28	125.15 (9.9)	27.80 (4.66)	9.02 (1.08)	8.91 (0.93)	73.45 (4.67)	74.56 (5.06)	10.08 (1.22)	9.51 (1.1)	70.71 (5.22)	74.90 (3.28)

**SPA, IAFO, SAFO measured in degrees
***SPL, IAFW, SAFW measured in mm
SD: standard deviation

Table 4.3: Comparison of female T6 mean morphometric measurements of Sts 14i, U.W. 88-189 and A.L. 288-1ae to African apes, contemporary humans and baboons.

Specimen	Species	Level	N	SPA (SD)**	SPL (SD)***	IAFW_R (SD)***	IAFW_L (SD)***	IAFO_R (SD)**	IAFO_L (SD)**	SAFW_R (SD)***	SAFW_L (SD)***	SAFO_R (SD)**	SAFO_L (SD)**
Sts 14i	*A. africanus*	T6	1	121.56	15.97	6.19	5.64	74.96	76.1	6.66	5.97	72.18	72.33
A.L. 288-1ae	*A. afarensis (cast)*	T6	1	121.22	Not present	6.39	5.60	73.07	63.68	6.05	Not present	65.68	Not present
U.W. 88-189	*A. sediba*	Mid thoracic	1	123.46	Not present	7.76	7.61	73.07	67.11	4.92	5.49	72.44	72.64
	Gorillas	T6	29	133.54 (8.84)	28.82 (3.65)	8.54 (1.26)	8.65 (1.23)	74.45 (5.13)	71.19 (5.87)	8.87 (1.18)	8.79 (1.08)	72.18 (5.54)	70.87 (6.26)
	Chimpanzees	T6	30	141.01 (6.4)	30.59 (3.12)	8.46 (0.95)	8.41 (0.99)	71.36 (5.26)	69.19 (4.31)	8.64 (1.1)	8.54 (0.97)	69.57 (4.86)	71.04 (5.47)
	Baboons	T6	28	152.20 (5.06)	26.93 (3.94)	6.62 (0.85)	6.43 (0.92)	62.66 (3.84)	60.97 (5.17)	6.64 (0.89)	6.40 (0.85)	59.21 (3.79)	61.75 (3.66)
	Contemporary humans	T6	28	121.21 (8.97)	28.60 (4.31)	8.98 (0.89)	9.14 (0.91)	76.17 (5.02)	75.50 (4.26)	9.39 (1.28)	9.28 (1.1)	70.28 (5.16)	74.35 (3.45)

**SPA, IAFO, SAFO measured in degrees
***SPL, IAFW, SAFW measured in mm
SD: standard deviation

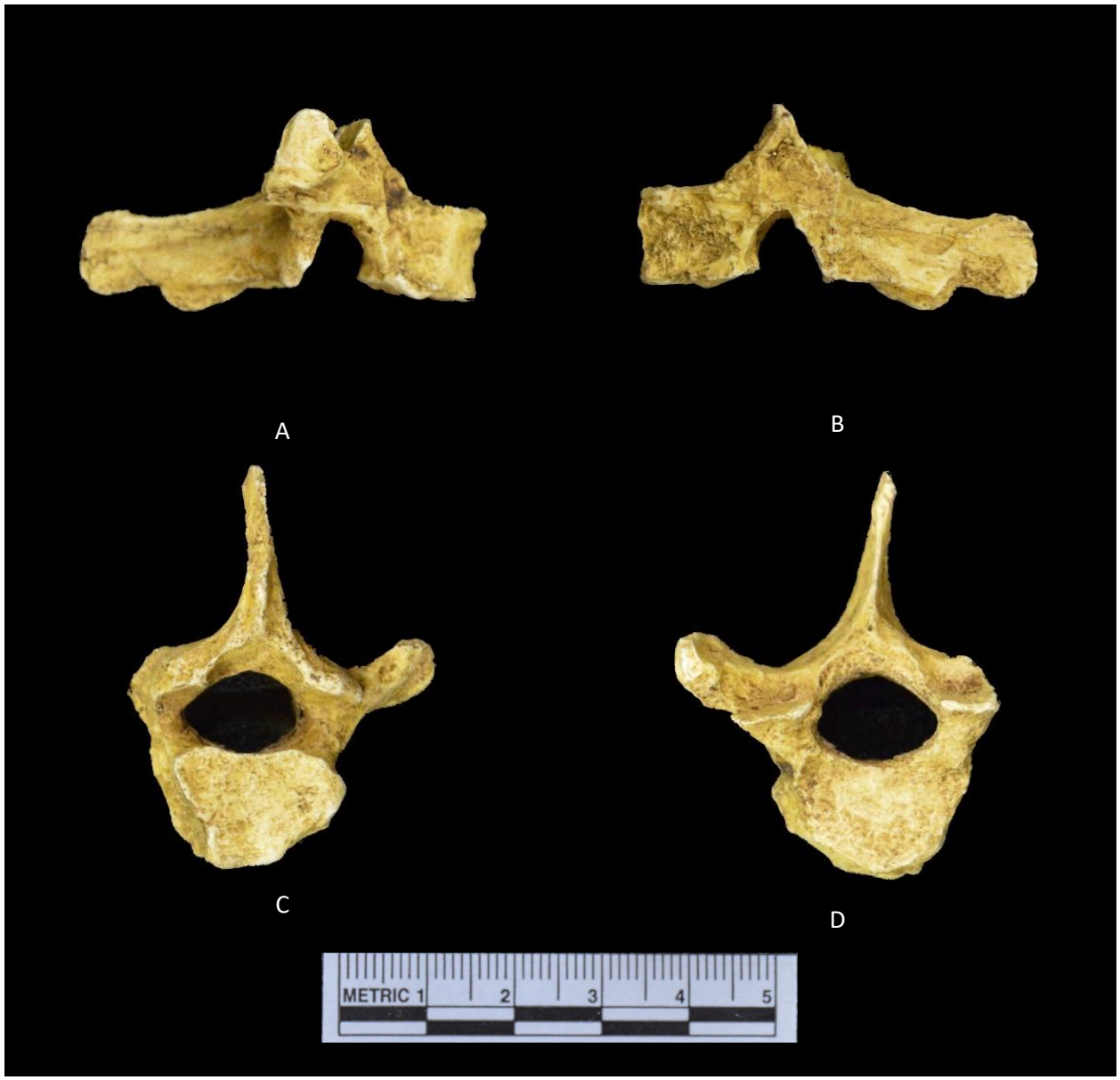


Figure 4.3: *Australopithecus sediba* (U.W. 88-11) upper thoracic vertebra. A: right lateral view; B: left lateral view; C: inferior view; D: superior view.

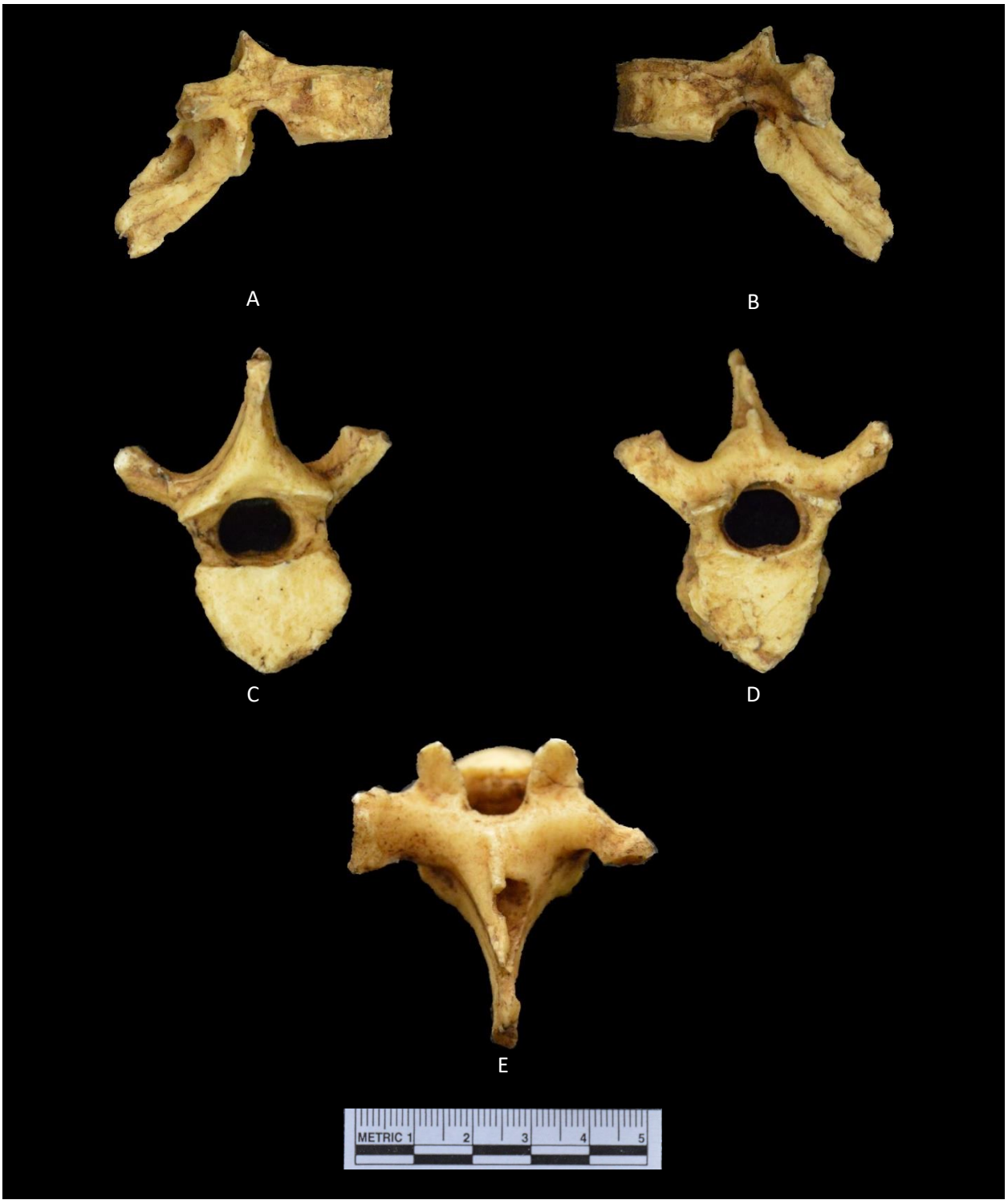


Figure 4.4: *Australopithecus sediba* (U.W. 88-37) mid thoracic vertebra. A: right lateral view; B: left lateral view; C: inferior view; D: superior view; E: posterior view.

U.W. 88-11 is compared to male T3 vertebrae of African apes, contemporary humans and baboons in Table 4.4. The SPA and SPL were most similar to baboons (153.12º and 30.65mm respectively). The IAFW was most similar to baboons on both sides (R=7.02mm; L=7.03mm), and SAFW to chimpanzees on the right (9.43mm) and baboons on the left (7.37mm). The IAFO was most similar to gorillas on the right (81.04º) and contemporary humans on the left (71.83º), with the right SAFO to chimpanzees (69.67º) and left to gorillas (81.38º).

U.W. 88-37 is compared to male T6 vertebrae of African apes, contemporary humans and baboons in Table 4.5. The SPA was most similar to gorillas (133.96º) and SPL to contemporary humans (31.62mm). The IAFW and SAFW on both sides were most similar to baboons, with the IAFO on the right to gorillas (76.83º) and chimpanzees on the left (70.02º). The SAFO was most similar to chimpanzees on the right (70.93º), and gorillas on the left (73.53º).

b. U.W. 88-188 and U.W. 88-189

U.W. 88-188 does not have a spinous process, with only the left neural arch being present. For the current study, 3D reconstruction from CT scans were utilized (courtesy of S. Williams), due to the original fossils being partially encased in matrix (as illustrated in Figure 4.5), and not allowing for adequate morphometric measurements. As presented in Figure 4.6, the right neural arch was digitally reconstructed and mirrored, but aligned to the original fossil material, and therefore only the left side was measured. The left IAFW measured 9.59mm, with the left IAFO being 68.64º. The left SAFW measured 7.85mm, and the left SAFO 70.20º.

Table 4.4: Comparison of male T3 (upper thoracic) mean morphometric measurements of U.W. 88-11 to African apes, contemporary humans and baboons.

Specimen	Species	Level	N	SPA (SD)**	SPL (SD)***	IAFW_R (SD)***	IAFW_L (SD)***	IAFO_R (SD)**	IAFO_L (SD)**	SAFW_R (SD)***	SAFW_L (SD)***	SAFO_R (SD)**	SAFO_L (SD)**
U.W. 88-11	*A. sediba (cast) MH1*	Upper thoracic	1	157.03	26.07	7.22	6.59	83.7	72.15	10.21	7.92	74.67	85.43
	Gorillas	T3	31	152.44 (9.59)	50.33 (8.82)	11.41 (1.76)	11.81 (1.8)	81.04 (5.74)	79.15 (5.49)	12.44 (1.84)	12.43 (1.82)	80.20 (7.63)	81.38 (9.56)
	Chimpanzees	T3	15	148.89 (7.22)	31.42 (4.16)	8.96 (1.21)	9.25 (1.84)	71.36 (4.02)	70.86 (4.38)	9.43 (1.31)	9.64 (1.62)	69.87 (4.96)	69.71 (5.91)
	Baboons	T3	23	153.12 (6.39)	30.65 (5.23)	7.02 (0.1)	7.03 (1.12)	55.31 (3.83)	54.64 (5.39)	7.42 (1.16)	7.37 (1.19)	49.84 (6.62)	51.38 (4.97)
	Contemporary humans	T3	30	137.16 (6.81)	30.94 (2.75)	11.07 (1.61)	10.39 (1.41)	75.13 (5.42)	71.83 (4.26)	11.40 (1.23)	10.82 (1.31)	69.52 (5.2)	72.04 (4.42)

**SPA, IAFO, SAFO measured in degrees
***SPL, IAFW, SAFW measured in mm
SD: standard deviation

Table 4.5: Comparison of male T6 mean morphometric measurements of U.W. 88-37 to African apes, contemporary humans and baboons.

Specimen	Species	Level	N	SPA (SD)**	SPL (SD)***	IAFW_R (SD)***	IAFW_L (SD)***	IAFO_R (SD)**	IAFO_L (SD)**	SAFW_R (SD)***	SAFW_L (SD)***	SAFO_R (SD)**	SAFO_L (SD)**
U.W. 88-37	*A. sediba (cast) MH1*	Mid thoracic	1	131.25	23.24	5.74	7.45	77.9	70.18	6.52	6.87	71.59	76.64
	Gorillas	T6	31	133.96 (8.31)	39.56 (7.63)	9.81 (1.47)	9.94 (1.47)	76.83 (5.48)	71.99 (6.72)	10.73 (1.67)	10.57 (1.52)	73.74 (4.89)	73.53 (5.31)
	Chimpanzees	T6	15	141.10 (6.58)	33.92 (5.57)	8.66 (0.76)	8.81 (1.14)	72.59 (2.82)	70.02 (6.42)	9.11 (1.34)	8.93 (1.1)	70.93 (4.98)	72.08 (5.61)
	Baboons	T6	23	150.25 (6.86)	32.10 (6.4)	7.48 (1.24)	7.50 (1.23)	61.05 (4.18)	61.19 (4.7)	7.40 (1.28)	6.98 (1.1)	58.34 (3.78)	61.67 (3.58)
	Contemporary humans	T6	30	122.19 (6.58)	31.62 (3.71)	10.03 (1.4)	9.85 (1.12)	73.78 (4.79)	73.90 (3.71)	10.50 (1.79)	9.84 (1.19)	69.08 (5.66)	73.27 (4.58)

**SPA, IAFO, SAFO measured in degrees
***SPL, IAFW, SAFW measured in mm
SD: standard deviation

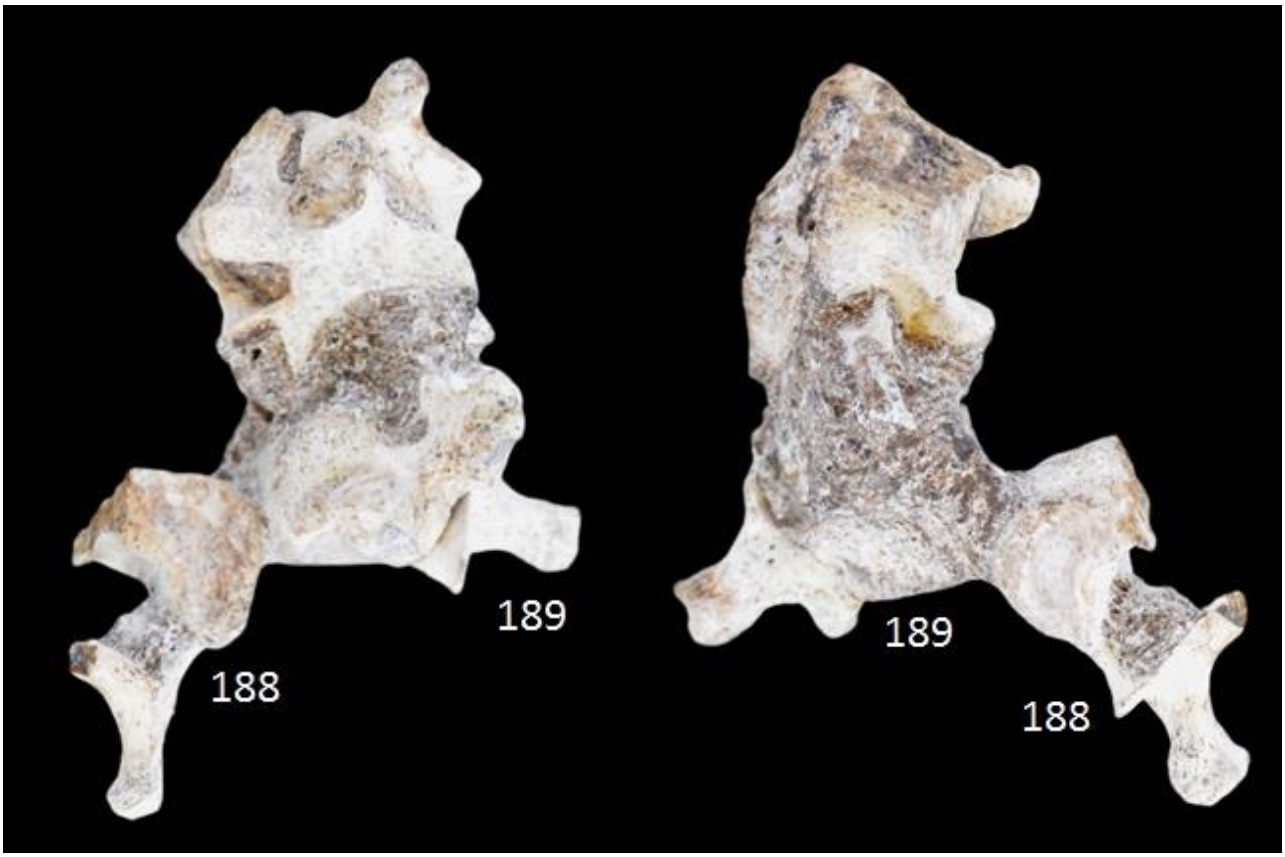


Figure 4.5: *Australopithecus sediba* (U.W. 88-188, U.W 88-189) in two views showing vertebrae partially encased in breccia matrix.

U.W. 88-189 (Figure 4.7), demonstrated a SPA of 123.46º, with no SPL measured, due to it not being fully present. The IAFW measured 7.76mm (right) and 7.61mm (left), with the IAFO being 73.07º (right) and 67.11º (left). The SAFW measured 4.92mm (right) and 5.49mm (left), with the SAFO being 82.44º (right) and 72.64º (left).

U.W. 88-188 is compared to female T3 vertebrae of African apes, contemporary humans and baboons in Table 4.6. Of the measurements obtained, the left IAFW was most similar to contemporary humans (9.61mm), with the left IAFO and SAFW to chimpanzees (70.69º and 8.97mm). The left SAFO was most similar to contemporary humans (71.92º).

U.W. 88-189 is compared to female T6 vertebrae of African apes, contemporary humans and baboons in Table 4.3. The SPA was most similar to contemporary humans (121.21º) and SPL was not measured. The IAFW on both sides were most similar to chimpanzees, with the IAFO on the right to gorillas (74.45º) and chimpanzees on the left (69.19º). The SAFW on both sides was most similar to baboons (6.64mm on the right, and 6.40 on the left). The right SAFO was most similar to gorillas (72.18º) and chimpanzees (71.04º) on the left.

4.2.3 *Australopithecus afarensis*

Australopithecus afarensis is represented in this sample as A.L. 288-1ae, which is a T6 vertebra from “Lucy” (Cook et al., 1983; Meyer et al., 2015). This was initially described by Johanson et al. (1982) and Williams and Meyer (2019).

A.L. 288-1ae (T6) (Figure 4.8) demonstrates a SPA of 121.22º, SPL was not measured as it was not complete. The IAFW measured 6.39mm (right) and 5.60mm (left), with IAFO being 73.07º (right) and 63.68º (left). The SAFW measured 6.05mm on the right, with no left SAF being present. The SAFO was measured as 65.68º on the right, with no SAF on the left. The spinous process was not fully preserved, and no deviation could be determined.

A.L. 288-1ae is compared to female T6 vertebrae of African apes, contemporary humans and baboons in Table 4.3. The left SAFW and SAFO are not presented. The SPA was most similar to the contemporary human group (121.21º). The spinous process was not complete, so SPL could not be compared. The IAFW on both sides was most similar to baboons (R=6.62mm; L=6.43mm), as was the right SAFW

(6.64mm). The IAFO was most similar to gorillas on the right (74.45º), and baboons on the left (60.97º). The right SAFO was most similar to chimpanzees (69.57º).

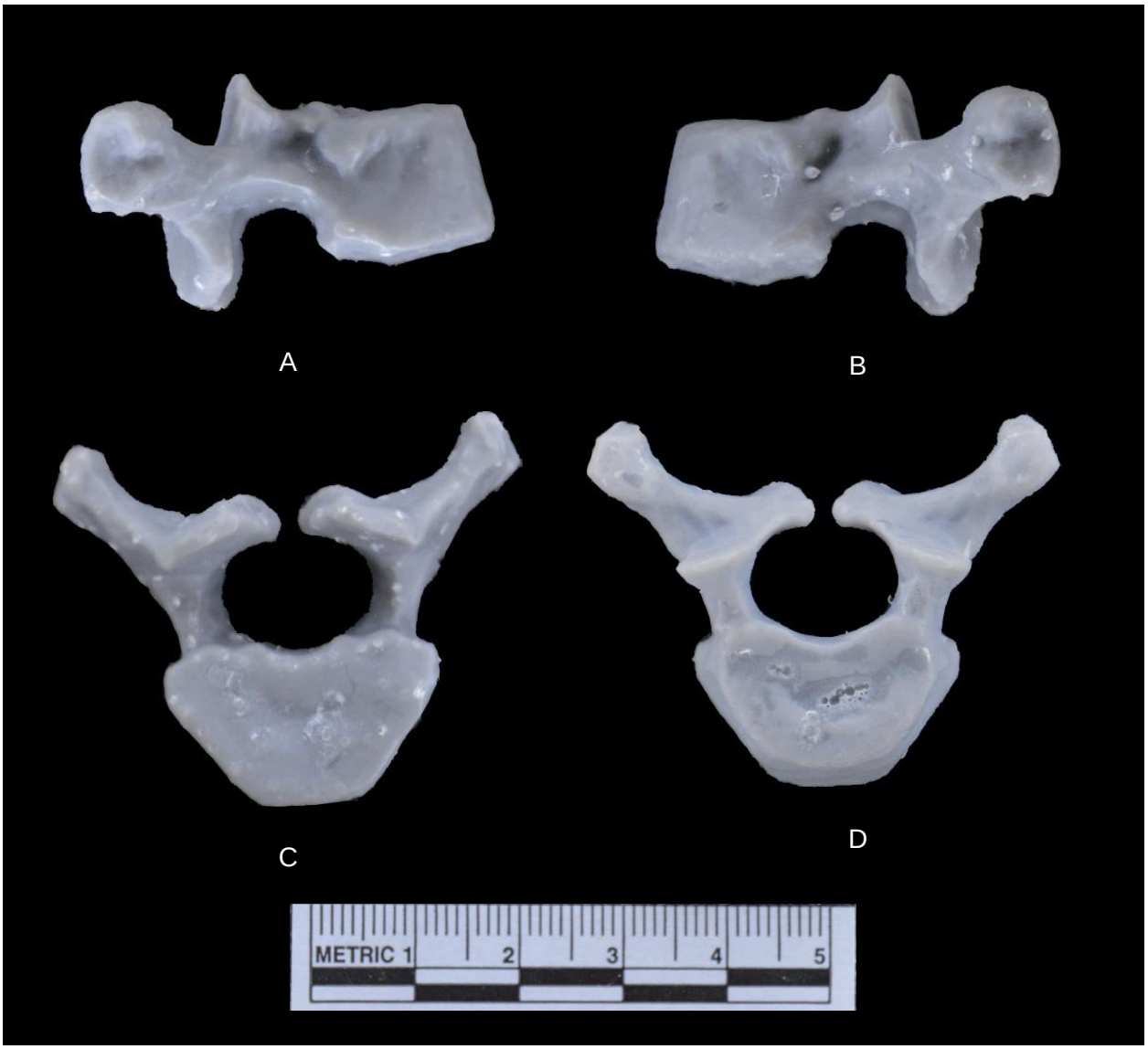


Figure 4.6: 3D reconstruction from CT scan of *Australopithecus sediba* (U.W. 88-188) upper thoracic vertebra. A: right lateral view; B: left lateral view; C: inferior view; D: superior view – note right neural arch reconstruction.

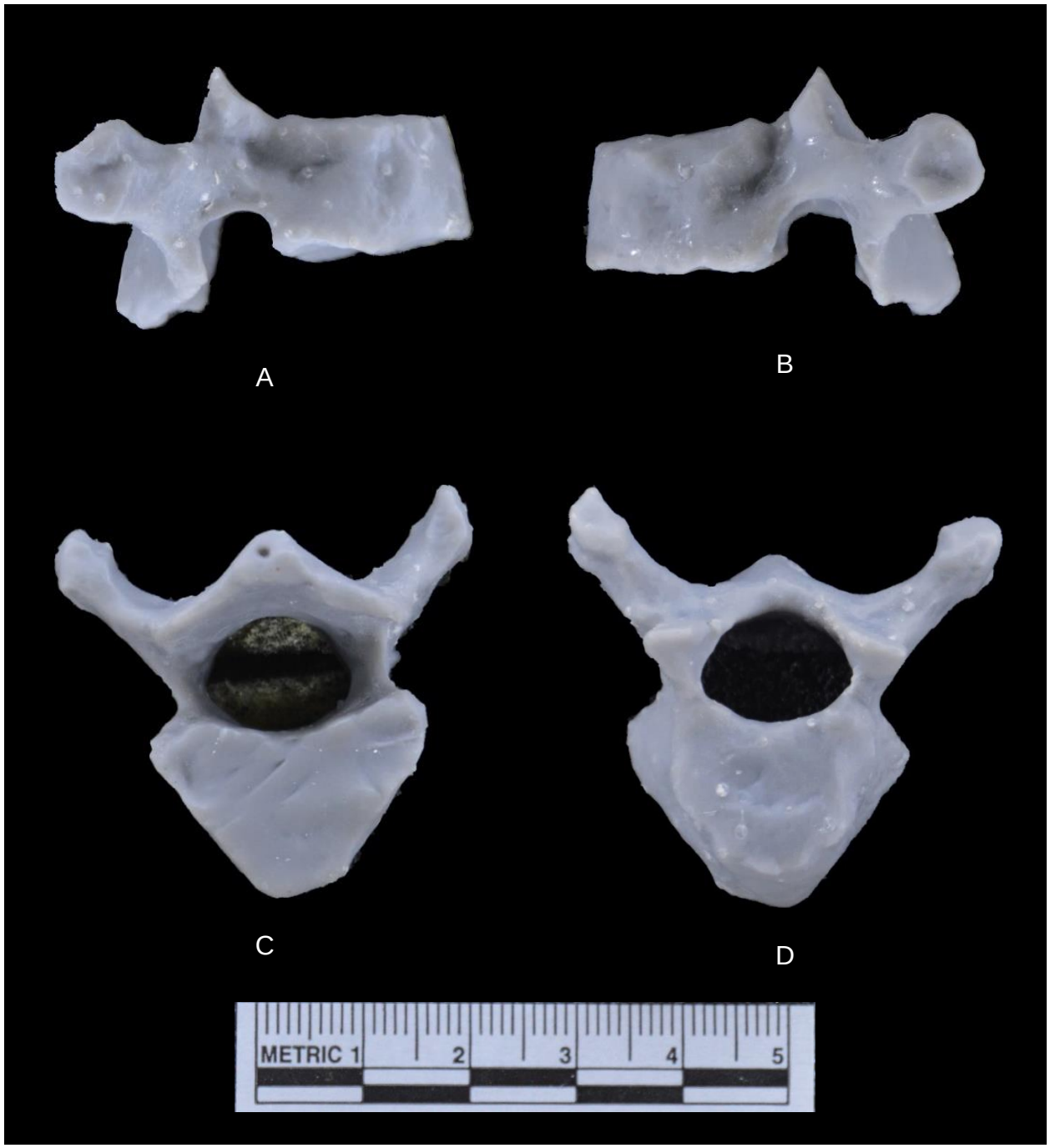


Figure 4.7: 3D reconstruction from CT scan of *Australopithecus sediba* (U.W. 88-189) mid thoracic vertebra. A: right lateral view; B: left lateral view; C: inferior view; D: superior view.

Table 4.6: Comparison of female T3 (upper thoracic) mean morphometric measurements of U.W. 88-188 to African apes, contemporary humans and baboons.

Specimen	Species	Level	N	SPA (SD)**	SPL (SD)***	IAFW_R (SD)***	IAFW_L (SD)***	IAFO_R (SD)**	IAFO_L (SD)**	SAFW_R (SD)***	SAFW_L (SD)***	SAFO_R (SD)**	SAFO_L (SD)**
U.W. 88-188	*A. sediba*	Upper thoracic	1	Not present	Not present	Not present	9.59	Not present	68.64	Not present	7.85	Not present	70.20
	Gorillas	T3	29	147.95 (9.0)	33.98 (4.59)	9.19 (1.26)	9.22 (1.35)	78.38 (4.93)	78.14 (5.38)	9.83 (1.6)	9.88 (1.58)	77.82 (4.9)	77.04 (5.41)
	Chimpanzees	T3	30	147.43 (7.67)	29.77 (3.0)	8.67 (1.06)	8.67 (0.99)	72.56 (4.12)	70.69 (3.14)	9.04 (1.19)	8.97 (0.91)	68.01 (4.59)	68.55 (4.5)
	Baboons	T3	28	156.14 (5.31)	26.10 (3.74)	6.10 (0.8)	6.32 (0.69)	56.54 (3.69)	56.58 (4.7)	6.52 (0.80)	6.40 (0.7)	50.13 (4.44)	53.85 (4.47)
	Contemporary humans	T3	28	135.64 (10.83)	27.34 (3.67)	10.18 (1.37)	9.61 (1.05)	74.46 (4.34)	71.54 (4.22)	10.76 (1.5)	10.37 (1.62)	68.23 (5.26)	71.92 (5.24)

**SPA, IAFO, SAFO measured in degrees
***SPL, IAFW, SAFW measured in mm
SD: standard deviation

Figure 4.8: *Australopithecus afarensis* (A.L. 288-1ae) T6 vertebra. A: right lateral view; B: left lateral view; C: inferior view; D: superior view.

4.2.4 *Australopithecus prometheus*

Australopithecus prometheus is represented in this sample by StW 573 (Little Foot). The vertebrae of the lower cervical spine and upper thoracic region are in a continuous breccia block (Figure 4.9) and for the purposes of the current study, we refer to the first thoracic vertebra currently free from matrix, which is the third in sequence, as

upper thoracic (T3) and the second thoracic vertebra currently free from matrix, which is the fourth in sequence, as mid thoracic (T6).

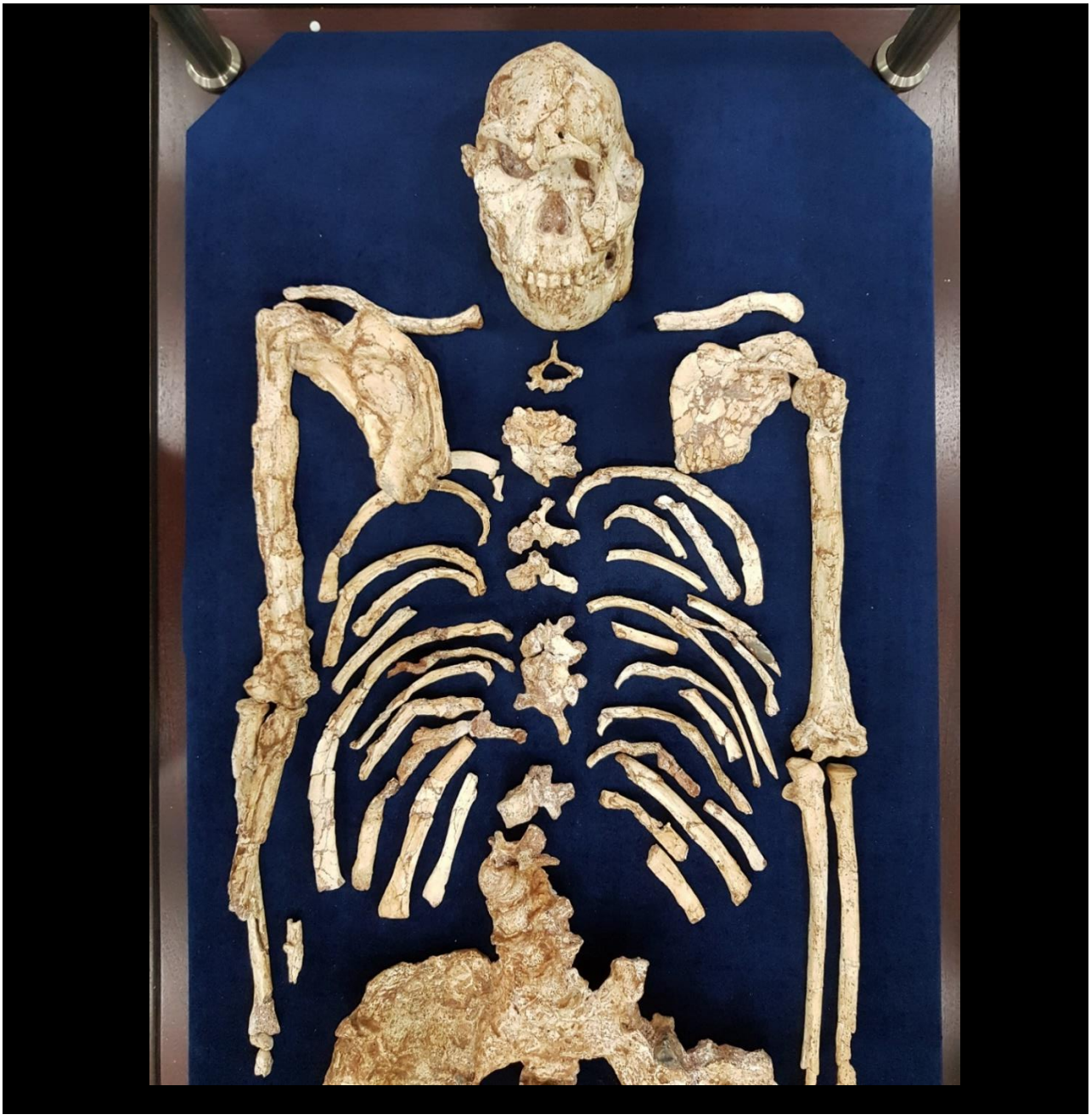


Figure 4.9: StW 573 skeleton, indicating the proposed description of first and second thoracic vertebrae currently free from matrix.

The StW 573 upper thoracic vertebra (first thoracic vertebra currently free from matrix) (Figure 4.10), demonstrates a SPA of 145.64º, with a SPL of 24.8mm. The IAFW measured 9.28mm (right) and 7.70mm (left), with IAFO being 65.72º (right) and 61.65º (left). The SAFW measured 7.55mm on the right, and 8.93mm on the left. The SAFO was measured as 79.53º on the right, and 65.24º on the left. The spinous process was deviated distally to the right.

Crompton et al. (2021) propose StW 573 to be female, although this has not been asserted and thus the first thoracic vertebra currently free from matrix is compared to male and female T3 vertebrae of selected African apes, contemporary humans and baboons in Table 4.7. The SPA is most similar to female chimpanzees (147.43º), and SPL was most similar to female baboons (26.10mm). The IAFW on the right was most similar to female gorillas (9.19mm) and male baboons on the left (7.03mm). SAFW was most similar to male baboons on the right (7.42mm) and female chimpanzees on the left (8.97mm). The IAFO was most similar to male chimpanzees on the right (71.36º) and female chimpanzees on the left (70.69º), with the right SAFO to female gorillas (77.82º) and left to female chimpanzees (68.55º).

The StW 573 mid-thoracic vertebra (second thoracic vertebra currently free from matrix) (Figure 4.11) demonstrates an SPA of 127.05º, with a SPL of 25.11mm. The IAFW measured 6.18mm (right) and 6.42mm (left), with IAFO being 76.52º (right) and 48.49º (left). The SAFW was not measured on the right and was 8.73mm on the left. The SAFO was not measured on the right, and 63.86º on the left. The spinous process was not deviated in relation to the lamina (as the body is not aligned to the posterior elements due to distortion and could therefore not be used as a reference point).

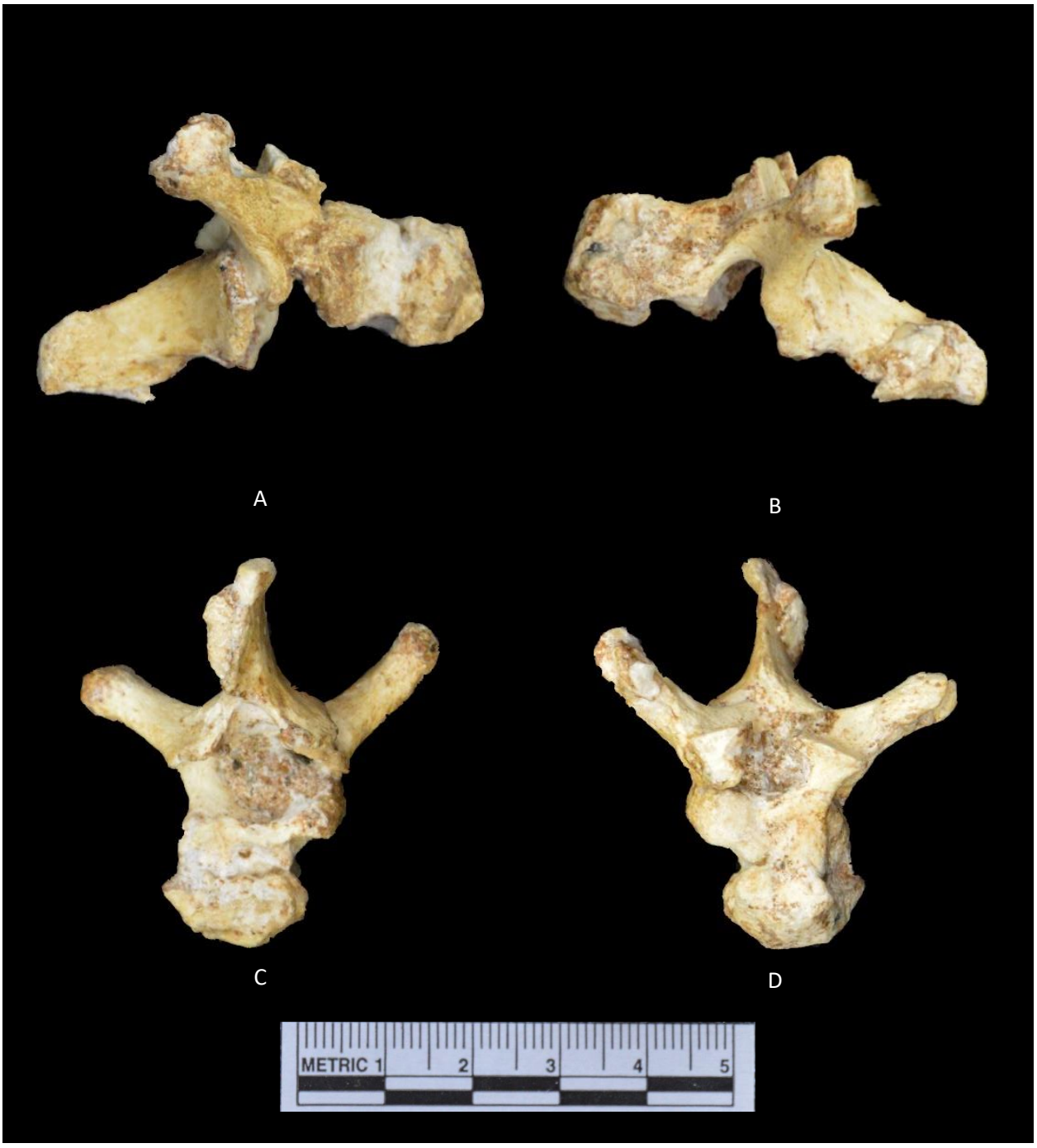


Figure 4.10: *Australopithecus prometheus* (StW 573) first thoracic vertebra currently free from matrix. A: right lateral view; B: left lateral view; C: inferior view; D: superior view.

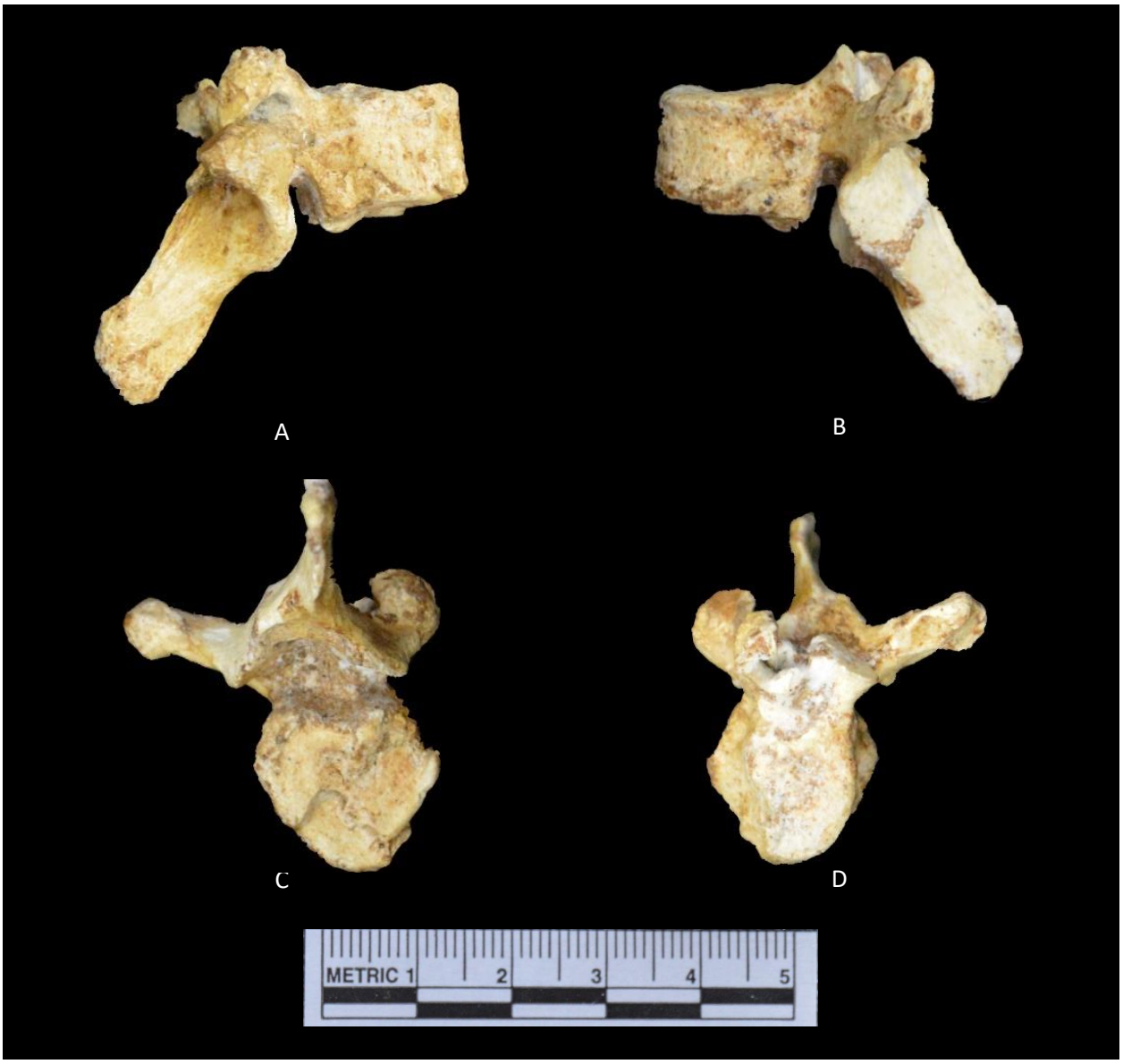


Figure 4.11: *Australopithecus prometheus* (StW 573) second thoracic vertebra currently free from matrix. A: right lateral view; B: left lateral view; C: inferior view; D: superior view.

The StW 573 second thoracic vertebra currently free from matrix is compared to male and female T6 vertebrae of selected African apes, contemporary humans and baboons in Table 4.8. The SPA is most similar to female gorillas (133.54º), and SPL was most similar to female baboons (26.93mm). The IAFW on both sides was most

similar to female baboons (right=6.62mm: left: 6.43m). SAFW was most similar to female gorillas on the left (8.79mm), with the right not being present. The IAFO was most similar to male gorillas on the right (76.83º) and female baboons on the left (60.97º), with the left SAFO to female baboons (61.75º) and right not being present.

4.3 Discussion

For the purposes of this study, all available *Australopithecus* fossil hominin samples with upper thoracic vertebrae were included. In many cases direct comparisons were not possible, as the spinous processes, transverse process and articular processes are damaged as they are fragile components of the vertebrae and liable to damage. In some cases, such as U.W. 88-188 and U.W. 88-189, which are preserved within matrix, the ability to utilize previous 3D scanning and printing, allowed for inclusion and comparison.

The following discussion will initially evaluate general trends within the fossil samples, followed by specific discussion per species.

Table 4.7: Comparison of T3 (upper thoracic) mean morphometric measurements of StW 573 to African apes, contemporary humans and baboons (male and female).

Specimen	Species	Sex****	Level	N	SPA (SD)**	SPL (SD)***	IAFW_R (SD)***	IAFW_L (SD)***	IAFO_R (SD)**	IAFO_L (SD)**	SAFW_R (SD)***	SAFW_L (SD)***	SAFO_R (SD)**	SAFO_L (SD)**
StW 573	*A. prometheus*	3	T3	1	145.64	24.80	9.28	7.70	65.72	61.65	7.55	8.93	79.53	65.24
	Gorillas	2	T3	29	147.95 (9.0)	33.98 (4.59)	9.19 (1.26)	9.22 (1.35)	78.38 (4.93)	78.14 (5.38)	9.83 (1.6)	9.88 (1.58)	77.82 (4.9)	77.04 (5.41)
	Chimpanzees	2	T3	30	147.43 (7.67)	29.77 (3.0)	8.67 (1.06)	8.67 (0.99)	72.56 (4.12)	70.69 (3.14)	9.04 (1.19)	8.97 (0.91)	68.01 (4.59)	68.55 (4.5)
	Baboons	2	T3	28	156.14 (5.31)	26.10 (3.74)	6.10 (0.8)	6.32 (0.69)	56.54 (3.69)	56.58 (4.7)	6.52 (0.80)	6.40 (0.7)	50.13 (4.44)	53.85 (4.47)
	Contemporary humans	2	T3	28	135.64 (10.83)	27.34 (3.67)	10.18 (1.37)	9.61 (1.05)	74.46 (4.34)	71.54 (4.22)	10.76 (1.5)	10.37 (1.62)	68.23 (5.26)	71.92 (5.24)
	Gorillas	1	T3	31	152.44 (9.59)	50.33 (8.82)	11.41 (1.76)	11.81 (1.8)	81.04 (5.74)	79.15 (5.49)	12.44 (1.84)	12.43 (1.82)	80.20 (7.63)	81.38 (9.56)
	Chimpanzees	1	T3	15	148.89 (7.22)	31.42 (4.16)	8.96 (1.21)	9.25 (1.84)	71.36 (4.02)	70.86 (4.38)	9.43 (1.31)	9.64 (1.62)	69.87 (4.96)	69.71 (5.91)
	Baboons	1	T3	23	153.12 (6.39)	30.65 (5.23)	7.02 (0.1)	7.03 (1.12)	55.31 (3.83)	54.64 (5.39)	7.42 (1.16)	7.37 (1.19)	49.84 (6.62)	51.38 (4.97)
	Contemporary humans	1	T3	30	137.16 (6.81)	30.94 (2.75)	11.07 (1.61)	10.39 (1.41)	75.13 (5.42)	71.83 (4.26)	11.40 (1.23)	10.82 (1.31)	69.52 (5.2)	72.04 (4.42)

**SPA, IAFO, SAFO measured in degrees
***SPL, IAFW, SAFW measured in mm
**** sex: 1=male; 2=female; 3=unknown
SD: standard deviation

Table 4.8: Comparison of T6 (mid thoracic) mean morphometric measurements of StW 573 to African apes, contemporary humans and baboons (male and female).

Specimen	Species	Sex****	Level	N	SPA (SD)**	SPL (SD)***	IAFW_R (SD)***	IAFW_L (SD)***	IAFO_R (SD)**	IAFO_L (SD)**	SAFW_R (SD)***	SAFW_L (SD)***	SAFO_R (SD)**	SAFO_L (SD)**
StW 573	*A. prometheus*	3	T6	1	127.05	25.11	6.18	6.42	76.52	48.49	Not present	8.73	Not present	63.86
	Gorillas	2	T6	29	133.54 (8.84)	28.82 (3.65)	8.54 (1.26)	8.65 (1.23)	74.45 (5.13)	71.19 (5.87)	8.87 (1.18)	8.79 (1.08)	72.18 (5.54)	70.87 (6.26)
	Chimpanzees	2	T6	30	141.01 (6.4)	30.59 (3.12)	8.46 (0.95)	8.41 (0.99)	71.36 (5.26)	69.19 (4.31)	8.64 (1.1)	8.54 (0.97)	69.57 (4.86)	71.04 (5.47)
	Baboons	2	T6	28	152.20 (5.06)	26.93 (3.94)	6.62 (0.85)	6.43 (0.92)	62.66 (3.84)	60.97 (5.17)	6.64 (0.89)	6.40 (0.85)	59.21 (3.79)	61.75 (3.66)
	Contemporary humans	2	T6	28	121.21 (8.97)	28.60 (4.31)	8.98 (0.89)	9.14 (0.91)	76.17 (5.02)	75.50 (4.26)	9.39 (1.28)	9.28 (1.1)	70.28 (5.16)	74.35 (3.45)
	Gorillas	1	T6	31	133.96 (8.31)	39.56 (7.63)	9.81 (1.47)	9.94 (1.47)	76.83 (5.48)	71.99 (6.72)	10.73 (1.67)	10.57 (1.52)	73.74 (4.89)	73.53 (5.31)
	Chimpanzees	1	T6	15	141.10 (6.58)	33.92 (5.57)	8.66 (0.76)	8.81 (1.14)	72.59 (2.82)	70.02 (6.42)	9.11 (1.34)	8.93 (1.1)	70.93 (4.98)	72.08 (5.61)
	Baboons	1	T6	23	150.25 (6.86)	32.10 (6.4)	7.48 (1.24)	7.50 (1.23)	61.05 (4.18)	61.19 (4.7)	7.40 (1.28)	6.98 (1.1)	58.34 (3.78)	61.67 (3.58)
	Contemporary humans	1	T6	30	122.19 (6.58)	31.62 (3.71)	10.03 (1.4)	9.85 (1.12)	73.78 (4.79)	73.90 (3.71)	10.50 (1.79)	9.84 (1.19)	69.08 (5.66)	73.27 (4.58)

**SPA, IAFO, SAFO measured in degrees
***SPL, IAFW, SAFW measured in mm
**** sex: 1=male; 2=female; 3=unknown
SD: standard deviation

4.3.1 The genus *Australopithecus*

Jones et al. (1992) discusses australopiths as being categorized as gracile (such as *A. africanus* and *A. afarensis*) or robust (such as *P. robustus* or *P. boisei*). They are described as ape-like and in many cases facultative primitive bipeds, with strong evidence suggesting arboreal behaviour and being adapted to life on the ground and in trees (Kappelman et al., 2016; Stern, 2000; Ward, 2002; Williams and Meyers, 2019). Approximately ten different species of australopiths have been identified from areas in east, central and southern Africa, with variations in size, diet, behavior, and environment they lived in (Reed et al., 2013).

In general, the articular facet widths for all australopiths in the current study were most similar to baboons. As indicated in Table 4.9, *A. sediba* is proposed to have a body mass in the region of 32-36kg, and *A. afarensis* 25.6kg (Holliday et al., 2018), which is similar to chacma baboon's average of 31.8kg (Kingdon et al., 2013), and it would therefore be expected to find similar morphometric measurements relating to size, as was the case in the current study. Sexual skeletal size dimorphism is proposed to be in the region of 15% for contemporary humans and some authors consider this to be similar in *A. afarensis* (Reno et al., 2003; Plavcan et al., 2005; Plavcan, 2018) although Richmond and Jungers (1995), Harmon (2006) and Gordon et al. (2008) indicate a similar postcranial dimorphic pattern in *Australopithecus* to gorillas and orangutans, with males being significantly larger than females. Measurements related to articular facet width in the current study were similar on most of the species, as was SPL and no definite support relating to dimorphism could be determined.

Table 4.9: Estimated body mass of fossil hominins utilized in this study (modified from Holliday et al. 2018).

Specimen	Estimated body mass (kg)
MH1	35
MH2	35.5
A.L. 288-1	25.6

Overall similarities in morphometric measurements in the current study would be expected, given the fact that samples were from the same genus. SPD was not a consistent morphometric measurement that could be utilized, as in many cases the spinous process was entirely or partially absent. This makes determination of a trend in comparison difficult to determine, especially, as will be discussed later, U.W. 88-37 exhibiting pathology that would directly impact SPD.

4.3.2 *Australopithecus africanus*

Sts 14 is considered to be an adult female representing *A. africanus.* Fossilized remains were found at Sterkfontein member 4, in South Africa, in a single block of breccia. The skeleton preserved 19 partial vertebrae (Ward et al., 2020).

Ward et al. (2020) describe Sts 14m and Sts 14i, with the articular facet orientation being approximately 5º from the coronal plane, with the superior facets facing slightly lateral, and the inferior facets slightly medial. The spinous process is described as being 55º from the inferior endplate. These are similar to the findings in the current study SPA (121.21º and 121.56º), and AFO (72.08º to 77.39º).

No SPD were noted in either Sts 14m or Sts 14i. As previously discussed in Chapter 3, various aspects should be considered in contribution towards SPD, with a relatively low overall incidence noted in the African apes, contemporary humans and baboons. As the evaluation is based on a single individual, no inference can be made regarding this feature in this species.

4.3.3 *Australopithecus sediba*

U.W. 88-11 and U.W. 88-37 (Malapa Hominin 1 – MH1) are considered to be from a juvenile male (Burger et al., 2010; Randolph-Quinney et al., 2016; Williams et al., 2018) with U.W. 88-188 and U.W. 88-189 (Malapa Hominin 2 – MH2) an adult female (Burger et al., 2010; Williams et al., 2018). Fossilized remains were found at Malapa, in the Cradle of Humankind, South Africa and dated to ca. 2.0 Ma (Berger et al., 2010; Dirks et al., 2010; Pickering et al., 2011), with seven vertebrae from MH1 and fifteen from MH2 (Williams et al., 2021).

Williams et al. (2018) described U.W. 88-11 and indicating a SPL measurement of 25.9mm and SPA of 158º to the coronal plane, which is similar to the findings in the current study SPL (26.07mm) and SPA (157.03º). They describe the SPA as being similar to the median of chimpanzees (Williams et al. 2018); however, in the current study it was found to be most similar to baboons. Williams et al. (2018) did however not compare to baboons, and focused comparisons to chimpanzees and contemporary humans. The spinous process angle is considered by Williams et al. (2018) to be quite horizontal and in the high end of human variation and close to the median of their chimpanzee sample. As previously discussed if considered a trait developed for

bipedalism (Latimer and Ward, 1993; Gomez-Olivencia et al., 2013; Plomp et al., 2019) a horizontal spinous process may support the proposal that members of the *Australopithecus* were not committed terrestrial bipeds (Ward, 2002; Kappelman et al., 2016; Williams and Meyers, 2019; Stern, 2000). However *A.sediba* is considered a derived bipedal with some retained adaptations to arboreal locomotion (Schmid et al., 2013, Williams et al., 2021).

U.W. 88-37 is a complete mid-thoracic vertebra, with a rounded penetrating defect on the right sided lamina (Randolph-Quinney et al., 2016; Williams et al., 2018) indicating a potential lytic bone lesion and described by Randolph-Quinney et al. (2016) as being a primary osteogenic tumour, in this case most likely an osteoid osteoma. Williams et al. (2018) describes the SPA as 124º, with a SPL of 30mm, which is similar to the current study findings of 131.25º and 23.24mm respectively and is most similar to gorillas (133.96º) and contemporary humans (36.65mm).

Spinous process deviations could be determined in U.W. 88-11 and U.W. 88-37, as the spinous processes were sufficiently intact. The two vertebrae are from MH1 but are not considered consecutive as previously indicated by Williams et al. (2018). U.W. 88-11 demonstrated distal deviation to the left, and U.W. 88-37 distal deviation to the right.

From the perspective of a proposed expanding neoplasm in the lamina (Randolph-Quinney et al., 2016) of U.W. 88-37, it may have been expected that the SPD would have been towards the left, due to the pressure from the right-side lamina enlargement from what is ostensibly a space occupying lesion. The fact that deviation is noted towards the side of the pathology, suggests that mechanisms other than effects of

a space occupying lesion, such as biomechanical adaptation may well be at play, as proposed in Chapter 3. Randolph- Quinney et al. (2016) proposed that MH1 would have had a level of dysfunction associated with movement of the shoulder blade and upper right quadrant of the back. Secondary muscle spasm may be associated with pain and inflammatory effects around a tumour (Saifuddin et al., 1998) and surrounding muscles such as trapezius, rhomboid, erector spinae and multifidus may have exerted abnormal load on the spinous process as a result of pain avoidance behaviour or muscle splinting resulting in the deviation identified. U.W. 88-11 demonstrated a deviation in the opposite direction to U.W. 88-37, but as discussed in Chapter 3, the progression and prediction of SPD is not always possible and these vertebrae were potentially three levels apart. The possibility exists that the SPD is a result of the contralateral increase in muscle demands, as part of compensation and adaptation for activity with pain avoidance, but a more complete vertebral series would be needed to investigate this proposed mechanism.

When considered locomotor propensity, Williams et al. (2021) evaluated the lumbar spine of MH2 and found it possessed a lumbar lordosis and other adaptations to bipedalism such as increased width of the intervertebral articular facets from the upper to lower lumbar column (pyramidal configuration). Arboreal and terrestrial bipedalism is suggested, with more arboreal activities as previously discussed based on the ribcage (Schmid, 1991; Schmid et al., 2013, Williams et al., 2021) which supports the current study's findings in relation to facet orientation being most similar to either chimpanzees or gorillas (as indicated in Table 4.4-4.6).

4.3.4 *Australopithecus afarensis*

A.L. 288-1 is considered an adult female and was found in the Hadar formation (Central Afar, Ethiopia) in the KH-1s deposit, with eight preserved vertebral elements (Johanson et al., 1982; Meyer et al., 2015; Williams and Meyer, 2019). Johanson et al. (1982), Cook et al. (1983) and Meyer et al. (2015) describe the A.L. 288-1ae vertebral level as T6. In the current study, casts were utilized from the Evolutionary Studies Institute, University of Witwatersrand, South Africa.

Aspects relating to size and morphometric measurements have been previously discussed. As was the case in other *Australopithecus* species in this study, orientation of articular facets tended to be most similar to chimpanzees and gorillas. This is consistent with the proposed arboreal adaptations (Schmid, 1991; Stern and Susman, 1983; Stern, 2000).

Kappelman et al. (2016) propose that this fossil presents evidence of injuries resulting from a fall from a significant height (possibly a tree) and indicates the potential for arborealism in this species. No indication is given of potential damage to the thoracic vertebra as a result of this proposed injury, and it is therefore unlikely to have affected the morphometric measurements in the current study.

A.L. 288-1 is described by Cook et al. (1983) as potentially having Scheuermann's disease, a form of juvenile osteochondrosis of the spine (Palazzo et al., 2014) with this diagnosis being based on the vertebral wedging and elongated vertebral body size (DiGiovanni et al., 1989) noted in the thoracic vertebrae. Farrell et al. (2012) propose that upright posture and habitual bipedal locomotion are not absolute requirements for the development of this condition, although Prabhat et al. (2021)

consider *A. afarensis* as the most terrestrially adapted australopith and may well have been susceptible to developing Scheuermann's disease. The anterior aspect and endplates are affected structurally in this condition (Palazzo et al., 2014) and the posterior elements may therefore only be affected by secondary mechanical strain from the increased kyphotic development. No spinous process was present in A.L. 288-1ae, so no determination could be made, and this would therefore require further investigation utilizing morphometric measurements in samples identified as having Scheuermann's disease to measurements obtained in the current study.

4.3.5 *Australopithecus prometheus*

StW 573, nicknamed "Little Foot", is a mature adult, that is proposed to be female by Crompton et al. (2021) and the fossilized remains were found in Sterkfontein Member 2 breccia in the Silberberg Grotto, with six thoracic vertebrae (Clarke, 2019; Clarke and Kuman, 2019). As described by Clarke (2019) these remains demonstrate significant taphonomic history, which may have affected the accuracy of the morphometric measurements in the current study. To date, no published descriptions of the vertebrae are available, and the classification of upper thoracic and mid thoracic vertebrae are based on observations of the fossil remains and images (Figure 4.8, 4.9 and 4.10) by the researcher and supervisors (Williams and Zipfel).

Regardless of sex, morphometric measurements showed the most similarity to *A. sediba* (MH2) in the *Australopithecus* comparison. Comparatively, both the T3 and T6 specimens had more correlation of morphometric measurements to the female primates

than males, which is consistent with the proposed female sex, and may be attributed to sexual dimorphism as previously discussed.

Spinous processes were sufficiently intact to evaluate SPD, with the upper vertebra exhibiting right distal deviation, and the mid thoracic vertebra exhibiting no deviation. Due to presenting taphonomic changes in these spinous process deviations needed to be determined differently to other specimens and was evaluated in relation to the lamina as opposed to the vertebral body. The lamina themselves may well have been affected by taphonomic changes and may not have been bilaterally equal in presentation and may have affected the accuracy of the SPD determination and SPD may not have been present in life.

Crompton et al. (2021) suggest that *A. prometheus* was an arboreal biped climber, and that gorilla may be a more informative extant species for locomotor comparison. This is supported in the current study as the articular facet orientations were most similar to female chimpanzees and gorillas and may be attributed to adaptations that would be expected to be aligned with similar habitual locomotor posture.

4.3.6 Considerations for bipedalism

Various traits have been presented in contemporary humans and great apes upper thoracic vertebrae as developed adaptations for bipedalism, and these will now be presented in relation to the *Australopithecus* specimens in the current study.

Human upper thoracic articular facets (superior and inferior) are proposed to be adapted for bipedalism and are more coronally orientated than great apes (Latimer and

Ward, 1993; Shapiro, 1993; Williams and Russo, 2015; Meyer et al., 2017; Plomp et al. 2019). In the current study the orientation of upper thoracic articular facets of *Australopithecus* were comparable to various hominines and baboons (Table 4.2 to 4.8) and no consistent pattern could be identified.

The spinous process angles in the *Australopithecus* species in the current study were found to be more caudally orientated when compared to the African apes and baboons (Table 4.2 to 4.8), but not compared to contemporary humans (except in the case of U.W.88-11). This feature is proposed by Latimer and Ward (1993), Gomez-Olivencia et al., (2013) and Plomp et al. (2019) to be an adaptation for bipedalism in contemporary humans (when compared to great apes) and may be an additional suggestion of *Australopithecus* being primitive obligate bipeds when terrestrial, with strong evidence of arboreal behaviour (Ward, 2002; Kappelman et al., 2016; Williams and Meyers, 2019; Stern, 2000).

Shorter spinous process length has been proposed by Schultz (1961), Latimer and Ward (1993), Gomez-Olivencia et al. (2013), Meyer (2016), Meyer et al. (2017) and Plomp et al. (2019) as a developed trait in contemporary humans (when compared to great apes) for bipedalism. In the current study, spinous processes length appears shorter in *Australopithecus* than other species comparisons although this may not be an accurate reflection on comparison, as the spinous processes are potentially subject to taphonomic damage. Most values were not similar to the contemporary humans, except for U.W.88-37 and Sts14m. Given the similarity to baboons spinous process lengths, this appears to be a consequence of size of species, as opposed to locomotor differences.

Spinous process deviations were noted in U.W. 88-11, U.W. 88-37 and StW 573. As discussed in the previous chapter and presented in Table 3.12, in the African apes and contemporary humans this may be considered a frequent feature in an individual, but not in baboons. *A.sediba* MH1 is considered to be a juvenile male (Randolph-Quinney et al., 2016; Williams et al., 2018) and the frequency of SPD was demonstrated to be higher in males in the previous chapter. This individual also presented evidence of a potential osteoid osteoma of the lamina (Randolph-Quinney et al., 2016) which had a direct impact on the spinous process and may therefore have been more predisposed to SPD as a consequence of this underlying pathology (Van Schaik et al., 1989; Mellado et al., 2011; Lawler et al., 2016). StW 573 is proposed to be a female (Crompton et al., 2021) and females appear to be less likely to present with SPD as discussed in the preceding chapter. Taphonomic changes are proposed by Lawler et al. (2016) as a potential causal category for SPD and significant taphonomic changes are seen in this fossil (Clarke, 2019) which may limit the ability to utilise the spinous process in this individual as a comparative feature.

When evaluating the findings of *Australopithecus* in the current study in relation to spinous process deviations, there does not appear to be sufficient consistency to allow for the presence of this feature in upper thoracic vertebrae to be proposed as a consequence of bipedalism.

CHAPTER 5

LATER STONE AGE AND CONTEMPORARY HUMAN MORPHOMETRIC COMPARISON

5.1 Introduction

This chapter focuses on potential differences in morphology and variability in measurements of Later Stone Age (LSA) humans to contemporary humans. For the purposes of this study, the humans remains from the Matjies River rock shelter (as a representative sample of LSA humans) are compared to contemporary human samples. This will allow for a determination of the potential effect of lifestyle and activity function on the structures measured and facilitate a discussion regarding locomotor propensity compared to functional activity.

5.2 Descriptive statistics for morphometric measurements between human sample groups

The LSA human specimens in the Matjies River collection are few in number, resulting in a considerably smaller group than the contemporary human sample, and do not have allocated sex. The results are therefore presented as a descriptive comparison of the entire contemporary human to LSA human sample groups**.** Figures 5.1 to 5.6 illustrate the visual comparison between LSA and contemporary human samples. The means values of morphometric measurements for the two groups are presented in Table 5.1, and the direct measurements of the LSA human in Table 5.2.

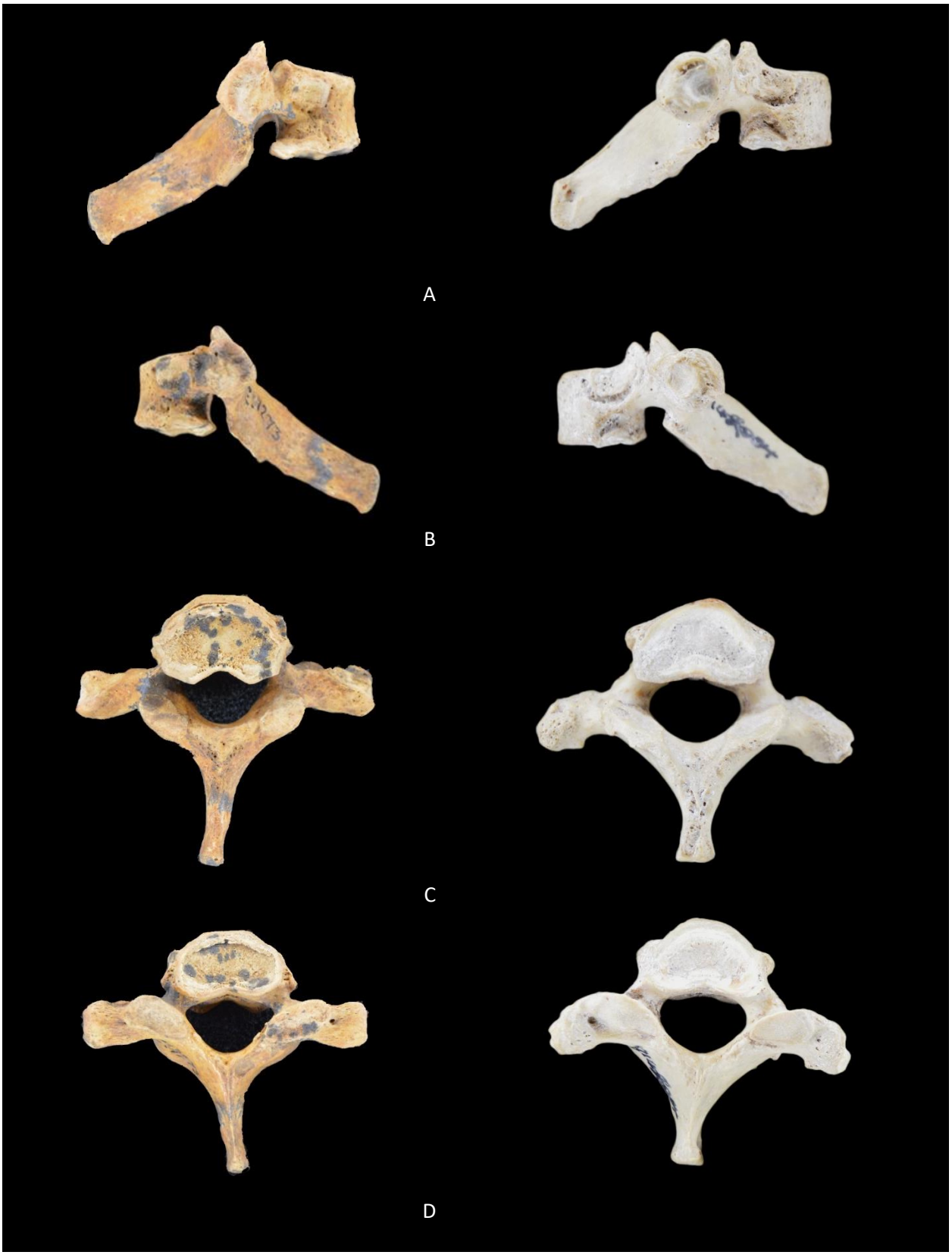


Figure 5.1: Comparison of LSA (left) and contemporary (right) human T1 Vertebra. A: right lateral view; B: left lateral view; C: inferior view; D: superior view.

Figure 5.2: Comparison of LSA (left) and contemporary (right) human T2 Vertebra. A: right lateral view; B: left lateral view; C: inferior view; D: superior view.

Figure 5.3: Comparison of LSA (left) and contemporary (right) human T3 Vertebra. A: right lateral view; B: left lateral view; C: inferior view; D: superior view.

Figure 5.4: Comparison of LSA (left) and contemporary (right) human T4 Vertebra. A: right lateral view; B: left lateral view; C: inferior view; D: superior view.

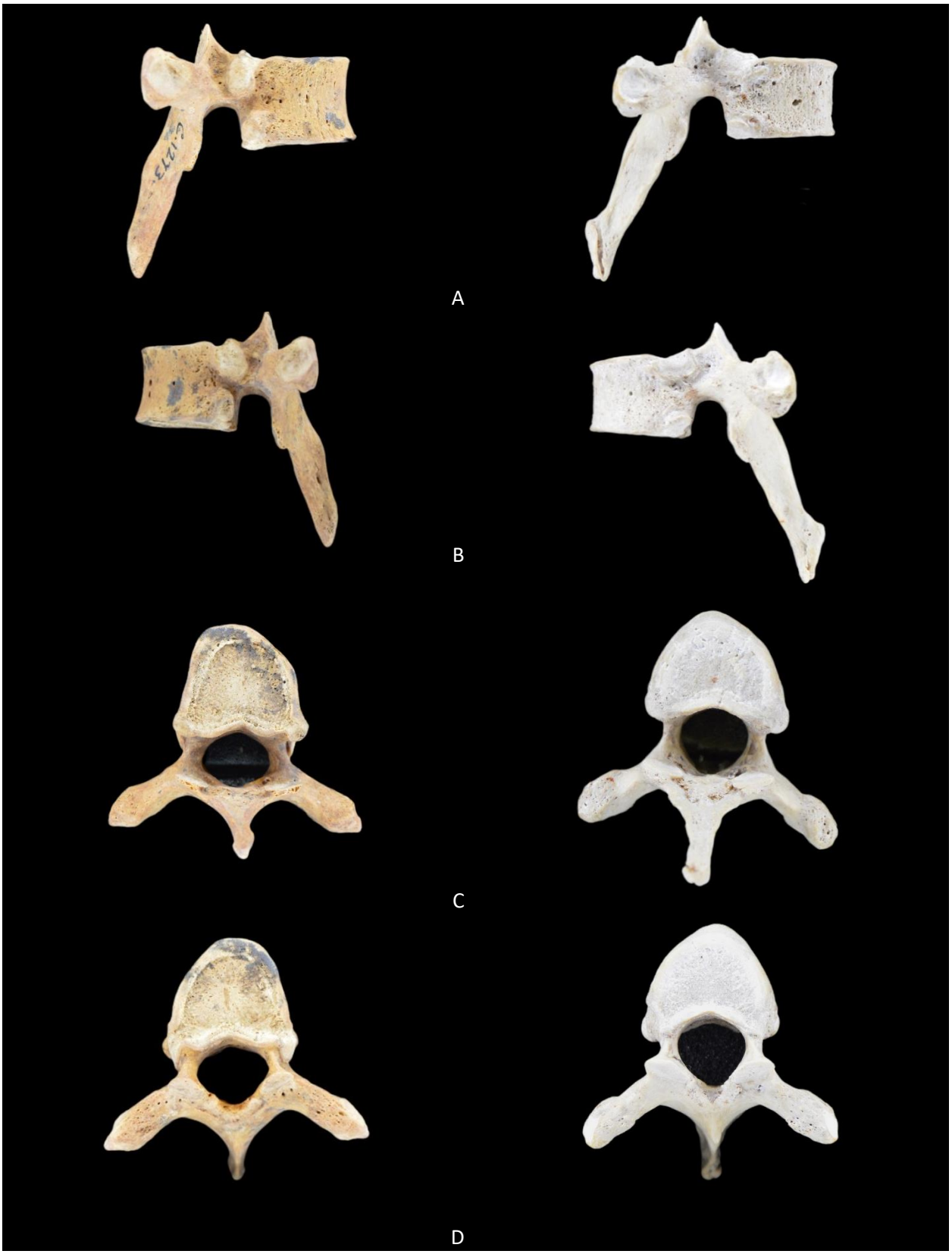


Figure 5.5: Comparison of LSA (left) and contemporary (right) human T5 Vertebra. A: right lateral view; B: left lateral view; C: inferior view; D: superior view.

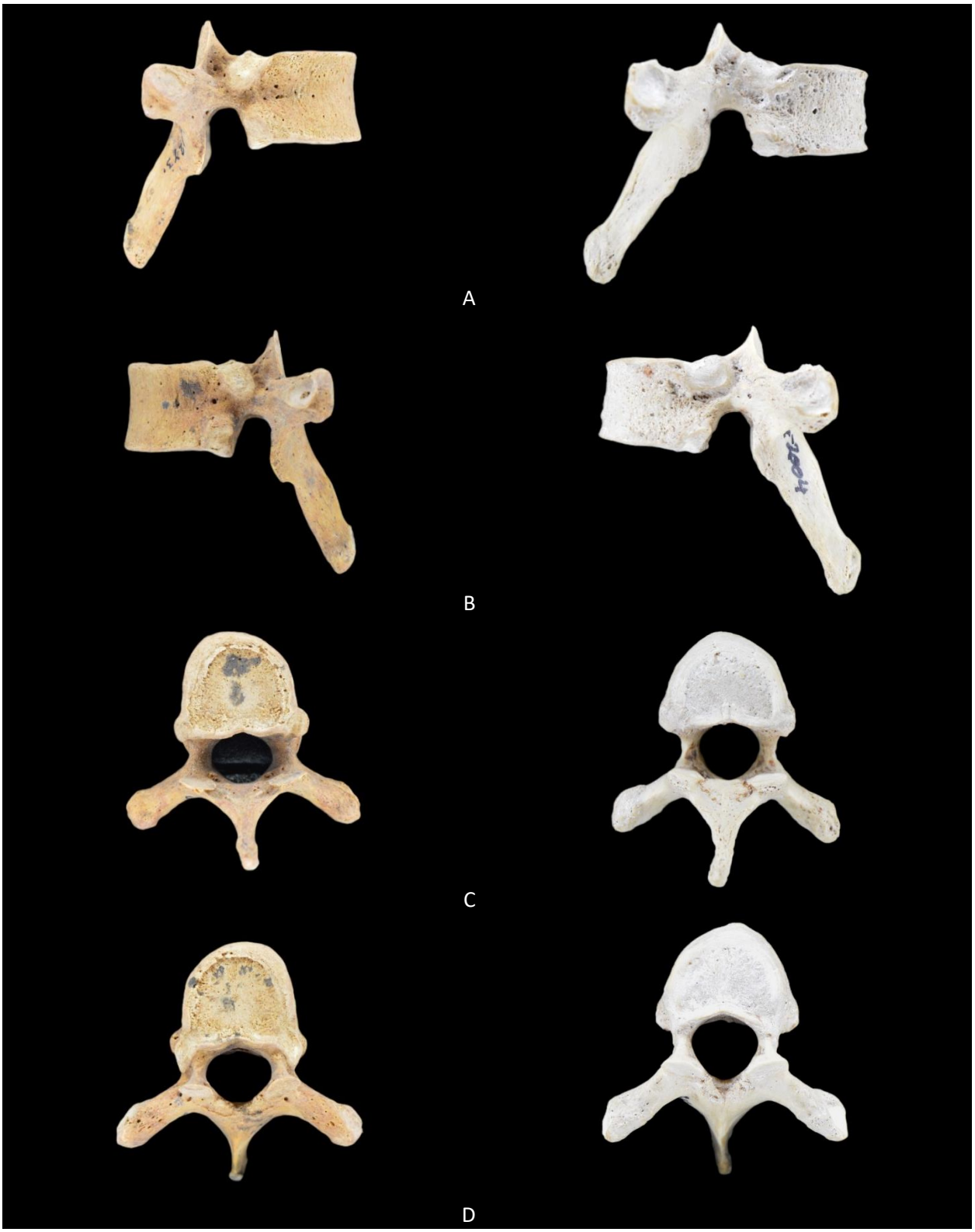


Figure 5.6: Comparison of LSA (left) and contemporary (right) human T6 Vertebra. A: right lateral view; B: left lateral view; C: inferior view; D: superior view

Table 5.1: Cross tabulation of LSA and contemporary humans mean values of morphologic measurements.

Measurement	Human sample	N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Minimum	Maximum
						Lower Bound	Upper Bound		
SPA_T1*	Human (contemporary)	58	142.03	8.290	1.089	139.85	144.21	119	156
	Human (Later stone age)	6	139.85	6.020	2.458	133.53	146.17	131	146
SPL_T1**	Human (contemporary)	58	31.82	3.521	0.462	30.89	32.74	25	42
	Human (Later stone age)	6	27.91	2.120	0.865	25.68	30.13	25	31
IAFW_R.T1**	Human (contemporary)	58	11.69	1.562	0.205	11.28	12.10	9	15
	Human (Later stone age)	6	10.50	1.251	0.511	9.19	11.81	9	13
IAFW_L.T1**	Human (contemporary)	58	11.93	1.674	0.220	11.49	12.37	8	15
	Human (Later stone age)	6	9.81	1.290	0.527	8.46	11.17	8	12
IAFO_R.T1*	Human (contemporary)	58	69.02	6.182	0.812	67.39	70.64	56	82
	Human (Later stone age)	6	67.18	8.225	3.358	58.55	75.81	51	74
IAFO_L.T1*	Human (contemporary)	58	66.81	4.985	0.655	65.50	68.12	57	78
	Human (Later stone age)	6	65.75	10.272	4.194	54.97	76.53	48	77
SAFW_R.T1**	Human (contemporary)	58	14.48	2.093	0.275	13.93	15.03	10	19

	Human (Later stone age)	6	12.76	2.621	1.070	10.00	15.51	9	17
SAFW_L.T1**	Human (contemporary)	58	14.56	2.353	0.309	13.94	15.18	9	20
	Human (Later stone age)	6	12.74	2.781	1.135	9.83	15.66	9	17
SAFO_R.T1*	Human (contemporary)	58	77.64	9.925	1.303	75.03	80.25	57	98
	Human (Later stone age)	6	76.31	6.920	2.825	69.05	83.57	67	85
SAFO_L.T1*	Human (contemporary)	58	78.03	8.266	1.085	75.85	80.20	60	95
	Human (Later stone age)	6	72.02	9.233	3.769	62.33	81.71	61	85
SPA_T2*	Human (contemporary)	58	139.45	8.722	1.145	137.15	141.74	111	155
	Human (Later stone age)	6	144.29	7.125	2.909	136.81	151.77	131	153
SPL_T2**	Human (contemporary)	58	30.86	3.782	0.497	29.86	31.85	20	39
	Human (Later stone age)	6	26.70	1.043	0.426	25.60	27.79	26	29
IAFW_R.T2**	Human (contemporary)	58	10.71	1.270	0.167	10.38	11.05	8	14
	Human (Later stone age)	6	10.27	0.864	0.353	9.36	11.17	10	12
IAFW_L.T2**	Human (contemporary)	58	10.46	1.536	0.202	10.06	10.86	7	15
	Human (Later stone age)	6	9.72	1.260	0.515	8.39	11.04	8	12
IAFO_R.T2*	Human (contemporary)	58	72.93	5.430	0.713	71.50	74.36	59	87

	Human (Later stone age)	6	73.02	6.630	2.707	66.06	79.98	64	81
IAFO_L.T2*	Human (contemporary)	58	71.43	4.489	0.589	70.25	72.61	58	80
	Human (Later stone age)	6	74.74	5.537	2.261	68.92	80.55	69	83
SAFW_R.T2**	Human (contemporary)	58	12.35	1.751	0.230	11.89	12.82	8	16
	Human (Later stone age)	6	11.20	1.337	0.546	9.80	12.61	10	14
SAFW_L.T2**	Human (contemporary)	58	11.95	1.728	0.227	11.49	12.40	9	16
	Human (Later stone age)	6	11.12	1.296	0.529	9.76	12.48	10	14
SAFO_R.T2*	Human (contemporary)	58	68.04	6.437	0.845	66.35	69.73	51	87
	Human (Later stone age)	6	67.66	2.004	0.818	65.56	69.76	65	71
SAFO_L.T2*	Human (contemporary)	58	69.92	4.872	0.640	68.64	71.21	58	83
	Human (Later stone age)	6	65.01	4.536	1.852	60.25	69.77	60	73
SPA_T3*	Human (contemporary)	58	136.43	8.928	1.172	134.08	138.77	114	156
	Human (Later stone age)	4	136.57	12.560	6.280	116.58	156.56	120	149
SPL_T3**	Human (contemporary)	58	29.21	3.676	0.483	28.24	30.17	22	37
	Human (Later stone age)	4	24.88	2.039	1.019	21.64	28.13	23	27
IAFW_R.T3**	Human (contemporary)	58	10.64	1.552	0.204	10.23	11.05	8	16

	Human (Later stone age)	4	9.03	0.522	0.261	8.19	9.86	9	10
IAFW_L.T3**	Human (contemporary)	58	10.01	1.300	0.171	9.67	10.36	7	13
	Human (Later stone age)	4	6.46	4.331	2.166	-0.43	13.36	0	9
IAFO_R.T3*	Human (contemporary)	57	74.81	4.908	0.650	73.51	76.11	64	86
	Human (Later stone age)	4	70.91	2.847	1.423	66.38	75.44	68	75
IAFO_L.T3*	Human (contemporary)	57	71.69	4.206	0.557	70.58	72.81	62	83
	Human (Later stone age)	4	71.28	6.826	3.413	60.42	82.14	63	80
SAFW_R.T3**	Human (contemporary)	57	11.10	1.392	0.184	10.73	11.47	8	14
	Human (Later stone age)	4	9.19	0.689	0.345	8.09	10.28	8	10
SAFW_L.T3**	Human (contemporary)	57	10.61	1.469	0.195	10.22	10.99	8	14
	Human (Later stone age)	4	8.57	1.295	0.648	6.51	10.63	7	10
SAFO_R.T3*	Human (contemporary)	57	68.91	5.219	0.691	67.52	70.29	54	79
	Human (Later stone age)	4	68.73	3.319	1.660	63.45	74.01	65	73
SAFO_L.T3*	Human (contemporary)	57	71.99	4.783	0.634	70.72	73.26	60	81
	Human (Later stone age)	4	72.40	3.180	1.590	67.33	77.46	70	77
SPA_T4*	Human (contemporary)	58	130.07	8.833	1.160	127.75	132.40	112	149

	Human (Later stone age)	3	127.59	8.942	5.163	105.38	149.80	117	133
SPL_T4**	Human (contemporary)	58	28.83	3.543	0.465	27.90	29.76	21	38
	Human (Later stone age)	3	24.19	3.481	2.010	15.54	32.83	20	27
IAFW_R.T4**	Human (contemporary)	58	10.20	1.513	0.199	9.80	10.59	7	14
	Human (Later stone age)	3	8.11	0.347	0.200	7.25	8.97	8	9
IAFW_L.T4**	Human (contemporary)	58	9.81	1.287	0.169	9.47	10.15	7	13
	Human (Later stone age)	3	8.78	0.368	0.213	7.86	9.69	8	9
IAFO_R.T4*	Human (contemporary)	58	74.03	4.402	0.578	72.88	75.19	64	83
	Human (Later stone age)	3	69.80	1.108	0.639	67.05	72.55	69	71
IAFO_L.T4*	Human (contemporary)	58	73.62	4.506	0.592	72.44	74.81	60	82
	Human (Later stone age)	3	76.25	5.406	3.121	62.82	89.68	72	82
SAFW_R.T4**	Human (contemporary)	57	11.15	1.538	0.204	10.74	11.56	8	15
	Human (Later stone age)	3	8.99	0.807	0.466	6.99	11.00	8	10
SAFW_L.T4**	Human (contemporary)	57	10.38	1.550	0.205	9.97	10.79	7	14
	Human (Later stone age)	3	9.08	0.483	0.279	7.88	10.28	9	9
SAFO_R.T4*	Human (contemporary)	57	69.93	5.064	0.671	68.58	71.27	58	81

	Human (Later stone age)	3	63.95	8.808	5.085	42.07	85.83	57	74
SAFO_L.T4*	Human (contemporary)	57	72.82	3.436	0.455	71.91	73.73	65	80
	Human (Later stone age)	3	69.77	2.891	1.669	62.58	76.95	67	73
SPA_T5*	Human (contemporary)	58	125.50	8.302	1.090	123.32	127.68	108	145
	Human (Later stone age)	2	115.62	6.046	4.275	61.30	169.93	111	120
SPL_T5**	Human (contemporary)	58	29.41	4.586	0.602	28.20	30.62	21	39
	Human (Later stone age)	2	23.23	6.530	4.618	-35.44	81.91	19	28
IAFW_R.T5**	Human (contemporary)	58	9.64	1.468	0.193	9.25	10.02	6	13
	Human (Later stone age)	2	8.51	0.506	0.358	3.96	13.06	8	9
IAFW_L.T5**	Human (contemporary)	58	9.30	1.309	0.172	8.96	9.65	6	13
	Human (Later stone age)	2	8.17	0.465	0.329	3.99	12.34	8	8
IAFO_R.T5*	Human (contemporary)	58	73.81	4.921	0.646	72.51	75.10	60	89
	Human (Later stone age)	2	74.01	6.654	4.705	14.22	133.79	69	79
IAFO_L.T5*	Human (contemporary)	58	73.87	4.806	0.631	72.61	75.13	62	87
	Human (Later stone age)	2	80.93	3.825	2.705	46.55	115.30	78	84
SAFW_R.T5**	Human (contemporary)	58	10.68	1.520	0.200	10.28	11.08	8	15

	Human (Later stone age)	2	8.69	0.850	0.601	1.06	16.33	8	9
SAFW_L.T5**	Human (contemporary)	58	10.02	1.326	0.174	9.67	10.37	8	13
	Human (Later stone age)	2	8.66	0.117	0.083	7.61	9.71	9	9
SAFO_R.T5*	Human (contemporary)	58	70.04	5.145	0.676	68.68	71.39	59	81
	Human (Later stone age)	2	60.60	4.533	3.205	19.87	101.32	57	64
SAFO_L.T5*	Human (contemporary)	58	74.21	3.672	0.482	73.25	75.18	60	80
	Human (Later stone age)	2	70.34	2.213	1.565	50.45	90.22	69	72
SPA_T6*	Human (contemporary)	58	121.71	7.769	1.020	119.67	123.76	103	139
	Human (Later stone age)	2	117.32	3.281	2.320	87.84	146.80	115	120
SPL_T6**	Human (contemporary)	58	30.16	4.258	0.559	29.04	31.28	19	40
	Human (Later stone age)	2	27.97	0.506	0.358	23.43	32.51	28	28
IAFW_R.T6**	Human (contemporary)	58	9.52	1.280	0.168	9.18	9.86	7	13
	Human (Later stone age)	2	9.35	0.672	0.475	3.32	15.39	9	10
IAFW_L.T6**	Human (contemporary)	58	9.51	1.077	0.141	9.22	9.79	8	12
	Human (Later stone age)	2	9.06	0.595	0.421	3.71	14.41	9	9
IAFO_R.T6*	Human (contemporary)	58	74.93	5.006	0.657	73.62	76.25	63	87

	Human (Later stone age)	2	71.49	3.366	2.380	41.25	101.73	69	74
IAFO_L.T6*	Human (contemporary)	58	74.67	4.029	0.529	73.61	75.73	65	86
	Human (Later stone age)	2	71.18	7.502	5.305	3.77	138.58	66	76
SAFW_R.T6**	Human (contemporary)	58	9.97	1.648	0.216	9.53	10.40	6	13
	Human (Later stone age)	2	9.53	0.440	0.311	5.57	13.48	9	10
SAFW_L.T6**	Human (contemporary)	58	9.57	1.176	0.154	9.26	9.88	6	12
	Human (Later stone age)	2	8.59	0.395	0.279	5.04	12.14	8	9
SAFO_R.T6*	Human (contemporary)	58	69.66	5.408	0.710	68.24	71.08	52	82
	Human (Later stone age)	2	65.99	1.633	1.155	51.31	80.66	65	67
SAFO_L.T6*	Human (contemporary)	58	73.79	4.072	0.535	72.72	74.86	63	84
	Human (Later stone age)	2	80.45	3.323	2.350	50.59	110.31	78	83

*SPA, IAFO, SAFO measured in degrees
**SPL, IAFW, SAFW measured in mm

Table 5.2: LSA human morphometric measurements and spinous process deviations per sample measured.

Specimen	Level	SPA**	SPL***	IAFW_R***	IAFW_L***	IAFO_R**	IAFO_L**	SAFW_R***	SAFW_L***	SAFO_R**	SAFO_L**	DRD*
P7 Matjies River Cave	T1	140.92	25.16	10.07	9.63	67.91	77.34	13.28	12.61	79.74	65.52	1
	T2	152.74	26.02	9.60	9.71	81.29	72.58	11.52	10.20	68.34	66.44	3
	T3	149.06	23.21	9.80	NP	68.81	63.44	9.58	8.54	72.89	69.99	1
211 Matjies River	T2	142.93	25.66	11.98	12.05	69.55	69.45	13.64	13.63	65.70	60.76	2
P1235	T6	119.64	28.33	8.88	8.64	69.11	65.87	9.84	8.87	64.83	78.10	4
P1271	T1	133.69	27.84	9.28	8.05	69.76	70.92	8.57	10.94	85.46	85.08	2
P1273	T1	131.30	29.53	12.56	11.83	50.98	47.57	16.78	16.62	69.97	68.06	1
	T2	131.38	26.52	9.77	8.80	75.37	78.72	9.68	10.73	68.87	64.84	1
	T3	120.31	26.75	8.71	8.21	74.55	80.07	8.93	9.63	68.88	72.39	2
	T4	117.30	25.66	7.98	8.90	70.03	82.43	8.33	9.34	73.69	73.00	1
	T5	111.34	27.85	8.15	8.50	69.30	83.63	8.09	8.58	63.80	71.90	1
	T6	115.00	27.61	9.83	9.48	73.87	76.48	9.21	8.31	67.14	82.80	1
P1274	T1	142.24	30.64	10.08	9.62	74.08	67.67	12.89	14.68	66.86	61.08	3
	T2	146.31	27.17	10.21	9.39	78.71	83.45	10.95	11.02	67.23	72.59	3
P1275	T1	145.71	28.49	9.57	9.14	71.42	61.49	12.18	8.68	80.07	80.84	2
	T2	147.33	28.56	10.05	8.48	63.52	74.85	10.86	11.06	65.27	60.00	1
	T3	143.24	26.54	8.74	8.43	71.80	70.26	8.35	6.75	64.78	76.89	1
	T4	133.48	26.69	8.51	8.37	68.60	72.41	8.76	8.52	56.54	68.87	2
P1451	T1	145.23	25.79	11.44	10.61	68.92	69.52	12.84	12.94	75.76	71.52	1
	T2	145.05	26.26	10.00	9.87	69.67	69.36	10.58	10.08	70.56	65.45	1
	T3	133.67	23.03	8.85	9.22	68.49	71.35	9.89	9.35	68.38	70.31	1
	T4	131.99	20.21	7.85	9.07	70.78	73.90	9.89	9.38	61.63	67.43	3
	T5	119.89	18.62	8.87	7.84	78.71	78.22	9.30	8.74	57.39	68.77	3

*DRD: 1=none; 2=distal left; 3=distal right; 4=proximal left; 5=proximal right
**SPA, IAFO, SAFO measured in degrees
***SPL, IAFW, SAFW measured in mm

5.3 Comparison of spinous process deviation region and direction in human sample groups

Comparison of frequencies of SPDRD will be presented per spinal level for each of the human sample groups and are represented in Table 5.3.

Table 5.3: Cross tabulation and frequency of spinous process deviation per spinal level comparing contemporary humans and LSA humans.

Level	Human group	Count and %	None	Distal Left	Distal Right	Proximal Left	Proximal Right	Total
T1	Contemporary humans	Count	47	3	8	0	0	58
		% within Species	81.0%	5.2%	13.8%	0.0%	0.0%	100.0%
	LSA Humans	Count	3	2	1	0	0	6
		% within Species	50.0%	33.3%	16.7%	0.0%	0.0%	100.0%
T2	Contemporary humans	Count	40	9	9	0	0	58
		% within Species	69.0%	15.5%	15.5%	0.0%	0.0%	100.0%
	LSA Humans	Count	3	1	2	0	0	6
		% within Species	50.0%	16.7%	33.3%	0.0%	0.0%	100.0%
T3	Contemporary humans	Count	34	13	11	0	0	58
		% within Species	58.6%	22.4%	19.0%	0.0%	0.0%	100.0%
	LSA Humans	Count	3	1	0	0	0	4
		% within Species	75.0%	25.0%	0.0%	0.0%	0.0%	100.0%
T4	Contemporary humans	Count	46	5	6	0	1	58
		% within Species	79.3%	8.6%	10.3%	0.0%	1.7%	100.0%
	LSA Humans	Count	1	1	1	0	0	3
		% within Species	33.3%	33.3%	33.3%	0.0%	0.0%	100.0%
T5	Contemporary humans	Count	45	6	5	0	2	58
		% within Species	77.6%	10.3%	8.6%	0.0%	3.4%	100.0%
	LSA Humans	Count	1	0	1	0	0	2
		% within Species	50.0%	0.0%	50.0%	0.0%	0.0%	100.0%
T6	Contemporary humans	Count	46	5	6	0	1	58
		% within Species	79.3%	8.6%	10.3%	0.0%	1.7%	100.0%
	LSA Humans	Count	1	0	0	1	0	2
		% within Species	50.0%	0.0%	0.0%	50.0%	0.0%	100.0%

5.3.1 T1 SPDRD

The contemporary humans sample demonstrated a frequency of deviations in 19.0% of specimens (n=11), whereas in LSA humans it occurred in 50.0% (n=3). Of the deviations noted, distal left deviation occurred in 5.2% (n=3) of the contemporary humans and 33.3%(n=3) of the LSA humans, with distal right deviation showing a frequency of 13.8% (n=8) in contemporary humans and 16.7% (n=1) in LSA humans. Neither group showed proximal deviations in either direction at this level.

5.3.2 T2 SPDRD

The contemporary humans sample demonstrated a frequency of deviations in 71.0% of specimens (n=18), whereas in LSA humans it occurred in 50.0% (n=3). Of the deviations noted, distal left deviation occurred in 15.5% (n=9) of the contemporary humans and 16.7%(n=1) of the LSA humans, with distal right deviation showing a frequency of 15.5% (n=9) in contemporary humans and 33.3% (n=2) in LSA humans. Neither group showed proximal deviations in either direction at this level.

5.3.3 T3 SPDRD

The contemporary humans sample demonstrated a frequency of deviations in 41.4% of specimens (n=24), whereas in LSA humans it occurred in 25.0% (n=1). Of the deviations noted, distal left deviation occurred in 22.4% (n=13) of the contemporary humans and 25.0% (n=1) of the LSA humans, with distal right deviation showing a frequency of 19.0% (n=11) in contemporary humans and was absent in LSA humans. Neither group showed proximal deviations in either direction at this level.

5.3.4 T4 SPDRD

The contemporary humans sample demonstrated a frequency of deviations in 20.7% of specimens (n=12), whereas in LSA humans it occurred in 66.7% (n=2). Of the deviations noted, distal left deviation occurred in 8.6% (n=5) of the contemporary humans and 33.3% (n=1) of the LSA humans, with distal right deviation showing a frequency of 10.3% (n=16) in contemporary human and 33.3% (n=1) in LSA humans. Proximal left deviations were absent in both groups, with contemporary humans showing 1.7% (n=1) proximal right deviation at this level.

5.3.5 T5 SPDRD

The contemporary humans sample demonstrated a frequency of deviations in 22.4% of specimens (n=13), whereas in LSA humans it occurred in 50.0% (n=1). Of the deviations noted, distal left deviation occurred in 10.3% (n=6) of the contemporary humans and were absent in the LSA humans, with distal right deviation showing a frequency of 8.6% (n=15) in contemporary humans and 50.0% (n=1) in LSA humans. Proximal left deviations were absent on both groups, with contemporary humans showing 3.4% (n=2) proximal right deviation at this level.

5.3.6 T6 SPDRD

The contemporary humans sample demonstrated a frequency of deviations in 20.7% of specimens (n=12), whereas in LSA humans it occurred in 50.0% (n=1). Of the deviations noted, distal left deviation occurred in 8.6% (n=5) of the contemporary humans and were absent in the LSA humans, with distal right deviation showing a

frequency of 10.3% (n=6) in contemporary humans and zero in LSA humans. LSA humans demonstrated 50% (n=1) proximal left deviation, and contemporary humans showing 1.7% (n=1) proximal right deviation at this level.

5.4 Discussion

The Matjes River rock shelter, where the LSA human remains were recovered, represents one of the largest shell middens in southern Africa, and is considered to be from the early Holocene period 9000 to 2000 BP (Sealy et al., 2006; L'abbe et al., 2008). The site has mainly archaeological remains consisting of shells, the debris from many meals of shellfish, animal bones, stone artefacts, and items manufactured out of ostrich eggshell, marine shell and ivory, with few plant materials (Sealy, 2006). Many of the skeletons are not complete due to disturbances of the graves and careless excavation and curation (Sealy, 2006). In addition, not all individuals are associated with viable upper thoracic vertebrae for use in the current study additionally limiting the sample size, with only one LSA human specimen allowing for a complete T1-T6 analysis. These individuals are considered to have been hunter-gatherers, with a mixed diet, including terrestrial food and low trophic level marine food such as shellfish (Sealy, 2006; Pfeiffer, 2012).

5.4.1 Comparative morphometric measurements

The comparison of SPL, IAFW and SAFW in Table 5.1 indicates that LSA humans' measurements were comparatively smaller than contemporary humans. Adult

stature of LSA humans is considered more petite than contemporary humans (Stock and Pfeiffer, 2001) with males being 160.9cm (Pfeiffer, 2012) and weighing 46.9kg (Sealy and Pfeiffer, 2000), and females 150.1cm (Truswell, 1976) and weighing 40.1kg (Sealy and Pfeiffer, 2000) on average. Dewar and Pfeiffer (2004) indicate that LSA humans may have habitually used squatting posture during life, based on their findings of increased talar extensions and squatting facets with the presence of facet extensions, separate facets and rounded joint surfaces, suggesting a lean body mass with joint flexion being unhindered. LSA humans are presented as utilizing hunting and gathering subsistence strategies reliant on terrestrial mobility (Stock and Pfeiffer, 2001) and Pfeiffer (2012) presents various reasons for the small size of these humans including dietary insufficiency, energetics and accident avoidance and life history, and propose a biocultural mix of dietary constraints and behavioral adaptations as the most plausible explanation for this pattern.

As presented in Table 5.1 the SPA and AFO measurements for both groups were similar, as would be expected within the same species.

5.4.2 Incidence of spinous process deviations in LSA and contemporary humans

The incidence of SPD was greater in the overall sample of the LSA humans, with 48.62% (n=11) overall incidence compared to 25.87% (n=90) in the contemporary humans. Of the spinous process deviations noted, distal deviations were the most common in both groups, with contemporary humans demonstrating 24.9% (n=86) and LSA humans 43.48% (n=10). When considering the frequency of SPD within an

individual's T1-T6 sequence, the LSA humans showed a higher frequency, with all the individuals used in the study having a deviation present, compared to the contemporary humans showing a 77.59% (n=45) frequency as presented in Table 3.12.

Sex of the individuals in the LSA human sample was not determined, however Cameron and Pfeiffer (2014) and Cameron and Stock (2018) did not find significant differences between sexes when evaluating biomechanical indicators of manual activities and terrestrial mobility. Female and male LSA humans would have undertaken different manual activities that would have exerted different loads on the upper limbs, which may have an impact on the T1-T6 spinous process as proposed in the current study. Female LSA humans would have been more involved with processing and gathering of food (Stock and Pfeiffer, 2001, 2004) and utilized tools that may have resulted in symmetrical upper limb loading such as digging sticks (extracting shellfish and digging underground storage) and grind stones (Stock and Pfeiffer, 2004; Cameron and Stock, 2018). LSA males would have been more involved with foraging, hunting and herding activities (Sealy and Pfeiffer, 2000; Sealy 2006). These hunting activities may well have resulted on directional loading and bilateral asymmetry where loading is a result of unimanual actions (Cameron and Stock, 2018). LSA men would have used spears and bow and arrows (Stock and Pfeiffer, 2004) which would cause this type of loading, and may have an impact on spinous processes given the actions required for these activities (Moore, 1992; Molnar, 2005). As presented previously in the current study, sex was demonstrated to impact the frequency of SPD in the contemporary human sample group, with males being more likely to present with this feature. Given this and the highlighted differences in activity functions in the LSA males and females, it

would be anticipated that differences in sex would be seen in SPD, and future studies would need to have increase sample sizes with the determination of included individuals sex to determine this impact.

5.4.3 Spinous process deviations in relation to lifestyle and activity function

Functional links to bony landmarks (hypertrophy of bone, in the form of a robust muscle attachment) are proposed as the direct result of increased stress and continual stress of a muscle in daily, repetitive tasks (Hawkey and Merbs, 1995; Mosley and Lanyon, 2002) and may require high rate, regularly repeated contracture to have an effect on the enthesis (Karakostis et al., 2019) which may be reasons for comparative changes within the two groups utilised. Hawkey and Merbs (1995) proposed a scoring system for muscular and ligamentous attachments for musculoskeletal stress markers, which has been utilized by Molnar (2006; 2010) to evaluate the effects of activity such as fishing, hunting, and gathering on Middle Neolithic populations in Gotland, Sweden, and demonstrated increased stress markers relating to archery and harpooning.

While various publications relating to archeologic populations utilize enthesis changes as a measure of changes related to activity and past behaviour (Hawkey and Merbs, 1995; Molnar, 2006; 2010), they have focused mainly on insertional areas of large muscles with specific sites such as gastrocnemius to the femur, and bones of the upper limb. As presented, the insertions of muscles such as trapezius, rhomboid and splenius cervicis to multiple thoracic spinous processes (Moore, 1993) applicable to the current study may similarly be considered an enthesis site (Aylott, 2012).

Spinous process deviations therefore appear to be more frequent within the LSA human grouping and it may be proposed that differences in activity related to cultural, behavioral, technology use and labour (Molnar, 2010) may well influence this specific morphology. Cameron and Stock (2018) evaluated biomechanical indicators of manual activities and terrestrial mobility and found that Cape coastal LSA humans presented with higher femoral strength indicators, proposed as a result of the complex terrain they lived in and the biomechanical cost of this, although upper limb loading patterns appeared similar between coastal and inland LSA humans. The highly terrestrial mobile foraging (Stock and Pfeiffer, 2001; 2004; Cameron and Stock, 2018) of the LSA humans could therefore be considered more physically demanding than contemporary humans. In addition, the physical activities such as digging stick and grind stones, predominantly in females (Stock and Pfeiffer, 2001; 2004; Cameron and Stock, 2018) and spears and bow and arrows predominantly in males (Sealy and Pfeiffer, 2000; Stock and Pfeiffer, 2004; Sealy 2006; Cameron and Stock, 2018) may have increased the upper limb loading either symmetrically or asymmetrically (Cameron and Stock, 2018). These physical activity factors related to lifestyle and activity function may therefore be proposed to result increased pressure on the T1-T6 spinous processes as enthesis points, and therefore the increased frequency of SPD in the LSA humans compared to contemporary humans.

5.4.4 Age related factors in spinous process deviations

Age related factors are a consideration for SPD as previously presented, and the contemporary human sample group had a recorded age of death range of 29-86 years,

with no accurate records of the LSA human ages at death. The age range for the contemporary humans is similar to the overall Raymond A. Dart Collection of Human Skeletons collections ages of deaths of 20-70 years (Dayal et al., 2009). While age may be proposed to have an effect on musculoskeletal stress markers with increased enthesial reaction (Molnar, 2006), life expectancy in the LSA humans is not considered to be high (Stock and Pfeiffer, 2001; Pfeiffer et al., 2019) and may therefore not have had a significant impact in the current study. In addition, as presented in Tables 3.13 and 3.14 relating to the contemporary human group, age or degenerative changes do not appear to be a significant factor in relation to SPD in the upper thoracic spine. It may therefore be proposed that although age of death is not noted for the LSA human group, it would not have had a significant impact on the current study findings.

CHAPTER 6

FINAL DISCUSSION AND CONCLUDING REMARKS

6.1 Final discussion

The current study attempted to evaluate and compare variations in morphology of the spinous processes and articular facets in the upper thoracic spine of hominines and baboons, with the goal of determining if differences existed, and if they are the result of a primary event such as locomotor behavior or a secondary event and influenced by lifestyle or physical activity in the case of humans and fossil hominins.

Muscle attachment sites and entheses such as the spinous processes of vertebrae (Aylott, 2012) have been used to infer cultural behaviour, technology use, labour difference or locomotion patterns (Molnar, 2010). Although the use of the spinous processes as a musculoskeletal stress marker has not been validated previously, it was proposed as a region that would allow for evaluation of altered biomechanics related to increased or continual functional stress of the muscle (from daily activity or posture) that may result in changes of bone morphology as a result of the increased forces of contracting muscle (Hawkey and Merbs, 1995; Benjamin et al., 2002; Mosley and Lanyon, 2002). The vertebrae selected for measurement and comparison in the current study were T1 to T6, as these spinous processes have insertion areas (enthesis) for the associated shoulder girdle as the main anchor for the scapula and are likely to be influenced by limb movement and cervical spine extension muscles (Slijper, 1942; Aiello and Dean, 1990; Kikuchi and Ogihara, 2021).

In hominoids the shoulder girdle is positioned on the back of the rib cage as opposed to its sides allowing for greater range of motion (Schultz, 1961; Latimer and Ward, 1993; Lovejoy, 2005), with additional upper limb morphological differences seen between humans and apes relating to lever arm advantages (Aiello and Dean, 1990). Locomotor propensity and its impact on morphology was considered in relation to the head balancing model (Slijper, 1946; Jaanuson, 1987; Smit, 2002), the thoracic shape (Schultz, 1961; Lovejoy, 2005), musculature relating to the upper thoracic region (Latimer and Ward, 1993; Shapiro, 1993; Diogo et al., 2017), shoulder girdle in humans and primates (Schultz, 1961; Aiello and Dean, 1990, Latimer and Ward, 1993; Lovejoy, 2005; Green and Alemseged, 2012; Green at al., 2012) and specific vertebral traits developed for bipedalism of the species included (Schultz, 1961; Latimer and Ward, 1993; Shapiro, 1993; Gomez-Olivencia et al., 2013; Williams and Russo, 2015; Meyer 2016; Meyer et al., 2017 and Plomp et al., 2019).

The model proposed for the current study was that upright posture and the resultant change in upper limb and cervical and thoracic spine biomechanics would have a commensurate effect on the morphology of the upper thoracic vertebrae. The spinous processes were specifically evaluated as they are considered as an enthesis site for muscles associated with changes to the cervicothoracic region for upright posture and shoulder girdle movement or stabilization. This is visually depicted in Figure 6.1, where contemporary human has been used as an example. The length of the associated muscles of the medial scapula and posterior cervical region, in comparison to apes to accommodate the requirements for upright posture and bipedal locomotion, are presented, with lengthened medial scapular and posterior cervical muscles in

contemporary humans, although possible greater force in African apes as a result of increased muscle mass

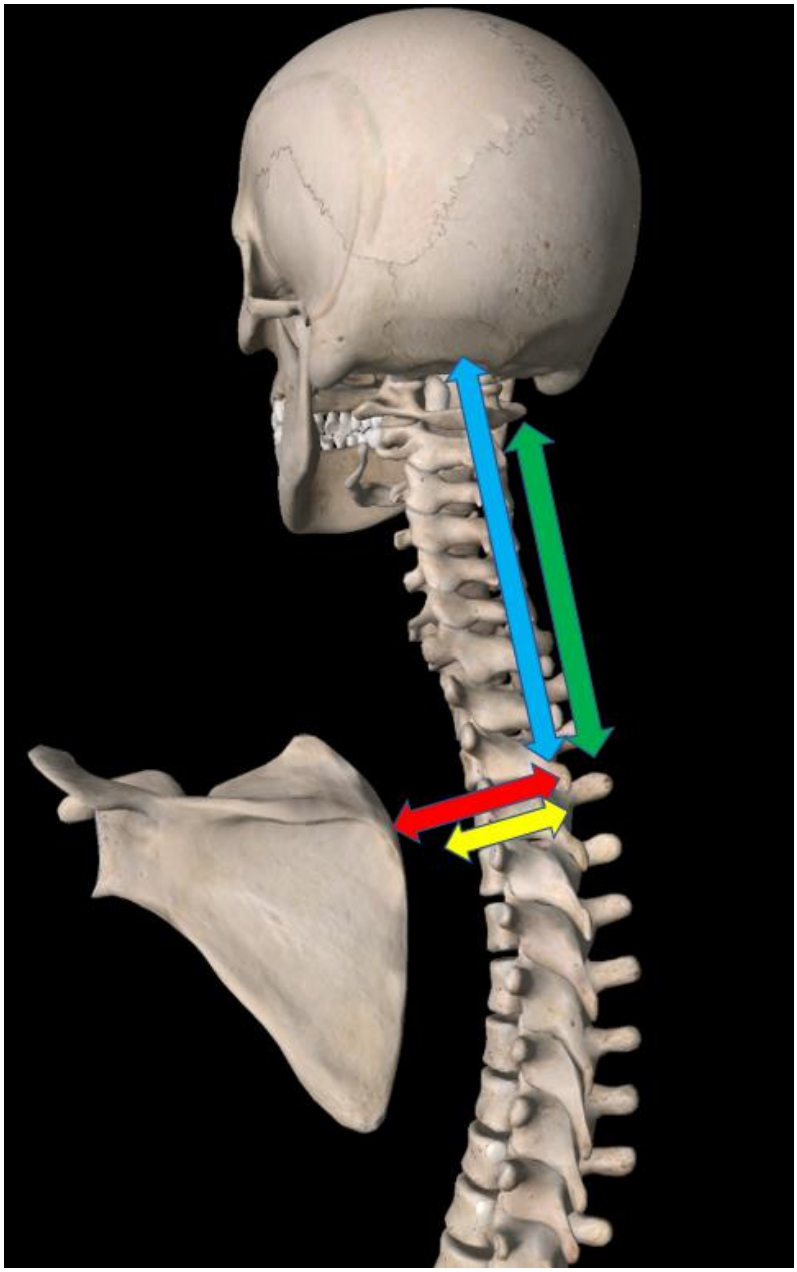


Figure 6.1: Visual depiction of potential changes to muscle length and force magnitudes in contemporary human to apes. Red arrow: human medial scapular muscle length; Yellow arrow: ape medial scapular muscle length; Blue arrow: human posterior cervical muscle length; Green arrow: ape posterior cervical muscle length (note increased magnitude due to greater muscle mass).

6.2 Summary of findings

6.2.1 Focus area one

In relation to focus area one, which was the comparison of differences and variability in the morphology measured between the selected African apes, contemporary humans and baboons (and related to proposed research questions 1 and 2), the following was determined:

a. The articular morphometric measurements (namely spinous process angle and length, and inferior and superior articular facet width and orientation), were found to be significantly different between the species presented, indicating the species-specific nature of these morphometric features.

b. Spinous processes were found to be shorter and more caudally oriented in contemporary humans than the African apes and baboons. This is consistent with previous research as developed traits in relation to bipedalism (Schultz, 1961; Latimer and Ward, 1993; Shapiro, 1993; Gomez-Olivencia et al., 2013; Williams and Russo, 2015; Meyer 2016; Meyer et al., 2017 and Plomp et al., 2019).

c. The frequency of SPD was not as high as anticipated in the overall sample of vertebrae, but when an individual's sequence of T1-T6 was evaluated, this incidence was significantly higher in all groups. Gorilla males showed the highest frequency overall and supports the findings of increased SPD frequency associated with larger species size, increased length of spinous process and male sex.

d. Age was considered (specifically in the contemporary human group) and

degenerative changes associated with ageing showed varied presentations, with each structure demonstrating degeneration in isolation or with concomitant second joint involvement but no uniformity. It was anticipated that age would have an impact on SPD, but when evaluating age ranges of the contemporary human's sample group, this was not the case, as older groupings did not show an increased frequency. Age did not therefore appear to be a significant contributing factor to the presence of SPD in the upper thoracic spine.

e. SPD was categorized (Figure 3.21) based on presentation into distal angular, proximal angular, proximal gradual, distal gradual and proximal gradual returning to the midline. No links between the proposed mechanisms and these regions of deviation were identified, with distal deviations being the most common and likely to be as a result of the distal area being the most sensitive to any dynamic or functional stresses imposed on it.

f. Locomotor propensity and SPD presentation did not appear to show a direct correlation. Bipedalism does not therefore appear to make this feature more frequent as was proposed in the current study, with quadrupedalism not demonstrating a direct link given the large difference in frequency between gorillas and baboons.

6.2.2 Focus area two

In terms of focus area two which was a comparative analysis of fossil hominins to allow for a determination of differences and variability in the measured morphology

compared to contemporary humans and other selected primates (and related to proposed research question 3) the following was determined:

a. The orientation of the spinous processes may be an additional suggestion of *Australopithecus* as being an obligate primitive biped with arboreal behaviour (Stern and Susman, 1983; Schmid, 1991; Ward, 2002; Schmid et al., 2013; Kappelman et al., 2016; Williams and Meyers, 2019; Stern, 2000; Crompton et al., 2021; Williams et al., 2021), as measurements were more closely aligned to this locomotor pattern in comparison to African apes and baboons.

b. The method utilized to determine measurements from photographic images is innovative and suggests that these may be a reliable approach to evaluation of vertebrae for comparative and study purposes, as the morphometric measurements obtained in the current study are supported by numerous previous descriptions of the specimens studied (Randolph-Quinney et al., 2016; Williams et al., 2018; Ward et al., 2020; Williams et al., 2021).

c. Size of fossil hominins were most similar to baboons (Kingdon et al., 2013; Holliday et al., 2018) but would be related more to size comparison than locomotor propensity.

d. The presentation of StW 573 vertebrae is unique to the current study and contributes to the overall data and information regarding australopiths.

e. U.W. 88-37 (Randolph-Quinney et al., 2016; Williams et al., 2018) and A.L. 288-1 (Cook et al., 1983) presented with pathology that may have had an impact on the presentation of SPD in these samples. In the extant hominid samples, pathology was an exclusionary factor, and comparison to specimens with similar pathology

may be considered to facilitate an understanding of the impact of pathology on spinous process deviation and articular morphology.

f. When evaluating the *Australopithecus* in the current study in relation to SPD, there did not appear to be sufficient consistency in presentation to allow for this feature to be proposed as an adaptation for bipedalism in the upper thoracic spine.

6.2.3 Focus area three

In terms of focus area three which was the evaluation of morphological variability in LSA humans and contemporary humans to determine the impact of lifestyle and activity function on the morphometric measurements obtained (and related to proposed research question 4) the following was determined:

a. Morphometric measurements related to size support previous research related to LSA humans having smaller stature and size than contemporary humans (Truswell, 1976; Sealy and Pfeiffer, 2000; Dewar and Pfeiffer, 2001; Stock and Pfeiffer, 2001; Pfeiffer, 2012).

b. The impact of sex on the compared sample groups could not be accurately determined due to no indications of sex in the LSA human sample group. It may be anticipated that males would have a higher frequency based on LSA human sex differences in activity functions, with males being more likely to have utilized asymmetrical loading patterns associated with hunting such as spears and bow and arrows (Sealy and Pfeiffer, 2000; Stock and Pfeiffer, 2004; Sealy 2006;

Cameron and Stock, 2018), and the indications of increased frequency of SPD in males in all selected primates with known sex in the current study.

c. Overall, the LSA humans sample group demonstrated an increased likelihood of SPD as a feature in the upper thoracic vertebrae. LSA human's lifestyle is presented as utilizing hunting, gathering and subsistence with a reliance on terrestrial mobility (Stock and Pfeiffer, 2001), and activity levels would be significantly different to contemporary humans. Spinous process deviations may therefore be proposed to occur more frequently as they may be susceptible to altered biomechanics related to increased and continual functional stress of a muscles in daily repetitive tasks associated with lifestyle and activity levels (Hawkey and Merbs, 1995; Mosley and Lanyon, 2002).

6.3 Limitations and recommendations

This study was not designed as a true incidence study where randomization of the sample would be required. However, the limited available collections of primate vertebrae pose a potential limitation in terms of such a study design. The sample of contemporary humans was selected randomly, based on the inclusion criteria, but collections utilized were not randomized. Future research should select samples that demonstrate spinous process deviations and evaluate morphometric measurements in relation to this feature being present. This would facilitate an understanding of the correlation between spinous process deviation in terms of mechanical stresses and pathologies.

A limited number of complete upper thoracic fossil hominin vertebrae are available. This therefore only allows comparison to single individuals in some cases, and given the variations noted in morphometric measurements in the larger comparative primate groups, this may not be an accurate representation of species.

Taphonomic changes could have a significant impact on spinous and articular processes of vertebrae in the fossil specimens. This is particularly evident in StW 573, which demonstrates various distortions, and in samples where articular or spinous processes could not be evaluated as they were either partially damaged or absent. These would influence the morphometric measurements noted and may have contributed to the variations found in the current study.

While the finding of LSA humans having an increased likelihood of SPD may infer that the contemporary humans are more sedentary resulting in lower frequency of SPD overall, this would need to be placed within the context of the current study sample groupings. Modern contemporary humans continue to demonstrate osteologic changes related to activity such as those presented by Shaher and Sayers (2018) where they identified the presence of occipital exostoses and proposed these to be a consequence of poor posture or poor postural habits related to current technologic developments. Karakostis et al. (2017) evaluated the Basel-Spitalfieldhoff contemporary human collection and found definite separations across occupational characteristics and defined enthesial patterns. The year of death of contemporary humans utilized in the current study ranged from 1942 to 1967, and the Raymond A. Dart Collection specimens as presented by Dayal et al. (2009) represent unclaimed bodies of migrant workers from Gauteng (previously Transvaal) Provincial hospitals, although since 1958

a bequeathment programme has contributed to the collection. The samples used therefore present different socioeconomic histories (Dayal et al., 2019), with many migrant workers in the period undertaking occupations such as mining (Vosloo, 2020) requiring significant physical activity. Given the socioeconomic factors of that period, and the use of modern current technologies purported to have an influence only developing recently, individuals utilized in the current study in life may have performed manual tasks requiring physical activity similar in intensity to the LSA humans, and it may not be possible to accurately determine this impact on features such as SPD. Future studies on contemporary humans may consider including occupation or physical activities as a component of evaluation of the morphometric measurements. This would facilitate a more accurate determination of the impact of current technology and postural changes on the morphology of the measured structures. The current study utilized a small LSA human sample size and potential variations may be a result of differences between individuals, and in some instances such as the T6, only a single vertebra was available for comparison. Relative percentages of presentations may therefore not give an accurate representation and future studies should include larger samples for comparison.

Outomuro and Johansson (2017) discuss the need to consider size effects in studies of biological shape, and in the current study size was not standardized. Future studies should consider standardizing measurements by utilizing a size proxy which would facilitate obtaining relative measurements that would be more comparable across species, specifically for length and linear measurements.

6.4 Concluding remarks

While numerous measurements and comparisons were carried out, overall, the current study did not show significant correlations in the groupings, with morphometric measurements and spinous process deviation appearing to relate more to species and potential sexual dimorphism within them, with lifestyle and activity levels in humans potentially increasing the frequency of SPD.

It may be therefore concluded that SPD is a consequence of various related factors that may interact to produce the changes noted, or in many cases may well be the result of random normal variations between individuals.

Spinous process deviations as a morphometric feature in the upper thoracic vertebrae are therefore not a reliable indicator of postural or locomotor behavior in the included primates and fossil hominins but may be indicators of lifestyle and activity levels in humans.

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Appendix 1: Details of chimpanzee, gorilla and baboon samples utilized.

Species	Specimen number	Sex*
Chimpanzee	ZIX49	M
	ZVII23	F
	ZVI35	M
	ZVII26	F
	ZVII24	M
	ZVIII10	F
	ZVI34	M
	ZIX52	F
	ZIX51	F
	FC116	M
	FC100	M
	CAMI13	M
	CAMI147	F
	CAMI205	F
	CAMI204	F
	CAMI206	M
	CAMI207	F
	CAMI218	F
	CAMI219	M
	CAMII62	M
	CAMI228	M
	M78	F
	CAMII301	F
	M86	F
	M105	F
	M148	F
	M155	F

	M169	F
	M158	F
	M172	F
	M184	F
	M186	F
	M234	F
	M254 3rd series	M
	M254 2nd series	F
	M273	F
	M272	M
	M275	F
	M277	F
	M299	F
	M352	F
	M348	F
	M424	F
	M440	M
	M724	M
Gorilla	MII2	F
	MII1	F
	Merfield Collection 21	M
	Merfield Collection 95	F
	MI29	F
	Merfield collection 89	F
	Merfield collection 35	F
	Merfield collection 20	M
	Merfield collection 57	F
	Merfield collection 96	F
	MI28	M

	M58	F
	Merfield collection 119	M
	Merfield collection 135	M
	Merfield collection 139	F
	Merfield collection 160	F
	Merfield collection 180	F
	Merfield collection 264	M
	Merfield collection 241	M
	Merfield collection 206	M
	Merfield collection 136	F
	Merfield collection 174	F
	Merfield collection 696	F
	Merfield collection 300	F
	Merfield collection 329	F
	Merfield collection 755	F
	Merfield collection 138	F
	Merfield collection 204	M
	Merfield collection 691	F
	Merfield collection 470	F
	Merfield collection 372	M
	Merfield collection 674	M
	Merfield collection 460	F
	Merfield collection 505	M
	Merfield collection 962	M
	Merfield collection 720	M
	Merfield collection 688	F
	Merfield collection 690	M
	Merfield collection 798	F
	Zenker collection VI 30	M
	Merfield collection 766	M

	Merfield collection 150	F
	Merfield collection 342	M
	ZI 30	M
	Merfield collection 717	M
	Merfield collection 786	F
	Merfield collection 729	F
	Merfield collection 490	F
	Merfield collection 687	M
	Cameroon trip one 98	F
	Merfield collection 877	F
	Zenker collection ZI 17	M
	Merfield collection M835	M
	Merfield collection 879	M
	Cameroon trip one 106	M
	Cameroon trip one 134	M
	Cameroon trip one 230	M
	Cameroon trip one 107	M
	French Congo 130	M
	French Congo 123	M
Baboon	Za 109	X
	Za 112	M
	Za 113	M
	Za 114	F
	Za 115	M
	Za 117	F
	Za 118	M
	Za 122	X
	Za 123	F
	Za 124	X

	Za 126	F
	Za 131	F
	Za 133	F
	Za 134	F
	Za 141	F
	Za 142	F
	Za 144	F
	Za 147	F
	Za 148	F
	Za 150	F
	Za 151	F
	Za 152	M
	Za 165	F
	Za 166	F
	Za 172	F
	Za 174	X
	Za 176	F
	Za 179	F
	Za 180	F
	Za 181	F
	Za 182	M
	Za 185	F
	Za 188	X
	Za 191	F
	Za 192	M
	Za 193	M
	Za 195	M
	Za 196	X
	Za 201	F
	Za 202	F

	Za 203	F
	Za 204	M
	Za 205	F
	Za 206	M
	Za 207	F
	Za 208	F
	Za 217	X
	Za 218	M
	Za 687	F
	Za 736	M
	Za 754	M
	Za 755	M
	Za 832	M
	Za 833	M
	Za 848	M
	Za 908	M
	Za 937	M
	Za 959	M
	Za 1032	F
	Za 1463	M
*Skeletons are identified as male (M) or female(F) if there is confidence of sex; (M) or (F) are probable males and females, and skeletons to which not sex can be attributed are marked X.		

Appendix 2: Contemporary human sample group details.

Specimen	Sex*
B14-2007	1
B9-2010	1
B30-2010	1
B14-2004	2
B23-2000	2
B76	1
B5-2011	1
B53-99	1
B98-2008	2
B41-2010	2
B1-2001	2
B74-2003	1
B55-2005	1
B31-2000	2
B25-2007	2
B17-2005	2
B41-2003	2
X0123 6515	2
X0216 7229	1
B20-2011	1

Specimen	Sex*
X3733 6614	2
B61-2012	1
X6678 0138	2
B58-2004	1
2685	1
2647	1
2653	1
2658	1
2662	1
2665	1
1363	1
1364	1
1365	1
1366	1
1367	1
1368	1
1371	1
1372	1
1373	1
1374	1

Specimen	Sex*
1375	1
1962	2
2986	1
2681	2
2682	2
1360	2
1369	2
1370	2
1378	2
1380	2
2700	2
2711	2
1879	2
1867	2
1886	2
1787	2
1795	2
1653	2

*1=male; 2=female

Appendix 3: ANOVA p values for comparison of all species (chimpanzees, gorillas, humans, baboons).

Sex	Measurement	Comparison	F	Sig.
Male	SPA_T1	Between Groups	53.494	0.001
	SPL_T1	Between Groups	144.990	0.001
	IAFW_R.T1	Between Groups	48.390	0.001
	IAFW_L.T1	Between Groups	43.245	0.001
	IAFO_R.T1	Between Groups	70.569	0.001
	IAFO_L.T1	Between Groups	91.711	0.001
	SAFW_R.T1	Between Groups	97.575	0.001
	SAFW_L.T1	Between Groups	118.152	0.001
	SAFO_R.T1	Between Groups	21.902	0.001
	SAFO_L.T1	Between Groups	28.942	0.001
	SPA_T2	Between Groups	34.662	0.001
	SPL_T2	Between Groups	95.152	0.001
	IAFW_R.T2	Between Groups	51.724	0.001
	IAFW_L.T2	Between Groups	31.507	0.001
	IAFO_R.T2	Between Groups	119.743	0.001
	IAFO_L.T2	Between Groups	121.677	0.001
	SAFW_R.T2	Between Groups	48.526	0.001
	SAFW_L.T2	Between Groups	54.928	0.001
	SAFO_R.T2	Between Groups	78.906	0.001
	SAFO_L.T2	Between Groups	76.845	0.001
	SPA_T3	Between Groups	26.091	0.001

	SPL_T3	Between Groups	74.731	0.001
	IAFW_R.T3	Between Groups	47.358	0.001
	IAFW_L.T3	Between Groups	49.497	0.001
	IAFO_R.T3	Between Groups	122.414	0.001
	IAFO_L.T3	Between Groups	110.216	0.001
	SAFW_R.T3	Between Groups	59.567	0.001
	SAFW_L.T3	Between Groups	51.421	0.001
	SAFO_R.T3	Between Groups	100.883	0.001
	SAFO_L.T3	Between Groups	88.380	0.001
	SPA_T4	Between Groups	38.818	0.001
	SPL_T4	Between Groups	40.129	0.001
	IAFW_R.T4	Between Groups	36.306	0.001
	IAFW_L.T4	Between Groups	33.373	0.001
	IAFO_R.T4	Between Groups	79.448	0.001
	IAFO_L.T4	Between Groups	69.360	0.001
	SAFW_R.T4	Between Groups	55.901	0.001
	SAFW_L.T4	Between Groups	48.240	0.001
	SAFO_R.T4	Between Groups	94.467	0.001
	SAFO_L.T4	Between Groups	80.089	0.001
	SPA_T5	Between Groups	53.558	0.001
	SPL_T5	Between Groups	24.471	0.001
	IAFW_R.T5	Between Groups	27.467	0.001
	IAFW_L.T5	Between Groups	21.770	0.001
	IAFO_R.T5	Between Groups	48.231	0.001
	IAFO_L.T5	Between Groups	44.697	0.001
	SAFW_R.T5	Between Groups	38.112	0.001

	SAFW_L.T5	Between Groups	44.171	0.001
	SAFO_R.T5	Between Groups	59.171	0.001
	SAFO_L.T5	Between Groups	48.155	0.001
	SPA_T6	Between Groups	69.129	0.001
	SPL_T6	Between Groups	10.720	0.001
	IAFW_R.T6	Between Groups	20.307	0.001
	IAFW_L.T6	Between Groups	20.224	0.001
	IAFO_R.T6	Between Groups	54.574	0.001
	IAFO_L.T6	Between Groups	26.522	0.001
	SAFW_R.T6	Between Groups	23.872	0.001
	SAFW_L.T6	Between Groups	37.792	0.001
	SAFO_R.T6	Between Groups	45.543	0.001
	SAFO_L.T6	Between Groups	34.147	0.001
Female	SPA_T1	Between Groups	32.494	0.001
	SPL_T1	Between Groups	96.504	0.001
	IAFW_R.T1	Between Groups	53.677	0.001
	IAFW_L.T1	Between Groups	53.486	0.001
	IAFO_R.T1	Between Groups	120.186	0.001
	IAFO_L.T1	Between Groups	76.904	0.001
	SAFW_R.T1	Between Groups	115.876	0.001
	SAFW_L.T1	Between Groups	100.088	0.001
	SAFO_R.T1	Between Groups	39.029	0.001
	SAFO_L.T1	Between Groups	52.662	0.001
	SPA_T2	Between Groups	23.381	0.001
	SPL_T2	Between Groups	39.098	0.001
	IAFW_R.T2	Between Groups	58.083	0.001

	IAFW_L.T2	Between Groups	38.036	0.001
	IAFO_R.T2	Between Groups	168.657	0.001
	IAFO_L.T2	Between Groups	165.471	0.001
	SAFW_R.T2	Between Groups	56.278	0.001
	SAFW_L.T2	Between Groups	64.787	0.001
	SAFO_R.T2	Between Groups	97.969	0.001
	SAFO_L.T2	Between Groups	68.305	0.001
	SPA_T3	Between Groups	28.019	0.001
	SPL_T3	Between Groups	24.065	0.001
	IAFW_R.T3	Between Groups	65.004	0.001
	IAFW_L.T3	Between Groups	55.687	0.001
	IAFO_R.T3	Between Groups	141.100	0.001
	IAFO_L.T3	Between Groups	119.101	0.001
	SAFW_R.T3	Between Groups	53.654	0.001
	SAFW_L.T3	Between Groups	54.788	0.001
	SAFO_R.T3	Between Groups	164.370	0.001
	SAFO_L.T3	Between Groups	115.702	0.001
	SPA_T4	Between Groups	40.159	0.001
	SPL_T4	Between Groups	22.606	0.001
	IAFW_R.T4	Between Groups	54.381	0.001
	IAFW_L.T4	Between Groups	48.127	0.001
	IAFO_R.T4	Between Groups	85.024	0.001
	IAFO_L.T4	Between Groups	69.672	0.001
	SAFW_R.T4	Between Groups	56.927	0.001
	SAFW_L.T4	Between Groups	49.218	0.001
	SAFO_R.T4	Between Groups	118.350	0.001

	SAFO_L.T4	Between Groups	115.447	0.001
	SPA_T5	Between Groups	49.821	0.001
	SPL_T5	Between Groups	5.146	0.002
	IAFW_R.T5	Between Groups	39.980	0.001
	IAFW_L.T5	Between Groups	47.748	0.001
	IAFO_R.T5	Between Groups	58.150	0.001
	IAFO_L.T5	Between Groups	30.788	0.001
	SAFW_R.T5	Between Groups	63.323	0.001
	SAFW_L.T5	Between Groups	51.858	0.001
	SAFO_R.T5	Between Groups	54.462	0.001
	SAFO_L.T5	Between Groups	42.323	0.001
	SPA_T6	Between Groups	84.744	0.001
	SPL_T6	Between Groups	4.563	0.005
	IAFW_R.T6	Between Groups	30.567	0.001
	IAFW_L.T6	Between Groups	38.087	0.001
	IAFO_R.T6	Between Groups	43.004	0.001
	IAFO_L.T6	Between Groups	42.535	0.001
	SAFW_R.T6	Between Groups	32.442	0.001
	SAFW_L.T6	Between Groups	45.014	0.001
	SAFO_R.T6	Between Groups	40.394	0.001
	SAFO_L.T6	Between Groups	34.445	0.001

Appendix 4: Comparison matrix of post-hoc p values for male morphometric measurements per species per vertebral level.

Measure		Gorilla	Chimpanzee	Baboon
SPA T1*	Chimpanzee	0.001		
	Baboon	0.006	0.084	
	Human (contemporary)	0.001	0.001	0.001
SPL_T1**	Chimpanzee	0.001		
	Baboon	0.001	0.024	
	Human (contemporary)	0.001	0.556	0.118
IAFWR_T1**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.076	0.001
IAFWL_T1**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.005	0.013	0.001
IAFO_R.T1**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.968	0.001
IAFO_L.T1**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	1.000	0.001
SAFW_R.T1*	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.001	0.001
SAFW_L.T1**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.001	0.001
SAFO_R.T1*	Chimpanzee	0.001		
	Baboon	0.001	0.689	
	Human (contemporary)	0.001	0.483	0.018
SAFO_L.T1**	Chimpanzee	0.001		
	Baboon	0.001	1.000	
	Human (contemporary)	0.001	0.041	0.008
SPA_T2*	Chimpanzee	0.026		
	Baboon	0.093	0.883	
	Human (contemporary)	0.001	0.001	0.001

SPL_T2**	Chimpanzee	0.001		
	Baboon	0.001	0.874	
	Human (contemporary)	0.001	0.988	0.976
IAFW_R.T2**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.234	0.001	0.001
IAFW_L.T2*	Chimpanzee	0.001		
	Baboon	0.001	0.009	
	Human (contemporary)	0.245	0.070	0.001
IAFO_R.T2*	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.849	0.001
IAFO_L.T2**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.994	0.001
SAFW_R.T2	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.010	0.023	0.001
SAFW_L.T2**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.002	0.030	0.001
SAFO_R.T2*	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.995	0.001
SAFO_L.T2**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	1.000	0.001
SPA_T3**	Chimpanzee	0.656		
	Baboon	1.000	0.360	
	Human (contemporary)	0.001	0.001	0.001
SPL_T3*	Chimpanzee	0.001		
	Baboon	0.001	0.996	
	Human (contemporary)	0.001	0.999	1.000
IAFW_R.T3*	Chimpanzee	0.001		
	Baboon	0.001	0.003	
	Human (contemporary)	0.857	0.001	0.001
IAFW_L.T3*	Chimpanzee	0.001		
	Baboon	0.001	0.001	

	Human (contemporary)	0.004	0.114	0.001
IAFO_R.T3**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.071	0.001
IAFO_L.T3*	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.944	0.001
SAFW_R.T3**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.077	0.001	0.001
SAFW_L.T3*	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.116	0.001
SAFO_R.T3*	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.999	0.001
SAFO_L.T3**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.691	0.001
SPA_T4**	Chimpanzee	0.875		
	Baboon	0.001	0.002	
	Human (contemporary)	0.001	0.001	0.001
SPL_T4**	Chimpanzee	0.001		
	Baboon	0.001	0.847	
	Human (contemporary)	0.001	0.201	0.965
IAFW_R.T4**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.965	0.001	0.001
IAFW_L.T4*	Chimpanzee	0.001		
	Baboon	0.001	0.024	
	Human (contemporary)	0.337	0.015	0.001
IAFO_R.T4*	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.437	0.001
IAFO_L.T4*	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.004	0.424	0.001
SAFW_R.T4*	Chimpanzee	0.001		

	Baboon	0.001	0.007	
	Human (contemporary)	0.965	0.001	0.001
SAFW_L.T4*	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.046	0.038	0.001
SAFO_R.T4*	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	1.000	0.001
SAFO_L.T4*	Chimpanzee	0.018		
	Baboon	0.001	0.001	
	Human (contemporary)	0.029	0.911	0.001
SPA_T5*	Chimpanzee	0.172		
	Baboon	0.001	0.040	
	Human (contemporary)	0.001	0.001	0.001
SPL_T5**	Chimpanzee	0.001		
	Baboon	0.001	0.696	
	Human (contemporary)	0.001	0.285	0.998
IAFW_R.T5*	Chimpanzee	0.002		
	Baboon	0.001	0.031	
	Human (contemporary)	0.808	0.019	0.001
IAFW_L.T5*	Chimpanzee	0.021		
	Baboon	0.001	0.014	
	Human (contemporary)	0.553	0.262	0.001
IAFO_R.T5*	Chimpanzee	0.036		
	Baboon	0.001	0.001	
	Human (contemporary)	0.366	0.511	0.001
IAFO_L.T5*	Chimpanzee	0.443		
	Baboon	0.001	0.001	
	Human (contemporary)	0.984	0.629	0.001
SAFW_R.T5*	Chimpanzee	0.001		
	Baboon	0.001	0.005	
	Human (contemporary)	0.891	0.003	0.001
SAFW_L.T5*	Chimpanzee	0.001		
	Baboon	0.001	0.003	
	Human (contemporary)	0.196	0.007	0.001
SAFO_R.T5*	Chimpanzee	0.064		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.758	0.001

SAFO_L.T5*	Chimpanzee	0.017		
	Baboon	0.001	0.001	
	Human (contemporary)	0.238	0.478	0.001
SPA_T6*	Chimpanzee	0.024		
	Baboon	0.001	0.004	
	Human (contemporary)	0.001	0.001	0.001
SPL_T6**	Chimpanzee	0.042		
	Baboon	0.002	0.923	
	Human (contemporary)	0.001	0.628	1.000
IAFW_R.T6*	Chimpanzee	0.057		
	Baboon	0.001	0.065	
	Human (contemporary)	0.940	0.016	0.001
IAFW_L.T6*	Chimpanzee	0.054		
	Baboon	0.001	0.026	
	Human (contemporary)	0.994	0.091	0.026
IAFO_R.T6**	Chimpanzee	0.008		
	Baboon	0.001	0.001	
	Human (contemporary)	0.140	0.873	0.001
IAFO_L.T6**	Chimpanzee	0.910		
	Baboon	0.001	0.001	
	Human (contemporary)	0.669	0.218	0.001
SAFW_R.T6*	Chimpanzee	0.017		
	Baboon	0.001	0.017	
	Human (contemporary)	0.956	0.058	0.001
SAFW_L.T6*	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.177	0.170	0.001
SAFO_R.T6*	Chimpanzee	0.357		
	Baboon	0.001	0.001	
	Human (contemporary)	0.005	0.704	0.001
SAFO_L.T6*	Chimpanzee	0.817		
	Baboon	0.001	0.001	
	Human (contemporary)	0.997	0.891	0.001

Appendix 5: Comparison matrix of post-hoc p values for female morphometric measurements per species per vertebral level.

Measure		Gorilla	Chimpanzee	Baboon
SPA_T1*	Chimpanzee	0.001		
	Baboon	0.970	0.001	
	Human (contemporary)	0.001	0.079	0.001
SPL_T1**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.259	0.001
IAFW_R.T1**	Chimpanzee	0.075		
	Baboon	0.001	0.001	
	Human (contemporary)	0.847	0.001	0.001
IAFW_L.T1**	Chimpanzee	0.006		
	Baboon	0.001	0.001	
	Human (contemporary)	0.941	0.001	0.001
IAFO_R.T1**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.980	0.001
IAFO_L.T1**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.950	0.001
SAFW_R.T1*	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.835	0.001	0.001
SAFW_L.T1**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	1.000	0.001	0.001
SAFO_R.T1*	Chimpanzee	0.001		
	Baboon	0.001	0.100	
	Human (contemporary)	0.001	0.010	0.001
SAFO_L.T1**	Chimpanzee	0.001		
	Baboon	0.001	0.158	
	Human (contemporary)	0.001	0.001	0.001
SPA_T2*	Chimpanzee	0.049		
	Baboon	0.969	0.014	

	Human (contemporary)	0.001	0.001	0.001
SPL_T2*	Chimpanzee	0.001		
	Baboon	0.001	0.024	
	Human (contemporary)	0.001	0.804	0.227
IAFW_R.T2**	Chimpanzee	0.198		
	Baboon	0.001	0.001	
	Human (contemporary)	0.014	0.001	0.001
IAFW_L.T2**	Chimpanzee	0.370		
	Baboon	0.001	0.001	
	Human (contemporary)	0.455	0.001	0.001
IAFO_R.T2*	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.433	0.001
IAFO_L.T2*	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.749	0.001
SAFW_R.T2**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.999	0.001	0.001
SAFW_L.T2*	Chimpanzee	0.003		
	Baboon	0.001	0.001	
	Human (contemporary)	0.969	0.001	0.001
SAFO_R.T2**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	1.000	0.001
SAFO_L.T2**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.659	0.001
SPA_T3*	Chimpanzee	0.997		
	Baboon	0.005	0.002	
	Human (contemporary)	0.001	0.001	0.001
SPL_T3**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.048	0.753
IAFW_R.T3*	Chimpanzee	0.394		
	Baboon	0.001	0.001	
	Human (contemporary)	0.017	0.001	0.001
IAFW_L.T3*	Chimpanzee	0.255		

	Baboon	0.001	0.001	
	Human (contemporary)	0.581	0.011	0.001
IAFO_R.T3**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.015	0.449	0.001
IAFO_L.T3*	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.914	0.001
SAFW_R.T3**	Chimpanzee	0.199		
	Baboon	0.001	0.001	
	Human (contemporary)	0.151	0.001	0.001
SAFW_L.T3**	Chimpanzee	0.056		
	Baboon	0.001	0.001	
	Human (contemporary)	0.819	0.002	0.001
SAFO_R.T3*	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.999	0.001
SAFO_L.T3*	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.003	0.089	0.001
SPA_T4**	Chimpanzee	0.031		
	Baboon	0.001	0.001	
	Human (contemporary)	0.064	0.001	0.001
SPL_T4*	Chimpanzee	0.232		
	Baboon	0.001	0.001	
	Human (contemporary)	0.002	0.313	0.002
IAFW_R.T4**	Chimpanzee	0.012		
	Baboon	0.001	0.001	
	Human (contemporary)	0.696	0.001	0.001
IAFW_L.T4**	Chimpanzee	0.228		
	Baboon	0.001	0.001	
	Human (contemporary)	0.769	0.003	0.001
IAFO_R.T4*	Chimpanzee	0.012		
	Baboon	0.001	0.001	
	Human (contemporary)	0.498	0.360	0.001
IAFO_L.T4*	Chimpanzee	0.002		
	Baboon	0.001	0.001	
	Human (contemporary)	1.000	0.001	0.001

SAFW_R.T4**	Chimpanzee	0.079		
	Baboon	0.001	0.001	
	Human (contemporary)	0.130	0.001	0.001
SAFW_L.T4*	Chimpanzee	0.528		
	Baboon	0.001	0.001	
	Human (contemporary)	0.403	0.019	0.001
SAFO_R.T4**	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.980	0.001
SAFO_L.T4*	Chimpanzee	0.001		
	Baboon	0.001	0.001	
	Human (contemporary)	0.196	0.137	0.001
SPA_T5*	Chimpanzee	0.002		
	Baboon	0.001	0.003	
	Human (contemporary)	0.002	0.001	0.001
SPL_T5**	Chimpanzee	1.000		
	Baboon	0.049	0.009	
	Human (contemporary)	0.342	0.090	0.891
IAFW_R.T5*	Chimpanzee	0.464		
	Baboon	0.001	0.001	
	Human (contemporary)	0.783	0.079	0.001
IAFW_L.T5**	Chimpanzee	0.356		
	Baboon	0.001	0.001	
	Human (contemporary)	1.000	0.078	0.001
IAFO_R.T5*	Chimpanzee	0.020		
	Baboon	0.001	0.001	
	Human (contemporary)	0.591	0.374	0.001
IAFO_L.T5**	Chimpanzee	0.122		
	Baboon	0.001	0.001	
	Human (contemporary)	0.992	0.002	0.001
SAFW_R.T5*	Chimpanzee	0.247		
	Baboon	0.001	0.001	
	Human (contemporary)	0.066	0.001	0.001
SAFW_L.T5**	Chimpanzee	0.232		
	Baboon	0.001	0.001	
	Human (contemporary)	0.942	0.014	0.001
SAFO_R.T5*	Chimpanzee	0.181		
	Baboon	0.001	0.001	

	Human (contemporary)	0.566	0.899	0.001
SAFO_L.T5**	Chimpanzee	0.471		
	Baboon	0.001	0.001	
	Human (contemporary)	0.329	0.001	0.001
SPA_T6*	Chimpanzee	0.003		
	Baboon	0.001	0.001	
	Human (contemporary)	0.001	0.001	0.001
SPL_T6*	Chimpanzee	0.359		
	Baboon	0.318	0.005	
	Human (contemporary)	0.997	0.266	0.436
IAFW_R.T6*	Chimpanzee	0.991		
	Baboon	0.001	0.001	
	Human (contemporary)	0.444	0.273	0.001
IAFW_L.T6*	Chimpanzee	0.849		
	Baboon	0.001	0.001	
	Human (contemporary)	0.355	0.067	0.001
IAFO_R.T6*	Chimpanzee	0.121		
	Baboon	0.001	0.001	
	Human (contemporary)	0.620	0.004	0.001
IAFO_L.T6*	Chimpanzee	0.493		
	Baboon	0.001	0.001	
	Human (contemporary)	0.016	0.001	0.001
SAFW_R.T6*	Chimpanzee	0.891		
	Baboon	0.001	0.001	
	Human (contemporary)	0.389	0.098	0.001
SAFW_L.T6*	Chimpanzee	0.833		
	Baboon	0.001	0.001	
	Human (contemporary)	0.341	0.058	0.001
SAFO_R.T6*	Chimpanzee	0.246		
	Baboon	0.001	0.001	
	Human (contemporary)	0.543	0.959	0.001
SAFO_L.T6**	Chimpanzee	1.000		
	Baboon	0.001	0.001	
	Human (contemporary)	0.070	0.045	0.001

Appendix 6: Male morphometric measurements obtained per species per vertebral level.

(SPA, IAFO, SAFO measured in degrees; SPL, IAFW, SAFW measured in mm)

Measurement	Species	N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Minimum	Maximum
						Lower Bound	Upper Bound		
SPA_T1	Gorilla	31	163.02	6.410	1.151	160.67	165.37	152	175
	Chimpanzee	15	151.27	6.843	1.767	147.48	155.06	134	162
	Papio	23	156.74	4.765	0.994	154.68	158.80	147	164
	Human (contemporary)	30	143.10	6.902	1.260	140.52	145.67	128	152
	Total	99	153.74	10.170	1.022	151.71	155.77	128	175
SPL_T1	Gorilla	31	66.74	11.803	2.120	62.41	71.07	37	85
	Chimpanzee	15	35.22	4.902	1.266	32.51	37.94	22	42
	Papio	23	29.86	5.689	1.186	27.40	32.32	22	40
	Human (contemporary)	30	33.06	3.213	0.587	31.86	34.26	27	40
	Total	99	43.19	17.738	1.783	39.65	46.73	22	85
IAFW_R.T1	Gorilla	31	14.05	2.526	0.454	13.12	14.97	9	20
	Chimpanzee	15	10.65	1.204	0.311	9.98	11.32	8	13
	Papio	23	8.21	1.088	0.227	7.74	8.68	7	10
	Human (contemporary)	30	11.73	1.502	0.274	11.17	12.29	9	15
	Total	99	11.47	2.796	0.281	10.92	12.03	7	20
IAFW_L.T1	Gorilla	31	13.97	2.508	0.450	13.05	14.89	9	19
	Chimpanzee	15	10.53	1.310	0.338	9.80	11.25	7	13
	Papio	23	8.28	1.237	0.258	7.75	8.82	6	10
	Human (contemporary)	30	12.05	1.701	0.311	11.42	12.69	8	15
	Total	99	11.55	2.824	0.284	10.98	12.11	6	19
IAFO_R.T1	Gorilla	31	87.26	15.731	2.825	81.49	93.04	60	130

	Chimpanzee	15	70.65	7.838	2.024	66.31	74.99	54	82
	Papio	23	42.68	10.591	2.208	38.10	47.26	28	73
	Human (contemporary)	30	68.91	6.035	1.102	66.65	71.16	56	82
	Total	99	68.83	19.723	1.982	64.89	72.76	28	130
IAFO_L.T1	Gorilla	31	82.15	11.478	2.061	77.94	86.36	66	108
	Chimpanzee	15	67.65	7.521	1.942	63.49	71.82	57	79
	Papio	23	43.45	8.301	1.731	39.86	47.04	29	65
	Human (contemporary)	30	67.54	4.542	0.829	65.85	69.24	60	77
	Total	99	66.54	16.513	1.660	63.24	69.83	29	108
SAFW_R.T1	Gorilla	30	18.40	2.755	0.503	17.37	19.43	13	26
	Chimpanzee	15	11.92	1.197	0.309	11.25	12.58	10	14
	Papio	23	8.90	1.411	0.294	8.30	9.51	7	12
	Human (contemporary)	30	15.21	2.098	0.383	14.42	15.99	10	19
	Total	98	14.20	4.179	0.422	13.36	15.04	7	26
SAFW_L.T1	Gorilla	30	18.68	2.498	0.456	17.75	19.61	14	23
	Chimpanzee	14	11.68	1.331	0.356	10.91	12.45	10	15
	Papio	23	8.63	1.455	0.303	8.00	9.25	6	11
	Human (contemporary)	30	15.03	2.065	0.377	14.26	15.80	11	19
	Total	97	14.16	4.330	0.440	13.28	15.03	6	23
SAFO_R.T1	Gorilla	30	104.91	14.528	2.652	99.48	110.33	58	123
	Chimpanzee	15	86.29	13.305	3.435	78.93	93.66	55	106
	Papio	23	91.16	12.331	2.571	85.82	96.49	64	105
	Human (contemporary)	30	80.29	7.759	1.417	77.39	83.19	63	93
	Total	98	91.30	15.485	1.564	88.19	94.40	55	123
SAFO_L.T1	Gorilla	30	110.17	14.515	2.650	104.75	115.59	60	128
	Chimpanzee	14	90.43	13.070	3.493	82.88	97.98	63	109

	Papio	23	91.82	15.859	3.307	84.96	98.67	62	110
	Human (contemporary)	30	78.87	8.602	1.570	75.66	82.08	60	95
	Total	97	93.29	17.957	1.823	89.67	96.91	60	128
SPA_T2	Gorilla	31	158.90	8.038	1.444	155.95	161.85	144	171
	Chimpanzee	15	151.45	7.236	1.868	147.44	155.46	137	164
	Papio	23	153.50	6.797	1.417	150.57	156.44	137	163
	Human (contemporary)	30	139.48	7.966	1.454	136.51	142.46	111	153
	Total	99	150.63	10.870	1.092	148.47	152.80	111	171
SPL_T2	Gorilla	31	56.42	9.823	1.764	52.82	60.03	32	72
	Chimpanzee	15	33.13	4.518	1.167	30.63	35.64	22	41
	Papio	23	31.39	5.733	1.195	28.91	33.87	22	41
	Human (contemporary)	30	32.34	3.033	0.554	31.21	33.47	25	39
	Total	99	39.78	13.055	1.312	37.18	42.38	22	72
IAFW_R.T2	Gorilla	31	11.62	1.797	0.323	10.96	12.28	7	15
	Chimpanzee	15	9.07	1.184	0.306	8.42	9.73	8	11
	Papio	23	7.22	0.964	0.201	6.81	7.64	6	9
	Human (contemporary)	30	10.82	1.200	0.219	10.37	11.27	9	14
	Total	99	9.97	2.191	0.220	9.53	10.41	6	15
IAFW_L.T2	Gorilla	31	11.58	2.086	0.375	10.81	12.34	6	16
	Chimpanzee	15	9.32	1.405	0.363	8.54	10.10	7	11
	Papio	23	7.42	1.244	0.259	6.88	7.96	5	10
	Human (contemporary)	30	10.71	1.459	0.266	10.17	11.26	7	15
	Total	99	10.01	2.274	0.229	9.55	10.46	5	16
IAFO_R.T2	Gorilla	31	81.70	6.480	1.164	79.32	84.08	73	96
	Chimpanzee	15	71.18	5.450	1.407	68.17	74.20	61	79
	Papio	23	51.88	4.748	0.990	49.82	53.93	41	62

	Human (contemporary)	30	72.82	5.904	1.078	70.62	75.03	61	87
	Total	99	70.49	12.460	1.252	68.00	72.97	41	96
IAFO_L.T2	Gorilla	31	82.36	8.308	1.492	79.31	85.40	68	102
	Chimpanzee	15	70.92	4.450	1.149	68.46	73.38	63	77
	Papio	23	51.12	4.196	0.875	49.31	52.94	43	59
	Human (contemporary)	30	71.70	4.753	0.868	69.93	73.48	60	80
	Total	99	70.14	12.943	1.301	67.56	72.72	43	102
SAFW_R.T2	Gorilla	31	14.66	2.948	0.530	13.58	15.74	10	21
	Chimpanzee	15	11.09	1.647	0.425	10.18	12.00	8	14
	Papio	23	8.09	1.116	0.233	7.61	8.57	6	10
	Human (contemporary)	30	12.68	1.482	0.271	12.13	13.23	8	15
	Total	99	11.99	3.174	0.319	11.36	12.63	6	21
SAFW_L.T2	Gorilla	31	14.47	2.683	0.482	13.49	15.46	9	21
	Chimpanzee	15	10.72	1.595	0.412	9.84	11.61	7	13
	Papio	23	7.69	1.054	0.220	7.24	8.15	6	9
	Human (contemporary)	30	12.29	1.746	0.319	11.64	12.94	9	16
	Total	99	11.67	3.189	0.320	11.03	12.30	6	21
SAFO_R.T2	Gorilla	31	87.82	13.625	2.447	82.82	92.82	62	128
	Chimpanzee	15	68.67	8.642	2.231	63.88	73.45	54	84
	Papio	23	44.07	10.337	2.155	39.60	48.54	31	76
	Human (contemporary)	30	67.78	6.408	1.170	65.38	70.17	51	79
	Total	99	68.68	19.023	1.912	64.89	72.48	31	128
SAFO_L.T2	Gorilla	31	83.38	10.189	1.830	79.64	87.12	66	112
	Chimpanzee	15	69.53	7.622	1.968	65.31	73.75	56	81
	Papio	23	48.47	9.500	1.981	44.36	52.58	33	75
	Human (contemporary)	30	69.17	4.996	0.912	67.30	71.04	58	78

	Total	99	68.87	15.234	1.531	65.83	71.90	33	112
SPA_T3	Gorilla	31	152.44	9.586	1.722	148.93	155.96	137	169
	Chimpanzee	15	148.89	7.215	1.863	144.90	152.89	138	164
	Papio	23	153.12	6.387	1.332	150.36	155.88	140	167
	Human (contemporary)	30	137.16	6.814	1.244	134.61	139.70	122	151
	Total	99	147.43	10.326	1.038	145.37	149.49	122	169
SPL_T3	Gorilla	31	50.33	8.815	1.583	47.10	53.56	29	68
	Chimpanzee	15	31.42	4.156	1.073	29.12	33.72	21	37
	Papio	23	30.65	5.216	1.088	28.40	32.91	22	38
	Human (contemporary)	30	30.94	2.749	0.502	29.92	31.97	27	37
	Total	99	37.02	10.782	1.084	34.87	39.17	21	68
IAFW_R.T3	Gorilla	31	11.41	1.761	0.316	10.76	12.05	7	15
	Chimpanzee	15	8.96	1.213	0.313	8.29	9.63	6	10
	Papio	23	7.02	0.996	0.208	6.59	7.45	5	9
	Human (contemporary)	30	11.07	1.611	0.294	10.47	11.67	8	16
	Total	99	9.92	2.317	0.233	9.45	10.38	5	16
IAFW_L.T3	Gorilla	31	11.81	1.798	0.323	11.15	12.47	7	16
	Chimpanzee	15	9.25	1.184	0.306	8.60	9.91	6	11
	Papio	23	7.03	1.115	0.233	6.55	7.51	5	10
	Human (contemporary)	30	10.39	1.414	0.258	9.86	10.92	7	13
	Total	99	9.88	2.298	0.231	9.42	10.34	5	16
IAFO_R.T3	Gorilla	31	81.04	5.743	1.032	78.93	83.15	73	94
	Chimpanzee	15	71.36	4.019	1.038	69.14	73.59	63	80
	Papio	23	55.31	3.826	0.798	53.65	56.96	47	62
	Human (contemporary)	30	75.13	5.421	0.990	73.10	77.15	64	86
	Total	99	71.80	10.893	1.095	69.63	73.98	47	94

IAFO_L.T3	Gorilla	31	79.15	5.488	0.986	77.14	81.16	62	89
	Chimpanzee	15	70.86	4.383	1.132	68.44	73.29	63	80
	Papio	23	54.64	5.387	1.123	52.31	56.97	43	63
	Human (contemporary)	30	71.83	4.263	0.778	70.24	73.43	65	83
	Total	99	69.98	10.338	1.039	67.92	72.05	43	89
SAFW_R.T3	Gorilla	30	12.44	1.842	0.336	11.75	13.13	9	16
	Chimpanzee	15	9.43	1.306	0.337	8.71	10.16	7	11
	Papio	23	7.42	1.157	0.241	6.92	7.92	5	10
	Human (contemporary)	30	11.40	1.232	0.225	10.94	11.86	8	13
	Total	98	10.48	2.420	0.244	10.00	10.97	5	16
SAFW_L.T3	Gorilla	31	12.43	1.822	0.327	11.76	13.09	9	18
	Chimpanzee	15	9.64	1.616	0.417	8.75	10.54	7	12
	Papio	23	7.37	1.186	0.247	6.86	7.88	5	10
	Human (contemporary)	30	10.82	1.310	0.239	10.33	11.31	8	13
	Total	99	10.34	2.409	0.242	9.86	10.82	5	18
SAFO_R.T3	Gorilla	30	80.20	7.627	1.392	77.35	83.05	68	98
	Chimpanzee	15	69.87	4.959	1.280	67.12	72.62	60	78
	Papio	23	49.84	6.616	1.380	46.98	52.70	38	65
	Human (contemporary)	30	69.52	5.198	0.949	67.58	71.46	54	79
	Total	98	68.22	12.819	1.295	65.65	70.79	38	98
SAFO_L.T3	Gorilla	31	81.38	9.564	1.718	77.87	84.89	67	105
	Chimpanzee	15	69.71	5.909	1.526	66.44	72.99	58	78
	Papio	23	51.38	4.969	1.036	49.23	53.52	41	59
	Human (contemporary)	30	72.04	4.418	0.807	70.39	73.69	60	80
	Total	99	69.81	12.960	1.303	67.23	72.40	41	105
SPA_T4	Gorilla	31	141.98	9.796	1.759	138.39	145.57	125	161

	Chimpanzee	15	144.42	5.960	1.539	141.12	147.72	133	154
	Papio	23	152.29	5.697	1.188	149.83	154.76	137	160
	Human (contemporary)	30	130.67	6.078	1.110	128.40	132.94	120	142
	Total	99	141.32	10.828	1.088	139.16	143.48	120	161
SPL_T4	Gorilla	31	45.61	8.551	1.536	42.48	48.75	24	61
	Chimpanzee	15	32.84	5.098	1.316	30.01	35.66	22	43
	Papio	23	30.78	6.409	1.336	28.00	33.55	22	41
	Human (contemporary)	30	29.62	3.462	0.632	28.33	30.91	23	38
	Total	99	35.38	9.387	0.943	33.51	37.26	22	61
IAFW_R.T4	Gorilla	31	11.11	1.950	0.350	10.39	11.82	6	15
	Chimpanzee	15	9.07	1.029	0.266	8.50	9.64	7	11
	Papio	23	7.20	1.003	0.209	6.77	7.64	6	9
	Human (contemporary)	30	10.76	1.460	0.267	10.22	11.31	8	14
	Total	99	9.79	2.159	0.217	9.36	10.22	6	15
IAFW_L.T4	Gorilla	31	10.90	1.788	0.321	10.24	11.55	7	14
	Chimpanzee	15	8.67	1.254	0.324	7.97	9.36	6	11
	Papio	23	7.14	1.149	0.240	6.65	7.64	6	10
	Human (contemporary)	30	10.20	1.382	0.252	9.69	10.72	7	13
	Total	99	9.48	2.059	0.207	9.07	9.89	6	14
IAFO_R.T4	Gorilla	31	78.84	5.204	0.935	76.93	80.75	65	89
	Chimpanzee	15	71.20	4.443	1.147	68.74	73.66	60	78
	Papio	23	59.60	3.849	0.802	57.93	61.26	53	69
	Human (contemporary)	30	73.61	4.559	0.832	71.91	75.31	64	82
	Total	99	71.63	8.499	0.854	69.93	73.32	53	89
IAFO_L.T4	Gorilla	31	77.46	4.371	0.785	75.86	79.06	69	87
	Chimpanzee	15	69.75	6.069	1.567	66.39	73.11	53	77

	Papio	23	57.53	6.480	1.351	54.73	60.33	46	73
	Human (contemporary)	30	72.47	4.115	0.751	70.94	74.01	60	82
	Total	99	70.15	9.028	0.907	68.35	71.95	46	87
SAFW_R.T4	Gorilla	31	11.89	1.767	0.317	11.24	12.54	8	15
	Chimpanzee	15	9.05	1.305	0.337	8.32	9.77	7	11
	Papio	23	7.29	1.007	0.210	6.85	7.72	6	9
	Human (contemporary)	29	11.69	1.530	0.284	11.11	12.27	8	15
	Total	98	10.32	2.428	0.245	9.83	10.80	6	15
SAFW_L.T4	Gorilla	31	12.07	1.981	0.356	11.34	12.79	8	17
	Chimpanzee	15	9.38	1.202	0.310	8.72	10.05	7	11
	Papio	23	7.00	1.165	0.243	6.50	7.50	5	10
	Human (contemporary)	29	10.88	1.583	0.294	10.28	11.49	7	14
	Total	98	10.12	2.496	0.252	9.62	10.62	5	17
SAFO_R.T4	Gorilla	31	77.51	6.328	1.136	75.19	79.84	63	90
	Chimpanzee	15	69.93	4.332	1.119	67.53	72.33	63	76
	Papio	23	51.78	4.694	0.979	49.75	53.81	45	66
	Human (contemporary)	29	70.06	6.118	1.136	67.73	72.38	58	81
	Total	98	68.11	11.137	1.125	65.87	70.34	45	90
SAFO_L.T4	Gorilla	31	76.37	6.301	1.132	74.06	78.68	53	89
	Chimpanzee	15	71.09	4.160	1.074	68.78	73.39	61	76
	Papio	23	55.28	5.748	1.199	52.79	57.77	44	66
	Human (contemporary)	29	72.28	3.454	0.641	70.97	73.60	65	80
	Total	98	69.40	9.562	0.966	67.49	71.32	44	89
SPA_T5	Gorilla	30	138.35	8.616	1.573	135.13	141.57	123	162
	Chimpanzee	15	143.59	8.046	2.077	139.14	148.05	126	153
	Papio	23	150.76	5.753	1.200	148.27	153.25	136	160

	Human (contemporary)	30	125.83	6.629	1.210	123.36	128.31	115	142
	Total	98	138.23	11.890	1.201	135.85	140.62	115	162
SPL_T5	Gorilla	30	42.90	7.809	1.426	39.98	45.82	21	57
	Chimpanzee	15	34.01	5.278	1.363	31.09	36.94	21	43
	Papio	23	31.55	5.919	1.234	28.99	34.11	21	41
	Human (contemporary)	30	30.92	4.035	0.737	29.41	32.42	24	39
	Total	98	35.21	7.903	0.798	33.62	36.79	21	57
IAFW_R.T5	Gorilla	30	10.58	1.551	0.283	10.00	11.16	7	14
	Chimpanzee	15	8.75	1.120	0.289	8.13	9.37	7	10
	Papio	23	7.31	1.236	0.258	6.78	7.84	5	9
	Human (contemporary)	30	10.21	1.563	0.285	9.63	10.80	6	13
	Total	98	9.42	1.926	0.195	9.03	9.81	5	14
IAFW_L.T5	Gorilla	30	10.21	1.707	0.312	9.57	10.85	6	13
	Chimpanzee	15	8.74	1.174	0.303	8.09	9.39	6	11
	Papio	23	7.14	1.104	0.230	6.66	7.62	5	9
	Human (contemporary)	30	9.67	1.509	0.275	9.10	10.23	6	13
	Total	98	9.10	1.853	0.187	8.73	9.47	5	13
IAFO_R.T5	Gorilla	30	76.37	5.962	1.088	74.14	78.59	63	89
	Chimpanzee	15	71.82	3.473	0.897	69.90	73.75	66	79
	Papio	23	61.23	2.930	0.611	59.96	62.50	56	66
	Human (contemporary)	30	74.14	5.203	0.950	72.20	76.08	63	89
	Total	98	71.44	7.543	0.762	69.93	72.95	56	89
IAFO_L.T5	Gorilla	30	73.72	5.259	0.960	71.76	75.68	61	87
	Chimpanzee	15	71.20	5.235	1.352	68.30	74.10	60	80
	Papio	23	59.79	4.373	0.912	57.90	61.68	51	66
	Human (contemporary)	30	73.22	4.544	0.830	71.52	74.92	67	87

	Total	98	69.91	7.428	0.750	68.42	71.40	51	87
SAFW_R.T5	Gorilla	30	11.56	1.909	0.348	10.85	12.27	7	15
	Chimpanzee	15	9.30	1.388	0.358	8.54	10.07	7	12
	Papio	23	7.35	1.177	0.245	6.84	7.86	5	9
	Human (contemporary)	30	11.24	1.576	0.288	10.65	11.83	8	15
	Total	98	10.13	2.318	0.234	9.66	10.59	5	15
SAFW_L.T5	Gorilla	30	11.32	1.765	0.322	10.66	11.98	7	15
	Chimpanzee	15	8.84	1.498	0.387	8.01	9.67	6	11
	Papio	23	6.95	1.080	0.225	6.48	7.42	5	9
	Human (contemporary)	30	10.50	1.355	0.247	9.99	11.00	8	13
	Total	98	9.66	2.233	0.226	9.21	10.11	5	15
SAFO_R.T5	Gorilla	30	75.58	5.722	1.045	73.45	77.72	67	86
	Chimpanzee	15	71.16	4.943	1.276	68.42	73.90	62	78
	Papio	23	57.08	4.330	0.903	55.21	58.95	48	64
	Human (contemporary)	30	69.41	5.081	0.928	67.51	71.30	60	81
	Total	98	68.67	8.546	0.863	66.96	70.39	48	86
SAFO_L.T5	Gorilla	30	76.32	5.137	0.938	74.41	78.24	67	87
	Chimpanzee	15	70.99	6.436	1.662	67.43	74.56	57	79
	Papio	23	60.01	5.602	1.168	57.58	62.43	51	79
	Human (contemporary)	30	73.57	3.954	0.722	72.09	75.05	60	80
	Total	98	70.84	8.068	0.815	69.22	72.45	51	87
SPA_T6	Gorilla	31	133.96	8.314	1.493	130.91	137.01	118	150
	Chimpanzee	15	141.10	6.582	1.699	137.46	144.75	123	149
	Papio	23	150.25	6.863	1.431	147.28	153.21	136	163
	Human (contemporary)	30	122.19	6.580	1.201	119.73	124.65	110	135
	Total	99	135.26	12.708	1.277	132.72	137.79	110	163

SPL_T6	Gorilla	31	39.56	7.627	1.370	36.76	42.35	16	52
	Chimpanzee	15	33.92	5.572	1.439	30.83	37.00	21	42
	Papio	23	32.10	6.403	1.335	29.33	34.87	23	42
	Human (contemporary)	30	31.62	3.714	0.678	30.23	33.01	25	40
	Total	99	34.57	6.896	0.693	33.19	35.94	16	52
IAFW_R.T6	Gorilla	31	9.81	1.471	0.264	9.27	10.35	7	13
	Chimpanzee	15	8.66	0.761	0.196	8.24	9.09	7	10
	Papio	23	7.48	1.239	0.258	6.94	8.01	5	10
	Human (contemporary)	30	10.03	1.397	0.255	9.51	10.55	7	13
	Total	99	9.16	1.654	0.166	8.83	9.49	5	13
IAFW_L.T6	Gorilla	30	9.94	1.474	0.269	9.39	10.49	6	13
	Chimpanzee	15	8.81	1.142	0.295	8.18	9.45	7	11
	Papio	23	7.50	1.229	0.256	6.97	8.03	5	11
	Human (contemporary)	30	9.85	1.123	0.205	9.43	10.27	8	12
	Total	98	9.17	1.601	0.162	8.85	9.49	5	13
IAFO_R.T6	Gorilla	30	76.83	5.477	1.000	74.78	78.87	63	86
	Chimpanzee	15	72.59	2.818	0.728	71.03	74.15	67	78
	Papio	23	61.05	4.177	0.871	59.25	62.86	54	68
	Human (contemporary)	30	73.78	4.787	0.874	71.99	75.57	64	83
	Total	98	71.54	7.574	0.765	70.02	73.06	54	86
IAFO_L.T6	Gorilla	31	71.99	6.723	1.207	69.53	74.46	58	83
	Chimpanzee	15	70.02	6.416	1.657	66.47	73.58	56	79
	Papio	23	61.19	4.699	0.980	59.16	63.22	51	68
	Human (contemporary)	30	73.90	3.714	0.678	72.52	75.29	65	86
	Total	99	69.76	7.269	0.731	68.31	71.21	51	86
SAFW_R.T6	Gorilla	31	10.73	1.670	0.300	10.12	11.35	6	13

	Chimpanzee	15	9.11	1.335	0.345	8.37	9.85	6	12
	Papio	23	7.40	1.284	0.268	6.84	7.95	5	9
	Human (contemporary)	30	10.50	1.788	0.326	9.84	11.17	6	13
	Total	99	9.64	2.062	0.207	9.23	10.05	5	13
SAFW_L.T6	Gorilla	31	10.57	1.523	0.274	10.01	11.13	6	13
	Chimpanzee	15	8.93	1.098	0.283	8.32	9.53	7	11
	Papio	23	6.98	1.101	0.230	6.51	7.46	5	9
	Human (contemporary)	30	9.84	1.194	0.218	9.39	10.29	6	12
	Total	99	9.27	1.860	0.187	8.90	9.64	5	13
SAFO_R.T6	Gorilla	31	73.74	4.889	0.878	71.94	75.53	63	82
	Chimpanzee	15	70.93	4.978	1.285	68.17	73.69	62	79
	Papio	23	58.34	3.780	0.788	56.71	59.98	48	66
	Human (contemporary)	30	69.08	5.659	1.033	66.97	71.19	52	82
	Total	99	68.32	7.576	0.761	66.81	69.84	48	82
SAFO_L.T6	Gorilla	31	73.53	5.314	0.954	71.58	75.48	64	87
	Chimpanzee	15	72.08	5.607	1.448	68.97	75.18	63	84
	Papio	23	61.67	3.577	0.746	60.12	63.22	55	69
	Human (contemporary)	30	73.27	4.576	0.836	71.56	74.98	63	84
	Total	99	70.48	6.793	0.683	69.12	71.83	55	87

Appendix 7: Female morphometric measurements obtained per species vertebral level.

(SPA, IAFO, SAFO measured in degrees; SPL, IAFW, SAFW measured in mm)

Measurement	Species	N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Minimum	Maximum
						Lower Bound	Upper Bound		
SPA_T1	Gorilla	29	158.28	7.500	1.393	155.43	161.13	140	172
	Chimpanzee	30	146.73	8.589	1.568	143.52	149.93	131	167
	Papio	28	159.38	7.881	1.489	156.33	162.44	146	174
	Human (contemporary)	28	140.90	9.557	1.806	137.19	144.60	119	156
	Total	115	151.30	11.378	1.061	149.20	153.40	119	174
SPL_T1	Gorilla	29	44.25	6.033	1.120	41.96	46.55	32	56
	Chimpanzee	30	32.20	3.108	0.567	31.04	33.36	26	38
	Papio	28	26.20	3.668	0.693	24.78	27.62	22	40
	Human (contemporary)	28	30.49	3.395	0.642	29.17	31.80	25	42
	Total	115	33.36	7.903	0.737	31.90	34.82	22	56
IAFW_R.T1	Gorilla	29	11.12	1.887	0.350	10.41	11.84	6	14
	Chimpanzee	30	10.08	1.102	0.201	9.67	10.49	8	13
	Papio	28	7.20	0.859	0.162	6.87	7.53	5	9
	Human (contemporary)	28	11.64	1.652	0.312	11.00	12.28	9	15
	Total	115	10.02	2.216	0.207	9.61	10.43	5	15
IAFW_L.T1	Gorilla	29	11.38	1.922	0.357	10.65	12.11	8	15
	Chimpanzee	30	9.95	1.088	0.199	9.54	10.35	7	12
	Papio	28	7.29	1.052	0.199	6.88	7.69	6	10
	Human (contemporary)	28	11.80	1.666	0.315	11.15	12.44	8	15
	Total	115	10.11	2.281	0.213	9.69	10.53	6	15
IAFO_R.T1	Gorilla	29	92.16	12.225	2.270	87.51	96.81	71	124

	Chimpanzee	30	70.38	7.063	1.290	67.75	73.02	56	90
	Papio	28	41.25	13.173	2.490	36.14	46.35	24	100
	Human (contemporary)	28	69.14	6.444	1.218	66.64	71.64	56	82
	Total	115	68.48	20.646	1.925	64.66	72.29	24	124
IAFO_L.T1	Gorilla	29	89.61	16.454	3.055	83.35	95.87	63	127
	Chimpanzee	30	67.52	7.972	1.455	64.54	70.49	53	86
	Papio	28	42.65	13.499	2.551	37.42	47.89	30	105
	Human (contemporary)	28	66.01	5.390	1.019	63.92	68.10	57	78
	Total	115	66.67	20.212	1.885	62.93	70.40	30	127
SAFW_R.T1	Gorilla	29	14.06	1.559	0.289	13.47	14.65	11	18
	Chimpanzee	30	10.84	1.429	0.261	10.30	11.37	8	14
	Papio	28	7.61	1.006	0.190	7.22	8.00	6	11
	Human (contemporary)	28	13.70	1.815	0.343	12.99	14.40	10	19
	Total	115	11.56	2.971	0.277	11.01	12.11	6	19
SAFW_L.T1	Gorilla	29	14.20	1.620	0.301	13.58	14.82	10	17
	Chimpanzee	30	10.68	1.241	0.227	10.22	11.15	9	14
	Papio	28	7.55	0.817	0.154	7.23	7.86	6	10
	Human (contemporary)	28	14.06	2.570	0.486	13.06	15.06	9	20
	Total	115	11.63	3.197	0.298	11.04	12.22	6	20
SAFO_R.T1	Gorilla	29	106.57	14.189	2.635	101.18	111.97	67	125
	Chimpanzee	30	85.22	8.723	1.593	81.96	88.47	64	100
	Papio	28	92.83	11.005	2.080	88.57	97.10	73	107
	Human (contemporary)	28	74.80	11.275	2.131	70.43	79.17	57	98
	Total	115	89.92	16.193	1.510	86.93	92.91	57	125
SAFO_L.T1	Gorilla	29	111.99	11.428	2.122	107.64	116.33	79	125
	Chimpanzee	30	87.27	9.254	1.689	83.81	90.72	73	107

	Papio	28	94.28	13.851	2.618	88.91	99.65	67	112
	Human (contemporary)	28	77.12	7.945	1.502	74.04	80.20	61	92
	Total	115	92.74	16.639	1.552	89.66	95.81	61	125
SPA_T2	Gorilla	29	154.48	7.868	1.461	151.48	157.47	139	167
	Chimpanzee	30	148.45	8.551	1.561	145.26	151.65	130	166
	Papio	28	155.55	6.006	1.135	153.22	157.88	143	170
	Human (contemporary)	28	139.41	9.615	1.817	135.68	143.14	116	155
	Total	115	149.50	10.239	0.955	147.61	151.39	116	170
SPL_T2	Gorilla	29	37.71	5.056	0.939	35.79	39.64	27	49
	Chimpanzee	30	30.31	2.890	0.528	29.23	31.39	25	36
	Papio	28	27.05	3.698	0.699	25.62	28.49	21	39
	Human (contemporary)	28	29.27	3.910	0.739	27.76	30.79	20	38
	Total	115	31.13	5.603	0.522	30.10	32.17	20	49
IAFW_R.T2	Gorilla	29	9.40	1.478	0.275	8.84	9.97	6	13
	Chimpanzee	30	8.71	0.936	0.171	8.36	9.06	6	11
	Papio	28	6.60	0.738	0.140	6.31	6.89	5	8
	Human (contemporary)	28	10.60	1.353	0.256	10.07	11.12	8	14
	Total	115	8.83	1.844	0.172	8.49	9.17	5	14
IAFW_L.T2	Gorilla	29	9.40	1.948	0.362	8.65	10.14	6	15
	Chimpanzee	30	8.68	0.892	0.163	8.34	9.01	7	10
	Papio	28	6.50	0.549	0.104	6.28	6.71	5	8
	Human (contemporary)	28	10.19	1.596	0.302	9.57	10.81	7	14
	Total	115	8.69	1.916	0.179	8.34	9.05	5	15
IAFO_R.T2	Gorilla	29	82.74	6.655	1.236	80.21	85.27	63	95
	Chimpanzee	30	70.85	4.221	0.771	69.28	72.43	63	83
	Papio	28	53.31	3.751	0.709	51.85	54.76	45	60

	Human (contemporary)	28	73.05	4.978	0.941	71.12	74.98	59	82
	Total	115	70.11	11.696	1.091	67.95	72.27	45	95
IAFO_L.T2	Gorilla	29	82.28	6.271	1.164	79.89	84.66	68	95
	Chimpanzee	30	69.70	4.497	0.821	68.02	71.38	60	79
	Papio	28	53.18	4.567	0.863	51.41	54.96	42	61
	Human (contemporary)	28	71.14	4.256	0.804	69.49	72.79	58	80
	Total	115	69.20	11.468	1.069	67.08	71.32	42	95
SAFW_R.T2	Gorilla	29	11.81	1.827	0.339	11.12	12.51	7	14
	Chimpanzee	30	10.15	1.294	0.236	9.67	10.63	8	13
	Papio	28	7.31	0.765	0.145	7.01	7.60	6	9
	Human (contemporary)	28	12.01	1.968	0.372	11.24	12.77	8	16
	Total	115	10.33	2.409	0.225	9.88	10.77	6	16
SAFW_L.T2	Gorilla	29	11.39	1.635	0.304	10.77	12.01	8	15
	Chimpanzee	30	10.00	1.201	0.219	9.55	10.45	7	13
	Papio	28	6.97	1.007	0.190	6.58	7.36	5	9
	Human (contemporary)	28	11.58	1.660	0.314	10.93	12.22	9	15
	Total	115	10.00	2.296	0.214	9.57	10.42	5	15
SAFO_R.T2	Gorilla	29	88.34	12.568	2.334	83.56	93.12	71	117
	Chimpanzee	30	68.32	6.064	1.107	66.05	70.58	56	79
	Papio	28	44.05	12.069	2.281	39.37	48.73	33	97
	Human (contemporary)	28	68.32	6.573	1.242	65.77	70.87	56	87
	Total	115	67.46	18.407	1.716	64.06	70.86	33	117
SAFO_L.T2	Gorilla	29	86.67	15.377	2.855	80.82	92.52	65	124
	Chimpanzee	30	68.60	6.830	1.247	66.05	71.15	58	84
	Papio	28	47.09	11.623	2.197	42.58	51.60	33	99
	Human (contemporary)	28	70.73	4.689	0.886	68.92	72.55	62	83

	Total	115	68.44	17.463	1.628	65.21	71.67	33	124
SPA_T3	Gorilla	29	147.95	9.001	1.671	144.53	151.38	123	161
	Chimpanzee	30	147.43	7.671	1.400	144.57	150.30	127	160
	Papio	28	156.14	5.305	1.003	154.08	158.20	147	168
	Human (contemporary)	28	135.64	10.825	2.046	131.44	139.84	114	156
	Total	115	146.81	11.034	1.029	144.77	148.85	114	168
SPL_T3	Gorilla	29	33.98	4.589	0.852	32.23	35.72	22	44
	Chimpanzee	30	29.77	2.996	0.547	28.65	30.89	23	36
	Papio	28	26.10	3.736	0.706	24.65	27.55	21	39
	Human (contemporary)	28	27.34	3.669	0.693	25.92	28.77	22	36
	Total	115	29.35	4.798	0.447	28.46	30.23	21	44
IAFW_R.T3	Gorilla	29	9.19	1.264	0.235	8.71	9.67	8	13
	Chimpanzee	30	8.67	1.061	0.194	8.28	9.07	7	11
	Papio	28	6.10	0.796	0.150	5.79	6.41	5	8
	Human (contemporary)	28	10.18	1.367	0.258	9.65	10.71	8	13
	Total	115	8.54	1.873	0.175	8.20	8.89	5	13
IAFW_L.T3	Gorilla	29	9.22	1.353	0.251	8.71	9.74	7	13
	Chimpanzee	30	8.67	0.986	0.180	8.30	9.04	7	10
	Papio	28	6.32	0.689	0.130	6.05	6.59	5	8
	Human (contemporary)	28	9.61	1.047	0.198	9.20	10.02	7	12
	Total	115	8.47	1.636	0.153	8.16	8.77	5	13
IAFO_R.T3	Gorilla	29	78.38	4.930	0.916	76.50	80.25	67	89
	Chimpanzee	30	72.56	4.115	0.751	71.02	74.10	63	80
	Papio	28	56.54	3.686	0.697	55.11	57.97	49	63
	Human (contemporary)	27	74.46	4.342	0.836	72.74	76.17	64	86
	Total	114	70.55	9.330	0.874	68.82	72.28	49	89

IAFO_L.T3	Gorilla	29	78.14	5.376	0.998	76.09	80.18	63	89
	Chimpanzee	30	70.69	3.135	0.572	69.52	71.86	63	77
	Papio	28	56.58	4.698	0.888	54.75	58.40	46	66
	Human (contemporary)	27	71.54	4.217	0.812	69.87	73.21	62	79
	Total	114	69.32	8.996	0.843	67.65	70.99	46	89
SAFW_R.T3	Gorilla	29	9.83	1.598	0.297	9.22	10.43	7	14
	Chimpanzee	30	9.04	1.193	0.218	8.59	9.48	6	12
	Papio	28	6.52	0.804	0.152	6.20	6.83	5	8
	Human (contemporary)	27	10.76	1.503	0.289	10.17	11.36	8	14
	Total	114	9.03	2.030	0.190	8.65	9.40	5	14
SAFW_L.T3	Gorilla	29	9.88	1.575	0.292	9.28	10.48	8	14
	Chimpanzee	30	8.97	0.905	0.165	8.63	9.31	7	11
	Papio	28	6.40	0.697	0.132	6.13	6.67	5	8
	Human (contemporary)	27	10.37	1.620	0.312	9.73	11.01	8	14
	Total	114	8.90	1.963	0.184	8.54	9.27	5	14
SAFO_R.T3	Gorilla	29	77.82	4.898	0.909	75.96	79.68	65	87
	Chimpanzee	30	68.01	4.592	0.838	66.29	69.72	60	79
	Papio	28	50.13	4.441	0.839	48.41	51.85	42	60
	Human (contemporary)	27	68.23	5.255	1.011	66.15	70.31	58	76
	Total	114	66.16	11.087	1.038	64.11	68.22	42	87
SAFO_L.T3	Gorilla	29	77.04	5.409	1.004	74.98	79.10	67	87
	Chimpanzee	30	68.55	4.501	0.822	66.87	70.23	59	76
	Papio	28	53.85	4.474	0.845	52.12	55.59	45	65
	Human (contemporary)	27	71.92	5.244	1.009	69.85	74.00	62	81
	Total	114	67.90	9.894	0.927	66.06	69.74	45	87
SPA_T4	Gorilla	29	137.08	10.812	2.008	132.97	141.19	115	158

	Chimpanzee	30	144.36	8.118	1.482	141.33	147.39	122	163
	Papio	28	155.20	5.484	1.036	153.08	157.33	142	168
	Human (contemporary)	28	129.43	11.144	2.106	125.11	133.75	112	149
	Total	115	141.53	13.078	1.220	139.11	143.94	112	168
SPL_T4	Gorilla	29	31.99	4.625	0.859	30.23	33.75	20	40
	Chimpanzee	30	29.90	3.014	0.550	28.77	31.02	24	37
	Papio	28	23.93	4.082	0.771	22.35	25.52	14	32
	Human (contemporary)	28	27.98	3.491	0.660	26.63	29.33	21	34
	Total	115	28.51	4.816	0.449	27.62	29.40	14	40
IAFW_R.T4	Gorilla	29	9.14	1.169	0.217	8.69	9.58	7	12
	Chimpanzee	30	8.30	0.752	0.137	8.02	8.58	7	9
	Papio	28	6.39	0.660	0.125	6.13	6.64	5	8
	Human (contemporary)	28	9.59	1.341	0.253	9.07	10.11	7	13
	Total	115	8.36	1.578	0.147	8.07	8.65	5	13
IAFW_L.T4	Gorilla	29	9.01	1.296	0.241	8.52	9.50	6	11
	Chimpanzee	30	8.38	0.996	0.182	8.01	8.76	6	10
	Papio	28	6.34	0.720	0.136	6.07	6.62	5	8
	Human (contemporary)	28	9.39	1.046	0.198	8.99	9.80	7	11
	Total	115	8.29	1.552	0.145	8.00	8.58	5	11
IAFO_R.T4	Gorilla	29	76.41	5.646	1.048	74.26	78.56	64	88
	Chimpanzee	30	72.27	4.140	0.756	70.72	73.82	64	80
	Papio	28	58.48	4.540	0.858	56.72	60.24	48	68
	Human (contemporary)	28	74.49	4.262	0.806	72.84	76.14	64	83
	Total	115	70.50	8.396	0.783	68.94	72.05	48	88
IAFO_L.T4	Gorilla	29	74.69	5.257	0.976	72.69	76.69	61	85
	Chimpanzee	30	69.53	4.883	0.892	67.70	71.35	62	82

	Papio	28	58.27	4.974	0.940	56.34	60.20	49	69
	Human (contemporary)	28	74.86	4.651	0.879	73.05	76.66	60	81
	Total	115	69.39	8.290	0.773	67.85	70.92	49	85
SAFW_R.T4	Gorilla	29	9.66	1.657	0.308	9.03	10.29	7	14
	Chimpanzee	30	8.73	1.070	0.195	8.33	9.13	7	11
	Papio	28	6.43	0.744	0.141	6.14	6.71	5	8
	Human (contemporary)	28	10.59	1.356	0.256	10.06	11.12	8	14
	Total	115	8.85	1.972	0.184	8.49	9.22	5	14
SAFW_L.T4	Gorilla	29	9.31	1.379	0.256	8.79	9.83	7	13
	Chimpanzee	30	8.85	1.191	0.218	8.40	9.29	6	11
	Papio	28	6.28	0.740	0.140	6.00	6.57	5	8
	Human (contemporary)	28	9.85	1.350	0.255	9.33	10.38	7	13
	Total	115	8.58	1.799	0.168	8.25	8.92	5	13
SAFO_R.T4	Gorilla	29	76.10	6.195	1.150	73.74	78.45	63	87
	Chimpanzee	30	70.49	3.807	0.695	69.07	71.92	62	79
	Papio	28	54.39	3.946	0.746	52.86	55.92	43	63
	Human (contemporary)	28	69.79	3.785	0.715	68.32	71.26	63	78
	Total	115	67.81	9.208	0.859	66.11	69.51	43	87
SAFO_L.T4	Gorilla	29	75.90	5.541	1.029	73.79	78.01	66	89
	Chimpanzee	30	70.66	3.991	0.729	69.17	72.15	63	81
	Papio	28	56.21	4.205	0.795	54.57	57.84	46	64
	Human (contemporary)	28	73.38	3.390	0.641	72.06	74.69	65	80
	Total	115	69.12	8.731	0.814	67.51	70.74	46	89
SPA_T5	Gorilla	29	133.60	9.387	1.743	130.03	137.17	116	151
	Chimpanzee	30	141.91	7.252	1.324	139.21	144.62	129	158
	Papio	28	150.15	4.784	0.904	148.29	152.00	142	161

	Human (contemporary)	28	125.15	9.903	1.871	121.31	128.99	108	145
	Total	115	137.74	12.223	1.140	135.48	140.00	108	161
SPL_T5	Gorilla	29	30.03	4.443	0.825	28.34	31.72	22	38
	Chimpanzee	30	30.33	2.702	0.493	29.32	31.34	23	35
	Papio	28	26.43	5.421	1.024	24.33	28.53	6	41
	Human (contemporary)	28	27.80	4.656	0.880	25.99	29.60	21	36
	Total	115	28.69	4.627	0.432	27.83	29.54	6	41
IAFW_R.T5	Gorilla	29	8.76	1.179	0.219	8.31	9.21	7	13
	Chimpanzee	30	8.35	0.707	0.129	8.09	8.61	7	10
	Papio	28	6.46	0.857	0.162	6.13	6.79	5	9
	Human (contemporary)	28	9.02	1.080	0.204	8.60	9.44	7	11
	Total	115	8.16	1.383	0.129	7.90	8.41	5	13
IAFW_L.T5	Gorilla	29	8.82	1.193	0.221	8.37	9.28	6	12
	Chimpanzee	30	8.35	0.742	0.135	8.07	8.62	7	10
	Papio	28	6.38	0.687	0.130	6.11	6.64	5	8
	Human (contemporary)	28	8.91	0.930	0.176	8.55	9.27	7	11
	Total	115	8.12	1.359	0.127	7.87	8.37	5	12
IAFO_R.T5	Gorilla	29	75.07	3.975	0.738	73.56	76.58	66	82
	Chimpanzee	30	71.40	4.796	0.876	69.61	73.19	64	81
	Papio	28	61.01	4.117	0.778	59.42	62.61	53	70
	Human (contemporary)	28	73.45	4.668	0.882	71.64	75.26	60	83
	Total	115	70.30	6.973	0.650	69.01	71.58	53	83
IAFO_L.T5	Gorilla	29	73.56	7.697	1.429	70.63	76.48	61	97
	Chimpanzee	30	69.55	4.975	0.908	67.69	71.40	59	81
	Papio	28	61.68	3.883	0.734	60.17	63.19	53	70
	Human (contemporary)	28	74.56	5.061	0.956	72.60	76.53	62	84

	Total	115	69.86	7.474	0.697	68.48	71.24	53	97
SAFW_R.T5	Gorilla	29	9.34	1.141	0.212	8.91	9.77	7	12
	Chimpanzee	30	8.80	0.840	0.153	8.48	9.11	7	10
	Papio	28	6.53	0.819	0.155	6.21	6.85	5	9
	Human (contemporary)	28	10.08	1.218	0.230	9.60	10.55	8	13
	Total	115	8.69	1.654	0.154	8.39	9.00	5	13
SAFW_L.T5	Gorilla	29	9.23	1.282	0.238	8.75	9.72	7	12
	Chimpanzee	30	8.60	1.068	0.195	8.20	9.00	7	11
	Papio	28	6.31	0.739	0.140	6.03	6.60	5	8
	Human (contemporary)	28	9.51	1.104	0.209	9.08	9.94	8	12
	Total	115	8.42	1.634	0.152	8.12	8.73	5	12
SAFO_R.T5	Gorilla	29	72.67	5.886	1.093	70.43	74.91	62	85
	Chimpanzee	30	69.67	5.502	1.004	67.61	71.72	61	84
	Papio	28	56.85	3.818	0.722	55.37	58.33	48	64
	Human (contemporary)	28	70.71	5.218	0.986	68.69	72.73	59	79
	Total	115	67.56	8.034	0.749	66.07	69.04	48	85
SAFO_L.T5	Gorilla	29	72.28	6.728	1.249	69.72	74.84	53	82
	Chimpanzee	30	69.74	4.831	0.882	67.94	71.55	59	80
	Papio	28	60.87	4.311	0.815	59.20	62.54	53	70
	Human (contemporary)	28	74.90	3.275	0.619	73.63	76.17	69	80
	Total	115	69.48	7.172	0.669	68.15	70.80	53	82
SPA_T6	Gorilla	29	133.54	8.836	1.641	130.18	136.90	116	155
	Chimpanzee	30	141.01	6.397	1.168	138.62	143.40	129	154
	Papio	28	152.20	5.063	0.957	150.23	154.16	140	160
	Human (contemporary)	28	121.21	8.966	1.694	117.73	124.68	103	139
	Total	115	137.03	13.416	1.251	134.55	139.51	103	160

SPL_T6	Gorilla	29	28.82	3.652	0.678	27.43	30.21	21	35
	Chimpanzee	30	30.59	3.117	0.569	29.42	31.75	23	35
	Papio	28	26.93	3.941	0.745	25.41	28.46	22	42
	Human (contemporary)	28	28.60	4.311	0.815	26.93	30.28	19	35
	Total	115	28.77	3.941	0.368	28.04	29.50	19	42
IAFW_R.T6	Gorilla	29	8.54	1.259	0.234	8.06	9.02	6	12
	Chimpanzee	30	8.46	0.950	0.174	8.10	8.81	6	11
	Papio	28	6.62	0.848	0.160	6.30	6.95	5	8
	Human (contemporary)	28	8.98	0.880	0.166	8.64	9.32	7	11
	Total	115	8.16	1.333	0.124	7.91	8.41	5	12
IAFW_L.T6	Gorilla	29	8.65	1.232	0.229	8.18	9.12	7	12
	Chimpanzee	30	8.41	0.992	0.181	8.04	8.78	6	11
	Papio	28	6.43	0.924	0.175	6.07	6.78	5	8
	Human (contemporary)	28	9.14	0.909	0.172	8.79	9.49	8	11
	Total	115	8.16	1.440	0.134	7.90	8.43	5	12
IAFO_R.T6	Gorilla	29	74.45	5.125	0.952	72.50	76.40	64	87
	Chimpanzee	30	71.36	5.259	0.960	69.40	73.33	60	80
	Papio	28	62.66	3.841	0.726	61.17	64.14	55	71
	Human (contemporary)	28	76.17	5.024	0.950	74.22	78.11	63	87
	Total	115	71.19	7.046	0.657	69.89	72.49	55	87
IAFO_L.T6	Gorilla	29	71.19	5.874	1.091	68.95	73.42	59	81
	Chimpanzee	30	69.19	4.312	0.787	67.58	70.80	60	77
	Papio	28	60.97	5.165	0.976	58.97	62.97	49	69
	Human (contemporary)	28	75.50	4.255	0.804	73.85	77.15	66	84
	Total	115	69.23	7.154	0.667	67.91	70.55	49	84
SAFW_R.T6	Gorilla	29	8.87	1.177	0.219	8.42	9.32	7	13

	Chimpanzee	30	8.64	1.098	0.200	8.23	9.05	7	10
	Papio	28	6.64	0.889	0.168	6.30	6.99	5	9
	Human (contemporary)	28	9.39	1.279	0.242	8.89	9.89	7	12
	Total	115	8.40	1.514	0.141	8.12	8.68	5	13
SAFW_L.T6	Gorilla	29	8.79	1.075	0.200	8.38	9.20	7	11
	Chimpanzee	30	8.54	0.965	0.176	8.18	8.91	7	11
	Papio	28	6.40	0.848	0.160	6.08	6.73	5	9
	Human (contemporary)	28	9.28	1.104	0.209	8.85	9.70	8	11
	Total	115	8.26	1.473	0.137	7.99	8.54	5	11
SAFO_R.T6	Gorilla	29	72.18	5.537	1.028	70.08	74.29	61	82
	Chimpanzee	30	69.57	4.859	0.887	67.76	71.39	60	78
	Papio	28	59.21	3.789	0.716	57.74	60.67	53	66
	Human (contemporary)	28	70.28	5.155	0.974	68.28	72.28	55	78
	Total	115	67.88	6.971	0.650	66.59	69.17	53	82
SAFO_L.T6	Gorilla	29	70.87	6.263	1.163	68.49	73.25	54	82
	Chimpanzee	30	71.04	5.472	0.999	69.00	73.08	57	83
	Papio	28	61.75	3.658	0.691	60.33	63.17	55	71
	Human (contemporary)	28	74.35	3.447	0.651	73.02	75.69	66	81
	Total	115	69.54	6.698	0.625	68.31	70.78	54	83

Appendix 8: Comparison of mean morphometric measurements (per species) between group mean and SPD group.

Measurement	Species	T1		T2		T3		T4		T5		T6	
		Mean of species	Mean of SPD specimens	Mean of species	Mean of SPD specimens	Mean of species	Mean of SPD specimens	Mean of species	Mean of SPD specimens	Mean of species	Mean of SPD specimens	Mean of species	Mean of SPD specimens
SPA*	Gorilla	160.73	165.39	156.76	156.89	150.27	149.16	139.61	138.63	136.01	133.66	133.76	133.6
	Chimpanzee	148.24	159.43	149.45	147.53	147.92	144.98	144.38	145.82	142.47	141.43	141.04	140.52
	Papio	158.19	160.67	154.63	157.44	154.78	158.39	153.89	152.23	150.42	145.54	151.32	152.38
	Human (contemporary)	142.03	143.03	139.45	139.81	136.43	137.59	130.07	134.97	125.50	123.93	121.71	124.59
SPL**	Gorilla	55.87	68.44	47.38	44.8	42.43	42.38	39.03	38.92	36.57	35.77	34.37	36.71
	Chimpanzee	33.21	39.02	31.25	31.8	30.32	31.27	30.88	30.73	31.56	32.34	31.70	31.02
	Papio	27.85	33.22	29.01	27.06	28.15	25.62	27.02	31.61	28.74	27.64	29.26	27.99
	Human (contemporary)	31.82	31.84	30.86	31.12	29.21	29.31	28.83	30.23	29.41	29.33	30.16	31.79
IAFW_R**	Gorilla	12.64	14.35	10.55	10.84	10.33	10.64	10.16	10.03	9.68	9.95	9.20	9.54
	Chimpanzee	10.27	11.73	8.83	8.68	8.77	9.1	8.56	8.5	8.48	8.64	8.53	8.51
	Papio	7.65	8.76	6.88	6.37	6.52	5.33	6.75	7.29	6.84	6.5	7.01	6.76
	Human (contemporary)	11.69	11.59	10.71	10.8	10.64	10.88	10.20	10.46	9.64	10.07	9.52	9.22
IAFW_L**	Gorilla	12.72	13.79	10.52	10.69	10.56	10.58	9.98	9.73	9.53	9.83	9.31	9.7
	Chimpanzee	10.14	11.12	8.89	8.9	8.86	9.07	8.48	8.42	8.48	8.77	8.54	8.58
	Papio	7.74	8.92	6.91	6.05	6.64	5.39	6.71	7.25	6.72	6.7	6.91	6.89
	Human (contemporary)	11.93	12.36	10.46	10.45	10.01	10.11	9.81	9.6	9.30	9.58	9.51	9.44
IAFO_R*	Gorilla	89.63	89.89	82.20	85.1	79.75	77.95	77.67	77.12	75.73	75.79	75.66	75.73

	Chimpanzee	70.47	73.33	70.96	70.6	72.16	73.39	71.91	71.95	71.54	70.85	71.77	71.69
	Papio	41.89	39.97	52.66	54.61	55.98	52.89	58.98	62.1	61.11	59.82	61.93	61.73
	Human (contemporary)	69.02	71.53	72.93	74.85	74.81	75.64	74.03	74.64	73.81	73.04	74.93	75.75
IAFO_L*	Gorilla	85.75	87.39	82.32	84.34	78.66	77.65	76.12	74.49	73.64	73.59	71.60	70.15
	Chimpanzee	67.56	71.5	70.10	68.68	70.75	71.43	69.60	70.61	70.10	68.76	69.46	69.08
	Papio	43.01	41.05	52.25	54.21	55.70	53.89	57.93	57.45	60.83	59.74	61.07	59.81
	Human (contemporary)	66.81	68.65	71.43	72.3	71.69	72.06	73.62	73.52	73.87	72.93	74.67	76.46
SAFW_R**	Gorilla	16.27	18.13	13.28	13.66	11.15	11.16	10.81	10.69	10.47	10.69	9.83	10.44
	Chimpanzee	11.20	12.27	10.46	10.15	9.17	9.66	8.83	8,74	8.97	9.2	8.80	8.58
	Papio	8.19	9.84	7.66	6.66	6.92	5.81	6.82	7.69	6.90	6.47	6.98	6.72
	Human (contemporary)	14.48	16.19	12.35	12.27	11.10	11.12	11.15	11.24	10.68	10.87	9.97	9.56
SAFW_L**	Gorilla	16.48	18.83	12.98	12.92	11.19	11.48	10.74	10.54	10.29	10.52	9.71	10.13
	Chimpanzee	11.00	11.39	10.24	10.01	9.19	9.64	9.03	8.93	8.68	8.98	8.67	8.57
	Papio	8.03	9.52	7.30	6.26	6.84	5.77	6.61	7.17	6.60	6.69	6.67	6.45
	Human (contemporary)	14.56	15.44	11.95	11.93	10.61	10.56	10.38	10.38	10.02	10.08	9.57	9.5
SAFO_R*	Gorilla	105.73	103.1	88.07	93.14	79.03	76.27	76.83	75	74.15	72.46	72.98	71.84
	Chimpanzee	85.58	90.5	68.44	66.07	68.63	69.6	70.31	70.94	70.16	69.65	70.03	70.06
	Papio	92.08	91.63	44.06	46.67	50.00	53.36	53.21	51.38	56.95	56.45	58.82	59.11
	Human (contemporary)	77.64	78.77	68.04	69.09	68.91	69.59	69.93	70.63	70.04	69.49	69.66	70.94
SAFO_L*	Gorilla	111.06	106.02	84.97	89	79.28	78.36	76.14	75.12	74.33	73.16	72.25	71.33
	Chimpanzee	88.27	94.73	68.91	65.96	68.94	69.64	70.80	70.21	70.16	70.38	71.39	71.13

	Papio	93.17	90.46	47.71	48.62	52.73	53.9	55.79	55.18	60.48	60.23	61.71	60.32
	Human (contemporary)	78.03	76.49	69.92	71.17	71.99	72.44	72.82	73.99	74.21	72.63	73.79	73.56

*SPA, IAFO, SAFO measured in degrees
**SPL, IAFW, SAFW measured in mm

Appendix 9: Cross tabulation of LSA and contemporary humans mean values of morphologic measurements.

(SPA, IAFO, SAFO measured in degrees; SPL, IAFW, SAFW measured in mm)

Measurement	Human sample	N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Minimum	Maximum
						Lower Bound	Upper Bound		
SPA_T1	Human (contemporary)	58	142.03	8.290	1.089	139.85	144.21	119	156
	Human (Late stone age)	6	139.85	6.020	2.458	133.53	146.17	131	146
SPL_T1	Human (contemporary)	58	31.82	3.521	0.462	30.89	32.74	25	42
	Human (Late stone age)	6	27.91	2.120	0.865	25.68	30.13	25	31
IAFW_R.T1	Human (contemporary)	58	11.69	1.562	0.205	11.28	12.10	9	15
	Human (Late stone age)	6	10.50	1.251	0.511	9.19	11.81	9	13
IAFW_L.T1	Human (contemporary)	58	11.93	1.674	0.220	11.49	12.37	8	15
	Human (Late stone age)	6	9.81	1.290	0.527	8.46	11.17	8	12
IAFO_R.T1	Human (contemporary)	58	69.02	6.182	0.812	67.39	70.64	56	82
	Human (Late stone age)	6	67.18	8.225	3.358	58.55	75.81	51	74
IAFO_L.T1	Human (contemporary)	58	66.81	4.985	0.655	65.50	68.12	57	78
	Human (Late stone age)	6	65.75	10.272	4.194	54.97	76.53	48	77
SAFW_R.T1	Human (contemporary)	58	14.48	2.093	0.275	13.93	15.03	10	19

	Human (Late stone age)	6	12.76	2.621	1.070	10.00	15.51	9	17
SAFW_L.T1	Human (contemporary)	58	14.56	2.353	0.309	13.94	15.18	9	20
	Human (Late stone age)	6	12.74	2.781	1.135	9.83	15.66	9	17
SAFO_R.T1	Human (contemporary)	58	77.64	9.925	1.303	75.03	80.25	57	98
	Human (Late stone age)	6	76.31	6.920	2.825	69.05	83.57	67	85
SAFO_L.T1	Human (contemporary)	58	78.03	8.266	1.085	75.85	80.20	60	95
	Human (Later stone age)	6	72.02	9.233	3.769	62.33	81.71	61	85
SPA_T2	Human (contemporary)	58	139.45	8.722	1.145	137.15	141.74	111	155
	Human (Later stone age)	6	144.29	7.125	2.909	136.81	151.77	131	153
SPL_T2	Human (contemporary)	58	30.86	3.782	0.497	29.86	31.85	20	39
	Human (Later stone age)	6	26.70	1.043	0.426	25.60	27.79	26	29
IAFW_R.T2	Human (contemporary)	58	10.71	1.270	0.167	10.38	11.05	8	14
	Human (Later stone age)	6	10.27	0.864	0.353	9.36	11.17	10	12
IAFW_L.T2	Human (contemporary)	58	10.46	1.536	0.202	10.06	10.86	7	15
	Human (Later stone age)	6	9.72	1.260	0.515	8.39	11.04	8	12
IAFO_R.T2	Human (contemporary)	58	72.93	5.430	0.713	71.50	74.36	59	87

	Human (Later stone age)	6	73.02	6.630	2.707	66.06	79.98	64	81
IAFO_L.T2	Human (contemporary)	58	71.43	4.489	0.589	70.25	72.61	58	80
	Human (Later stone age)	6	74.74	5.537	2.261	68.92	80.55	69	83
SAFW_R.T2	Human (contemporary)	58	12.35	1.751	0.230	11.89	12.82	8	16
	Human (Later stone age)	6	11.20	1.337	0.546	9.80	12.61	10	14
SAFW_L.T2	Human (contemporary)	58	11.95	1.728	0.227	11.49	12.40	9	16
	Human (Later stone age)	6	11.12	1.296	0.529	9.76	12.48	10	14
SAFO_R.T2	Human (contemporary)	58	68.04	6.437	0.845	66.35	69.73	51	87
	Human (Later stone age)	6	67.66	2.004	0.818	65.56	69.76	65	71
SAFO_L.T2	Human (contemporary)	58	69.92	4.872	0.640	68.64	71.21	58	83
	Human (Later stone age)	6	65.01	4.536	1.852	60.25	69.77	60	73
SPA_T3	Human (contemporary)	58	136.43	8.928	1.172	134.08	138.77	114	156
	Human (Later stone age)	4	136.57	12.560	6.280	116.58	156.56	120	149
SPL_T3	Human (contemporary)	58	29.21	3.676	0.483	28.24	30.17	22	37
	Human (Later stone age)	4	24.88	2.039	1.019	21.64	28.13	23	27
IAFW_R.T3	Human (contemporary)	58	10.64	1.552	0.204	10.23	11.05	8	16

	Human (Later stone age)	4	9.03	0.522	0.261	8.19	9.86	9	10
IAFW_L.T3	Human (contemporary)	58	10.01	1.300	0.171	9.67	10.36	7	13
	Human (Later stone age)	4	6.46	4.331	2.166	-0.43	13.36	0	9
IAFO_R.T3	Human (contemporary)	57	74.81	4.908	0.650	73.51	76.11	64	86
	Human (Later stone age)	4	70.91	2.847	1.423	66.38	75.44	68	75
IAFO_L.T3	Human (contemporary)	57	71.69	4.206	0.557	70.58	72.81	62	83
	Human (Later stone age)	4	71.28	6.826	3.413	60.42	82.14	63	80
SAFW_R.T3	Human (contemporary)	57	11.10	1.392	0.184	10.73	11.47	8	14
	Human (Later stone age)	4	9.19	0.689	0.345	8.09	10.28	8	10
SAFW_L.T3	Human (contemporary)	57	10.61	1.469	0.195	10.22	10.99	8	14
	Human (Later stone age)	4	8.57	1.295	0.648	6.51	10.63	7	10
SAFO_R.T3	Human (contemporary)	57	68.91	5.219	0.691	67.52	70.29	54	79
	Human (Later stone age)	4	68.73	3.319	1.660	63.45	74.01	65	73
SAFO_L.T3	Human (contemporary)	57	71.99	4.783	0.634	70.72	73.26	60	81
	Human (Later stone age)	4	72.40	3.180	1.590	67.33	77.46	70	77
SPA_T4	Human (contemporary)	58	130.07	8.833	1.160	127.75	132.40	112	149

	Human (Later stone age)	3	127.59	8.942	5.163	105.38	149.80	117	133
SPL_T4	Human (contemporary)	58	28.83	3.543	0.465	27.90	29.76	21	38
	Human (Later stone age)	3	24.19	3.481	2.010	15.54	32.83	20	27
IAFW_R.T4	Human (contemporary)	58	10.20	1.513	0.199	9.80	10.59	7	14
	Human (Later stone age)	3	8.11	0.347	0.200	7.25	8.97	8	9
IAFW_L.T4	Human (contemporary)	58	9.81	1.287	0.169	9.47	10.15	7	13
	Human (Later stone age)	3	8.78	0.368	0.213	7.86	9.69	8	9
IAFO_R.T4	Human (contemporary)	58	74.03	4.402	0.578	72.88	75.19	64	83
	Human (Later stone age)	3	69.80	1.108	0.639	67.05	72.55	69	71
IAFO_L.T4	Human (contemporary)	58	73.62	4.506	0.592	72.44	74.81	60	82
	Human (Later stone age)	3	76.25	5.406	3.121	62.82	89.68	72	82
SAFW_R.T4	Human (contemporary)	57	11.15	1.538	0.204	10.74	11.56	8	15
	Human (Later stone age)	3	8.99	0.807	0.466	6.99	11.00	8	10
SAFW_L.T4	Human (contemporary)	57	10.38	1.550	0.205	9.97	10.79	7	14
	Human (Later stone age)	3	9.08	0.483	0.279	7.88	10.28	9	9
SAFO_R.T4	Human (contemporary)	57	69.93	5.064	0.671	68.58	71.27	58	81

	Human (Later stone age)	3	63.95	8.808	5.085	42.07	85.83	57	74
SAFO_L.T4	Human (contemporary)	57	72.82	3.436	0.455	71.91	73.73	65	80
	Human (Later stone age)	3	69.77	2.891	1.669	62.58	76.95	67	73
SPA_T5	Human (contemporary)	58	125.50	8.302	1.090	123.32	127.68	108	145
	Human (Later stone age)	2	115.62	6.046	4.275	61.30	169.93	111	120
SPL_T5	Human (contemporary)	58	29.41	4.586	0.602	28.20	30.62	21	39
	Human (Later stone age)	2	23.23	6.530	4.618	-35.44	81.91	19	28
IAFW_R.T5	Human (contemporary)	58	9.64	1.468	0.193	9.25	10.02	6	13
	Human (Later stone age)	2	8.51	0.506	0.358	3.96	13.06	8	9
IAFW_L.T5	Human (contemporary)	58	9.30	1.309	0.172	8.96	9.65	6	13
	Human (Later stone age)	2	8.17	0.465	0.329	3.99	12.34	8	8
IAFO_R.T5	Human (contemporary)	58	73.81	4.921	0.646	72.51	75.10	60	89
	Human (Later stone age)	2	74.01	6.654	4.705	14.22	133.79	69	79
IAFO_L.T5	Human (contemporary)	58	73.87	4.806	0.631	72.61	75.13	62	87
	Human (Later stone age)	2	80.93	3.825	2.705	46.55	115.30	78	84
SAFW_R.T5	Human (contemporary)	58	10.68	1.520	0.200	10.28	11.08	8	15

	Human (Later stone age)	2	8.69	0.850	0.601	1.06	16.33	8	9
SAFW_L.T5	Human (contemporary)	58	10.02	1.326	0.174	9.67	10.37	8	13
	Human (Later stone age)	2	8.66	0.117	0.083	7.61	9.71	9	9
SAFO_R.T5	Human (contemporary)	58	70.04	5.145	0.676	68.68	71.39	59	81
	Human (Later stone age)	2	60.60	4.533	3.205	19.87	101.32	57	64
SAFO_L.T5	Human (contemporary)	58	74.21	3.672	0.482	73.25	75.18	60	80
	Human (Later stone age)	2	70.34	2.213	1.565	50.45	90.22	69	72
SPA_T6	Human (contemporary)	58	121.71	7.769	1.020	119.67	123.76	103	139
	Human (Later stone age)	2	117.32	3.281	2.320	87.84	146.80	115	120
SPL_T6	Human (contemporary)	58	30.16	4.258	0.559	29.04	31.28	19	40
	Human (Later stone age)	2	27.97	0.506	0.358	23.43	32.51	28	28
IAFW_R.T6	Human (contemporary)	58	9.52	1.280	0.168	9.18	9.86	7	13
	Human (Later stone age)	2	9.35	0.672	0.475	3.32	15.39	9	10
IAFW_L.T6	Human (contemporary)	58	9.51	1.077	0.141	9.22	9.79	8	12
	Human (Later stone age)	2	9.06	0.595	0.421	3.71	14.41	9	9
IAFO_R.T6	Human (contemporary)	58	74.93	5.006	0.657	73.62	76.25	63	87

	Human (Later stone age)	2	71.49	3.366	2.380	41.25	101.73	69	74
IAFO_L.T6	Human (contemporary)	58	74.67	4.029	0.529	73.61	75.73	65	86
	Human (Later stone age)	2	71.18	7.502	5.305	3.77	138.58	66	76
SAFW_R.T6	Human (contemporary)	58	9.97	1.648	0.216	9.53	10.40	6	13
	Human (Later stone age)	2	9.53	0.440	0.311	5.57	13.48	9	10
SAFW_L.T6	Human (contemporary)	58	9.57	1.176	0.154	9.26	9.88	6	12
	Human (Later stone age)	2	8.59	0.395	0.279	5.04	12.14	8	9
SAFO_R.T6	Human (contemporary)	58	69.66	5.408	0.710	68.24	71.08	52	82
	Human (Later stone age)	2	65.99	1.633	1.155	51.31	80.66	65	67
SAFO_L.T6	Human (contemporary)	58	73.79	4.072	0.535	72.72	74.86	63	84
	Human (Later stone age)	2	80.45	3.323	2.350	50.59	110.31	78	83