THE VERTEBRAL COLUMN IN HUMANS AND SELECTED NON-HUMAN PRIMATES AND THE FUNCTIONAL STRUCTURE OF ITS TRANSITIONAL ELEMENTS.

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Thesis presented for the degree of Doctor of Philosophy at
The University of Cape Town.
February 4, 2000.

DECLARATION:

I declare that this thesis is my own, unaided work. It is being submitted for the degree of Doctor of Philosophy, to the University of Cape Town. It has not been submitted before for any degree or examination at any other University.

Signed by candidate

Signature removed

4th this day of February 2000

DEDICATION:

To my wife Agnes Mary Namazzi Naalongo and my children who remained in Uganda; for their understanding to cope without me for almost four years, while I was in South Africa pursuing this work, and for their unwavering support.

ABSTRACT

This study applies morphometric analyses to the thoracic vertebral column of primates. Vertebral counts are conducted and vertebral patterns examined. The sample for morphometric measurements consists of 112 humans, 27 gorillas, 22 chimpanzees, 8 orang-utans, 68 vervets and 77 baboons but for the counts the numbers are much higher. The six species exhibit orthograde (human), semi-orthograde (chimpanzee and gorilla), pronograde (baboon and vervet) and suspensory (orang-utan) patterns of locomotion. Measurements of vertebral components are taken on the 7th to 21st vertebrae (C7-L2 in humans). Various ratios are calculated and standardised by the species body weight. The Spearman Rank Correlation Test and the Chi-square Test indicate no sexual dimorphism in respectively morphometric and counts data, and therefore both sexes are pooled.

The positions of the longest spine and of the greatest spinous leverage do not always coincide. In humans and chimpanzees the greatest leverage is in the lumbar region (V21), and on the longest spinous process is at V13. The placement of the greatest leverage on V21 is necessary in the region to maintain lordosis in humans and to some extent in chimpanzees. The strain caused by the high leverage at V21 in humans might contribute to the causes of the lower back pain, common in humans. The highest spinous process leverage and the longest spinous process of pronogrades are in the midthorax where they help to resist lateral bending and thus stabilise the trunk in the midline, important in quadrupedal locomotion. When only the upper vertebral regions are considered, in the gorilla and orang-utan, the highest spinous leverage the longest spinous process coincide at V7, or at V8. This leverage helps in the support the relatively heavy heads.

The leverages of the transverse processes are important for all primate locomotion. The lateral flexion leverage (Lattran ratio) helps to stabilise the back in the mid-sagittal plane, and is higher in orthograde and semi-orthograde

primates than in pronogrades. Extending the back is necessary in primate postures but more so in orthograde and pronograde primates. Therefore the ventrodorsal extension leverage (Vdtran ratio) of the transverse process is relatively high in monkeys and humans. The orang-utan has the lowest Lattran and Vdtran ratios, probably because the slow suspensory activity of this species which factor puts less demand on flexion and extension of the vertebral column.

The number and size of thoracic facet (zygapophyseal) angles are also adapted to locomotion. In the orang-utan, gorilla, chimpanzee, human, baboon and vervet, there are respectively 2, 3, 4, 5, 9, and 12 pairs of thoracic facet angles that are above 110 degrees. It is suggested that range of movements in the vertebral column and trunk depend on the *number* of facet angles that are wider than 110 degrees.

The transitional vertebrae are specialised by having larger facet areas, larger pedicle areas and larger pedicle ratios than other pedicles in the thoracic region. Pedicles and facets at the cervicothoracic (C-T) transition in the study are relatively more developed, having larger areas than those at the thoracolumbar (T-L) transition. It is not clear why these differences exist, since the weight of the individual and the attachments of the psoas muscles act on the T-L transition, causing considerable stress on it. On the other hand the developments of the bony parts at the C-T transition might be influenced by support they give to the heavy heads and by the highly developed limb muscles for brachiating, in the apes.

The position of the T-L transition in relation to the total number of the pre-sacral vertebrae differs with posture and locomotion.

The pattern of the relation between the position of the T-L joint and the ribs is important in the stability of the trunk. This study indicates that the terrestrial pronogrades (baboons) have the most stable pattern followed by the arboreal pronogrades (vervets). The human pattern is probably not as stable.

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Acknowledgements

Many people and institutions have assisted me with ideas and facilities for a project of this nature. I would therefore like to convey my sincere appreciations to all of them. The following are specially mentioned.

The University of Cape Town for the financial support without which, I would not have embarked on this work. They are Professor B.B Rawdon, Head of Department of Anatomy and Cell Biology, University of Cape Town and Professor Beverly Kramer, Head of Department of Anatomical Sciences, University of the Witwatersrand. In addition to those two just mentioned are Dr Francis Thackery, Director Transvaal Museum, Derek R Howlett, Curator, Powell-Cotton Museum, Kent, England, Pauline Jenkins of the British Museum of Natural History and Ms Drunkrow of the South African Museum, Cape Town.

I would also like to thank Professor P.J.M Ssebuwufu, Vice-chancellor, Makerere University, Kampala, Uganda and Professor J. Epelu-Opio, Deputy Vice-chancellor, Makerere University for their wide-ranging support to me.

Makerere University as my employer is acknowledged for the financial support, whenever it was possible, and for granting me a study-leave to pursue this research.

I am also indebted the Head of Department of Human Anatomy, Makerere University, and to the Head of Department of Veterinary Anatomy, Makerere University, her staff and colleagues who have had to put up with my absence.

The technical staff at the above institutions are all appreciated.They are, Fred Ladner, Jacob and Elijah of the Department of Anatomical Sciences, University of the Witwatersrand; Chris Motumi and Mbulelo, formerly students at the University of Cape Town; Caroline Powrie, Fatima Samodien, Barbara Breytenbach, Bruce Dando and Keith Hall, all from the Department of Anatomy and cell Biology, University of Cape Town; Andrew Kiwanuka, Bill Serumaga, Ben Kisitu and Kange, Faculty of Medicine, Makerere University.

On the academic front I have benefited from very useful suggestions which helped me to visualise the project better and I would like to thank all those who have helped me in that respect. However Professor P.V. Tobias is singled out for having found time in his busy schedule to discuss this project with me 1996. His suggestions have been very valuable. I should also mention my initial correspondence, about four years ago, to the Department of Anatomy and Cell Biology, University of Cape Town, to which Professor W.J. Els replied with very good advice. Professor Epelu-Opio as my former head of department contributed professionally during the initial stages of the project proposal.

Last but not the least my heart felt gratitude goes to Professor Alan G Morris and Dr Graham J Louw, both of the Department of Anatomy and Cell Biology. Professor Alan Morris was instrumental in recommending funding; I am very grateful. Further more himself and Dr Graham Louw have been my supervisors. I am contented that they have done their best to help me.

Chapter 1

AIM AND INTRODUCTION

The general aim of this study is to identify the morphological (anatomical) adaptations of the thoracic vertebral column in different forms of primate posture or locomotion. The forms of locomotion include pronogrady (arboreal and terrestrial quadrupedalism) semi-orthogrady or semi-pronogrady (knuckle-walking and suspensory locomotion), and full-orthogrady (habitual bipedalism).

The following are the specific approaches planned so that the study achieves the above general aim.

i) Establishing the comparative morphological adaptations of the thoracic vertebral column using morphometric methods.

ii) Identifying particular morphometric features of the cervicothoracic and thoracolumbar transitional vertebrae.

iii) Identifying the relative positions of the transitional vertebrae within the pre-sacral vertebral column, in relation to the total number of pre-sacral vertebrae, in different primate species that have various postures and forms of locomotion.

The vertebral column is found in the mid-line of the dorsal aspect of the body, from which position it gives support and rigidity, as well as flexibility to the body. It protects the spinal cord and receives cumulative forces emanating from diverse activities of the individual. Such activities can be various forms of locomotion. For example, leaping, climbing, swinging, running, quadrupedal and bipedal walking, or can be a form of occupation such as standing or sitting upright (general orthogrady), lifting/carrying objects and digging up food from the ground. It is reasonable to assume that such activities influence the anatomical features of the skeleton, including the vertebral column. The skeletal morphology responds and adapts to patterns of load placed upon it by various activities (Ward, 1991). In this connection, Hayama et al., (1992) were able to induce lordosis in monkeys. A series of studies carried out by the Suo-sarumawashi Japanese Monkey Performance group, subjected pronograde monkeys to long-term training aimed at producing a stable upright posture. The pronograde posture is the quadrupedal posture that an animal adopts when walking or standing on all the four limbs. The lordosis that developed continued to exist even when the monkeys resorted to their normal pronograde posture. Keith (1923) pointed out that modern life styles might cause vertebral column disorders. Shapiro(1993b) noted that, the primate vertebral column can adapt to various postures in which the individual moves and so it is affected by the activities of the individual.

The vertebral column consists of vertebrae whose number and structure vary with the following.

(i) Their position within the individual
(ii) The individual
(iii) The population group, species and sex (Allbrook, 1955; Herman et al., 1992; Gilsanz et al., 1992, 1994).

In primate research, postural and locomotion behaviour, including bipedalism, have been extensively studied by many authors. The authors include Tuttle (1967, 1981), Walker (1969, 1979), Jenkins (1974), Fleagle (1988), Stern (1971), Fleagle et al., (1981), Oxnard (1984), Lovejoy (1975), Stern and Susman (1983), Jungers (1985a), Doran (1993), Shapiro (1995), Shapiro and Jungers (1988, 1994) to mention a few. A good understanding of the anatomy is necessary for a clear explanation of how the primate body is manipulated during movement.

The origin and development of bipedalism are of interest to anthropologists and to the public generally. Indeed an erect trunk supported by the lower limbs resulting in habitual bipedalism is a feature that clearly identifies humans from other primates.

For a long time researchers believed that bipedalism evolved hand in hand with relatively large brains, free manipulative hands, tool-making and reduced canines (Washburn, 1963). However, the discovery of australopithecines, that probably practised bipedalism about three million years ago, caused scientists to realise that human features evolved in a mosaic fashion. That means, primitive features continued to exist in particular species side by side with advanced features in the later forms (McHenry, 1975; Johanson and White, 1979; Leakey and Hey, 1979; Stern and Susman, 1983; Latimer and Lovejoy, 1990).

One way of understanding human morphology and bipedalism is through the study of comparative morphology. In order to uncover the morphological adaptations of the vertebral column, primates that practise different modes of postures and locomotion are investigated.

In studies of fossil vertebrae and other skeletal specimens, the functional requirements of locomotion and other activities can possibly be deduced by examining bony remains, i.e. by noting the markings that muscles leave on the bones. The constraints which morphology places on the range, that is the movement of one part of the body against another, can also be generally deduced from such studies. However, such deductions are usually general speculations, since they can never be observed or tested due to the fact that the individuals in question are dead and possibly, the species is extinct.

Anatomical, behavioural and experimental studies on the hind limb of primates have identified similarities between humans and other primates (Stern, 1971; Fleagle et al., 1981; Oxnard, 1984). Other studies have also identified unique structural aspects of the human lower limb related to bipedalism (Jenkins, 1972; Lovejoy, 1975; Jungers, 1985a, 1988a). Using information from such studies, inferences have been made on posture and locomotion of the last common ancestor shared by African apes and humans.

It must be understood that morphological requirements for standing and walking on two legs cannot be a preserve of the lower limb and pelvis only. Fundamentally, efficient bipedal gait and posture also depend on the ability to balance the pre-sacral vertebral column or trunk on the pelvis and lower limb. The unique aspects of the human vertebral column should be noted when we consider bipedal evolution. There is no doubt that this point has been known by researchers for a long time (Keith, 1923; Robinson, 1972; Rose, 1975; McHenry and Temerin, 1979; Tuttle, 1981; and many others). In comparison with other regions such as the limbs, there have been relatively fewer studies on the vertebral column in primates.

In order for anatomists to understand the evolutionary aspects of locomotion and bipedalism, all relevant primate anatomy should be studied. Thus more understanding of the anatomy of the vertebral column of humans and other primates in relation to the form of locomotion, is one of the major intentions of this study. The study focuses on the morphometric features of the thoracic vertebral column, in primates of different postural and locomotive behaviours. Relatively more work has been done on the lower lumbar region. Indeed this is why the lower lumbar region is not mainly part of this research (Wells 1963; Abitbol 1987a and b; Singer 1989; Ward 1991; Shapiro 1995 and many others mentioned later in this literature review). The transitional elements, i.e. the vertebrae at the cervicothoracic and thoracolumbar junctions of the spine, are part of this study because of their particular and strategic functional position.

Comparative research may also clarify those postural features that are common to all primates, but are erroneously attributed to humans. Unlike the main characteristics of the lower limb, the basic postural features of the back do not easily distinguish humans from other primates. For example, while humans are the only primates that fully extend the knee and hip joints during bipedalism, they are not the only primates whose backs are habitually held almost perpendicular to the ground. Hence, they are not the only ones whose posture can be classified as orthograde. The orthograde position is one in which an animal or its trunk is in the upright posture, usually vertical to the ground. Many primate species can stand or sit in this posture but they cannot sustain standing or walking in the upright posture for a long time or over a long distance. Such animals can only achieve a general upright posture that can be referred to as semi-orthogrady, (general orthogrady or postural bipedalism), (Shapiro, 1991a). The existence of such primates complicates the comparative study of aspects of the vertebral column related to full orthogrady (habitual bipedalism). On the other hand, the existence of semi-orthograde primates may enable researchers to make comparisons between the transitional forms of orthogrady and the fully orthograde forms (humans).

There has been a tendency by paleoanthropologists to overlook the difference between general orthogrady (postural bipedalism) and bipedalism, as far as the structure of the vertebral column is concerned. This has resulted in viewing all aspects of the human vertebral column as specifically designed for bipedal locomotion. Clearly, it is not only in humans among the primates, that the vertebral column can be positioned in the upright posture. Possibly some of the features of the human vertebral column may also be linked with the postural bipedalism of other primates, rather than with only the human form of bipedalism (Shapiro, 1991a).

Some researchers tend to regard humans and all hominoids as orthogrades. This on the one hand has been good because it has brought out those features commonly shared by humans and hominoids on one side, versus features of the non-hominoids on the other side. For instance, a short lumbar region and increased sacral areas for back muscle attachment, due to loss of the tail and tail musculature, are now accepted as human and hominoid features according to Slijper, (1946) and Benton, (1967). However *Proconsul,* a primitive pronograde hominoid lacked a tail, pointing to the fact that taillessness is not solely a consequence of upright posture and upright locomotion (Ward, et al., 1991). Considering all hominoids as orthograde masks the specialisation of bipedalism. It also disregards the fact that many hominoids (the African apes) largely practise pronograde locomotion, that is quadrupedalism (Reynolds and Reynolds, 1965; Kortlandt, 1975; Susman, 1984; Tuttle and Watts, 1985; Doran, 1989). By considering the hominoids together or separately, the researchers can identify consistent vertebral features that can distinguish between the primates of different postural behaviours within one phylogenetic group. If such features are seen to persist across the groups, then possibly adaptations to general orthogrady can be separated from specific adaptations to orthogrady (Shapiro, 1991a).

A proper comparative analysis of the morphology of the primate back is also necessary to dispel the notion that all aspects of the human vertebral column are geared to bipedalism. A good comparison might help to show the differences in the anatomy of the vertebral column of primates, which use different forms of posture and locomotion (Shapiro,1991a).

In view of the above-mentioned, some attempts have been made to carry out morphometric, biomechanical and electromyographic studies of the primate vertebral column. In some of such studies, Rose (1975) observed that humans have a greater increase in the diameter of consecutive lumbar vertebral bodies. This characteristic was attributed to compression forces through the vertebral column due to the upright posture. Increasing diameter of the vertebral bodies is now regarded as a functional feature of the human vertebral column.

Humans and lesser apes have five or more lumbar vertebrae and as such, they exhibit the primitive lumbar morphology of an ancestor with an upright trunk. The great apes have secondarily evolved adaptations that support terrestrial pronogrady by having a reduced lumbar region of three to four vertebrae and osteologic locking mechanisms (epizygal contacts). It should be noted however that the orang-utan is rarely, if ever, a terrestrial pronograde, yet has a reduced lumbar region, as in the African apes.

In order to distinguish between postural bipedalism and habitual bipedalism, the spinal musculoskeletal arrangements and their functional integration in locomotion should be well understood. A biomechanical approach is likely to expose the linkages between the morphological adaptations to general postural orthogrady, (upright posture) and the adaptations to a full orthograde posture of habitual orthogrady, as found in humans only (Shapiro, 1991a; Ward, 1991).

Electromyographic studies have been published by Shapiro and Jungers (1994; 1998). Electromyographic (EMG) studies by Shapiro (1991a) have demonstrated similarities in actions of spinal muscular contractions in chimpanzee, gibbon, baboon and orang-utan, during quadrupedalism. Shapiro (1991a) observes a similarity between the results of EMG studies of the above groups and earlier EMG studies of the human spinal musculature. The EMG pattern of the orang-utans walking upright is different from the patterns in the above primates. Similarities were observed between the recruitment patterns and functions of the back muscles in non-primate quadrupedalism, ape quadrupedalism, ape bipedalism and human bipedalism (Shapiro, 1991b). These were remarkable findings in view of the differences in postures of these species. The findings depict the complex nature of locomotion and underscore the necessity for more studies on the other aspects of the spine.

It has been suggested that if parameters such as the individual body weight and size are identical, postural differences in locomotion should be explainable by contrasting vertebral column structure (Shapiro, 1991a). However, postures of primates overlap and hence variations in primate locomotion can primarily be a matter of opinion (Napier, 1976) or of degree (Shapiro, 1991a). This is due to the fact that primates are highly adaptable and can take to different means of locomotion depending on the prevailing situation. For instance, posture and locomotion vary with feeding, foraging and habitat, and therefore comparing the postural behaviour of even co-specific primates living in different places can produce dissimilar results according to Fontaine, (1990). Defining and categorising primate locomotion has therefore been a difficult exercise. It has also been pointed out that forms of locomotion in primates have been differently defined by observers, a fact that has compounded the above problem.

In spite of the difficulties mentioned in categorising primate postural and locomotive behaviour, the fact is that many primates are specialised in their morphology in certain postures and activities. These activities may comprise only a part of their postural behaviour. The morphological specialisation can to a reasonable extent, be contrasted among primate groups, and the contrasts can be related to primate locomotion and postural behaviours.

Knowledge of primate postural behaviour is vital in the understanding of primate morphology. Positonal behaviour is defined as postural and locomotor behaviour (Prost, 1965). However, movements (dynamic actions) result in the greatest strain in bone and soft tissue rather than the static position of the species (Ward, personal communication 24th March 1999). It is within the above limitation that the postural behaviours of the primates, whose vertebral columns are investigated in this research and are summarised below. Refer to Figures 1.1 to 1.4 on primate locomotion.

(1) Cercopithecoids (Old World monkeys)

(Figures 1.1 and 1.6)

The Catarrhine infra-order consists of the Old World (Africa and Asia) primates that include the super-family of the Cercopithecoidea (Old World monkeys) and Hominoidae (all apes and humans). The Old World monkeys include the rhesus monkey (macaque), vervet monkey, *Colobus*, mandrill and baboon (*Papio*). Catarrhines have only two premolars among thirty-two teeth. Their nose has narrow and the nostrils face ventrally. There is a long bony tube that supports the eardrum on of inner side. The Old World monkey family has ischial callosities that are cornified sitting pads. Two cercopithecinae species are considered, from the subgroup cercopithecinae (the African Old World monkeys) in this study. These were selected because they have divergent ways of locomotion as explained. The species are:

(i) *Cercopithecus aethiops* (vervet monkey)

(Figure 1.1)

Vervet monkeys and many Old World monkeys are arboreal quadrupedal locomotors. All monkeys keep their vertebral columns upright when they are sitting and climbing. On the ground, they practise some bipedalism. In *C.aethiops* leaping accounts for only 10% of the locomotive activity, according to Fleagle (1988). The digits of the vervet limbs have retained the ancestral grasping ability of primates that is so essential in arborealism. During quadrupedalism the vertebral column of the vervet monkey is kept in the horizontal position.

(ii) *Papio ursinus* (Chacma baboon)

Baboons are mainly terrestrial quadrupedal monkeys. They prefer to inhabit flat open areas with few trees (Altmann and Altmann, 1970) though in some parts, such as the Western Cape Peninsula in South Africa and Eastern Uganda, they can be found on high forested ground. They are thus adaptable, and can climb trees in search of a resting-place or food (Altmann and Altmann, 1970; Rose, 1974). During

Figure 1.1

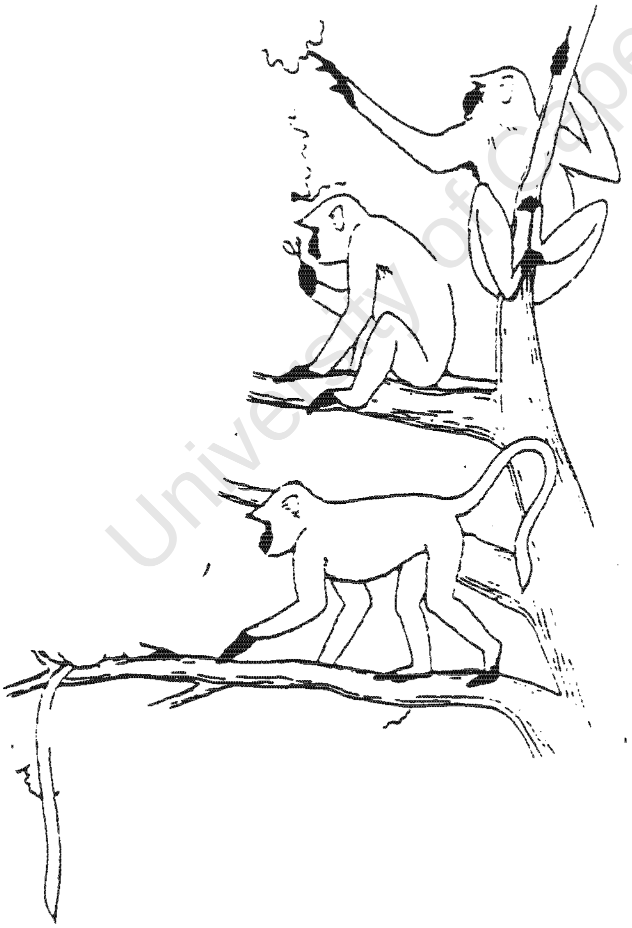
Quadrupedalism

a) Ground quadrupedalism in baboon (immediately below) and leaf monkey (bottom of page). The vertebral column is kept in the horizontal posture during locomotion. From Zihlman (1982).

Figure 1.1

Quadrupedalism

b) Arboreal quadrupedalism in leaf monkey. The vertebral column can be kept horizontal or vertical to the ground. From Zihlman (1982).



quadrupedal walking on the ground or when standing, their soles and palms are placed in a digitigrade posture (Rose, 1979a). Climbing and walking in trees remains quadrupedal, leaping being a very rare exercise. Their vertebral column is kept in the horizontal position during quadrupedal locomotion.

(2) Hominoids (Great apes) (Figures 1.3 - 1.4)

The great apes belong to the super-family Hominoidea that includes the family of gibbons (Hylobatidae), chimpanzees, gorillas and humans (Hominidae) as well as the evolutionary ancestors of all these groups. Ward and Colin Grooves agree that the great apes should be technically included in Hominidae (Ward personal communication, 24th March 1999). The hominoids are characterised by a broad chest and the absence of a tail. The gibbons possess ischial callosities just like the Old World monkeys but, like the chimpanzees and gorillas, their upper limbs are long and lower limbs are short, indicating that these primates indulge in suspending activities during locomotion. The chimpanzees and gorillas are identified from the gibbons by their greater size and the absence of the callosities. Like the humans, the apes have the Y-cusp pattern in the lower molars.

(i) *Pongo pygmaeus* (orang-utan) (Figure 1.2b)

The orang-utan is known for its slow careful movements. Swinging and brachiating are very limited, in preference to quadrupedal suspensory movements beneath branches even during feeding (Mackinnon, 1974; Tuttle, 1986). The primate displays extremely cautious quadrumanous climbing (that is climbing with all the four limbs and feet), and bridges gaps by reaching out to branches (Doran, 1989). When climbing in the upright posture, it keeps the spine upright (Cant, 1987) and exhibits widely abducted limb postures. The young usually scramble on the maternal body across gaps bridged cautiously by the mother. On the ground, the large males usually practise bipedalism (Rodman, 1979b). The males may sometimes swing and brachiate while the females tend to practise quadrumanous scrambling and quadrupedal walking

(Sugardjito, 1982). Orang-utans, as stated above, keep their spine mostly in the horizontal posture and to a less extent in the upright posture.

(ii) *Pan troglodytes* (common chimpanzee) (Figure 1.3, 1.4c)

Chimpanzees are predominantly terrestrial, quadrupedal knuckle-walkers according to Tuttle, (1986). The support of the body is placed on the bent dorsal aspects of their middle phalanges which Napier (1976) also calls knuckles and not on the palmar aspects as in other primates such as monkeys. Knuckle-walkers have long fore limbs, giving them a posture that is neither fully bipedal nor fully quadrupedal (Napier, 1976).

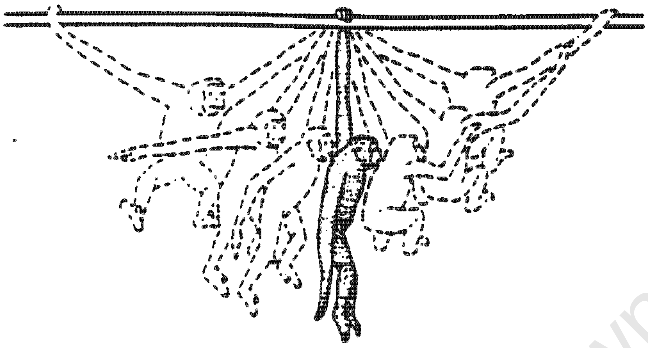
Chimpanzees, however, do climb trees in which the adults can move quadrupedally, although they sometimes suspend themselves with one arm and swing to bridge gaps (Goodall, 1986; 1995). During arboreal locomotion, females are more quadrupedal than males. Males climb and scramble more, and are more bipedal on the ground than females (Doran 1989,1993). Most arboreal movements of chimpanzees frequently involve abducted limb postures, especially of the fore `limb. In both sexes, knuckle-walking takes about 86% of all the terrestrial locomotor activity, quadrumanous climbing and scrambling 11%, arm swinging and bipedalism 1%, and leaping 1-2% (Doran, 1989). Arboreal locomotion accounts for only 16% of overall locomotive activities, as most of the time chimpanzees prefer to stay on the ground (Napier, 1976).

(iii) *Gorilla gorilla* (gorilla)

Adult gorillas are largely terrestrial, quadrupedal knuckle-walkers that keep their vertebral column (spine) in semi-erect posture. They spend 80% of their time on the ground, and frequently sleep on the ground (Tuttle and Watts, 1985). According to these authors terrestrial knuckle-walking covers 94% of the distance or area that the mountain

Figure 1.2

a) Brachiation in siamang. The vertebral column and trunk are vertical to the ground. The body pivots at a point and swings like a pendulum. From Napier and Napier (1985).



b) Suspension, swinging and brachiation in orangutan *(Pongo pygmaeus)*. The vertebral column can be kept horizontal or vertical to the ground. From Young (1962).

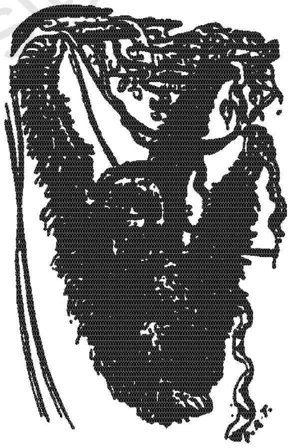


Figure 1.3

Knuckle-walking

Knuckle-walking in the chimpanzee. The vertebral column posture is between the vertical and horizotal positions. From Napier and Napier (1985).

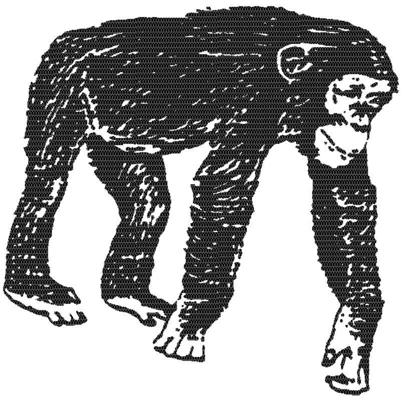


Figure 1.4

Bipedalism

a) Bipedalism in Japanese Macaque monkey. The vertebral column is nearly vertical to the ground. From Napier (1977).

Figure 1.4

b) Bipedalism in the gibbon. The vertebral column is in the upright posture during acrobatic displays. From Eimerl and De Vore (1966).

Figure 1.4

c) Bipedalism of the chimpanzee. The vertebral column is almost erect. The posture is rather crouched showing the bent-knee-bent-hip posture. From Le Gros Clark (1965).

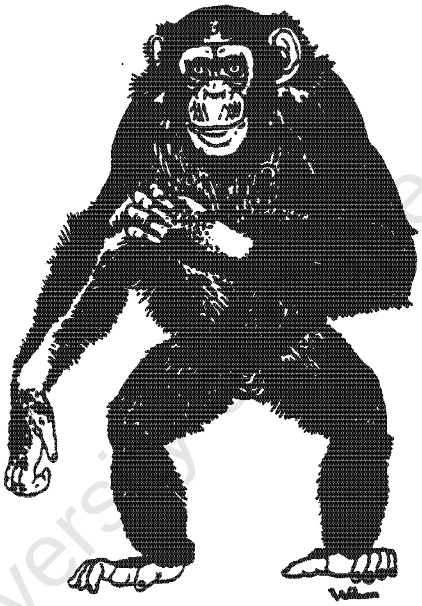


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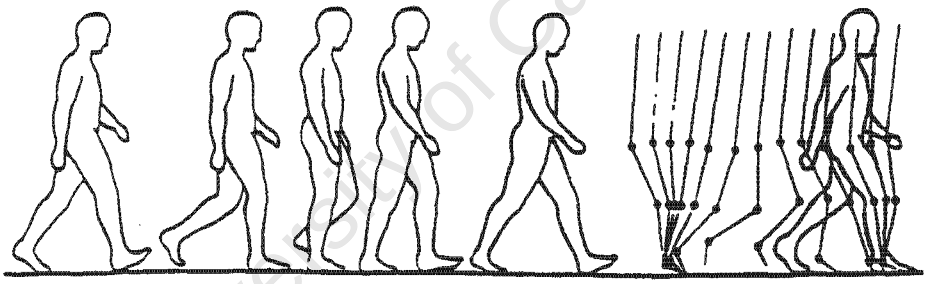
Figure 1.4

Bipedalism

d) Bipedalism in modern humans. The vetebral column is straight and vertical to the ground. The centre of gravity is through the midline of the body, swings forward and backward between the hindlimbs. The body tends to follow the centre of gravity during walking in order to maintain its balance. From Aiello and Dean (1990).



gorilla covers during its activities. Climbing, bipedalism, leaping and brachiation or bridging is rare in mountain gorillas (Tuttle and Watts, 1985). When bipedalism occurs in gorillas it is usually for aggressive displays (Tuttle, 1967). The young and nesting females climb trees (Napier, 1976), and in such a situation they are seen to be very cautious in their movements, engaging in bridging and arboreal quadrupedalism (Tuttle, 1986).

Lowland gorillas are also terrestrial knuckle-walkers. They however engage more in tree climbing but feed, nest and rest on the ground (Dixon, 1981; Fleagle, 1988).

(3) Hominids

The hominids belong to the family Hominidae that, according to the Simpsonian classification, includes modern humans and those ancestors down to where the human line diverges from the apes (Aiello and Dean, 1990). The hominids are characterised by bipedal locomotion, a large brain in relation to the body size and a reduced dentition particularly in the anterior part of the mouth (Le Gros Clark, 1964 and Pilbeam, 1972). However, the above features do not clearly identify fossil hominids. For instance in *A. afarensis*, the dentition is more similar to the Miocene apes (*Dryopithecus* and *Sivapithecus*) than to modern humans (Conroy, 1997; Conroy and Pilbeam, 1975). On the other hand, *A.aferensis* differs from the latter two, which also differ from each other in very many ways. The relative size of the brain of australopithecines was in the range of monkeys and apes (Aiello and Dean, 1990). Bipedalism as such does not distinguish modern humans from the great apes, and researchers such as Ward and Groves, include the great apes in Hominidae (Ward, through a comment, 24th March 1999). Bipedalism also defines australopithecines as hominids although their bipedalism was different from that in the modern *Homo sapiens*, and possibly was practised together with other forms of locomotion.

(i) *Homo sapiens sapiens* (humans) (Figure 1.4 d)

Humans are the only primates that sustain bipedalism during locomotion. Humans are therefore known to be habitually bipedal.

Gorillas, chimpanzees, orang-utans and monkeys engage in some degree of bipedalism, but for short periods only. Habitual bipedalism, that is sustained locomotion on two legs, has been mastered only by humans. Human walking has been described in detail under Chapter 4, in this literature because of its importance. It suffices to say here that humans can stand and walk, while keeping their spines in the upright position, for a long period. Other primates can sustain their spine and trunk in the upright posture only when sitting, climbing and swinging; when standing, the posture of such primates is described as crouched and cannot be maintained for long. However, humans and other primates share the characteristic of being able to keep their vertebral column upright, when sitting.

Humans are terrestrial bipeds. Anthropologists would like to find out why, when and how the human posture was adopted (Shapiro, 1991a). In order to answer the above questions, many studies on the evolution of bipedalism have been carried out by many researchers. Among these are Lovejoy et al., (1973), McHenry and Temerin, (1979), Rodman and McHenry, (1980), Lovejoy, (1981), Carrier, (1984), McHenry, (1986), Shapiro, (1991a) and Shreeve, (1996). Shapiro (1991a) is of the view that we must first find answers to the questions of when and how we became bipedal. Then we can investigate why we became bipedal. Shapiro (1991a) also notes that clarifying the anatomical relations of primates would help to throw more light on the evolution of the human unique locomotion. The human traits, which are primarily or solely related to bipedalism, as well as chronological anatomical changes brought about by bipedalism, can possibly be identified through the comparative anatomical studies of primates.

(ii) *Australopithecus*

The fossil vertebrae of Australopithecines are not part of this study, although observations of these bones would be interesting. They are mentioned here and in other sections of the background literature because they are important in the locomotion of early primates.

The australopithecines are ancestral hominids that lived in late Pliocene times, from roughly 5 to 2 million years ago. Although the earliest forms possessed some ape-like features, the group demonstrates a distinct evolutionary line, one branch of which gave rise to genus *Homo*. The morphological and behavioural biology of the Australopithecines is of much interest since these are regarded as the first hominids to practise human-like bipedalism. *Australopithecus africanus* lived in South Africa and perhaps East Africa 3-2½ million years ago (Robinson 1972; Leakey and Walker, 1976; Conroy, 1997).

Studies of the foot and pelvic bones of *A. africanus* have shown that this extinct species could stand erect on two legs, had a lumbar curve (Robinson, 1972), and could walk in some bipedal fashion. Its vertebrae show weight-bearing adaptations to terrestrial bipedalism, such as increasing diameters and size of the vertebral bodies from the proximal to the distal segments (Ward and Latimer, 1991). However, the lumbar vertebral column of *A. africanus* exhibits primitive features, such as relatively small cross-sectional areas of the vertebral body surfaces (McHenry, 1991). In humans, the cross-sectional areas of the lumbar vertebrae and of the pedicles are large relative to the size of the individual. The human lower lumbar pedicles are wider, relative to their height (length) and size of the individual, than those of the quadrupedal primates. Furthermore, the lumbar regions in *A. africanus* and in the Nariokotome *H.erectus* have 6 vertebrae (Walker and Leakey, 1993) as in some monkeys, while in humans and apes it has fewer, usually 5 and 3-4 respectively (Leakey and Lewin, 1992). Some humans though have six lumbar vertebrae (Allbrook, 1955; Kaufman 1974).

Unlike humans *A. africanus* has a long lumbar region, in spite of the fact that some features of its postcranial skeleton indicate a bipedal posture. The status of *A. africanus* is hence interesting as far as its vertebral column, posture and development of its bipedalism are concerned. This species has thus generated much discussion among anthropologists.

Justification of this study

This study uses morphometric methods to investigate the primate vertebral column in relation to posture and locomotion of the various primate groups mentioned earlier. Particularly, the thoracic region including the cervicothoracic and thoracolumbar transitional vertebrae are focused on by the study. The focus has been put on these areas because the lower region of the vertebral column has been covered by some other researchers, (Wells 1963; Abitbol 1987a and b; Shapiro 1995 and many others cited later in this literature).

Although this study relates to the primate vertebral column, and in particular the thoracic vertebral column, literature has also been reviewed on the other parts of the postcranial skeleton (limbs and pelvis) of living and extinct primates. This has been done for several reasons.

(a) Such parts as, for instance, the pelvis and the limbs are vital in the consideration of locomotion of any animal group.

(b) All parts of the skeleton and indeed the body are functionally synergists. Therefore, the different parts of the skeleton interact with one another and with the vertebral column during locomotion and other activities. The background literature on the bony pelvis and the some parts of the appendicular skeleton are therefore also reviewed.

(c) There has been relatively more research interest on the pelvis and the appendicular skeleton of primates and on their modification to various forms of locomotion, than on the vertebral column. A great deal of literature therefore exists on the above aspects and its omission might mean leaving out some important information about primate locomotive adaptations. Such information could be useful in understanding the findings of this study.

Chapter 2

BACKGROUND: THE FUNCTIONAL STRUCTURE OF THE PRIMATE VERTEBRAL COLUMN

Embryology

The segmental nature of the vertebral column reflects its origin from embryological segmentation of somites. The mesodermal cells of the sclerotomal area of the somite have a chondrogenic tendency. Extracellular elements of tissues surrounding the notochord also influence formation of chondrocytes from which the vertebrae are formed (Holtzer and Detwiler, 1953). The cells from the sclerotomal portion of the somite migrate from either side of the mid-line, towards the notochord. These cells begin the formation of the primordial centra of vertebrae. Soon the sclerotomal cells from each somite pair are condensed in the caudal part and at the same time become loosely packed in the cranial part. The dense caudal portion of the somite migrates caudally to fuse with the cranial portion of the adjacent somite behind. Thus a primordial centrum formed by the fusion of the caudal and cranial portions of adjacent somite, and the centrum is located between two myotomes. The centrum is finally located between two myotomes. More mesenchymal cells move dorsal and lateral to the centra to form the primordia for the neural arches and ribs respectively. In the human embryo some cells migrate from the condensed caudal portion of the somite to a more cranial position. These migratory cells differentiate into the intervertebral disc (Prader, 1947). The intervertebral disc will be described later in this chapter on page 19. Centres of ossification are formed on the centra and other parts of the vertebrae. Endochondral ossification follows in stages culminating in the bony vertebrae.

General overview

Early accounts of anatomy on primates put more emphasis on human anatomy, than on other primates. In the text such as, "The Anatomy of the Gorilla" by Raven (1950), the vertebral column is minimised, except for two pages on all muscles of the back. Recent accounts of primate anatomy however, have given reasonable coverage to the vertebral column (Aiello and Dean, 1990; Ward, 1991; Shapiro, 1991a; Gebo, 1993). The information given under this chapter is largely based on the above accounts as well as on others mentioned later.

All the five types of vertebrae (cervical, thoracic, lumbar, sacral and coccygeal) are present and are well developed in the primates but the coccyx in humans and ape is stunted, due to lack of a tail. The ribs normally articulate with only the thoracic vertebrae, although cervical ribs and lumbar ribs may occur (Allbrook, 1955).

The number of vertebrae varies widely in primates and so does the length of the various regions of the vertebral column, especially the thoracic, lumbar, sacral and coccygeal regions (Schultz, 1961). The variation of thoracic, lumbar and sacral vertebrae depends on the level at which the thoracolumbar and lumbosacral transitional joints occur in different individuals and species (Abitbol, 1987b).

There are usually 33 vertebrae in humans (C7, T12, L5, S5, and CY4) and 31-32 in great apes where there are fewer lumbar vertebrae, namely 3-4. In total there are normally 22 thoracic, lumbar and sacral vertebrae in monkeys, apes and humans (Abitbol, 1987b) in spite of the regional variations in the different species. In the apes the vertebral formula is either C7, T13, L3, S6 or C7, T13, L4, S5 (Schultz, 1961).

A short and wide vertebral column is mechanically relatively more stable than a narrow, long one (Jungers, 1984; Ward, 1991). Short lumbar regions that are common in hominoids and atelines (Spider monkeys) enhance orthogrady, according to Johnson and Shapiro (1998). Short backs are also adaptable to brachiation (Erikson, 1963); bridging and vertical clinging (Cartmill and Milton, 1977; Jungers, 1984).

Primates such as the *colobus* monkeys that practise quadrupedal running, leaping and springing have long lumbar regions according to Keith (1923), Schultz (1961) and Fleagle (1988).

The length of the vertebral column and/or any of its regions does not only depend on the number of vertebrae but also on the lengths of the individual vertebrae (Schultz, 1961). It is therefore important when making comparisons between vertebral columns of individuals or groups of primates to take those two factors into account.

In comparison with monkeys and prosimians, the apes and humans are characterised by shorter lumbar regions in relation to the total presacral column length. The apes have a relatively shorter lumbar region than humans in comparison with the total length of the presacral vertebral column, (Schultz, 1961). It must be noted however that the length of the cervical region varies with the length of the vertebral bodies. The length of the other regions depends on increase or reduction of the number of vertebrae as well as their lengths.

The progression of the size of individual cervical vertebrae tends to be in the craniocaudal direction. In humans the fifth and sixth vertebrae have the shortest bodies, the length again increasing progressively caudally from the seventh (Martin and Saller, 1959). In the gorilla the seventh cervical and the first thoracic have the shortest bodies, while the longest are the second and third thoracic vertebrae (Martin and Seller, 1959). The lumbar vertebrae are wider transversally in relation to the other vertebrae in humans than in other primates. In human the dorsal (posterior) length of the body of each lumbar vertebra decreases (from the first lumbar) towards the fifth lumbar vertebrae. The ventral (anterior) lengths of the lumbar vertebrae increase resulting in "increasing dorsal wedging" of the lumbar vertebrae. The wedging is expressed as the "lumbodorsal index" as devised by Cunningham in 1886 (Aiello and Dean, 1990). This is the ratio of the dorsal length of the body of a vertebra to the ventral length of its body. Humans have a marked dorsal wedging of the last lumbar vertebra. This means that they have a low lumbodorsal or lumbovertebral index when compared to great apes.

The lumbovertebral index of the last lumbar however has a considerable range of variation between humans and apes, resulting in a degree of overlap of this index. Other individual lumbar vertebrae in humans and apes may also show marked dorsal wedging (Rose, 1975). Therefore human lumbar lordosis is not entirely attributed to the wedging of the last lumbar vertebra only (Aiello and Dean, 1990).

Vertebral morphology

Vertebrae are generally similar in all mammals. The usual vertebral features are, the vertebral body, neural arch (pedicles and laminae), vertebral foramen, vertebral notch, spinous process, transverse processes and pairs of prezygapophyses and postzygapophyses (Figure 2.2, 2.7).

The vertebral foramina of all vertebrae in a vertebral column combine to form a vertebral canal in which the spinal cord is protected. In humans and other orthograde primates the vertebral column is in the median vertical axis. In quadrupeds the vertebral column is in the median horizontal position. There are curvatures within the vertebral column, which have been discussed in detail later. Vertebrae vary with their positions (regions) within the body and with the posture and locomotion of each species.

The body is ventral and cylindrical except in the first and second where it is modified or specialised. There are significant sexual and geographical differences among the vertebral body diameters in humans observed by Hermann et al., (1993), Gilsanz et al., (1994), and MacLaughlin and Odale (1992). Such differences are of forensic, anthropological, and pathological importance. The cranial surface of the body, known as the head (caput), is convex, while the caudal surface is slightly excavated (concave).

Where epiphyses of the bodies of adjacent vertebrae exist, they are connected by intervertebral discs. In humans the vertebral epiphyses are ring-like while in apes they are complete discs covering the body articular surfaces (Aiello and Dean, 1990). The body has a dorsal crest for the attachment of a dorsal (posterior) ligament and on either side of the crest is a groove for blood vessels.

The vertebral (neural) arch strides over the body with its laminae forming the roof of the vertebral canal (vertebral foramen) and protects the spinal cord. The vertebral canal is extremely wide at the level of C1-C7/T1 and at the lower thoracic and upper lumbar regions because of the respective spinal cord enlargements at or near these regions.

The base of the arch has the pedicles that are indented cranially and caudally, forming the incisura vertebralis. The incisurae of adjacent vertebrae form the intervertebral foramen at each articulation for the roots of the spinal nerves.

Each vertebra has processes for attachment of muscles. The spinous process is dorsal and projects dorsally. The transverse processes are found lateral to the vertebral body projecting laterally. On each vertebra there are two cranial and two caudal zygapophyses (facets) that form joints between adjacent vertebrae. The zygapophyseal orientation determines the range of movements that can occur between adjacent vertebrae and in each region of the column. Adjacent vertebrae also articulate at an intervertebral disc that lies between the vertebral bodies. The disc consists of collagen and gelatinous material that facilitates cushioning and bending movements.

The thoracic and lumbar vertebral arches carry mammillary processes between the cranial articular and transverse processes. Caudally between the caudal articular and the transverse processes are accessory processes, especially on the thoracic vertebrae of the pig. In most primates there are pointed accessory processes on the dorsal aspect of the laminae, just lateral to the post zygapophyses (Gebo, 1993; Aiello and Dean 1990). The processes decrease in size caudad. The accessory processes also occur on both thoracic and lumbar vertebrae of carnivores and various species of primates. On the human lumbar vertebrae these processes are poorly developed.

The intervertebral articulation and the intervertebral disc

The intervertebral articulations consist of symphyses between the vertebral bodies, and synovial zygapophyseal joints between the articular processes. Thick but flexible pads, known as vertebral discs, are located between the bodies of adjacent vertebrae. The discs account for about 16% and 25% of the length of the vertebral column in, respectively, domestic mammals and humans. The rest of the vertebral column is formed by bone (Dyce et al., 1987). The discs degenerate with age and the degeneration can be a cause of back pain. Each disc has an eccentrically placed nucleus pulposus and a lateral annulus fibrosus. The nucleus pulposus is derived from the embryonic notochord, and in young animals retains the semifluid texture of the embryonic notochord. The nucleus pulposus acts as a shock absorber and helps to spread compressive forces to which the column is subjected. Later in life the nucleus pulposus may escape, pressing on the spinal cord and nerve roots causing pain. In some cases it may become calcified, diminishing the resilience and flexibility of the spinal column. The annulus fibrosus is an encircling fibrous tissue, obliquely passing between the bodies of adjacent vertebrae, merging with their cartilagenous plates.

The vertebrae are also joined by synovial interfacet (zygapophyseal) joints.These cause varying degrees of mobility in different regions of the individual spine, and in different species. The surfaces of the cervical and cranial thoracic facet joints are tangential to the axis of the vertebral body. Therefore rotation is the major movement encouraged in these joints, although a lesser degree of flexion and extension is also possible. In the lumbar regions the facet joint surfaces are parallel to the axis of the vertebral column, restricting the movements to the sagittal plane (flexion and extension). More details of the facet joints are given later in this chapter on page 42.

Vertebrae are again held together by strong ligaments, such as the interarcuate ligaments between the laminae of the vertebral arches. The other ligaments are the interspinous and intertransverse joining adjacent spinous and transverse processes. Lastly there are the long ligaments dorsal and ventral to the vertebral body.

A) Regional Differentiation in Primate Vertebral Columns

Cervical Vertebrae (Figure 2.1)

The number of cervical vertebrae is the most constant in all mammals, being seven usually, except in manatees and sloth (Schultz, 1961).

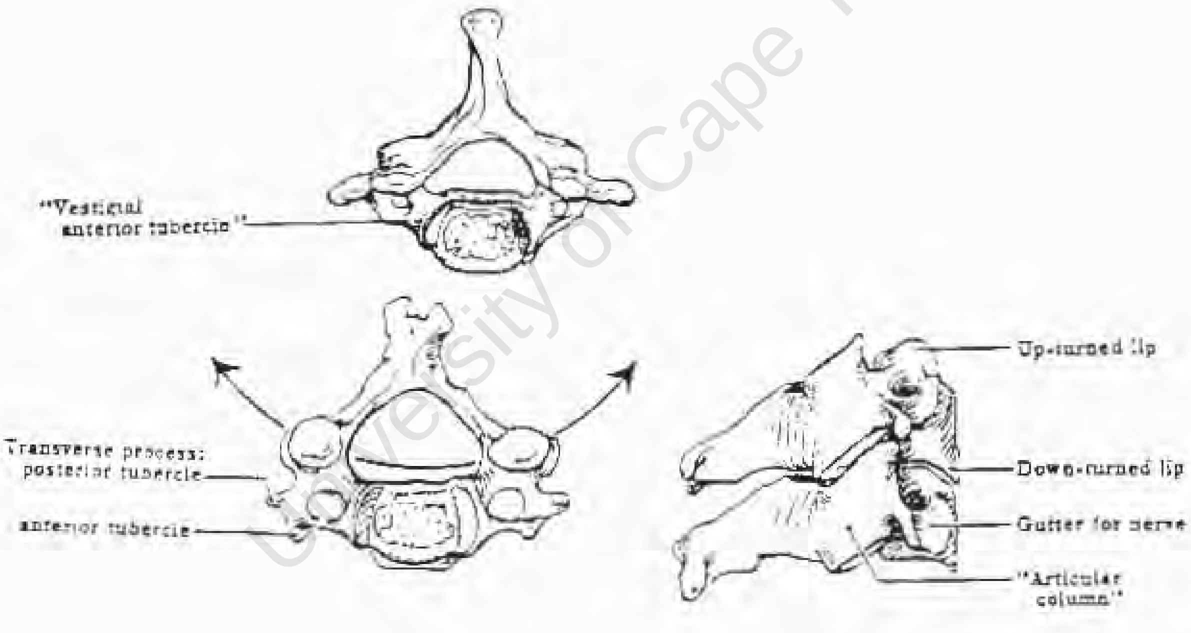
A primate cervical vertebra has a transverse foramen in each of its transverse processes. Typically its body is kidney-shaped, when viewed cranially and saddle-shaped when viewed from the side. The cranial articular surface of the body projects with the "uncinate processes" towards the cranial vertebra forming an atypical synovial joint that is known as "uncovertebral joint". The prezygapophyses face dorsocranially and the postzygaphyses face ventrocaudally. The spinous processes are frequently bifid especially in humans (Allbrook, 1955), and are relatively much longer in the great apes, especially in the male gorilla and male orang-utan.

The long spinous processes improve the leverage for the neck musculature

Figure 2.1

Cervical vertebrae

The seventh cervical vertebra. Note the superior articular processes that are facing dorsocranially. From Anderson (1977).



necessary to support the relatively large heavy head of the great apes (Schultz, 1961). The spinous processes of Asian Prosimian *Loris tardigradus* are relatively long despite the fact that *Loris* does not have a relatively large head (Slijper, 1946). The author suggested that, in both *Loris* and great apes the elongation of the cervical spines compensates for head-support lost by the reduction of the postcondylar portion of the occiput.

Walker (1970) noted a "sensory zone" of hairless cornified skin around the tips of the elongated spines of the sixth and seventh cervical vertebrae and those of the first, second and third thoracic vertebrae in the African Prosimian (*Perodicticus).* The zone is a grooming area during "peaceful social interactions" but this is a highly specialised adaptation.

Thoracic vertebrae and thorax (Figure 2.2 and 2.3)

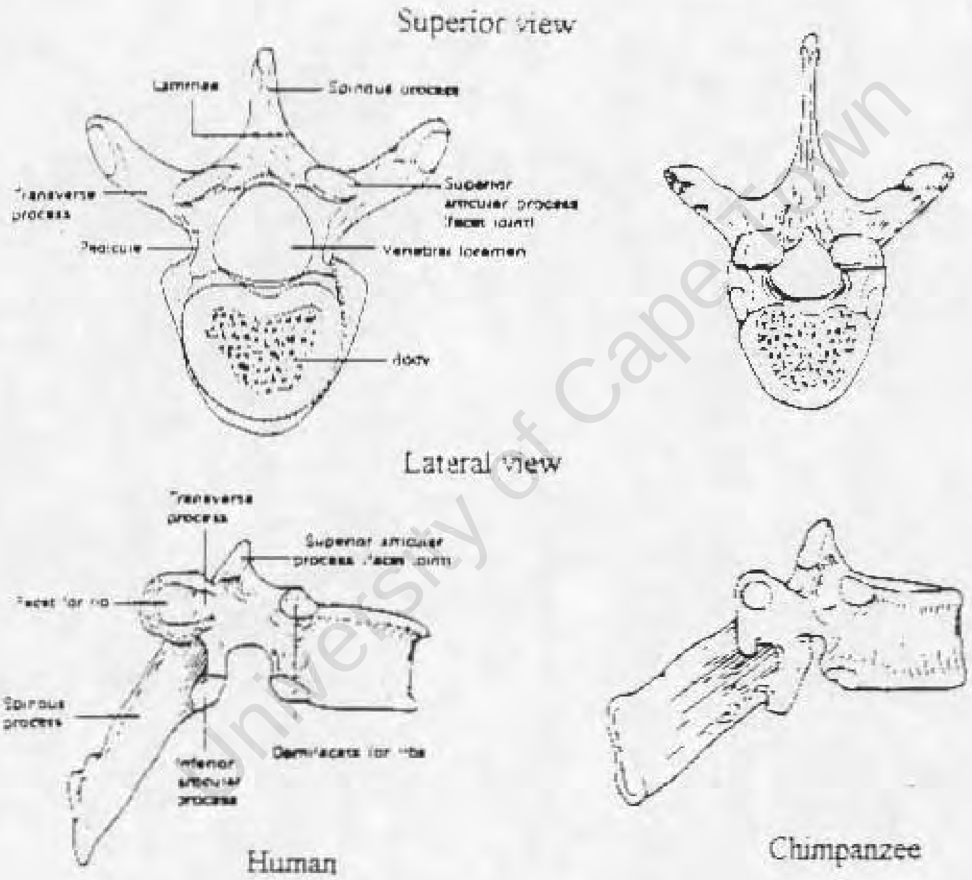
As expected, the primate thoracic vertebrae have rib articular facets (demifacets) cranially and caudally on the body and on the transverse processes. A rib articulates with the demifacets of two adjacent vertebrae and with the transverse process of its corresponding number. However, the first thoracic vertebra in humans and the last two thoracic vertebrae in both humans and apes carry single complete costovertebral facets on their bodies. Therefore the corresponding ribs articulate fully with the bodies of these vertebrae. The facets on the transverse processes of the last two thoracic vertebrae are absent and the last two ribs are attached to these transverse processes by ligaments rather than synovial joints (Aiello and Dean, 1990).

The thoracic prezygapophyses face dorsally and the postzygapophyses ventrally. In the first thoracic vertebra the prezygapophyses are still cervical type, facing dorsocranially. In the last thoracic vertebra, which is usually T12 in human and T13 in apes, the postzygapophyses have the typical lateral orientation of the lumbar facet joints (Aiello and Dean, 1990). The thoracic and other presacral vertebrae can be sequenced easily according to the size (volume) of the vertebral body. The volume (that is length times surface area) generally increases steadily down to the second lumbar (sometimes to the last lumbar vertebra) (Aiello and Dean, 1990). The cross-sectional shape of the thoracic vertebrae changes in a caudal direction, the cranial vertebrae being "kidney" shaped (as in the cervical vertebrae), but around the fourth thoracic

Figure 2.2

Thoracic vertebrae

The human and chimpanzee thoracic vertebrae. The superior articular processes face dorsally and are in the coronal plane. From Anderson (1977).



vertebra the shape changes to a "heart" form. The most caudal three thoracic vertebrae are again "kidney" shaped, like the adjacent upper lumbar vertebrae (Aiello and Dean, 1990). The thoracic spinous processes make a sharp angle caudally, more so in humans than in apes, completely covering the vertebral canal and hence the spinal cord. The processes are flattened from side to side but the first and second thoracic vertebrae have bulbous tips, while the last three are stubby and project less acutely, like those of the lumbar vertebrae, (Aiello and Dean, 1990). The last thoracic vertebra has two tubercles, namely the cranial mammillary processes and the accessory tubercles.

The relative length of each thoracic vertebra and therefore the lengths of the thoracic regions vary among the taxa, just like the number of vertebrae (Schultz, 1961). The lorisines have the greatest number of thoracic vertebrae amongst primates (Schultz, 1961).

The number of rib-bearing thoracic vertebrae and the shape of the rib cage vary in primates even within genus or species. In the hominoids the rib cage is broad mediolaterally and flattened dorsoventrally, the ribs being curved and the vertebrae more ventrally placed. In contrast, the non-hominoids have narrow, deep rib cages (Keith, 1923, Schultz, 1961, Ankel, 1972). The differences of the thoracic cage are related to the movement in the forelimb that affects the position of the scapula upon the thoracic cage (Keith, 1923; Schultz, 1961, Jenkins et al., 1978). However, some non-hominoids, namely *Perodicticus, Tarsus, Ateles, Brachyteles* and *Colobus* tend to have hominoid-shaped thoracic cages (Ankel, 1972).

The Thoracolumbar transitional vertebra (Diaphragmatic vertebra)

The last thoracic vertebra is the transitional vertebra between the thoracic and lumbar regions. It is sometimes called the diaphragmatic vertebra (Erikson, 1960). It has thoracic shaped prezygapophyses and lumbar orientated postzygapophyses but is usually regarded as thoracic. In humans and great apes it is often the last-rib bearing vertebra, but in other primates there are usually one to three more rib-bearers caudal to it (Shapiro, 1995). However in some humans and apes ribs might continue in a caudal direction after the joint transitional change. In such a situation it is difficult to determine the position of the transition between the thoracic and lumbar regions. Traditionally the position of the last pair of ribs is used to determine the transition. Maximum sagittal flexion in humans is alleged to occur at the transitional joint vertebra that is at the thoracolumbar joint transition, according to Kashimoto et al., (1982). According to Jenkins (1974) this is not necessarily the case in other primates and non-primate mammals.

The diaphragmatic vertebra is the last vertebra of the thoracic series. If the zygapophyseal change is considered, then the vertebra subjacent to the diaphragmatic vertebra is the first lumbar regardless of whether it is carrying a rib or not (Erikson, 1960).

According to Shapiro (1993a) more morphometric research is needed on the primate thoracic vertebral column, because most of the research in this region so far has been on counts of vertebrae and comparative qualitative aspects only.

Lumbar vertebrae (Figure 2.4)

It is difficult to consider adjacent regions of the vertebral column in isolation from each other, since they effect each other functionally. Although focus is on the thoracic vertebrae in this study, the lumbar and other vertebrae are also put in perspective, so that their interaction with the other vertebrae in locomotion and postural behaviour is recognised.

Lumbar vertebrae can be identified by their size, shape (orientation) of their zygapophyses and by the absence of rib facets. Their number in the vertebral column depends on how they are defined. Thus by the zygapophyseal definition, the number of lumbar vertebrae is increased and the thoracic vertebrae decreased. The increase or decrease depends on the presence of rib-bearing vertebrae, (caudal to the transitional vertebra), that will lose their thoracic status by having lumbar zygapophyses.

Research by Schultz (1961), Erikson (1960) and Washburn (1963) shows that by either definition, the most numerous lumbar vertebrae are found in leaping prosimians such as *Lepilemur, Indri, Propithecus, Avahi*, and ironically in *Loris* that is a slow-moving quadrupedal prosimian.

The atelines (e.g. *Ateles, Brachyteles, Lagothrix, Alouatta*) have relatively few vertebrae in the lumbar region, although not fewer than those of the great apes (Rosenberger and Strier, 1989). *Pan, Gorilla* and *Pongo* have the fewest

Figure 2.3

Human thoracic vertebrae

Thoracic vertebrae (human). The superior articular facets are in the coronal plane facing dorsally. The inferior articular facets are in the same plane facing ventrally. From Anderson (1977).

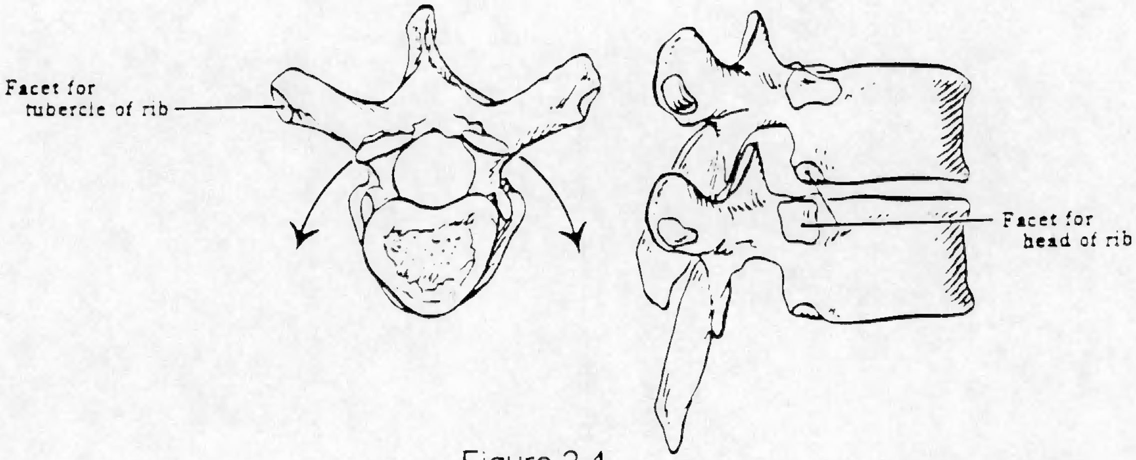
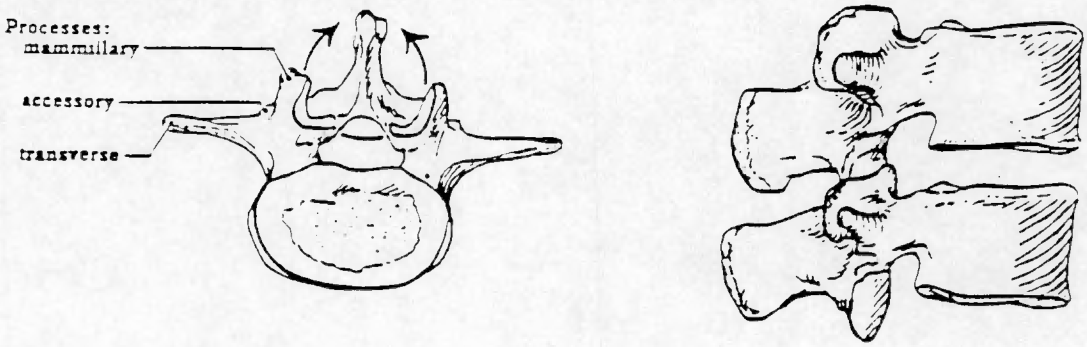


Figure 2.4

Human lumbar vertebrae

The superior articular facets lie in the sagittal plane facing medially. The inferior articular facets lie in the same plane but facing laterally. From Anderson (1977).



numbers of lumbar vertebrae among the hominoids (Aiello and Dean, 1990). Keith (1923) suggested that the reduction of lumbar vertebral number in the hominoids is related to orthograny and brachiation.

Although cercopithecoids generally have a uniform number of lumbar vertebrae, those that leap frequently such as *Presbytis* and *Colobus* have relatively longer lumbar regions, than quadrupedal non-leapers (Fleagle, 1977a, 1977b; Rose, 1978). This increased length is largely due to the increase in craniocaudal length of each vertebra but definitely not to an increase in number (Ward, 1991). The long lumbar region of leapers is also accompanied by strong back muscles for leaping (Erikson, 1963 and Fleagle, 1988).

In the hominoid lumbar region, the diaphragmatic vertebra is also usually the bearer of the last rib, so by either definition the number of lumbar vertebrae remains the same. Secondly, the lumbar region is short relative to the trunk length and to the presacral spine length, due to the fact that the lumbar vertebrae are relatively fewer and shorter if compared to those of non-hominoids (Schultz, 1961; Benton, 1967; Ankel, 1972).

Keith (1923) attributed certain hominoid features to orthograny and brachiation but similar features were exhibited by some non-hominoid primates that engage in various different postural behaviours. Keith (1923) did not delineate between features for the orthograde posture and features of primates that keep their spines erect when sitting or climbing (mere postural features). More explanation was necessary, from researchers like Cartmill and Milton (1977) who, for example, noted that lumbar reduction in atelines enables these primates to control the trunk during bridging across the gaps in trees. For the purposes of bridging, these primates had long thoracic regions. Their lumbar regions were comparatively short, in order to reduce the trunk to manageable length, and had nothing to do with orthograny.

Cartmill and Milton (1977) again noted that *Galago* (bushbaby), *Perodicticus*, (potto and Loris) have an elongated thorax just as hominoids and atelines, possibly to help in jumping (Walker ,1969).

Jungers (1984) observed that the lesser apes have a reduced lumbar region that was thought by the researcher to prevent buckling of the trunk in climbing, jumping and landing. Although cercopithecoids have a long lumbar region (compared to apes), that enables them to leap and jump, the region exhibits negative allometry. This means that the larger the cercopithecoid is, the shorter the lumbar region (Jungers, 1984), helping them to gain spine rigidity and stability. According to Shapiro (1993), this may be consistent with the findings of Hurov (1987) that vervets use their spinal flexibility to increase stride, while larger-bodied patas monkeys do not. However, the above author suggests that more research should be carried out on the primate spine length and flexibility in order to understand its relation to locomotion better.

The consecutive caudal increase of transverse diameters of lumbar vertebral bodies is highest in humans (Rose 1975). Though the lumbar vertebral surface area scales isometrically (proportionately) in non-human hominoids, the area of the intervertebral surface is larger in humans, and increases with the body weight of the individual (Shapiro, 1991a; Ward, 1991). Schultz (1961) was of the view that the large diameter and surface area increase in humans must be due to compressive forces from bipedal locomotion.

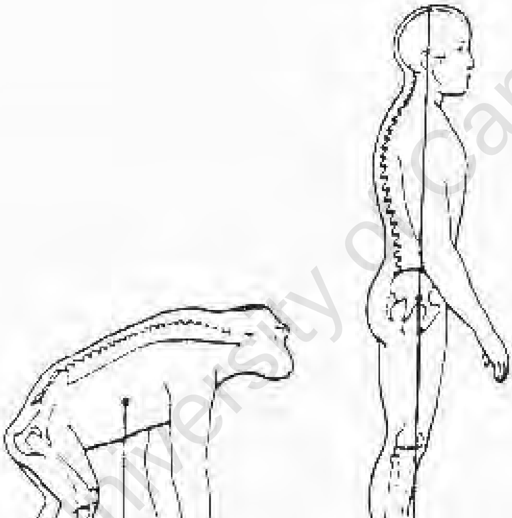
The human lumbar vertebrae are wedged and play a part in the establishment of lordosis in the region. Lordosis due to wedging is enhanced by a sharp lumbosacral angle. Lordosis is also accentuated by the wedging between the sacral disc or body of the first sacral vertebra and the body of the last lumbar (usually L5) (Nissan and Gilad, 1986; Bogduk and Twomey, 1987). It must be noted that there are other primates, especially hominoids, which have lordosis and a lumbosacral angle but these features are not as pronounced as they are in humans (Schultz, 1961). On the other hand pronograde primates can develop lordosis if trained to become bipedal (Preuschoft et al., 1988; Hayama et al., 1992). Thus according to Abitbol (1987a), the ontogenic development of lordosis and the lumbosacral angle coincided with the adoption of bipedalism. The lumbar lordosis promotes stability necessary for bipedalism, by placing the centre of gravity of the individual directly over the hip joints (Figure 2.5).

The mammillary tubercle of the lower thoracic vertebrae (towards the lumbar region), widens to become the mammillary process of the first and other lumbar vertebrae, located on the lumbar articular processes. The accessory processes are attachment points for the lumbar head of extensor caudae lateralis, longissimus and intertransversarii muscles. In most primates the accessory processes are prominent and pointed in the first few lumbar vertebrae, but

Figure 2.5

Centre of gravity

The centre of gravity and supporting rectangle of the pedestal in chimpanzee quadrupedalism and human bipedalism. From Aiello and Dean (1990).



caudally they are reduced or absent. In hominoids they are small bumps that are highly reduced (Shapiro, 1993). However, Ward (Comment, 24th March 1999) states that hominoids, except hylobatids and early forms such as *Proconsul* and *Kenyapithecus* have no trace whatsoever of any accessory processes.

The lumbar prezygapophyses are typically concave and face medially, while the postzygapophyses are convex, facing laterally. These joints are designed to guide ventral flexion and limit and lateral movements (or slipping). This type of articulation in the primate lumbar region is also found in the vertebral column of other vertebrates, including reptiles and birds (Aiello and Dean, 1990). It is supposed to be the primitive form of vertebral articulation. Most of the rotation of the human thoracolumbar column occurs in the lumbar region (Bogduk and Twomey, 1973, 1987).

In humans, the sequence of the size of the lumbar bodies increases proportionally with the distances between the prezygapophyses or the postzygapophyses, these distances also increase towards the caudal aspect but decrease in great apes. The lumbar facet joints become less mediolaterally orientated and more ventrodorsally orientated at the lumbosacral articulation. For example, the postzygapophyses of the last lumbar vertebra are ventrally orientated, such that they secure the last lumbar from sliding ventrally off the highly angled promontory of the sacrum (lumbosacral angle). In the great apes the promontory does not have a sharp angle and the facet joints have not changed from their mediolateral orientation.

Sacrum and Coccyx

The sacrum articulates with the ossa coxae and consists of several vertebrae that are fused to form a single unit (Abitbol, 1987b). Hominoids have more sacral vertebrae than most non-hominoids. The increase in the number of sacral vertebrae in hominoids is often at the expense of lumbar vertebrae (Abitbol, 1987b). In apes L4 can be sacralised, but in humans it is not (Allbrook, 1955). In humans, in 10-15% of cases it is L5 that is sacralised (Abitbol, 1987b). Sacralisation can be complete or partial, involving only part of a vertebra, such as a transverse process. It must be pointed out that the apes usually have 3-4 lumbar vertebrae, while humans normally have 5 and sometimes 4 or 6. In sacralisation the last lumbar vertebra becomes sacralised in apes and humans, reducing the lumbar vertebrae by one.

Prehensile-tailed primates have a wide distal sacral aperture of the neural canal for the well-developed nervous system to the prehensile muscles in the tail (Ankel, 1972).

Coccygeal vertebrae are rudimentary in humans and apes, showing only reduced bodies, except the first which shows some transverse processes and facet joints. In the human foetus, there are at least six segments in the coccygeal region but these are reduced to three in the adult, because the last three to four are fused into one. However, in tailed primates, more so in those having prehensile tails, the coccygeal vertebrae are numerous and relatively well developed. In prehensile tails the vertebrae have high neural and ventral arches to protect and guide the vessels to the tail.

Modal Patterns of Vertebral Arrangement

Bornstein and Peterson (1966) found 14 numerical patterns in 1239 vertebral columns belonging to various human populations in the Americas, while Kaufman (1974) observed only seven patterns in 462 vertebral columns South African indigenous population.. The number of numerical patterns observed by Allbrook (1955) in 206 vertebral columns from Central and East African indigenous population is 18. However the approach that Allbrook (1955) uses to identify the vertebrae in thoracic and lumbar regions is not clearly stated. It is not stated whether Allbrook applies the conventional approach that uses the presence of ribs, or whether he applies the modern method of counting using changes in the zygapophyses. The most common model pattern observed by Bornstein and Peterson (1966), and Kaufman (1974) consists of 7 cervical, 12 thoracic and 5 lumbar, making a total of 24 presacral vertebrae (PSV). The next common pattern is C7 T12 L6 making a sum of 25 PSV, and the third is C7 T13 L5 (25 PSV). According to the above studies there is a higher incidence of 25 PSV in the males than in the females, and a higher incidence of 23 PSV in the females. That is, the specific variation of 23 PSV occurred almost twice as often in the females (7.9%), than in the males (4.2%). The PSV of 25 is more than twice as often in the males (6.8%) than in the females (3.0%). The layout below shows the vertebral patterns as observed by Bornstein and Peterson (1966). Kaufman did not use the conventional rib identification for the vertebrae but used other criteria, such as shape of joints/zygapophyses and spinous process.

The variation of human PSV patterns

Table 6.0

Cervical	Thoracic	Lumbar	PSV Pattern	Frequency
7	11	5	23	12%
7	12	4	23	
7	11	6	24	8.9%
7	12	5	24	
7	13	4	24	
7	12	6	25	9.8%
7	13	5	25	

This table is modified from Bornstein et al., (1966).

C) Functional Specialisation of parts of Primate Vertebrae

Vertebral Body

Functionally the vertebral column may be divided into anterior (ventral) and posterior (dorsal) elements. The anterior element consists of the vertebral body (and disc) while the posterior element consists of the pedicles, laminae and zygapophyses. In order to assess morphological expression of load transmission between the anterior and posterior elements, the "size" of the cross-sectional area of the anterior element, pedicles and laminae has to be measured (Shapiro 1993a). The surface area of the vertebral body gives a reflection of the weight transmission (compression force) through the anterior column including the disc. The assumption here is that the size of a given portion of a vertebra is related to the magnitude of the forces acting upon it (Davis, 1961). Due to the bipedal posture and locomotion, the surface areas of the vertebral bodies of lower lumbar vertebrae of humans are large relative to the species body size or weight (Shapiro, 1993b). There is a decrease in the vertebral body surface areas between the penultimate and the last lumbar (LL) vertebrae in human and some habitual pronograde primates. This feature is therefore not due to bipedalism as previously thought (Shapiro, 1993b).

In hominoids the surface areas of the vertebral bodies increase progressively along the column and then decrease at the last lumbar (Shapiro 1991a, 1993b). Work by Shapiro (1991a) shows that in hominoids the areas of the vertebral body are correlated significantly with overall animal body weight. When humans are eliminated from the hominoid sample, the correlation becomes closer. This indicates that humans have relatively larger vertebral body areas in comparison to their weight (Shapiro, 1993b).

In spite of other human-like features of *Australopithecus africanus*, its vertebral bodies are not human-like. That is, *A.africanus* has relatively small vertebral surface areas. This feature was noted as a characteristic of australopithecine thoracolumbar vertebrae (Robinson, 1972; Sanders, 1990).

The expectations of earlier studies of the vertebral body area were that orthograde primates have relatively larger vertebral body areas than pronograde primates (Preuschoft,1978 and Shapiro,1991a). A second expectation was that body area "profiles" would have values that increase progressively along the column caudally in orthograde primates, since the caudal (lower) end bears weight of the trunk. In pronogrades, since weight is distributed among the limbs, it is expected that the body area values would be more or less constant. Among the hominoids only the humans have vertebral body areas that are larger than expected, in comparison to the overall body weights in this group. The most orthograde non-human hominoid, the gibbon, has the smallest values of the absolute vertebral body area. Among the non-human hominoids vertebral body area is correlated significantly with body size.

Increases of the vertebral body areas along the column appear to be a common feature among both pronograde and orthograde primates (Preuschoft, 1978; Preuschoft et al., 1988; Shapiro, 1991a). These increases are due to axial load increases (Badoux, 1968). However, at the last lumbar vertebra the area decreases in humans (Davis, 1961), but in all nonhuman primates the lumbar vertebral body area decreases caudally (Shapiro, 1993a). This has resulted in the relative increase in pedicle size of the human L5 or last lumbar in other hominoids, as the case may be. The pedicles of the last lumbar participate in transmission of forces from the vertebral body area to the pelvis and lower limbs. The similarity in the transmission pattern or in the profile of the vertebral forces among different orthograde and pronograde primates can be explained as follows.

Compressive loads (Figure 2.6) placed on the axial skeleton of quadrupedal primates are responsible for the forces experienced by the vertebral column (Slijper, 1946; Badoux, 1974). Thus the resultant epaxial and hypaxial forces that maintain the stability of the bow produce an axial load throughout the column. The craniocaudal differences in the vertebral body surfaces and compressive load is less extreme in quadrupeds. In biped the increase in the vertebral surfaces are considerable, and are an adaptation to these forces (Rose, 1975).

Spinous process

The primate spinous process and its interaction with the back musculature have been examined by researchers such as Ward (1991) and Shapiro (1991a). The following account is primarily based on work by the above and others mentioned later. The spinous processes act as bony levers for muscles of extension, the most important within the lumbar region being the erector spinae and multifidus (Shapiro, 1991a). According to Shapiro (1991a) the dorsal projection of the spinous process does not register different values among closely related primates. The spinous process inclination has been investigated by Latimer and Ward (1993) and Jellema et al., (1993). The inclination is the spinous "craniocaudal orientation". It is referred to as the angle "S" formed between a coronal plane and a line passing from the base to the tip of the spinous process (Figure 2.7). A spine at an angle of less than 90° is caudally orientated and a spine at an angle of more than 90° is cranially orientated (Shapiro, 1991a). Generally the thoracic spinous processes would point caudally at an angle less than 90° (Ankel, 1972).

In the primate lumbar region, the spinous process inclination varies but is usually cranially orientated. However in the lumbar region, reference to the inclination must be accompanied by a clarification of whether one is referring to the cranial or caudal edges of the spine, since the two edges may be inclined in

Figure 2.6

Maximum bending moment during axial loading

In the drawing below the rectangle blocks represent long (A) and short (B) vertebrae. The arrow represents the maximum bending moment during axial loading of the vertebral column. The shorter bodies would result in smaller moment. From Ward (1991)

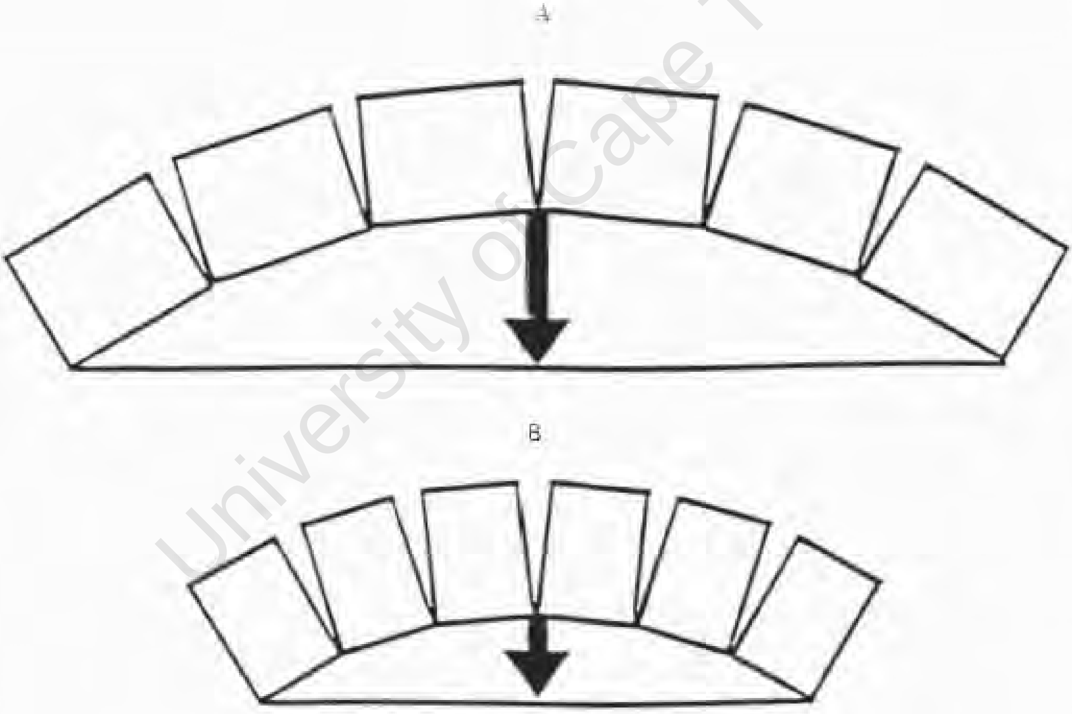
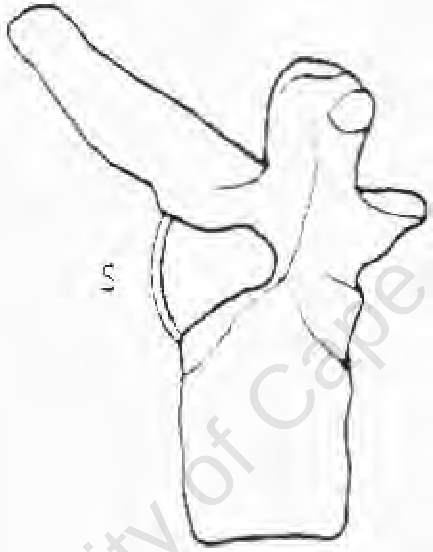


Figure 2.7

The angle of the spine

The leverage of the spinous process depends on the angle 's' the process makes with the body of a vertebra, and not on the length of the process. A spinous process that makes a large angle, that is almost 90 degrees with a vertebra, has a higher leverage than a spinous process of the same length making a smaller (acute) angle with the body of the vertebra. (From Slijper, 1946)



Increasing the angle S raises the tip of the spinous process further from the centre of the vertebral body, i.e. the axis of movements. The further the tip of the spinous process is from the axis, the longer is the lever arm of the spinous process and hence the greater the leverage of the spinous process.

different directions (Clauser, 1980).

The cranially inclined spine of the lumbar region meets the spine of the anticlinal vertebra at a transition that may or may not coincide with the diaphragmatic vertebra. The anticlinal lumbar vertebra is the vertebra whose spine tends to be vertical. Its spine is neither caudally nor cranially inclined, and the diaphragmatic vertebra is the thoracic vertebra at the thoracolumbar transitional joint.

In hominoids, the lumbar spinous processes have square dorsal edges. The difference between the inclination of the lumbar spinous processes in hominoids and other primates is visible but difficult to quantify, due to the anatomical nature of the spinous processes in this region (Shapiro, 1991a). Researchers have not come to a uniform method of quantification of this structure (Ward, 1991). For these and other reasons stated later no spinous angular measurements were taken in this study.

The question as to why the inclination of the spinous processes varies has still to be answered. Slijper (1946) reasoned that each spinous process is orientated perpendicularly to the line of force of the most important muscle acting on it. If more than one important muscle acts on a spine, the orientation of the spine is intermediate to the perpendicular of the forces of those muscles (Shapiro, 1991a). In most primates, the post-diaphragmatic spinous processes are cranially orientated, which, according to Slijper (1946), shows that spinalis muscles is acting on these spines. The caudally inclined spinous processes are responsible for the extension of the trunk through the action of the multifidus.

The interspinous distance and the craniocaudal expansion of the dorsal end of the spinous processes need further investigations (Shapiro, 1991a). Erikson (1963) explained that the "broad" interlocking spines of *Ateles* seem to limit mobility of the spine. As noted by Gambaryan (1974), these wider expansions of the spinous processes reduce interspinous spaces for the supraspinous ligaments and interspinous ligaments, making the lumbar region rigid. The same researcher observed in carnivores that narrow spinous process tips increase spinal flexibility in the sagittal plane, because the ligaments and muscles have more space to attach on in order to effect movement.

Since the spinous process is a vital muscular attachment, it is important to examine how its absolute length, its perpendicular length or height and its angle of inclination relate to the back muscular action and locomotion. Badoux (1968), observed that the further dorsally the spinous process projects the further the outermost fibres of the erector spinae muscle will be placed, relative to the axis of the vertebra which is near the centre of the vertebral disc. Haher et al., (1989) remarked that longer spines would improve moments for transversospinal muscles.

Slijper (1946) pointed out that the angles the spinous processes make with the long axis of the vertebral column are related to the lines of action of the important muscles acting on these processes. The above author also noted that the spinous processes are orientated perpendicularly to the most important muscle fibres acting on them to provide the greatest mechanical advantage for the muscular action.

Shapiro (1991a) suggested that in order to compare the leverages in primates, for example, the leverage of multifidus muscle in extension, a measurement has to be devised to reflect the lever arm of the process on which the muscle attaches. The lever arm of the multifidus is considered to be the perpendicular distance from the centre of rotation of a vertebra, to the tip of the spinous process. The leverarm is a projection of the spinous process, expressed in the formula (SPL+ h)+ (1/2) SDC (Figure 5.1). The variations in the angle of orientation of the spinous processes do not affect the projected lever arm, but may be related to the economic use of material (Shapiro, 1991a, 1995). This may imply that the angle of inclination of a spinous process might not be the major factor in the forces generated by the back muscles. This further explains why this angle was not included among the measurements in the study.

In humans, the centre of rotation of a vertebra lies in the centre of the disc (Pennal et al., 1972). Shapiro (1991a, 1995) suggests that in the non-human primates it is reasonable to assume that the centre of rotation is also in a similar position. Therefore the lever arm for extension of erectores spinae or multifidus is given by the following formula:

The variable spine = $(s + h) + (c/2)$ (Shapiro, 1991a), (Figure 5.1) where:

s = SPL = spinous process perpendicular length/ height
h = vertebral foramen height
c = SDC = Cr. Vert. body mid-line sagittal diameter
$c/2$ = $1/2$ SDC = radius from the centre of the cranial articular surface of the vertebra to its dorsal surface

From the variable spine "Spine Ratio" the can be calculated by using a consistent size variable and a relative comparison of leverage in primates of different body weight (size) can be possible.

Thus, The Spine Ratio = $(s + h) + c/2 \div {}^{3}\sqrt{}$ Body Weight.

In order to make comparisons across taxa of different sizes, the ratios from linear values are divided by the cube root of the species body weight (Sneath and Sokal, 1973; Jungers, 1985a, 1985b; Shapiro, 1993a, 1995). The cube root of the species body weight is applied in order to put the weight into a form comparable to linear value since the ratios being compared are from linear measurements. The body weight has a direct relationship to volume which is proportional to the third power of linear dimensions (Shapiro 1991a, and Jungers, 1985b)

Henneberg et al. (1989) however state that in all Old World monkeys, apes and humans the weight of the body scales to the exponent of two times the body length. They argue that because the primate body is elongate and not spherical, the weight scales approximately to the square root of the body length. On the other hand, Shapiro (1993a; 1995) who has also carried out studies similar to the current research, has supported the use of the cube root of the body weight in the formulae (personal communication, see Statistic methods). After discussions with other authorities, Shapiro's approach has been followed in this study. This point about the application of the cube root has been discussed further under the section on Statistic methods.

Since the estimates of the species body weight and how they are applied are arguable, some authors have used the "geometric mean" instead of the body weight. The "geometric mean" is defined as "the equivalent of the n^{th} root of the product of n linear variables" of one vertebra that is not included in the analysis (Mosimann, 1970; Mosimann, 1979; Shapiro, 1991a). The "geometric mean" is supposed by the above authors to be more accurate because it is calculated for each individual and is not an estimate. The diaphragmatic vertebra is usually the one from which the geometric mean is determined, because for some reason it appears to be highly correlated with the species means of the body weight (Johnson and Shapiro, 1998) (r = .95 across species).

Though the geometric mean is mentioned this study did not use the geometric mean. It was not used because the diaphragmatic vertebra, which is recommended for use in the geometric mean, is at the same time part of the study, as it is a transitional vertebra. Henneberg (direct communication) also pointed out that substituting the geometric mean of linear dimensions of a vertebra for the weight leads to circular reasoning. This is so because other vertebrae are expressed as fractions of one particular vertebra of the same spine.

The spine ratio also evaluates the "efficiency" of extension produced by, for example, multifidus muscle in orthograde and pronograde primates of similar phylogeny (Shapiro, 1991a). According to Keith (1923) the spine ratio should be larger in orthograde primates than in pronograde ones. Ward (1991) noted that as monkeys become larger the spinous process becomes longer to reflect the larger erectores spinae. The lever arm similarities in *Indri* and *Propithecus* have no relation to body weight (size) (Shapiro, 1995). The relatively long extensor lever arm in *Indri* should theoretically facilitate powerful back extension during leaping and/or vertical clinging (Shapiro, 1995).

Spinous process Extensor leverage or lever arm

The extensor leverage for muscles attaching to the spinous process is not necessarily greater in those primates in which erect posture dominates the locomotion repertoire. Exceptions are among the prosimians, such as *Indri* and *Propithecus* that do have relatively longer extensor lever arms than *Varecia* for most of the lumbar column. The difference in the spine ratio among the prosimians (i.e. *Indri and Propithecus* on the one hand and *Varecia* on the other) could be a reflection of differences in function, but not necessarily due to orthograde vs. pronograde posture. For example, it could be related to the fact that *Indri* and *Propithecus* practise leaping more than *Varecia* (Walker, 1979;

Gebo, 1987; Dagosto, 1989).

In hominoids the spine lever arm again does not seem to exhibit orthograde and pronograde dichotomy. For example the relative values of the lever arm of the spines in the gibbons, which are relatively orthograde primates, are not similar to those of humans, and in the upper lumbar region, their range comes within the values of pronogrades such as gorillas and orang-utan.

However, the difference in the lever arm of pronograde and orthograde primates may exist, but because of the approach to the analysis of the problem the results could have been influenced by the following factors (Shapiro, 1991a):

- The axis of rotation could have been placed at the facet joints, and not at the centre of the disc where it were supposed to be.
- The differences may not be in the lever arm but perhaps in shape and orientation of the spinous process e.g. in the direction of "pull" of a muscle and in the ability of the spines to "lock", thus preventing hyperextension.
- The presence of human lumbar lordosis which "elongates the lever arms of muscles" (Preuschoft, 1978). In the absence of this lordosis, the human spinous process leverages are not significantly different from those of chimpanzees. Thus it may be a combination of the spinous process lever arm, spinal curvature and pelvic orientation that allow for a reorganisation of human back muscles for bipedalism. So, analysing the lever arm without considering the other factors that come into play might not show the difference between the muscle leverages of primates using different forms of locomotion.

It is possible that there might be no differences in extensor leverages of the spinous processes of orthograde and pronograde primates. This means that the "extensor leverage" might be as equally important in pronograde quadrupedalism as it is in orthograde locomotion. The electromyographic data (Shapiro, 1991b) supports this view, since multifidus shows similar recruitment patterns in both quadrupedal and bipedal walking. Multifidus also comes into play during galloping in the vervet monkey (Shapiro, 1991b) and cat (English, 1980; Zomlefer et al., 1984).

Transverse process and the thorax

The roots of the lumbar transverse processes have been studied by Shapiro (1991a) and Ward (1993). It was pointed out that these transverse processes originate from different levels of the vertebra in different taxa. In monkeys they originate from the vertebral body while in great apes they are rooted from the neural arch and in humans even higher (Erikson, 1963; Ward, 1993).

The position of the tips of the transverse processes is also critical because it is associated with the reorganisation of back musculature. The iliac blades in apes are flared laterally and expanded, influencing the insertions of erector spinae and quadratus lumborum to more dorsolateral positions. The transverse process position affects iliocostalis action since the ribs are attached to the transverse processes by ligaments (Schultz, 1961). The dorsal migration of the transverse processes increases the distance of the erector spinae from the axis of bending, and so increases the moment of these muscles to counteract back flexion. The changes also affect the actions of transversospinal muscles (i.e. semispinalis, multifidus, rotatores), psoas major as well as quadratus lumborum (Shapiro, 1991b).

In monkeys the muscles have become relatively longer and acquired greater rotational and lateral flexion leverage for greater mobility. In great apes the orientation of the lumbar transverse processes is important in the extension of the trunk and hence stability. Ward (1991) suggests that the above changes have no correlation to body weight in primates. However, in African bovids the transverse processes become more perpendicular relative to the sagittal plane as the species become larger, showing a weight relationship (Halpert, et al. 1987 1991a, Gambaryan, 1974).

The levels of the roots of thoracic primate transverse processes are high and constant at the junction of the laminae and the pedicles (Aiello and Dean, 1990). However the level of their tips might vary in different species. The more dorsally positioned the transverse processes or their tips are, relative to the axis of extension, the better the leverage of longissimus and iliocostalis during their bilateral contraction. In maintaining the erect posture, these long muscles must resist flexion of the trunk by bilateral contraction (Shapiro, 1991a; Ward, 1991.

1993). Thus atelines and gibbons that practise more "antipronograde" postures and movements have transverse processes arising high above the junction of the body and pedicle (i.e. at the root of neural arch), with tips projecting horizontally. The great apes and humans have their transverse processes arising even higher at the pedicle-lamina junctions with tips projecting dorsally (Benton, 1967, 1974; Shapiro, 1991a; Ward, 1991).

The tips lie further dorsally in primates that tend to practise orthogrady (atelines and hominoids) than in primates that rely primarily on pronograde postures. Shapiro (1995) found that in Indrids the tips are located more dorsally than in *Varecia*. This arrangement is understood to improve the leverage of *Indri* back extensors, which explanation agrees well with the leaping and orthogrady of *Indri*. The *Varecia* arrangement is the best for quadrupedalism/pronogrady (Walker, 1979; Gebo, 1987; Dagosto, 1989).

The higher and more lateral the tips of the transverse processes are relative to the ventral surface and axis of the vertebral body, the better are the leverages for lateral flexion of multifidus, iliocostalis and quadratus lumborum.

Lumbar transverse processes which are cranially orientated may improve leverage for lateral flexion by keeping the "moment of arm" of the spinal muscles large (Gambaryan, 1974). The cranial orientation of the transverse processes improves the leverage of the spinal extensor muscles that insert on the dorsal surfaces of the processes by moving their attachment points forward to the axis of extension, which is at the centre of the caudal end of each vertebra.

Gambaryan (1974) observed in carnivores that the cranioventrally orientated transverse processes occurred with strong intertransversal muscles attached to their narrow tips, which gave lateral flexibility to the lumbar spine. In quadrupeds, Gambaryan (1974) noted that expanded (flattened) transverse processes increase the area for attachment of the muscles and promote rigidity by limiting lateral movements, and encouraging sagittal plane movements. Shapiro (1993b) was of the view that more studies should be carried out to clarify the shape, position and orientation of the transverse processes of primates.

The lever arm for lateral movement is known as the Lattran (lateral leverage of transverse process) and is expressed as:

Lattran = (½) a (Shapiro, 1991a, 1995) (Figure 5.3), where:

' a ' is the distance between the tips of the right and left transverse processes of the same vertebra (TPP).

The lateral leverage, also known as the Lattran Ratio is given in the following formula by Shapiro, (1991a):

Lattran Ratio = Lattran ÷ $\sqrt[3]{\text{Species Body Wt.}}$

= $(1/2)\, a / \sqrt[3]{\text{Species Body Wt.}}$

The lateral movement lever arm for iliocostalis and quadratus lumborum, and hence the Lattran ratio, would be relatively larger at each vertebral level in orthograde primates than in pronograde ones (Keith, 1923).

Comparing the transverse process leverages of different taxa is more complicated because of the differences in position of the bases (in lumbar) and tips (in thorax) of transverse processes in different primates. Measuring and comparing the lever arm directly would therefore give biased results.

The position of the tip of the transverse process relative to the ventral aspect of the vertebral body, is the measurement that is taken. This measurement is applied to obtain a fair quantification of the leverage for the long muscles inserting on the tips. The more dorsally places the tips of the transverse processes are, the better is the leverage for extension (Shapiro, 1991a, 1995). The axis of rotation of a vertebra in humans is in the centre of the intervertebral disc. Shapiro (1991a, 1995) assumed that in other primates, the centre was similarly located. Selbie et al. (1993) experimentally confirmed that in the cat (quadruped) spine, the centre of rotation was located in the intervertebral disc during extension, flexion and rotation.

The point to note in this measurement is that, even if the axis of rotation differs among the primates, it is always ventral to the transverse processes. Therefore the most ventral aspect of the vertebral body, and not its axis, is taken as a point of reference for the measurement of parameter "b" (Figure 5.3) (Shapiro, 1991a, 1995). The ventrodorsal transverse process ratio (Vdtran ratio) is expressed as b/c by Shapiro (1995) where:

b = TPV = the vertical distance between the transverse process tip(s), and the most ventral coronal plane of the vertebral body.

c = the cranial sagittal diameter (SDC) of the vertebral body (the median ventrodorsal height (or length) of the cranial surface of the vertebral body).

If the tips are more ventral than the most ventral coronal plane of the vertebral body, then the distance is taken to be negative. According to Keith (1923), the tips of the transverse process would be more dorsal in orthograde primates than in pronograde ones. The Vdtran ratio would be larger in orthograde primates.

The validity of this formula (b/c) depends on the fact that c does not differ significantly relative to body weight among primate taxa (Shapiro, 1995). This is why it is not necessary to rationalise this ratio by using a constant (i.e. body weight /size).

Lateral Leverage of the Transverse Process (Lattran) Ratio

The lever arm for lateral movement or Lattran ratio at the lumbar transverse process is not necessarily longer in the orthograde than in pronograde primates (Shapiro, 1991a), although some researchers predicted that the lever arms for iliocostalis and quadratus lumborum are longer in orthograde primates (Keith, 1923). Such prediction is based on the assumption that the lateral balance is more important in orthograde positional behaviour than in pronograde postures.

It has been shown that mammalian quadrupedal walking also demands axial morphology that restricts lateral bending of the trunk. This gives a rigid attachment for the propulsive hind limb muscles by stabilising the trunk and pelvis (Carlson et al., 1979; English, 1980; Carrier, 1984). In other words, longissimus and iliocostalis play a stabilising role in quadrupedalism by bilateral contraction during each hind footstep (Carlson et al., 1979; Zomlefer et al., 1984 and English, 1980). The restriction of lateral bending distinguishes mammalian quadrupedalism from the reptilian quadrupedalism, whereby lateral undulations increase stride and propulsion (Carrier, 1987). Electromyographic data provided by Shapiro (1991b) suggest that back muscles that produce or restrict lateral trunk movements are equally important for both pronograde quadrupedalism and orthograde behaviour, such as arm swinging and bipedalism.

Ventrodorsal (Vdtran) Ratio or Ventrodorsal Transverse Tip Leverage

The position of the root and the orientation of the lumbar transverse processes were in distinct positions that varied in the different groups of primates Benton, 1967; Shapiro, 1991a). Shapiro's work (1991a, 1995) considered positions of the tips of the transverse processes onto which iliocostalis and quadratus lumborum are inserted (Figure 5.3). From the formula b/c, Shapiro (1991a) noted that a Vdtran of 1.0 indicates that the tips of the transverse processes lie at the level (height) of the dorsal surface of the vertebral body. A higher value of Vdtran means that the tips are dorsal to the dorsal surface of the vertebral body, and a value less than 1.0 indicates that the tips lie ventral to the dorsal aspect of the vertebral body. A negative value indicates that the tips are ventral to the ventral aspect of the vertebral body.

The *Hylobates* have values close to 1.0, great apes and humans more than 1.0 and *Cebus, Cercopithecus, Indri, Propithecus* and *Varecia* less than 1.0 (Shapiro, 1991a).

The position of the transverse process could have some relation to body size (weight). This has been noted by studies by Halpert et al., (1987) in African bovids, and Shapiro (1991a) in platyrrhines such as *Cebus*, prosimians such as *Varecia, Hylobates* and in other hominoids. Shapiro (1991a) strongly recommends further investigations on the position of the transverse processes and particularly the position of its tips.

Vertebral canal or Vertebral foramen

The size and shape of the vertebral foramen or canal can be determined and compared among primates. In humans the vertebral canal is said to have peculiar features not explainable by the size (weight) of the human body (MacLarnon 1993). The size of the vertebral canal gives an approximation of the size of the spinal cord. MacLarnon (1987) identifies differences in the vertebral canal of humans and modern primate species, in the lumbar and sacral regions. Generally, there is little variation in the spinal cord and vertebral canal dimensions of the modern primate species. In fact, according to MacLarnon (1987) the size of the spinal cord relative to body size (weight) appears to have little variation among modern mammals. The above researcher finds that the vertebral canals (hence spinal cords) in two Eocene primate species are relatively small in the cervical and thoracic areas in comparison to modern primates. Again, the vertebral canals in the lumbar region of these fossils are of similar relative size to those of modern primates. Brown et al., (1985) find that the vertebral canal in the cervical and thoracic regions of *Homo erectus* fossil (KNM-WT 15000) is relatively small, compared to that of modern humans. The vertebral canal in the lumbar region, is found to be about the same size as in humans by Brown et al., (1985). It might therefore be that the present form of primate spinal cord and vertebral column, achieved its current form much earlier than during the last few million years of separate hominid evolution. The difference between the size of the spinal cord of *Homo erectus* (KNM-WT 1500) and modern humans is speculated to be due to the young age of the *Homo* specimen. This *Homo erectus* was only about 11 years at time of death (Walker and Leakey, 1993).

The vertebral canal and cord dimensions scale proportionately to body weight. Therefore, if body weight is taken into account, all the dimensions of canal and cord (e.g. height and width at any level, volume and weight) are found to be positively correlated to the body weight (MacLarnon, 1987). Except at the lower lumbar regions where the spinal cord is absent and at or near C1, it is possible to estimate the dimensions of the spinal cord from the vertebral canal dimensions. The human lumbar enlargement is located slightly higher than the beginning of the lumbar region. The vertebral canal is also occupied by meninges, blood vessels. These and the absence of the spinal cord at certain levels do affect estimated size. This is why the results obtained here should not be regarded as the accurate size of the spinal cord. The method can however be applied to rare or extinct specimens, such as fossils.

According to MacLarnon (1987) the heights and widths at the levels of the cervical and lumbar enlargements give the largest values for the dimensions along the vertebral canal. The minimum values are at the thoracic level in the primates investigated. The height of the vertebral canal decreases from C7 into the thoracic region in most modern primates, but in humans, orang-utans, gorillas and KNM-WT1500 fossil there is an increase at C7 that continues into the upper thorax (MacLarnon, 1987). In humans, the average height of the lumbar canal decreases in the cranial lumbar region and in modern primates the lumbar canal height steadily decreases throughout the region (Hinck et al., 1965; Twomey and Taylor, 1988; MacLarnon, 1987). In most modern primates there is a lumbar enlargement after which the canal width decreases towards the sacrum. The width of the lumbar canal varies much more than the height in humans and primates investigated by the above, and at the last lumbar the canal width tends to decrease towards the first sacral vertebra. In species with a prehensile tail, the width of the lumbar vertebral canal shows a rising profile into the sacrum (MacLarnon, 1987).

Larsen and Smith (1981) noted that in humans the height and width at the level of the cervical enlargement do not increase after puberty. Opinions vary as to when maximum sizes of the canal and cervical enlargement are achieved. Larsen and Smith (1981) state that it is two years while Wholey et al., (1958) suggest 3-6 years and Hinck et al., (1962) 18 years. In the thoracic region the increase in dimensions (growth) may be observed up to 10 years or adolescence (MacLarnon, 1987).

Articular facets (zygapophyses)

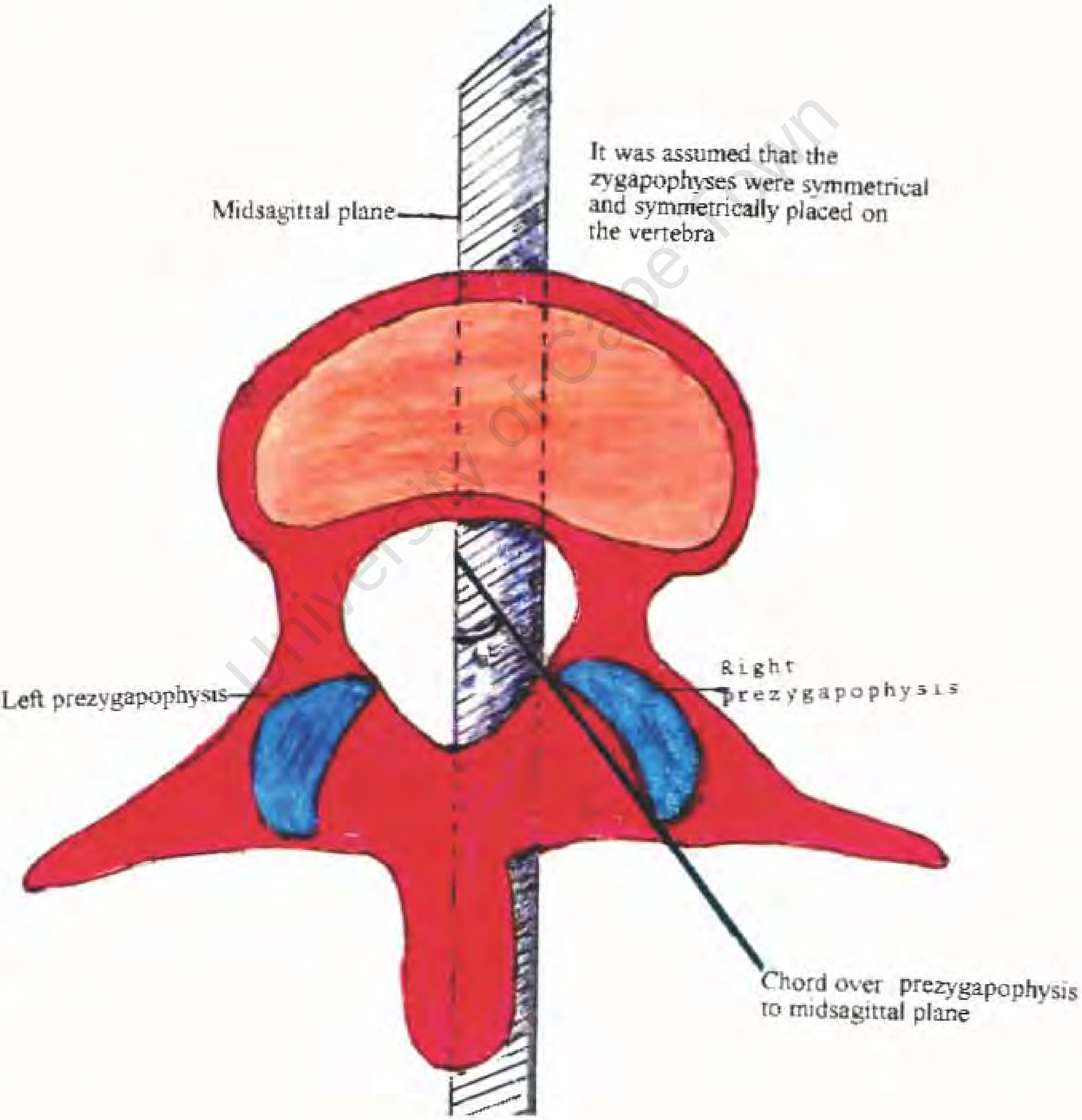
The angle or plane of orientation of the zygapophysis has been described by by Shapiro (1991a) and Latimer and Ward (1993). It is the angle formed between the chord of the curved articular surface of the zygapophysis and the median plane of the vertebra (Figure 2.8). More details on the facet angle and facet area measurements have been covered under "Methods". If the facet angle is 90°, it means that the angle is in a horizontal plane, (i.e. coronal plane) of the vertebra. In such case the joint articular surfaces of the prezygapophyses face dorsally (Shapiro, 1991a). The angles between zero and 90 degrees are for the medially incined articular surfaces and the angles between 90 and 180 degrees are for the laterally inclined (Shapiro, 1991a). The lumbar vertebrae are vertebrae that have prezygapophyseal angles that lie between zero and 90 degrees. Conversely, the thoracic vertebrae have prezygapophyseal angles that are between 90 and 180 degrees.

If the zygapophyseal joint is more sagitally orientated, it means that the articular surfaces of the prezygapophyses face more medially and those of the postzygapophyses face more laterally, as in lumbar vertebrae. The thoracic

Figure 2.8

The facet (zygapophyseal) angle and its estimation

The facet angle "a" is the angle between a chord that passes over the anterior facet to the midsagittal plane. In its estimation two assumptions are made. The first assumption is that the right and left facet surfaces are equal and symmetrical. The second asssumption is that the facets are equidistant from one another in relation to the midsagittal plane of the vertebra.



zygapophyses resist ventral displacement of one vertebra on another. An intermediate orientation of joints would resist both rotation and ventral displacement (Bogduk and Twomey, 1987).

Human clinical studies by Singer et al., (1989a and b) and computer modelling observations by Scholten and Veldhuizen (1985) have clearly demonstrated the vertebral joint structure and their movements. According to Shapiro (1991a) there is very little variation in the angles of prezygapophyses of closely related non-human primates even as their positional behaviour differs immensely.

Humans have a distinctive pattern of change of the orientation of their prezygapophyses along the vertebral column in the lumbar region, from the upper lumbar vertebrae to the first sacral vertebra. The pattern shows an increasing divergence of the distance or gap between the lumbar zygapophyseal articulations in a caudal direction towards the first sacral vertebra. This is in contrast to the convergence of this distance in other hominoids, such as *Pan* (Odgers, 1933) and non-hominoids Shapiro, (1991a). Latimer and Ward (1993) point out that the increasing obliquity of the zygapophyses, and the widening of the laminae and of the vertebral bodies are a result of lordosis and hence unique to bipedalism. The zygapophyseal angles and shape (curvature) need to be analysed more closely because of their importance in stabilising the vertebral column against ventral displacement (Shapiro, 1991a). Halpert et al. (1987), for example, note that the larger African bovids tend to have more curved zygapophyses for spinal rigidity. Shapiro (1991a) observes that the articular facets are flatter in gorillas than in smaller hominoids.

As a result of lordosis which in humans is accentuated by the sharp lumbosacral angle and wedging between L5 and S1 and between L4 and L5, these lower vertebrae would tend to slip ventrally on one another (Davis, 1961; Bogduk and Twomey, 1987). The zygapophyseal angle at these levels is 45 and 50 degrees (Kenesi and Lesur, 1985; Bogduk and Twomey, 1987). This angle is a good compromise in providing resistance to slipping and at the same time allowing rotation (Bogduk and Twomey, 1987).

Zygapophyseal shape, angle and movements

As already mentioned above, the zygapophyseal shape and angle of orientation is important in influencing movements in particular regions of the vertebral column. In rotational movements of the human vertebral column, the axis of rotation is located at the posterior aspect of the intervertebral disc (Cossette et al., 1971; Bogduk and Twomey, 1987). This is in contrast to the common assumption that the axis of rotation lies at or near the zygapophyseal joints (Gregersen and Lucas, 1967; Haher et al., 1989). A rotational axis through the zygapophyseal joints level would probably be functionally problematic because it would subject the vertebral column and discs to great shearing moments (Shapiro, 1991a). Markoff (1972) noted that in the thoracic region, the freedom of rotation facilitated by the coronal arrangement of the thoracic zygapophyseal joints would be unsafe for the joints between T10 and T12 inclusive, in view of the short floating ribs at this vertebral level. This problem is however addressed by (prominent mammillary) epizygal processes on the above vertebrae; the processes in some are quite developed on the diaphragmatic vertebra. The processes form a "mortise" joint with the coronally orientated prezygapophyses, thus restricting the rotational movement, in the absence of the rib girders (Singer et al., 1989a, 1989b; Singer, 1989). According to Ward (personal communication 24 March 1999) loads can be transmitted through the posterior elements ONLY in the lordotic posture, when the zygapophyseal joints are not parallel, but sliding to each other, that is, when the caudal zygapophyses contact the pars articularis.

Thoracic and lumbar zygapophyseal angles have been measured in several species of monkeys, namely *Cercopithecus*, *Cebus*, *Lagothrix*, and in some hominoids giving interesting results. Shapiro (1991a) reports the thoracic angles to be more than 110 degrees in monkeys, and generally less than 110 degrees in hominoids. In the same study Shapiro reports that *Ateles*, *Alouata*, and some prosimians (*Indri*, *Propithecus* and *Varecia*), have angles that are greater than 110 degrees in the lower three thoracic vertebrae. In hominoids (gibbon, great apes, and human) the angles are reported by the same researcher to be 106 and 114 degrees which values cover a wider range than those reported on great apes by other studies.

In spite of the dichotomy between hominoids and non-hominoids there is penultimate lumbar vertebra. Regarding pedicle shape, at LL only the pedicles of human and gibbon increase dramatically in width relative to length. The shape of the pedicles of the great apes remains constant in this respect (Shapiro, 1991a).

The value of the ratio between the pedicle width and the pedicle length (PW/PL) increases at LL in humans and the gibbon but the ratio does not increase in the great apes. In the other taxonomic groups, the reduction of the relative size of the pedicle at L1 and the relative widening of the pedicle at LL is characteristic of both pronograde and orthograde primates. Shapiro (1991a) is of the view that the reduction in the value of the ratio is not related to the increase in the vertebral body area at or near the vertebra in question.

There appears to be a pattern unique to humans and gibbons. Thus following the rib definition of the lumbar vertebrae, only humans and gibbons show progressive increase in the size of the pedicle relative to the vertebral body area throughout the lumbar region (i.e. L2-LL).

D) Vertebral Column Curvatures and Compression Forces

The curves of the vertebral column can be viewed from the lateral aspect of the body as the cervical, thoracic, lumbar and sacral curves (Figure 2.9). They are vital in balancing the trunk on the sacrum during bipedalism in humans.

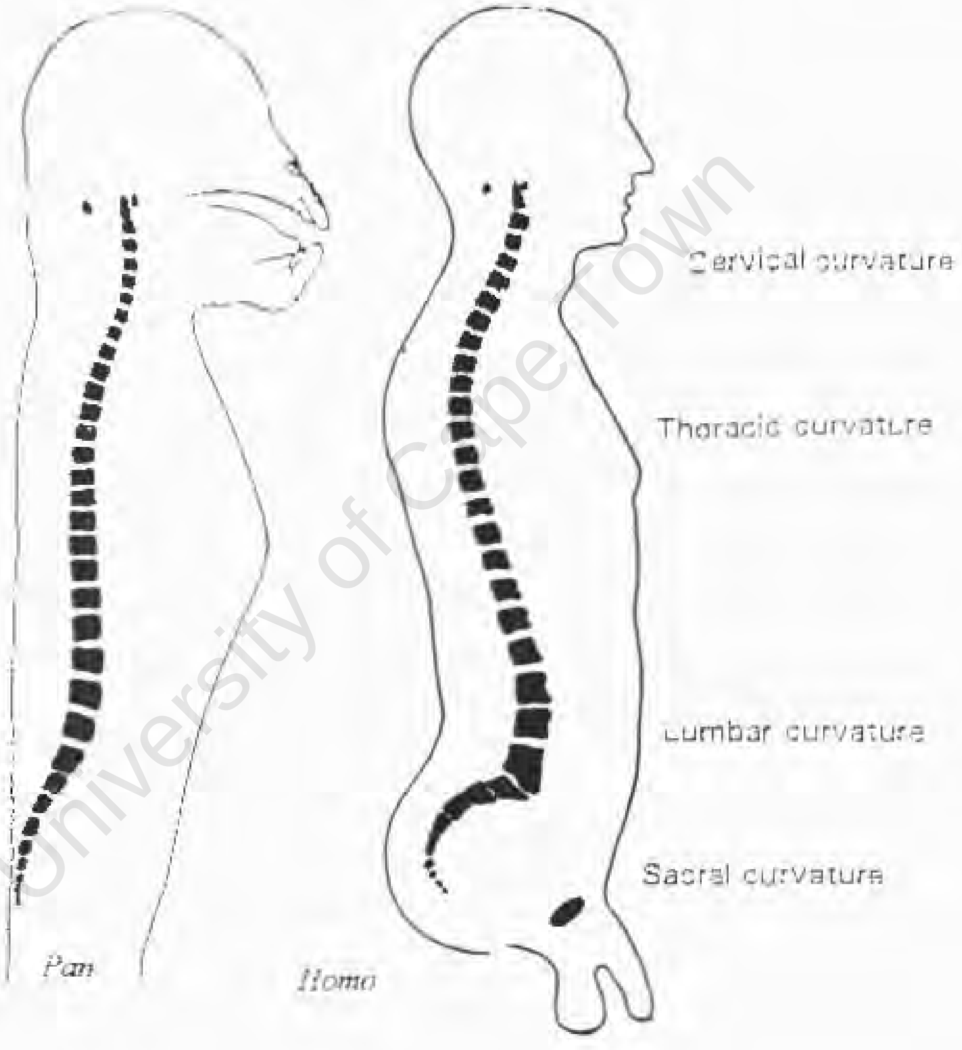
The thoracic and sacral or pelvic curves are concave ventrally, and are known as primary curvatures because they appear early during foetal life and persist thereafter. The sacral curve displays a powerful promontory at the lumbosacral junction or angle, which angle is also established before birth in humans.

The cervical and lumbar curves are secondary or compensatory, since they appear later, and are maintained by ligaments, muscles and, especially in the lumbar region, by the bony structures (vertebrae) themselves. The cervical curvature appears late during intrauterine life. It is further accentuated, firstly when the child begins to hold up its head (3-4 months postnatally), and secondly when it starts to sit (about 9 months postnatally). The view that the cervical curve appears late in intrauterine life has however been challenged by Bagnall et al., (1977), who has studied radiographic pictures of 195 human foetuses, ranging between 8-23 weeks. It was observed in that study that 83%

Figure 2.9

Curvatures of the vertebral column

Midsagittal sections of the primate trunk, through the vertebral column of the chimpanzee and human, showing the curvatures. In humans the curvatures are better developed than in the chimpanzee. There is also a well developed lordotic curve in humans which supports the human bipedal posture.



of the foetuses possess a cervical curve when ossification centres became radio-opaque at about 9.5 weeks of gestation. The observations also emphasise the importance of early onset of foetal movements as a factor in the appearance of an identifiable cervical curve. In the adult humans the cervical curve is the least accentuated; it is convex ventrally, extending between the atlas and the second thoracic vertebra.

Graf et al., (1995) investigated the functional anatomy of the head and neck in quadrupeds. They noted that when at rest both bipeds and quadrupeds flex their atlanto-occipital, atlanto-axial and third cervical joints. At rest the cervical and thoracic articulations in the rabbit, cat, guinea pig and monkey, were held in extremely extended position. The humans articulations of the lower cervical spine were seen to be kept at the midpoint position between maximal flexion and maximal extension, a position that Graf et al., (1995) presume to be related to permanent bipedalism of humans. The authors think that mechanical bony structures, such as specifically shaped articular processes and ligaments, may be responsible for the intrinsic configuration of the cervical curvature.

The thoracic curve is concave ventrally running between the second and twelfth (last) thoracic vertebrae (Warwick et al., 1973). In the upper thoracic region there is often a slight lateral curvature convex to the right in the right handed people and to the left in the left handed (Warwick et al., 1973).

The lumbar curve in humans appears in life at 12-18 months, when walking begins. It is convex ventrally, extending between the last thoracic vertebra to the lumbosacral angle, the convexity of the lower three lumbar vertebrae being more pronounced. The curve is more pronounced in the females than the males, as is also the cervical curve (Knussman and Finke, 1977).

The lumbar curvature is enhanced by the lumbar vertebral bodies, which are wedge-shaped, their longer aspect facing ventrally. If for example, five lumbar human vertebrae are serially articulated outside the body, they form a lumbar curve even without the disc between them (Tobias, 1982).

Rose (1975) made a detailed dimensional study of lumbar vertebrae in humans and noted that the size and shape of the vertebral bodies are equally concerned with the bending and compressive stresses. Rose (1975) further observed that in humans, only the fifth lumbar vertebral body regularly displays greater ventral length (i.e. ventral wedgedness). Rose therefore pointed out that other factors must also contribute to the lumbar curvature, namely the ability of the intervertebral disc to conform; the sexual dimorphism in the first sacral vertebra; and the structure of the pelvis. Clearly Rose (1975) and Tobias (1982) do not agree to some extent on the causes of the lumbar curvature and more studies might be appropriate to clarify this issue. Ground reaction forces are a critical component of musculoskeletal loads during dynamic activities, and could influence the curvatures (Ward, personal communication 24th Mar. 1999).

The ratios of the length of bones (i.e. the vertebral bodies) to the thickness of the discs are 77:23; 82:18; 65:35 in the cervical, thoracic and lumbar regions respectively. On average bone contributes 75% and the disc only 25% (Basmajian, 1975). Using imaging, Boos et al. (1993), noted that in healthy adult persons the water content of the discs was significantly less in the evenings than in the mornings. Green and Silver (1981) observed that astronauts returning from space missions were about an inch taller than their pre-mission height, may be as a result of weightlessness or lack of compression forces. Literature was not available as to whether this increase of height was maintained permanently or lost later.

The intervertebral discs not only link and hold vertebrae together but facilitate intervertebral movements, and due to their elasticity/pliability, they allow tilting and may be a limited degree of torsion between the vertebral bodies. They therefore make the vertebral column receptive to changes and compression forces. The impact of the forces directed vertically through the column is however largely expended by its sinuous curvatures. The effects of the weight, muscle traction and thrust from the feet from walking, running and jumping are also smoothened out by the curvatures and to lesser extent by the discs.

The disposition, shape (geometrical arrangement) and other properties of the zygapophyseal joints, as well as the complex arrangements of ligaments between the adjacent vertebrae, also play a vital part in the movements of the vertebral column. Although the movement between adjacent vertebrae is limited to small ranges, the aggregate change along the whole column is considerable, in terms of bending and axial rotation (Selbi et al., 1993; Dumas et al., 1993).

When the vertebral bodies are viewed from their ventral aspect, they are seen to increase in width from about the second cervical to the third lumbar, in relation to the weight experienced along the column. The serialisation of increasing vertebral size is much less evident in the quadrupedal, obliquely walking apes (Tobias, 1982). After the last lumbar vertebra the width diminishes rapidly to the coccygeal apex. In the last two lumbar vertebrae there is an inverse relationship between the areas of the cranial and caudal surfaces of the their vertebral bodies and pedicle sizes. This suggests that the last vertebra does not bear all the forces but transmits some of these compressive forces from the spine to the pelvis (Davis, 1961).

Clinical and biomedical analyses have shown that functionally the vertebrae and the vertebral column should be regarded as having a ventral (or anterior) and dorsal (or posterior) elements (columns). Such studies have been carried out by White and Hirsch, (1971), Huttov and Cyron, (1978), Shah et al., (1978), Adams and Huttov, (1980, 1983), Denis, (1983), Jayson, (1983) and Scales et al., (1988). The dorsal column that consists of the zygapophyses and neural arches has been shown by the above researchers to take part in the weight transmission in humans. For a long time it was strongly believed that only the vertebral bodies and discs (i.e. the ventral elements/column) were the ones that bear the load through the vertebral column. In an attempt to measure the "stiffness" between the intervertebral joints, studies have been carried out in vitro in isolated "motion segments", consisting of two vertebrae with all their ligaments and disc intact (Nachemson, 1966; Markolf, 1972). Forces of various magnitudes and direction are loaded to a motion segment with and without the posterior element in place. It has been observed in such experiments that the zygapophyseal joints (i.e. posterior elements) resist 16% of the compressive force during the upright position. Other studies, however, show that during flexion of the spine, as occurs in erect sitting, whereby lordosis is usually flattened out, the compressive force is transmitted via the disc/body (i.e. ventral elements).

The pars articularis is that part of the lamina between the prezygapophyses and postzygapophyses of each side. Some studies suggest that in the lumbar vertebrae, compressive load can be transmitted across the zygapophyses through contact of the tip of the zygapophysis with pars interarticularis (Adams and Huttov, 1980, 1983). Similar conclusions have been drawn from loading experiments, using pressure recording paper at the zygapophyseal joints (Yang and King, 1984). Strain gauge measurements have also demonstrated the facet-lamina contact or transmission and have shown that axial compressive loading produces compression strains near the bases of the pedicles as well as on the dorsal and ventral surfaces of pars interarticularis.

Extension, that is to say "posterior offset loading", brings increased compressive strain in the bases of the pedicles, and compressive as well as tensile strains in the pars interarticularis. In contrast, flexion of the spine, i.e. "anterior offset loading", brings smaller compressive strains in the same areas (Shah et al., 1978; Lin et al., 1978; Jayson, 1983). Now if the zygapophyses, pedicles and laminae are involved in resisting the load during spine extension (or in any posture), the morphology of these structures must differ in pronograde and orthograde animals (Shapiro, 1995).

The vertebral column of quadrupeds has been likened to a horizontal bow made of the lined vertebrae. The string of the bow is likened to the rectus abdominis muscles that prevent hyperextension or sagging of the bow (Badoux, 1974; Preuschoft, 1978; Preuschoft et al., 1988) (Figure 2.6). The pronograde spine is not subjected to prolonged vertical weight (loading) as is the orthograde spine. The compressive forces along the spine of a pronograde primate will be resisted largely by anterior part (i.e. vertebral bodies and discs) (Figure 2.6). It might be speculated that the more orthograde a spine is the larger the relative size of the dorsal elements, since the larger part of the compressive force will be transmitted through this area.

Finally, in spite of the resilience of the spine injuries can occur. Spinal injuries can occur in forced flexion or extension, impact on the back, falling headlong or landing on feet from a height, carrying loads on the head or lifting up such loads. Serious back injures can result in paralyses of various degrees depending on the severity and level of the spinal cord segments affected. The vertebral column is therefore maintained in position by strong ligaments and muscles that help it to resist unnecessary strenuous movements.

Chapter 3

BACKGROUND: MUSCLES OF THE BACK

A) General structural arrangement

The muscles controlling trunk and back movements are attached to the vertebrae, ribs, skull and fascia. Shapiro (1991a) claims that anatomical literature has not been specific on the attachments of human back intrinsic muscles, adding that various authors have treated them as one mass (erector spinae) except in the thoracic and cervical regions. However there are many detailed accounts of the anatomy that attempt to specify these attachments reasonably in the human (Gardner et al., (1965); Warwick et al., (1973); Bogduk (1973, 1980); Moore (1982); MacIntosh and Bogduk (1986)). In order to understand the role of the vertebral column in the movements of an animal, a clear knowledge of the attachments and actions of the back muscles is necessary. According to Warwick et al., (1973) the trunk muscles in humans consist of the following six groups (Figures 3.1 a, b, 3.2, 3.3, and 3.4).

- Deep back muscles
- Suboccipital muscles
- Thoracic muscles
- Abdominal muscles
- Pelvic muscles
- Perineal muscles

For the purposes of this study only the deep back muscles will be described, because these are the ones that have the closest relation to the vertebral column (Warwick et al., 1973).

Figure 3.1 a
Surface land-marks of the back

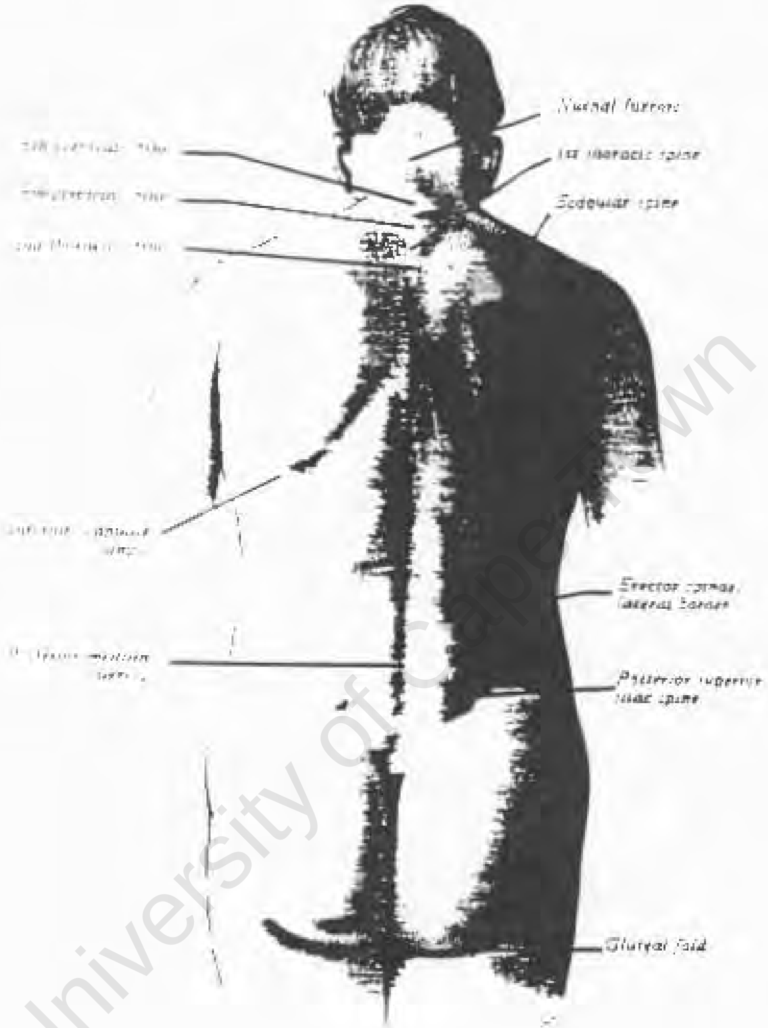


Figure 3.1 b

Deep muscles of the back

The erector spinae is displayed on the right. On the left the muscle has been removed except its longissimus cervicis portion. From Warwick et al. (1973)

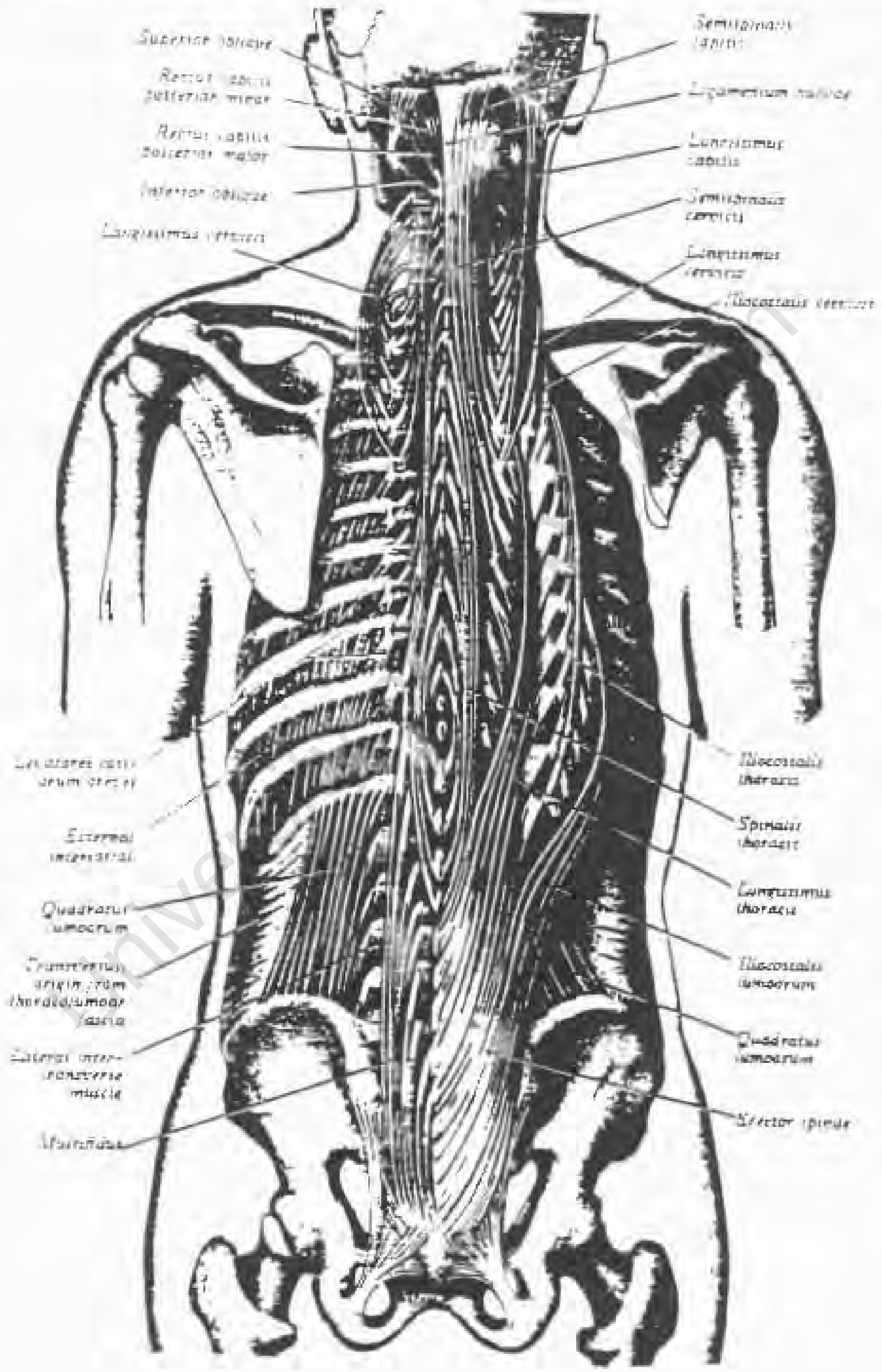


Figure 3.2
A transverse section through the middle of erector spinae muscle showing its close relation to the spinous and transverse processes. From Warwick et al. (1973)

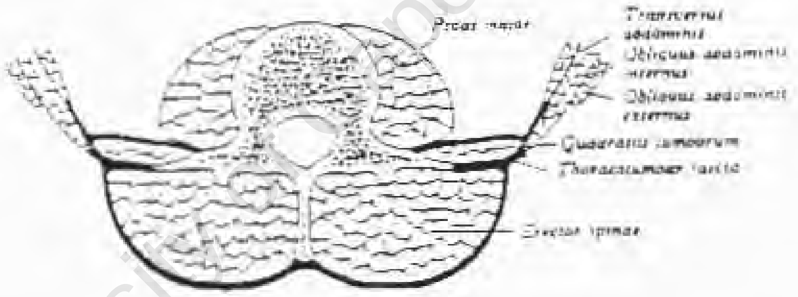


Figure 3.3

Muscles of the back. Note their close relation with the vertebral processes and the ribs:-

Spinalis with the spinous processes, longissimus thoracis with the ribs and thoracic transverse processes, longissimus capitis with the spinous and transverse processes in the cervical and upper thoracic regions, semispinalis capitis with the cervical spinous processes and the transverse processes in the upper thoracic region and iliocostalis mainly with the ribs and 3-4 lower cervical transverse processes. The ribs are attached to the vertebral bodies and transverse processes through strong costovertebral ligaments. Therefore the action of muscles such as iliocostalis on the vertebral column should not be under-rated. From Moore (1982).

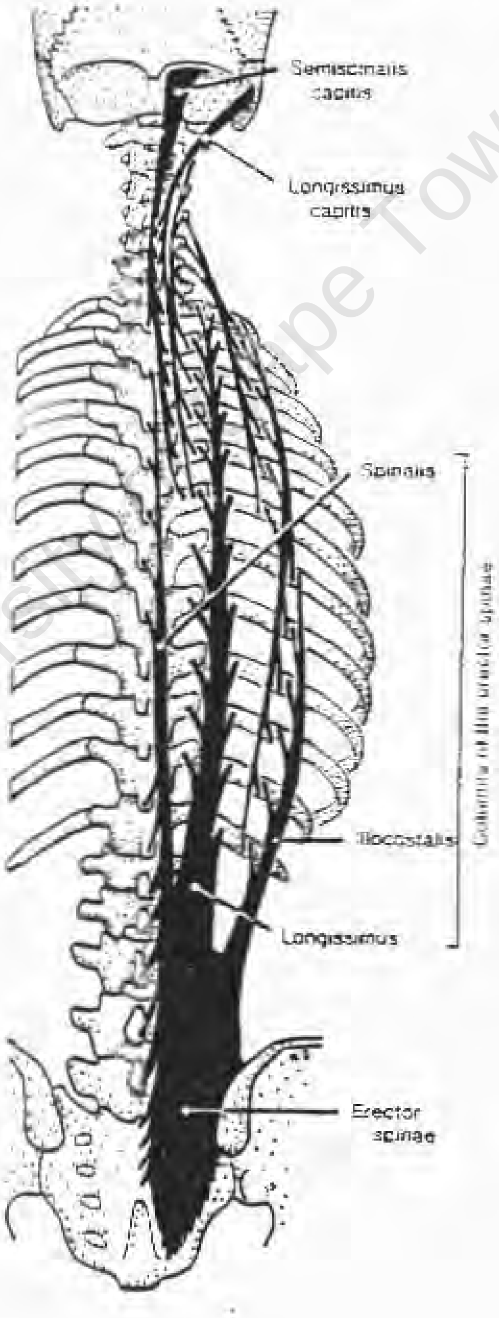
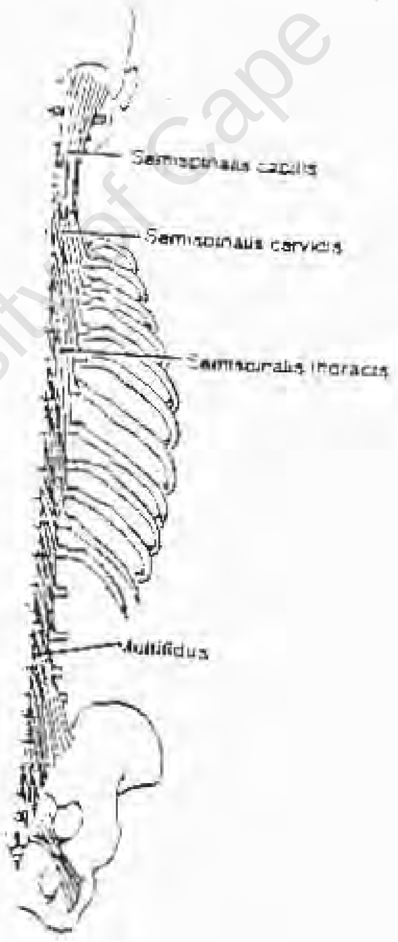


Figure 3.4

Deep muscles of the back
Note the deep oblique layers of the back muscles i.e. transversospinalis consisting of semispinalis, multifidus, and (not shown in the drawing) rotators. From Moore (1982)



i) Erectore spinae (sacrospinalis)

This muscle consists of a longitudinal series extending from the sacrum to the base of the skull and splits into three columns namely, iliocostalis, longissimus and spinalis muscles. The fibres of erectore spinae generally run in the cranial direction. The longissimus division however extends laterally from the spines to the transverse processes. This division of longissimus may be referred to as the spinotransversus muscle in contrast to the deeper muscle known as the transversospinalis. The erectore spinae has two origins:

- A strong aponeurotic covering of the fleshy origin of multifidus that arises from the sacral spines (i.e. median sacral crest), lumbar and thoracic spines. It also has an origin from the sacral transverse processes (lateral sacral crest) and adjacent ligaments.
- A fleshy origin from the interosseous sacroiliac ligament and the part of the iliac crest above this.

In the gorilla, Raven (1950) gives the origin of erectore spinae as the lumbodorsal fascia and crest of the ilium and categorically doubts the origins on the sacroiliac ligament and sacrum. At about the level of the last rib, the human erector spinae divides into three columns that ascend dorsally onto the thorax where they are inserted into the ribs and vertebrae. Additional tendinous slips arise from the above insertions to continue with the three columns cranially into the neck, (specifically onto the posterior tubercles of the cervical transverse processes). The three columns of erector spinae are arranged as follows:

(a) Spinalis

This narrow column is medial, runs along the spines and consists of several slips that extend into the thoracic spines as spinalis thoracis. Inconstant slips of this muscle also extend into cervical spines as spinalis cervicis, and extensions into the head as spinalis capitis which sometimes blend with semispinalis capitis (Warwick et al., 1973).

The spinalis cervicis when present has attachments onto the spines of the axis, and occasionally on the spines of C3, C4, C7, T1 and T2. In the gorilla spinalis cervicis, when present, is difficult to separate from semispinalis cervicis (Raven, 1950). Spinalis capitis is not mentioned in the gorilla by Raven.

(b) Longissimus

This muscle consists of longissimus thoracis, longissimus cervicis and longissimus capitis running to the thorax, neck and head respectively. Longissimus thoracis is the largest intermediate column comprising the bulk of erector spinae. In the lumbar region, where it is still fused with iliocostalis lumborum, some fibres are attached on the whole length of the dorsal surfaces of the transverse processes. More fibres are attached on the accessory processes of the lumbar vertebrae, as well as on the middle layer of the thoracolumbar fascia. In the thoracic region, its insertion is on the tips of the transverse processes of all the thoracic vertebrae by rounded tendons, and by fleshy parts to the lower 9-10 ribs, between their angles and tubercles (Warwick et al., 1973). According to Raven (1950), the thoracic insertions in the gorilla are into "the costotransversal articulations of all the ribs".

The longissimus cervicis muscle originates medial to the above muscle. The attachments for longissimus are via long tendons to the transverse processes of T1 to T4/T5 and to the posterior tubercles of the transverse processes of C2 to C6.

Longissimus capitis lies between the longissimus cervicis and the semispinalis capitis, starting from the transverse processes of T1 to T4/T5 and from the articular processes of C3/C4 to C7. It is inserted at the mastoid process, deep to splenius capitis and the sternocleidomastoid muscles. It must be noted that longissimus is the only column of erectore spinae to reach the skull through this part.

EMG analyses of this muscle in primate quadrupedalism also show consistent activity as the contralateral foot touches down, as in cats and dogs. Its activity pattern at ipsilateral touchdown, is variable (less consistent) among the primates than among the non-primates (Shapiro and Jungers, 1994).

However in the baboon longissimus activity is as in non-primates, that is it has two consistent bursts of activity, one at contralateral touchdown and the other at ipsilateral touchdown.

(c) Iliocostalis (iliocostalis lumborum, thoracis and cevicis)

This muscle is also referred to as iliocostocervicalis (Warwick et al., 1973). It is the smaller of the lateral part of erectore spinae, extending from the ilium to the transverse processes and angles of the ribs as follows:

- The iliocostalis lumborum is inserted into the angles of the lower six ribs, by flat tendons, and onto the tips of the lumbar transverse processes (Bogduk and Twomey, 1987).
- The iliocostalis thoracis runs from the upper borders of the angles of the lower six ribs, medial to the insertions of the iliocostalis lumborum. It inserts onto the angles of the upper six ribs and to the dorsum of the transverse process of the seventh cervical vertebra.
- The iliocostalis cervicis arises from the angles of the 3rd to 6th ribs medial to the insertion of iliocostalis thoracis and inserts to the posterior tubercle of the transverse processes of C4-C6.

This muscle has a relatively low activity in the baboon as shown by its EMG activity pattern (Shapiro and Jungers 1994), but when it acts it does so during contralateral foot touchdown and to a lesser extent during ipsilateral touchdown. This pattern resembles the patterns of the other two back muscles, as well as the pattern reported for cat quadrupedalism. In the chimpanzee iliocostalis shows a different recruitment pattern from the pattern shown by multifidus and longissimus. Unlike these muscles, the chimpanzee iliocostalis is active consistently only around the touchdown of the contralateral foot; its action at the ipsilateral touchdown is very variable (inconsistent) as that of the multifidus.

ii) Transversospinalis

Transversospinalis muscle is deep to erectore spinae muscle. This muscle has numerous slips that run obliquely craniomedially between the transverse processes and the spines. It has three layers, namely semispinalis, multifidus and rotatores.

a) Semispinalis

This is the superficial part of transversospinalis. Its bundles span 4-6 segments and consist of semispinalis thoracis, semispinalis cervicis and semispinalis capitis. The thoracic part starts from the upper thoracic transverse processes and the cervical part from the lower cervical articular processes (Gardner et al., 1965; Moore, 1982). However Warwick et al. (1973) give the origins of the thoracic part as being from the transverse processes of T6 to T10, and the origin of semispinalis cervicis as T1 to T5/T6 transverse processes. Their insertion is on the spines of C6 to T4 and C2 to C5, respectively. Semispinalis capitis is a relatively broad muscle with vertical fibres, arising from the tips of the transverse processes of the

- upper six or seven thoracic vertebrae and sometimes including C7
- articular processes of C4, C5 and C6
- the spine of C7 or T1

Its insertion is cranial on the occipital bone, between the superior and inferior nuchal lines.

(b) Multifidus

The muscle consists of tendinous fascicles lying under the semispinalis muscle, in the groove lateral to the vertebral spines, from the sacrum to the axis. The fascicles arise from the following places.

- dorsum of the sacrum
- aponeurosis of the spine
- posterior superior iliac spine and dorsal sacral iliac ligaments
- lumbar mammillary processes
- all thoracic transverse processes
- articular processes of the lower four cervical vertebrae

Each fascicle passes obliquely cranially and medially. The fascicle lengths vary from those connecting adjacent vertebrae to those connecting two, three and even four vertebrae. They are most developed in the thoracic region, but are found along the whole spine length.

EMG studies were carried out by Shapiro and Jungers (1994) on multifidus in baboon, orang-utan and chimpanzee, during quadrupedal walking; they observed that the activity pattern of this muscle in the above species resembles that reported for the cat. But the activity pattern during the touchdown of the contralateral foot is more consistent in the primates, while the pattern at the touchdown of the ipsilateral foot is more variable among the primates.

(c) Rotatores

Rotatores are small quadrilateral muscles each connecting the cranial and dorsal aspects of the transverse processes to the caudal and lateral surfaces of the laminae of the cranially adjacent vertebra. They are usually eleven in number. The first are between T1 and T2 and the last being between T11 and T12, depending on the presence of a thirteenth thoracic vertebra the last may be between T12 and T13, and the total number may then be twelve.

iii) <u>Interspinales and Intertransversarii</u>

These are interspinous and intertransverse muscles, which are well developed in the cervical and lumbar regions, and generally absent in the thoracic spine. The interspinous muscles connect the bifid tubercles of adjacent spines of cervical and lumbar vertebrae, and lie along the interspinous ligaments. The intertransversarii (anterior and posterior) connect adjacent respective tubercles of the transverse processes. According to Gardner et al. (1965), the most cranial intertransverse muscle is the posterior rectus capitis lateralis. The intertransverse muscles are well developed in the lumbar region.

B) **Action of the back muscles**

The more longitudinal a course of the back muscle is, the more the muscle will influence flexion and extension of the vertebral column (Gardner et al., 1965). The erector spinae is the chief extensor of the back, while the prevertebral and abdominal muscles are the flexors. According to Basmajian (1975) much of the back extension and flexion takes place in the lumbar region. Warwick et al., (1973) adds that the longissimus thoracis and cervicis extend the vertebral column and can bend it laterally, while longissimus capitis extends the head and turns the face to the side of the muscle that is acting unilaterally. The iliocostal cervicales are extensors and lateral flexors. Spinales are also identified as extensors. Shapiro (1991a, 1991b), noted that the above mentioned muscles stabilise the trunk in quadrupedal primates, and that longissimus as well as iliocostalis extend the lumbar region and stabilise the trunk during bipedal walking. Other authors have similar accounts on longissimus and iliocostalis (Waters and Morris, 1972). The immediately mentioned muscles also continue to give stabilisation during swinging and climbing (Shapiro and Jungers, 1988, 1994).

Multifidi are the main rotators of the trunk aided by rotatores, semispinales, external and internal oblique, quadratus lumborum and psoas major. As already mentioned, all the above muscles stabilise the trunk in human and other forms of primate locomotion (Waters and Morris, 1972). In tailed primates, the most caudal fascicles of multifidus form the extensor caudae medialis muscle. The multifidus force is indicated by the dorsal projection of the spinous process, which can be referred to as the multifidus lever arm. In *Indrid*, which mostly leap, this lever arm is relatively longer than in those prosimians which leap less frequently (Shapiro, 1995). A similar relationship is manifest when the lever arms in *Indrid*, hominoids and atelines are compared (Shapiro, 1991a). The difference in the lever arms reflects more efficient back muscle leverage of the indrids. However, among the closely related primates the dorsal projections of the spinous process (lever arm), do not show much variation.

The head is mainly rotated by splenius, semispinalis capitis and sternocleidomastoid muscles. It should be noted that the tubercle of the atlas is free and has no muscle attachments. So while the atlas can be extended and flexed together with the neck, it can freely rotate independent of other movements in the region.

Quadratus lumborum and psoas major inserting on the ventromedial and ventrolateral aspects of the transverse processes respectively, also act together with multifidus, longissimus and iliocostalis muscles to stabilise the trunk during bipedalism (Waters and Morris, 1972).

Boyd et al., (1965) noted that quadratus lumborum fixes the last rib during respiration. The leverages of longissimus, iliocostalis, psoas major and quadratus depend on the shape and position on the vertebral body, and the orientation of the tips of the transverse processes. The tips could be orientated to point cranially, caudally, ventrally or dorsally, and their position could be dorsal or ventral to the dorsal surface of the vertebral body.

According to Gardner et al., (1965), during full flexion of the back, as in bending to touch the toes, the erector spinae relaxes and the strain is taken over by ligaments. On reversing this movement, that is in extension of the back, the erector spinae is inactive at first, and the initial phase of extension is carried out by the iliofemoral ligaments, the hamstrings and glutei maximi. Therefore lifting a load or unbending suddenly from a fully flexed posture, is biomechanically disadvantageous, and can injure the back ligaments, intervertebral discs and muscles. The back muscles are prime movers with postural and synergistic functions in locomotion. For example, when one stands on one leg the erector spinae contracts and helps to keep the balance. During walking the erector spinae of either side contracts alternately as the weight shifts from one supporting foot to another.

Though electromyographic (EMG) observations on the function of primate limb muscles during quadrupedalism have been well documented, the same is not true for the back muscles. Shapiro and Jungers (1994) however carried out EMG analyses of the multifidus, longissimus and iliocostalis in the baboon *(Papio anubis)*, chimpanzee *(Pan troglodytes)*, and orang-utan *(Pongo pygmaeus)* during quadrupedalism. The recruitment patterns of the above muscles indicate that they restrict trunk movements during quadrupedalism by contracting during touchdown of one or both feet, but becoming more active with touchdown of the contralateral foot. It was also observed that the EMG patterns of the back muscles were similar in primate and non-primate mammals. The EMG patterns for the chimpanzee, gibbon and human, when walking bipedally, are also reported to be similar (Shapiro and Jungers 1994); the orang-utan bipedal EMG pattern differs from that of the other above primates however. This fundamental similarity in the back muscle function across species and locomotive behaviours is consistent with data that are mentioned later. That data indicate that there is conservatism in the evolution of the neural control of the tetrapod hind limb movements. However, the data do not rule out the fact that some aspects of primate neural circuitry are unique as can be shown by EMG studies based on fore limb muscles and spinal lesions.

Quadrupedalism in primates and non-primate mammals has been investigated in various studies by Prost (1965), Kimura et al., (1979), Rollinson and Martin (1981), Larson and Stern (1987,1989) and Demes et al., (1994). In the studies just cited, it was observed that primates prefer to use a diagonal-sequence gait, referred to as Lh-Rf-Rh-Lf, rather than the lateral-sequence gait, Lh-Lf-Rh-Rf. (R = right, L = left, h = hind and f = front, in reference to the limbs). However, other studies have also shown that the diagonal-sequence gait is not used exclusively by primates (Prost 1965). Rollinson and Martin (1981) hypothesised that a diagonal-sequence gait is more stable for primates than the lateral-sequence gait, because the centre of gravity is more posteriorly located in primates than in other mammals. Kimura et al., (1979) point out that in order to propel themselves, primates use "front-steering, rear-driving", rather than "front-steering, front driving". The propulsion of the primates from the rear is a result of most of their weight being supported by the hind limbs, and freeing the fore limbs for other manipulations (Kimura et al., 1979; Vilensky 1989; Vilensky and Larson 1989). However other studies have shown that both primates and non-primates predominantly use their hind limbs for propulsion (Demes et al., 1994, Pandy et al., 1988).

Convincing evidence has also been brought to show that the location of the centre of gravity is towards the posterior. The increased weight of the hind limbs does not adequately explain how it influences the primates to prefer the diagonal sequence-gait. The difference in the location of the centre of gravity between cats and primates has been reported to be marginal by Velinsky (1989), and Velinsky and Larson (1989). These authors noted that although the diagonal-sequence gait is preferred in primates, the lateral-sequence gait is also common in primates. They therefore suggested that the reasons for the preference for the diagonal-sequence gait might be in the neural control mechanisms, rather than in the morphological set-up. EMG analyses also show that there is similarity in the activity patterns for muscles of the hind limbs of primates and non-primate, and between mammals and other tetrapods, thus suggesting that there is an evolutionary conservatism in this region.

The EMG analyses for the muscles in the fore limb have different activity patterns for quadrupedal primates and non-primates. These variations are not simply due to biomechanical factors but possibly the result of advanced neural control of the limb, culminating in locomotive and manipulative activities and in being manipulatable (Vilensky and Larson 1989; Larson and Stern 1989). From the above studies, it can be seen that further investigations on the primate muscular movements are still necessary from all aspects. Studying the morphometric aspects of the vertebral column elements can be one of the ways of understanding how the leverage of the axial muscles and associated forces affect the movements in the area, and locomotion of the individual in general. EMG studies by Shapiro and Jungers (1988) indicate basic similarity in the recruitment patterns of muscles of the back of humans on the one hand, and non-human hominoids. This similarity in a way might be related to the conservatism of the muscles of the hind limb that has been mentioned above, in primate and non-primate quadrupedalism. The conservatism of the activity pattern of the back muscles across species raises the question, whether or not back muscle function differs with various types of locomotive behaviour. Examining the morphometry of the vertebral columns of primates that manifest different postures and locomotion might give some indication of the answer to the above question.

According to studies mentioned in the above paragraphs, there might be resemblances between primates and non-primates in the recruitment patterns of back muscles during quadrupedalism. According to Shapiro and Jungers (1994), the activity patterns for the back muscles of the baboon (*Papio anubis*), more closely resemble the patterns for cats and dogs than the patterns for other hominoids, in this case chimpanzee and orang-utan. The above authors further note that the chimpanzee also deviates in some ways from the non-primate patterns by, a) having variable activity patterns of longissimus throughout the swing phase, and b) having no ipsilateral activity pattern of the iliocostalis.

Now the deviations in the back muscles of chimpanzees are also found in the patterns of bipedal EMG, indicating a resemblance between the back muscle activity patterns of the quadrupedal hominoid and a bipedal hominoid (Shapiro and Jungers 1994). From EMG studies these authors further show that the chimpanzee uses its three long muscles similarly during quadrupedalism and bipedalism, in spite of the different mechanical demands placed on the back by quadrupedalism and bipedalism. In both quadrupedalism and bipedalism, multifidus and longissimus respond to the touchdown of each foot, but more so on the contralateral burst; the iliocostalis responds only to the contralateral touchdown. It is clear that the same basic activity patterns of back muscles controls the trunk in quadrupedalism and bipedalism. The recruitment pattern of iliocostalis and to some extent of longissimus in chimpanzee quadrupedalism is more similar to that of a chimpanzee walking bipedally, than to that of a cat walking quadrupedally (Shapiro and Jungers 1994). The recruitment pattern for iliocostalis during bipedalism in orang-utan is similar to the recruitment pattern for the same muscle in bipedalism of the chimpanzee, gibbon and human (Shapiro and Jungers 1988). Its activity is associated with the touchdown of the contralateral foot and with restricting excessive movement of the trunk in the direction of that contralateral foot. The multifidus and longissimus contract bilaterally with the touchdown of each foot in the chimpanzee, gibbon and human, but in the orang-utan the two muscles respond to contralateral touchdown only, as the iliocostalis does.

The baboon, chimpanzee and orang-utan exhibit similar recruitment patterns for each of the three back muscles during quadrupedalism (Shapiro and Jungers 1994). The above primate patterns are also similar to those reported for non-primate mammals. That is, both primates and non-primates studied by the above authors show that each of the back muscles, except iliocostalis in chimpanzees, contracts bilaterally with or just before touchdown of each foot.

Zomlefer et al., (1984) noted cats that in walking the back muscles do not initiate movements but "compensate for and minimise movements of the trunk". This stabilises the pelvis and provides a rigid origin for muscles acting on the hind limb (English 1980). The study by Zomlefer et al., (1984) agrees with what Carlson et al., (1979) and English (1980) noted in cat quadrupedalism, where only limited angular movements in the sagittal and frontal planes were noted. In spite of the above similarities between the EMG patterns of primates and those of other mammals, the chimpanzee has the following differences. First, as mentioned earlier the chimpanzee does not recruit the iliocostalis at ipsilateral touchdown (i.e. recruits it only at contralateral touchdown). Secondly, when both ipsilateral and contralateral activities are present in the chimpanzee EMG, they are about the same amplitude. The explanation for the unique activity of the chimpanzee iliocostalis may lie in the position of the muscle itself. The iliac blades being mediolaterally expanded in the chimpanzee, the iliocostalis lies more laterally than in monkeys and cats. This position gives the iliocostalis an advantage of being an efficient leverage for lateral flexion, which enables it to counteract movements of the trunk on contralateral touchdown, during both quadrupedalism and bipedalism. In the orang-utan the iliocostalis is also laterally situated, and its contralateral activity is indeed present, while the ipsilateral is minimal. Lastly, overall body shape, that is thoracic width and depth might result in kinematic differences in the muscle activity patterns in quadrupedalism in the chimpanzee and orang-utan on one side versus the other quadrupeds, such as baboon and cat.

During bipedalism in the chimpanzee, gibbon and human the more medially placed multifidus and longissimus contract bilaterally with each step. This controls the sagittal plane movements of the trunk. The laterally placed iliocostalis contracts unilaterally, at contralateral touchdown, and thus controls the trunk movement in the oblique and frontal planes (Shapiro and Jungers, 1994). In the chimpanzee, muscles which control the quadrupedal trunk movements (stabilisers of the pelvis) are responsible for the control of the sagittal and lateral trunk movements (Shapiro, 1991a). In the orang-utan there is an awkward bipedal gait because this species is not normally bipedal; in fact it has not been seen walking bipedally in the wild (Sugardjito, 1982). So it is not surprising that the activity patterns for the back muscles of the orang-utan, during bipedalism, are different from the patterns for the other hominoids (Sugardjito 1982). All the three back muscles of orang-utan respond only to contralateral touchdown during bipedalism. This indicates that control of the trunk movements from side-to-side (frontal plane balance) is critical in bipedalism. In the chimpanzee, gibbon and human, where bipedalism is relatively more developed and more easily to practised than in the orang-utan the activity patterns of the back muscles that are associated with contralateral touchdown are more amplified. This means that these muscles are highly being activated during bipedalism, and are therefore important for that exercise. The activation of the back muscles that are associated with contralateral touchdown prevents the trunk from swaying from side to side during bipedalism, in the chimpanzee, orang-utan and human. The orang-utan, which has naturally specialised in suspensory movements, has to struggle during bipedalism by exaggerating the activity and movements of the muscles associated with contralateral touchdown. Therefore, the orang-utan has an unusual bipedal gait. In the orang-utan it can therefore be seen that, in spite of the earlier mentioned similarities between the activity patterns for back muscles in primates and other mammals, the patterns may differ between quadrupedal and bipedal walking. It is speculated by Shapiro and Jungers (1994) that the activity patterns of the back muscles in vertical climbing and bipedalism might be similar. They propose that this might mean that the ancestor of bipedal *Homo* would not have had to undergo major changes in the back muscles in the course of evolution to bipedalism, assuming that the ancestor was a vertical climber.

Chapter 4

BACKGROUND: THE BIOMECHANICS OF THE PRIMATE POSTCRANIAL SKELETON AND ITS ADAPTATIONS FOR THE ERECT POSTURE

A) Orthograde posture and balance

The postcranial skeleton supports the muscles, and acts as a lever system to facilitate muscle action. In humans, apes and other primates, the postcranial skeleton differs in shape and relative, size and these differences are reflected in the length of the limbs and the trunk. Biomechanics and locomotion in early hominids have been studied by Biewener (1990), Duncan et al., (1994), Langdon et al., (1991) McHenry (1994) and Susman (1989) from whose studies the literature below is obtained.

In a primate standing upright, it is essential that the body centre of gravity remains directly over the rectangle or triangle formed by the supporting feet (Figure 2.5). Four-footed animals have a large supporting rectangular base formed by the outer margins of the four feet, and therefore have little difficulty in maintaining their balance (Figure 2.5). Since the base prescribed by the feet in humans is small, a little displacement of the centre of gravity can move it outside the supporting triangle, easily causing an imbalance. The postcranial skeleton of a primate that has to sustain locomotion in an upright posture must therefore meet the structural requirements of maintaining this balance. Although the central nervous system and muscles play a vital role in maintaining balance, this should be viewed in terms of co-ordination of an already existing and conforming bony structure, especially in humans. It is difficult to maintain an erect posture if the bony framework does not conform to it. The centre of gravity in humans is located in the mid-line, just anterior to the second sacral vertebra (MacConaill and Basmajian, 1969). When a person is standing at rest in the upright position, the line of the centre of gravity perpendicular to the ground bisects the lines joining the following body points with each other (Figure 2.5):

- Mastoid processes
- Anterior (ventral) aspect of the two shoulder joints
- Dorsal close to the hip joints (Tardien, et al; 1993)
- Anterior aspect of the knee joints
- Anterior aspect of the ankle joints

The muscular activity necessary in maintaining the upright posture in humans is minimal and economical due to the interplay of ligaments. For example, the strong iliofemoral ligament binds the femur to the ilium anteriorly and prevents the trunk from falling backward at the hip joint (Figure 4.1). In chimpanzee bipedalism, the bent-knee-bent-hip posture is uneconomical, since it puts much strain on the hamstring, gluteal and quadriceps muscles (Aiello and Dean, 1990). (Figures 4.1 and 4.2). The ability of humans to sustain standing and balancing comfortably in the bipedal posture is a result of certain features of the human postcranial skeleton that are not present in the other primates, e.g. in the chimpanzees. When a chimpanzee stands in the upright position, its pelvis rotates at the hip joint, raising the trunk, but at the same time bringing the ischium closer to the femur (Figure 4.2). This has the effect of shortening and reducing the leverage of the hamstring muscles (Figure 4.2).

The human pelvis has a small angle at the greater sciatic notch. That acute angle allows the trunk to be held upright without the ischial tuberosity abutting onto the posterior aspect of the femur. This means that the human pelvis need not rotate to bring the trunk in the upright posture. This reduced angle between the ilium and ischium enables the upper part of the trunk (vertebral column) to be maintained in a vertical posture without hindering or straining the hamstring muscles (Figures 4.1). The angle is very wide in the apes, resulting in the need for rotation of the pelvis and the above problems.

There are spinal curves, particularly the lumbar curve in humans, which are vital in placing the centre of gravity within the rectangle of the human feet. The curves also help in balancing the trunk upright on the sacrum, as has been

Figure 4.1

Chimpanzee and human gluteal muscles (lateral view)
In the chimpanzee gluteus medius and gluteus minimus act as medial rotators and extensors of the hip during locomotion. In humans the two muscles are abductors and lateral stabilisers of the trunk. From Conroy (1997).

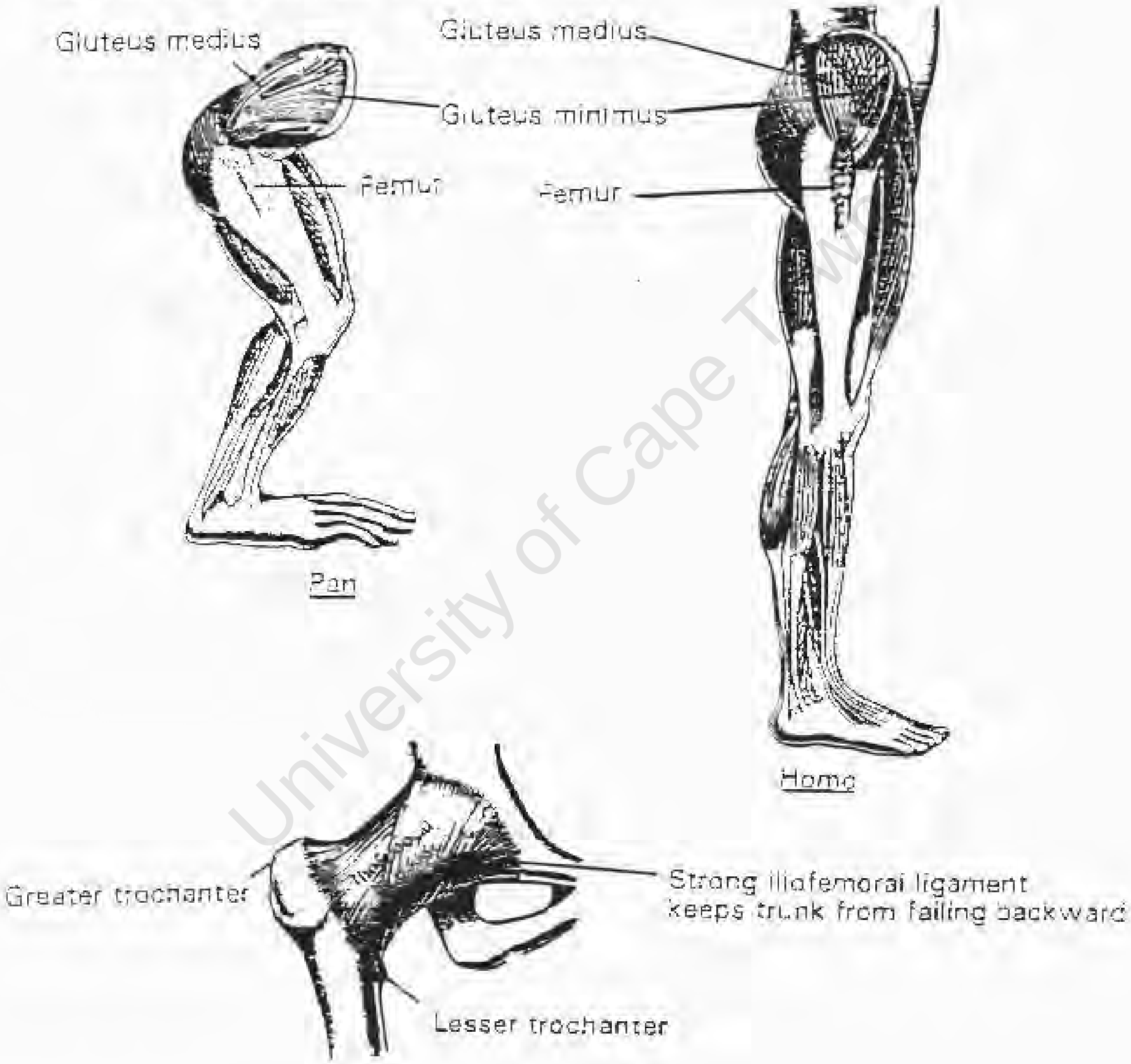
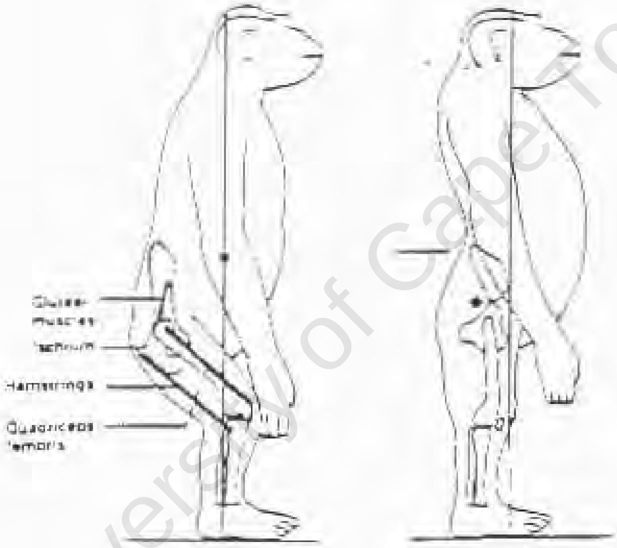


Figure 4.2

Adjusting to the bipedal posture

In chimpanzee bipedalism the centre of gravity is towards the ventral aspect of the trunk. In humans the centre of gravity is towards the midline. If the chimpanzee were to adopt a proper human erect and bipedal posture, the angle of their sciatic notch (marked with an asterisk in the figure) would have to be reduced dramatically, as it is in humans. This would bring the sacrum and hence the trunk to a more upright natural posture. A pronounced lumbar curve, at the position indicated by the arrow, would also have to be established to maintain the balance. From Aiello and Dean (1990).



discussed, by creating lordosis (Figures 2.5 and 2.9). The height (depth) of the pelvis is relatively reduced in humans thus keeping the centre of gravity low near the hip joint. The low centre of gravity encourages stability in the erect posture. The pelvis has lateral pillars, for muscle attachment of the hip abductors/stabilisers (glutei minima and maxima) that are important for the leg-swing in bipedalism (Figure 4.1).

The surfaces of the human knee and ankle joints are relatively larger and hence more stable and more extendible, and therefore are more suitable for bipedal demands (Jungers, 1988a).

Various indices or ratios can be calculated and used to compare the proportional differences of the bones in primates (Aiello and Dean, 1990). In such comparisons some human characteristics have been found to be much closer to the isometric relationships found in Old World monkeys, such as colobines and cercopithecines, than to any large ape (Aiello and Dean, 1990). For instance, both arboreal Old World monkeys and humans have relatively long lower limbs in comparison to their upper limbs. However, the normally terrestrial Old World monkeys, namely macaques and baboons, and New World monkeys as well as the large apes deviate from the above pattern by having longer upper limbs relative to their lower limbs.

According to Aiello and Dean (1990), all australopithecines had non-human body proportions, such as short lower limbs relative to the upper limbs. Fossils of *Homo erectus* species and later hominid taxa appear to have body proportions within the range of modern humans. Their hind limbs are well adapted for bipedal locomotion (Tobias, 1965).

B) **Postcranial long bones, joints and bipedalism**

Vertebral articular surfaces are like special joint surfaces. Joint surfaces and cross sections of bones are proportional in size to the amount of force that they experience (Aiello and Dean, 1990). For example, the midshaft circumference of the femur (FMC) in humans is larger than the equivalent measurement of the humerus (HMC), since the former experiences relatively greater forces due to standing and walking. The size of the joint surfaces differs markedly between species using different locomotion patterns (Schultz, 1961; Robinson, 1972; Jungers, 1988a). Thus, humans have unexpectedly large surface areas at the cranial articular surface of the first sacral vertebra. According to Schultz (1961), the gorilla can only achieve such area sizes if it were double its weight. In respect of sizes of joint surfaces, *Australopithecus afarensis* (AL 288-1) is midway between humans and apes (Schultz, 1961). While this might mean poorly developed bipedalism in *A. afarensis* (Jungers, 1988c), latest allometric data notes that adult humans with small bodies have relatively small lower limb joints. So small joints of the "Lucy" specimen at Hadar might be a reflection of just her small body size rather than a major difference in her locomotion pattern (Ruff, 1988). This means that analyses of bony and joint indices should take into account the relative body weight if they are to be reasonable comparisons. If midshaft circumferences of long bones and their joint articular surfaces bear a relationship to locomotion, as stated in the above studies, it might be reasonable to examine such locomotive relationships in the vertebral column bodies and vertebral column articulations. The quadrupedal bipedal ancestor could have been like a knuckle-walking African ape, a fist-walking orang-utan, the upright swinging gibbon or quite a different animal (Begun, 1992). The time when bipedalism appeared cannot be exactly be pointed out but is approximated to be about 3.9 - 4.2 million years ago (Conroy, 1997), as also is indicated by the Laetoli footprints (Tuttle, 1985, 1987), Day (1987). The behavioural pressures that brought about this unique form of locomotion can make for another long discussion, but were possibly environmental (climatic) changes that brought about behavioural changes. Bipedalism has its own shortcomings, and the reasons why it should have been selected for are not clear in view of these shortcomings. For instance, in running, bipedalism is slow, less agile and uses relatively much energy (Conroy, 1997). The following reasons however have been advanced as to why the bipedal form of locomotion was preferred to quadrupedalism:

- Cost-effectiveness of bipedalism in oxygen use during *walking* long distances when compared to quadrupedalism. Bipedalism has been found to be bio-energetically more efficient than quadrupedalism (Rodman and

McHenry, 1980; Jablonski and Chaplin, 1993).

- Bipedalism enables the individual to expose a much smaller surface area to the sun, especially in an open grassland savannah with few trees.
- Bipedalism frees the hands for tool-use, collection, picking and carrying food, and for parental care of the infants.
- A combination of some or all of the above reasons.

It should be noted that, recent fossil evidence has shown that bipedalism evolved well before the use of stone-tools (Conroy, 1997). Bipedalism also evolved before acquisition of a large brain and other hominid features such as the short canines and dental complex (Rose, 1991; Coppens and Senut, 1991). Conroy (1997) points out that two of the most basic requirements for effective and efficient bipedalism are:

- The position of the centre of gravity of the body, which must be lower and within the pelvis in bipedalism than in quadrupedalism for stability (Figures 1.4 and 2.5).
- The lower limb must be able to move quickly through a relatively wide arc to provide the propulsive force to the stride and support (Figure 4.1).

Conroy (1997) states that all the gluteal muscles attach on or near the iliac blades such that they are wrapped around it, while the vertebral column is at the centre, creating a wheel-and-axle lever (Figure 4.3). Conroy (1997) further notes that in order to improve the stability of the trunk in hominids, the muscles are wrapped on the ilia around the vertebral column in an ever-increasing distance from the centre (vertebral column).

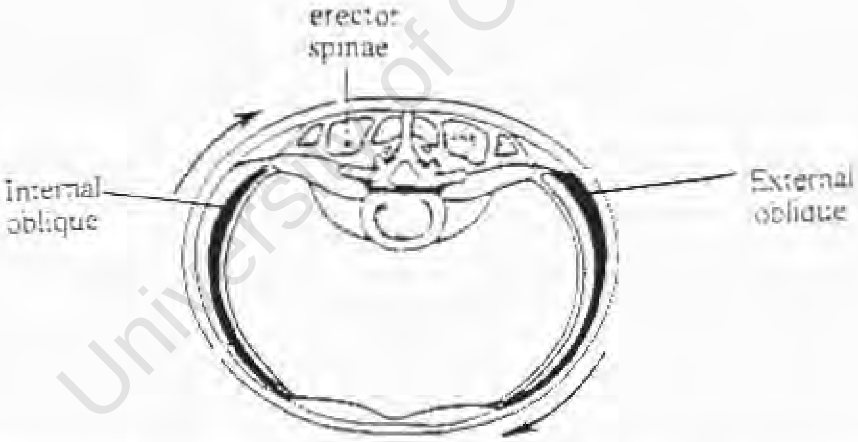
In bipedalism, the lesser gluteal muscles (gluteus medius and minimus) are the most critical in maintaining the lateral stability of the trunk. Through their attachment from the lateral aspect of the ilium to the greater trochanter of the femur, they act as abductors of the lower limb (Figure 4.1) and steadying the hip during bipedal walking. Failure for these abductors to act would cause the hip to collapse on the unsupported side during each stride (Saunders, 1953). When the apes try bipedal walking, they tend to bend laterally, because their lesser gluteal muscles are positioned more anterolaterally. From that position,

Figure 4.3

The pelvis and the vertebral column. The wheel-and-axle pelvic arrangement.

Pan: Iliac external surface facing dorsally.

H.sapiens. Iliac external surface facing laterally and "wrapped around" the vertebral column.



A cross section of the human trunk at about the level of the first lumbar vertebra. The force of the erector spinae muscle is applied directly to the vertebral column which acts as the axle of the wheel, while the force of the abdominal oblique muscles is applied to the ilia (the wheel). From Conroy (1997).

the lesser gluteal muscles act as flexors and medial rotators of the hip rather its abductor (Stern and Susman, 1983, 1987 and 1991).

In humans the biomechanical stresses due to the individual body weight are counterbalanced by the lesser gluteal muscles, resulting in the formation of a supporting pillar along the ilium between the iliac crest and the acetabulum. The presence of this pillar in the lateral position is important osteological evidence of the presence of efficient control and lateral balancing of the trunk (Conroy, 1997). Other features of the bipedal ilia are that they are broader from front (ventral) to back (dorsal), and have prominent anterior and posterior iliac spines, which respectively provide strong attachments for the flexors and extensors of the hip joint (Conroy, 1997).

According to Conroy (1997), larger mammals support their body weight on less bent limbs than small mammals. This posture, evident in bipedalism, decreases the stress on the muscles that support the individual while standing or moving (Biewener, 1990).

The morphological features of the postcranial skeleton of the australopithecines are of interest to evolution of locomotion in humans and primates. This is so because the austrolopithecines were the first hominids to practise a bipedal-like mode of locomotion, although the extent to which they practised bipedalism and aborealism is a highly debatable issue (Tuttle, 1981, 1985, Conroy 1997). Allometric comparison of the length of the limbs and of the body weight in monkeys, apes and fossil hominids such as *A. afarensis* shows that the latter has unique limb proportions among the hominoids (Jungers, 1982, 1988 b & c; Jungers and Stern, 1983). However, although body proportions of *A. afarensis* from Hadar are compatible with bipedalism, its type of locomotion was different from the human gait (Conroy, 1997).

The upper limb of *A. afarensis*, in spite of its proportional similarity to that of humans, has features that could indicate an arboreal form of locomotion, according to Tuttle (1981), Marzke (1983), Stern and Susman (1983), Susman et al. (1984), Senut and Tardieu (1985), Senut (1989), Senut and Tobias (1989), Heinrich et al., (1993). The glenoid cavity of the scapula is directed more cranially indicating a swinging limb position (Conroy 1997. However, powerful gripping activities such as holding sticks, pounding with stones or throwing objects as in *A. africanus*, have been speculated in *A.afarensis* (Marzke, 1983; Marzke and Shackley, 1986; Ricklan, 1987). The pelvis and lower limb of *A. afarensis* have both human and pongid features (Conroy 1997 Lovejoy (1975), Stern and Susman (1983), Susman et al., (1984) and Berge (1994) are as follows:

The concavity of the ventral aspect of the sacrum, and the transverse processes of the first sacral vertebra are poorly developed. These features imply a poor lordosis and weak ligaments connecting the sacrum with the ilium resulting in a less stable sacral iliac joint that cannot sustain the trunk in the erect posture for a long time (Conroy, 1997). The surface area of the body of the last lumbar and the surface area of the body of the first sacral vertebra of *A. afarensis* are relatively small. These surfaces are clearly not adapted to bearing compression forces from the bipedal posture (McHenry, 1991).

In *A. afarensis* the vertical displacement of the centre of gravity has been contained by the relative extreme width of her pelvic inlet in combination with the horizontal rotation of the pelvis (Rak, 1991).

There are arguments for supporting the adaptation of fossil hominids such as *A. afarensis* to obligate bipedalism since arborality was no longer selectively valuable (Lovejoy, 1988; Latimer and Lovejoy, 1989; Latimer, 1991). They argue that A.Afarensis was an obligate biped that had lost many critical climbing adaptations. These researchers identified a number of adaptations to bipedalism in *A. afarensis*, e.g. the unopposable big toe, and a strong iliofemoral ligament to fix the hip.

The postcranial skeleton of *A. africanus* consists of some mid-thoracic and lumbar vertebrae, sacrum, pelvis, some ribs and part of a femur with a head, neck and shaft. Since all these bones including the vertebral bodies are slender, it can be concluded that they belong to a small gracile animal, about 122 to 137 cm in height (Robinson, 1972). It is important to note that as in the *Homo erectus* skeleton (WT1500) from the West of Lake Turkana (Latimer and Ward, 1993), there are six lumbar vertebrae in *A. africanus*. In the humans there are five lumbar, and in apes three to four. As in the other australopithecines, the vertebrae of *A. africanus* though small, appear to be adapted to the requirements of weight bearing in bipedalism. This adaptation is shown by increasing vertebral body diameters from the proximal to the distal segments of the vertebral column (Latimer and Ward, 1993). However, in spite of this increasing size of the cross-sectional area of the vertebrae, the areas of the lumbar and sacral vertebrae are still relatively very small for human-like bipedalism (McHenry, 1991). In humans, the vertebrae also conform to certain other characteristics in addition to the increasing cross-sectional area of the body. For example, the surface area of the vertebral bodies of the lower lumbar vertebrae and the pedicles of the same are large. The pedicles of the lower lumbar vertebrae of humans are wider relative to their length than those of the non-human (quadrupedal) primates. It should also be noted that, in spite of some human-like features found in australopithecine vertebrae, the last lumbar vertebra of *A. africanus* does not have the human-like features. Its pedicles and vertebral surface area are relatively small, and the pedicles are short (Shapiro, 1993a).

The vertebral column of *A. africanus* shows a lumbar curve that is similar to the human lordosis, which implies that there is a human-like posture in *A. africanus* (Robinson, 1972). The bones of the foot of *A. africanus* were bipedal (Clarke and Tobias, 1995). The *A. robustus* foot was also non-grasping, hence human-like (Susman and Brain, 1988). Possibly these variations only imply the mosaic pattern of human bipedal evolution, and hence show the complexity of the anatomical adaptations to primate posture and locomotion (McHenry, 1975).

The presence of ape-like semicircular canals in australopithecines supports the observation that the postcranial skeleton of these primates was less specialised and that their locomotion included arborealism and semi-bipedalism (Spoor, 1993 and Spoor et al., 1994).

It can be seen in the literature just reviewed that various primates have struggled to achieve an erect posture and possibly bipedalism. The reason for this struggle could be that bipedalism gives a vantage view, in a flat savana grassland. Such a view may be crucial for survival of the individual and species.

Generally, bipedalism demanded body structural adjustments. According to electromyographic (EMG) studies by Shapiro and Jungers (1988), the adjustments were possibly not drastic in the back muscles. The electromyographic recruitment patterns support this view because the patterns tend to be similar in primates of different postural behaviour, when they are engaged in similar activities. The EMG recruitment patterns of the long back muscles monitored in chimpanzees and the gibbon, when practising bipedalism, were consistent in both groups, and with the recent EMG data on the same muscles in humans (Shapiro and Jungers, 1988). The above researchers therefore suggest that there is a basic similarity in the mechanical constraints placed on the back during bipedalism among the above three hominoids. They conclude that human (habitual) bipedalism probably did not involve a major change in the back muscle action or function, but rather an improvement in the mechanical advantage and architecture of these muscles. In view of the limited experimental EMG data that could be found on the back muscle activities of primates, it is not possible to comment further on the above conclusion. If the differences are in the mechanical advantage, then the skeleton of the spine, especially the leverages of the spinous and transverse processes, can probably reflect these differences. Hence the importance of this study.

In summary, the above account shows how primate locomotion and indeed habitual bipedalism are complex activities, evolved over millions of years. Bipedalism developed in a mosaic fashion. This means that ape-like features may be found occurring side by side with human like features, such as bipedalism (McHenry, 1975). There is therefore not a single muscular or bony structure that can be identified as being solely responsible for sustaining the full bipedal posture in humans or other primates. So posture is a result of an integrated effort of organs, parts and regions of the body, including the skeleton. It is with the above known facts and background, that this study of the primate vertebral column has been approached.

Chapter 5

MATERIALS AND METHODS

A) Materials

The structure of the thoracic vertebral column was investigated in cercopithecoid (vervet monkey and baboon), *Pongo*, *Pan*, *Gorilla* and *Homo*. The thoracic region was selected for study because, except for human clinical studies, it has received relatively little attention from functional morphologists, judging from literature available. In this study, morphometric measurements were carried out on prepared disarticulated skeletons of vertebral columns of various primate species. The measurements were made in millimetres using digital callipers. Gross observations on the number of vertebrae were made. Transitional vertebrae, which occur at the cervicothoracic and thoracolumbar transitions were of particular interest to this study because some of them are unique by having cervicothoracic or thoracolumbar features. The species studied represent a reasonable spectrum of locomotive behaviour found in primates. The details of the specimens are given in the Tables 5.1, 5.2 and 5.3. All the specimens that were investigated were from mature individuals, and particularly the vertebrae were completely ossified. Their epiphyses were completely fused to the vertebral bodies. The other vertebral components or processes were also fused accordingly. The following points were also taken into account:

- Only complete vertebral columns (i.e. those verified by thorough examination to have no accidentally missing vertebrae) were finally studied.
- Specimens having malformations and diseases such as arthritis, spinal bifida, spondylosis etc. (Allbrook, 1955) were not considered for morphometry.
- Efforts were made to ensure that both sexes were reasonably

represented in the samples (Table 5.1)

Sources of the specimens used in the study (Table 5.1)

Source	Species	Numbers
The South African Museum Cape Town South Africa	Chacma Baboon *(Papio ursinus)*	8
The Drennan Museum Dept. of Anatomy & Cell Biology Faculty of Health Sciences University of Cape Town South Africa	Modern human (*Homo sapiens sapiens*)	11
The Dart Collection Dept. of Anatomical Sciences University of the Witwatersrand 7 York Road, Park Town 2193 Johannesburg, South Africa	Vervet monkey *(Cercopithecus aethiops)*	68
	Chacma baboon *(Papio ursinus)*	69
	Orang-utan *(Pongo pygmaeus)*	1
	Chimpanzee *(Pan troglodytes)*	2
	Modern human (*Homo sapiens sapiens*))	56
The Transvaal Museum Pretoria South Africa	Chimpanzee *(Pan troglodytes)*	2
	Orang-utan *(Pongo pygmaeus)*	1
The Galloway Collection Dept. of Human Anatomy Makerere University P.O.Box 7062, Kampala Uganda, East Africa	Human (Modern *Homo)*	207
The Natural History Museum Cromwell Road London SW7 5BD	Orang-utan *(Pongo pygmaeus)*	14
The Powell-Cotton Museum Quex Park Birchington, Kent England	Gorilla *(Gorilla)*	27
	Chimpanzee *(Pan troglodytes)*	18

The following are the groups of primates studied because they have different ways of posture and locomotion. Details of their locomotion and postures are described in Chapter 1.

Cercopithecoidea

i) *Cercopithecus aethiops* (vervet monkey)

ii) *Papio ursinus* (chacma baboon)

Hominoidea

i) *Pongidae* (great apes)

- a) *Pongo pygmaeus* (orang-utan)
- b) *Pan troglodytes* (common chimpanzee)
- c) *Gorilla gorilla* (gorilla)

ii) Hominids

Homo sapiens sapiens (Human)

The samples in Table 5.2 represent the *maximum* numbers of sample that were initially available, as well as the numbers available for the morphometric measurements, and for counts studies. Not all specimens were appropriate for particular investigations, measurements and tests. The numbers vary accordingly as reported in particular appropriate tables in the results.

Maximum number of specimens available for data collection *

(Table 5.2)

	Available	Counts	Morphometrics
Vervet monkey	68	68	61
Chacma baboon	77	77	72
Orang-utan	16	16	8
Common chimp.	22	22	20
Gorilla	27	27	27
Modern human	274	274	112

* The sample for apes and monkeys were relatively low compared to the human sample, because the resources dictated the places that were visited

in order to access the samples and the length of time that was spent in each place. The apes specimens in particular were scattered in various places in small numbers. The results should therefore be viewed with these limitations of sample sizes in mind.

B) **Methods**

The various functional aspects of vertebrae, together with their mechanisms of articulation with each other and with muscular components, have been adequately dealt with under the appropriate subheadings in Chapters 2, 3 and 4. For example, extensive information related to important studies on the spinous processes can be found in detail under the section on the spinous process in Chapter 2. This section on "Methods" is therefore deliberately brief as it is precisely tailored to cover and explain only those aspects relevant to:

- Manipulation and measurement of the various components of vertebrae in the study.
- Significance of the above measurements in primates in the study.
- Procedures for handling of the above data (data analysis).

Each vertebral column was first properly identified. Its elements were arranged in their serial order from the first cervical to the sacrum using the following features:

- shape and size of the vertebral body
- inclination, length and shape of the spinous process
- orientation and articulation of the zygapophyseal facets
- presence or absence of rib facets
- the shape and position of the transverse processes
- position and shape of rib facets or demifacets

After the above exercise, morphometric measurements were taken on the vertebrae, starting from the seventh vertebra (C7) to the twenty-first (V21) inclusive, using digital calipers. The twenty-first vertebra in humans corresponds to L2. This range of vertebrae was chosen after an initial pilot study showed that the cervicothoracic and thoracolumbar transitional vertebrae would be well covered within this range in all the primates under investigation.

The transitional elements are:

(a) V7, V8 and V9 (C7, T1 and T2)

(b) V17 / V18, V19 and V20 / V21 (T10 / T11, T12 and L1 / T13)

Depending on species and sometimes individuals, the thoracolumbar transitional elements vary from the seventeenth vertebra (V17) to the twentieth first (V21), while the cervicothoracic transitional elements almost invariably are fixed starting from C7 to T2 (i.e. V7 to V9).

Vertebral counts

Vertebral counts were carried out in this study on the samples listed in Table 5.2, under the counts column. During the exercise, the presacral vertebrae (PSV) of each vertebral column were carefully arranged and articulated. The number of vertebrae in each portion of the column and the total number in each vertebral column were recorded down. As mentioned earlier, only complete vertebral columns were considered. The presence of a cervical rib would not have resulted in re-classifying the seventh cervical vertebra as a thoracic. The presence of a lumbar rib did not affect the total presacral vertebrae since the vertebra would still be presacral whether it had a rib or not. First the count of the vertebrae according to the position of the thoracolumbar joint transition was recorded, and then the count according to the position of the last ribs was carried out. The last lumbar vertebra was regarded as sacralised (and counted as sacral) if it showed the following features.

An enlarged transverse process that formed part of the sacroiliac joint, and was involved in the formation of a sacral foramen even on one side. The fusion of bodies to osteophytic growths was not regarded as sacralisation. According to Kaufman (1974), the above criteria were also used in earlier investigations by Lanier (1939), and Bornstein and Peterson (1966).

Measuring equipment and unit of measure

TESA digital calipers were used to make various measurements on vertebrae in millimetres. The dimensions mentioned below are defined, used or recommended for use, in vertebral column studies by researchers such as Shapiro (1991a), Ward (1991), Latimer and Ward (1993), Walker and Leakey (1993) and MacLarnon (1993). Using these dimensions certain vertebral column ratios shown below can be calculated.

Dimensions

The measurements and assessments are made with the assumption that the 'size' of a given part of a vertebra is related to the magnitudes of the forces acting on it as noted by Davis (1961). The measurements can then be used to quantify the action of the muscles or the forces they generate, in terms of relative ratios. The ratios indicate the leverages at the respective parts or processes of the vertebral column. It is *assumed* by Shapiro, (1991a) that the species with similar forms of posture and/or locomotion would have relatively similar ratios, and vice versa.

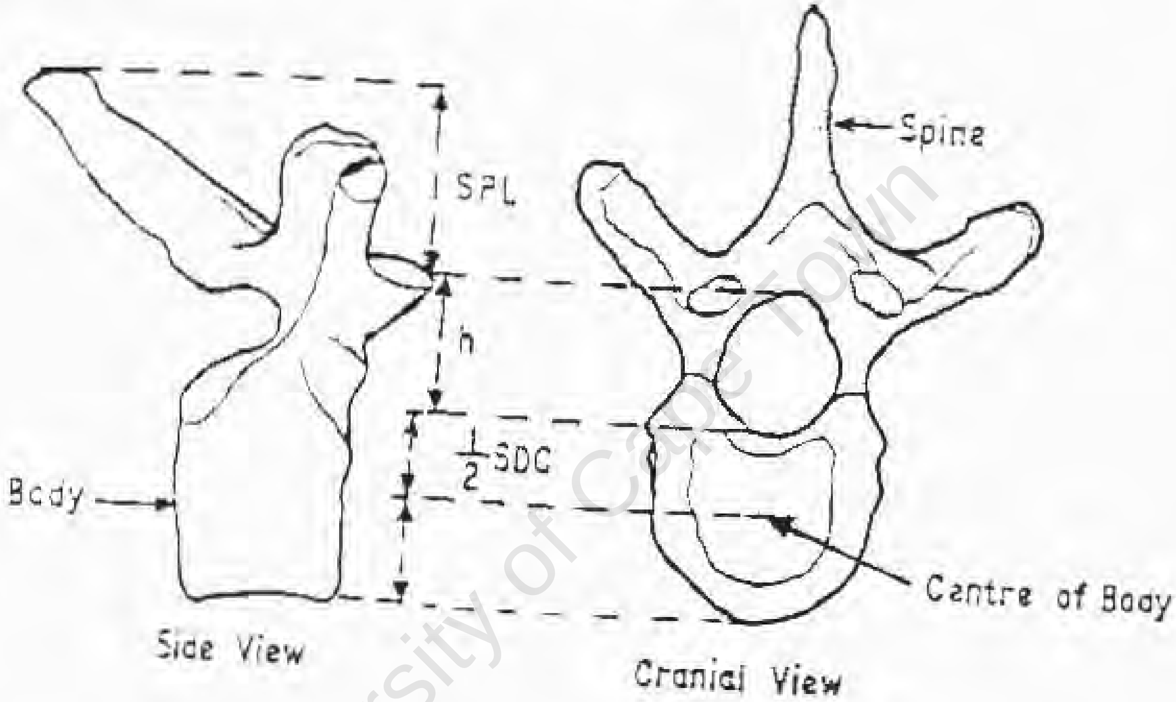
Ward (personal communication) cautioned about "the use of ratios as they can be misleading, as allometric relations will cause apparent differences across taxa that might not be functionally relevant although there are potential justifications for their use". When making the above assumption one should be aware that not only posture or locomotion (functional variations) of a species may affect the results, but variations in size may also affect the results in a study of this nature. However, formulae that minimise the effect of varying sizes of species have been obtained from the literature, and have been used.

Spinous Process perpendicular Length (SPL)

This is the perpendicular distance measured in a ventrodorsal plane, from the cranial base of the spine to a (line) tangent to the tip of the spine

Figure 5.1

The spinous process *perpendicular* (projected) length (height).



SPL – Spinous Process Perpendicular Height

SDC – Sagittal Body Diameter Cranial

h – Vertebral foramen height cranial

(Figure 5.1) (Shapiro, 1991a). It is not the absolute (true) length of the spine though it is sometimes wrongly referred to as the "spinous process length". More details on the spine have been covered under the spinous process literature review. The measurement indicated by 'SPL' or 's' is applied in the calculation of the lever arm for extension. The lever arm indicated here is for multifidus and parts of erector spinae that have attachments and action on the spinous process (Moore, 1982). The "Variable spine" and "Spine ratio" calculations are carried out according to the following formulae (Figure 5.1):

The Variable Spine = $(s + h) + c/2$ (Shapiro, 1991a), where:

s = SPL = Spinous Process perpendicular Length/Height

h = Vertebral foramen height measured from the dorsal aspect of the cranial surface of the vertebral body to the ventral surface of the spine.

c = SDC = Vertebral body sagittal diameter (cranial)

$c/2$ = ½SDC = the radius of the cranial articular surface of the vertebra to the dorsal aspect of the same surface.

The Geometric Mean discussed earlier in this literature review was not adopted for use in this research. It was not used because:

1) The diaphragmatic vertebra, which is recommended for the calculation of the geometric mean, was part of the study as a transitional vertebra. The vertebra from which the geometric mean is derived should not be part of those being investigated (Shapiro, 1991a), in order not to bias the results. Shapiro (1991a) claims that where it can be freely applied, the geometric mean can give better accurate results than the estimated species body weight. This is so because the geometric mean is calculated for each individual specimen and is highly correlated with the weight of the individual (r = .95 across species).

2) Other authorities (personal communication) are of the view that

"substituting the geometric mean of linear dimensions of vertebrae for body weight leads to circular reasoning. In this method the dimensions of vertebrae are expressed as fractions of a size, of one particular vertebra of the same vertebral column. This process may show differences between vertebrae in the same vertebral column, but not between animals who have different sizes of vertebral columns in relation to body weight".

The species body weight is recommended by authors such as Shapiro (1991a) as a consistent body variable, to enable a relative comparison of muscle leverage in primates of different sizes (weight).

The final variable that is considered in respect of the spine is known as the "Spine Ratio", and is given by the following formula:

The Spine Ratio = $(s + h) + c/2 \div \sqrt[3]{\text{Body Wt}}$. The use of the cube root is explained in the Statistical Methods later.

Average species body weight and cube root of species body weight

(Table 5.3)

Species	Sex	Av. Spc. Wt. in g	C- root	Source
Gorilla	M	164,350	54.78	Jungers (1985b)
	F	75, 700	42.30	Fleagle (1988)
Orang-utan	M	79,600	43.02	Fleagle (1988)
	F	37,750	33.55	Fleagle (1988)
Chimpanzee	M	51,500	37.21	Fleagle (1988)
	F	40,300	34.28	Fleagle (1988)
Vervet	M	4,460	16.46	Kavanagh (1983)
	F	3,125	14.62	Kavanagh (1983)
Baboon	M	22,200	28.11	Kovacs (1993)
	F	13,500	23.81	Kovacs (1993)
Human	M	57,200	38.53	Kark (1954
	F	55,200	38.08	Kark (1954)

Key: C-root stands for cube root of the average body weight of a species.

In some cases the above averages were not given by the above authors.

but were calculated from the data of the weight given by the same authors. In South African indigenous populations, Kark (1954) found that the average body weight of the individual was about Kg 57 in contrast to Kg 65 in North America and Europe. In Central and East Africa it is even lower. The average weight given by Kark (1954) has been adopted in calculations on the human data because the human specimens in this study are indigenous to South, East and Central Africa.

The Spinous Process Length (SL) (Figure 5.2A)

This is the absolute length of the vertebral spine. Its measurement in figure 5.2A is taken from the cranial base of the spine, along its craniodorsal surface to its tip. It does not enter any important calculations beyond relative length comparisons of the spinous process.

Vertebral Foramen (Figure 5.2C)

The gross dimensions of the vertebral foramen/canal and spinal cord are positively correlated. They can therefore be used to make deductions on each other although with reservastions. (The spinal cord is absent in parts of the canal and there are other structures, such as the meninges and blood vessels and fluids. The structure should be taken into account since they occupy part of the canal). Gross morphological studies of the spinal cord and the vertebral canal have centred on the cervical and lumbar regions. Such studies have used radiographic and computerised tomography but correlation for magnification errors have not been made on the radiographic measurements. Larsen and Smith (1981) found that radiographic measurements sometimes made overestimations of vertebral canal dimensions. Lastly, the canal height and width have been differently defined by various researchers. The definitions and methodology used here are by MacLarnon (1987). The height (h) is the maximum dorsoventral diameter, and the width (w) is the maximum transverse diameter, of the vertebral foramen of each vertebra (Figure 5.2C). They are measured with calipers, while the cranial end of the vertebra is directed to the person taking the measurements. When measuring the height, one of the pointers of the calipers is placed on the "floor" of the canal (dorsal surface of the vertebral body) in the mid-sagittal plane. The second pointer is moved until it touches the "roof" (dorsum) of the canal still in the mid-sagittal plane. The width is measured by placing the caliper pointers in the mid-transverse (coronal) plane of the vertebral canal with the pointers just protruding to the other end. They are then opened to touch the inner "sides" (lateral surfaces) of the canal, thus measuring the maximum diameter (width) at that level. The vertebral foramen area at a particular level can be calculated from the above as the area of an ellipse from the formula below:

The Vertebral Foramen Area = pi x w/2 x h/2 sq. units

The vertebral foramen ratio is the square root of the above area divided by the cube root of the body weight of the species. The ratio can be applied to make comparisons of size of the vertebral canal and spinal cord in various primate groups.

Sagittal vertebral body Diameter (SD) (Figures 5.2A, 5.3)

This is the ventrodorsal (mid-sagittal) distance at the midpoint of the vertebral body articular surface; it is the shortest mid-line distance ventrodorsally along the body articular surface. It can be measured on the cranial or caudal aspects of the vertebral body articular surfaces, and denoted respectively as SDC and SDCD or 'c' (Figure 5.3). The cranial sagittal diameter (SDC) is applied in the estimation of the "Variable Spine", Spine Leverage and Spine Ratio.

Transverse vertebral body Diameter (TD) (Figure 5.2A)

This is the greatest distance across the articular surface of the vertebral body, measured mediolaterally (transversely). It is denoted as 'g' or TDC and TDCD, for respectively the cranial and caudal aspects. The articular surface area of the vertebral body gives a reflection of the weight (compressive force or pressure) that may be transmitted through it and the disc, to the other parts of the vertebral column. It is estimated by the following formula:

The Vertebral body area = Area of an ellipse (Shapiro 1993a)
= π (½ SDCD x ½ TDCD)

= π (1/2G x 1/2g)

Accordingly, the cranial and caudal transverse and sagittal diameters of the vertebral body are used to calculate the corresponding areas of the vertebral body.

Transverse Process Projection (TPP or 'a')

This is the distance between the opposite tips of the transverse processes of a single vertebra (Figure 5.3). It could be referred to as the "span" of the transverse processes. It is important in determining the lever arm of a vertebra, for unilateral flexion. The lever arm for unilateral flexion is known as the Lattran (i.e. Lateral leverage of the Transverse process) (Shapiro 1991a and 1995). The Lattran is given by Shapiro (1991a) as:
Lattran = a/2 (see Figure 5.3) where,
a = the distance between the tips of the right and left transverse processes of the same vertebra (TPP). a/2 is half of the length. Hence a/2 is the length of one transverse process (its lever arm as measured from the mid-line sagittal plane of a vertebra)

The "lateral flexion leverage" (Lattran ratio) for back muscles can be calculated from the Lattran, for each species by again applying a consistent variable of the species. The formula is given as follows:
Lattran Ratio = Lattran ÷ $\sqrt[3]{\text{Body Wt}}$ (Shapiro, 1991a)

The Lattran Ratio indicates the lateral flexion leverage for stabilising the back and counteracting lateral flexion of the back by muscles that have attachments into the dorsal aspect of the transverse processes (Moore 1982; Shapiro, 1995). Such muscles include the erectores spinae. The Lattran ratio also gives the leverage of quadratus lumborum that is attached to the ventral aspect of lumbar transverse processes. Although this muscle is attached to the lumbar transverse processes, it is important in thoracic movements because it fixes the lumbar region while appropriate thoracic movements are taking place. Thoracic movements cannot take place in isolation of the other regions of the vertebral column.

Distance between the Transverse Process tip and the Ventral surface of the Vertebra (TPV or 'b') (Figure 5.3)

This distance is the perpendicular height from the tip of a transverse process of a vertebra to the horizontal (coronal) plane at the most ventral surface of the vertebral body (Figure 5.3).

The "Transverse process level" or the "Ventrodorsal transverse process ratio" (Vdtran Ratio) is given by the following formula using the measurement of TPV or "b":

Vdtran ratio = TPV / SDC = b/c (Figure 5.3) (Shapiro, 1995), where:

b – TPV = the perpendicular height from the transverse process tip(s) to the most ventral aspect of the vertebral body

c = mid-sagittal diameter of the vertebral body cranial surface.

The Vdtran (Ventrodorsal transverse process) ratio gives the relative position of the tips of the transverse processes from the ventral aspect of the vertebral body. Reference can also be made to the section on the transverse process in Chapter 2. Since the rector spinae is inserted on the ribs that are in turn anchored to the vertebal body and transverse process, the position of the transverse process might be regarded as the approximate distance of erector spinae from the axis of bending, and gives the moment of these muscles when they counteract flexion of the trunk (Shapiro, 1991a).

Directly comparing the lever arm of the transverse processes in different primate groups would give biased results because the location of the roots and the tips are at different levels, relative to the ventral aspect of the

Figure 5.2

Measurements on vertebrae. 'c' – sagittal diameter, 'g' – transverse diameter of the vertebral body, 'd' – pedicle width, 'e' pedicle length. 'h' – height and 'w' width of the vertebral foramen.

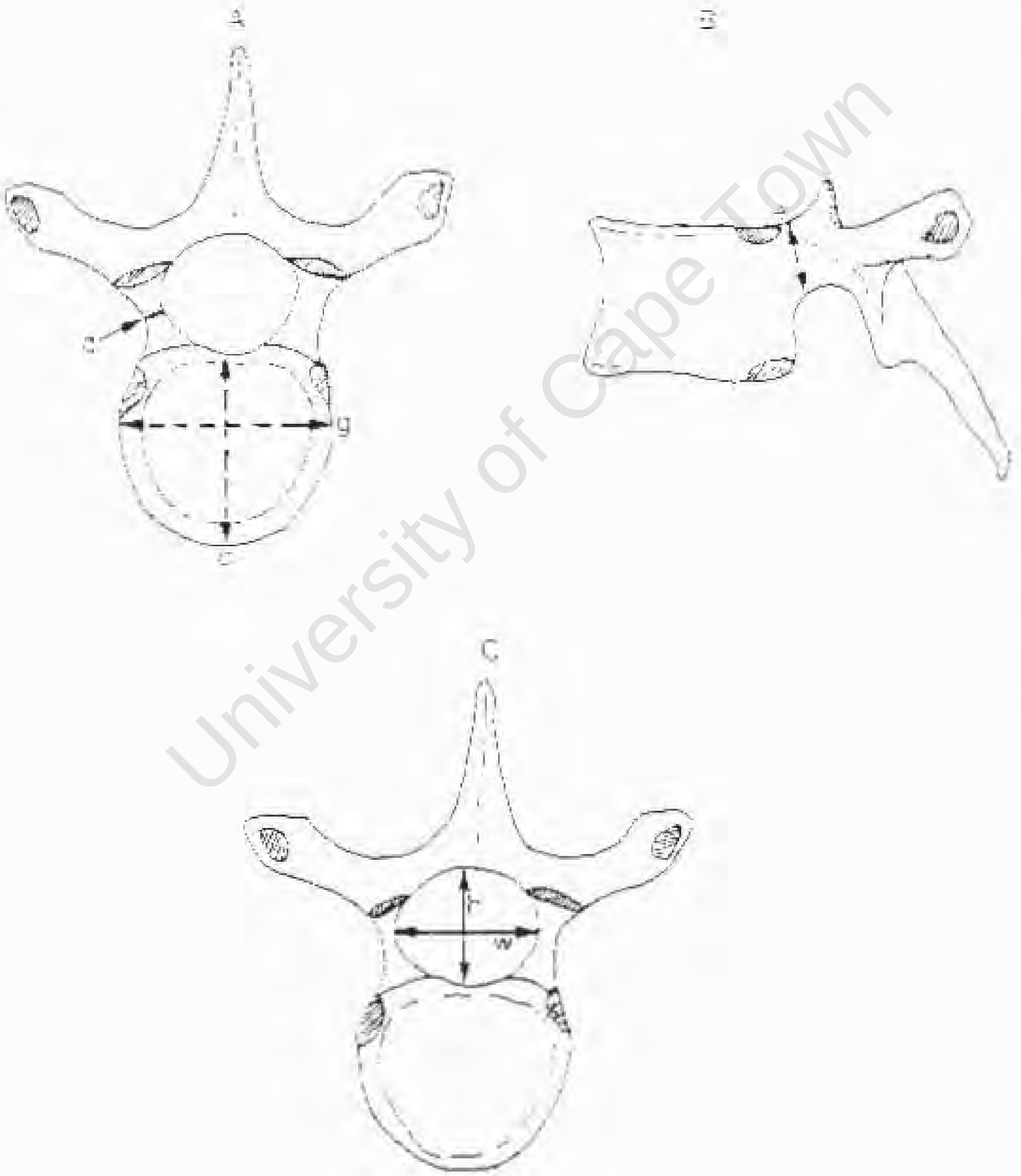
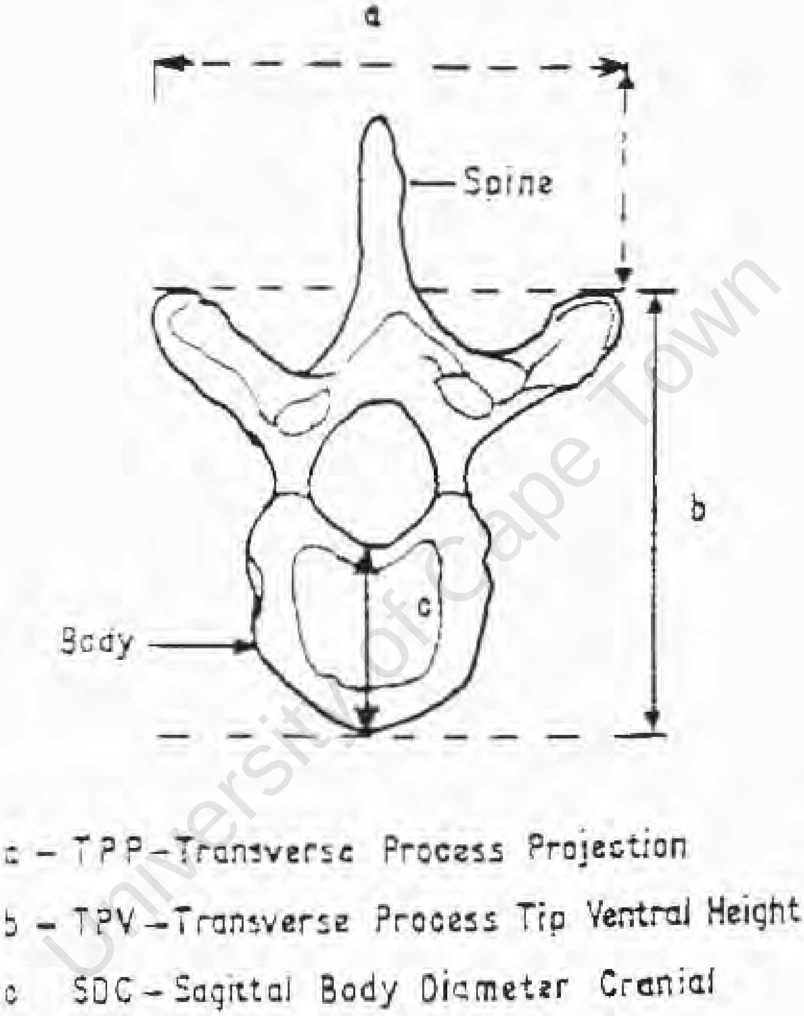


Figure 5.3

The transverse process. a - "span" of the transverse process, b - ventrodorsal height to the tip of the transverse process.



vertebral body. The lever arm for extensor leverages of the back musculature, e.g. longissimus and iliocostalis, is best compared when the relative level of the transverse process tips is taken into account, as in the case of Vatran ratio. The further dorsal the transverse process lies relative to the axis of extension, the better are the leverages for extension by longissimus and iliocostalis when they contract bilaterally. The further the tip of the transverse process lies relative to the axis for lateral flexion, the better is the leverage of iliocostalis for lateral flexion when they contract unilaterally (Shapiro, 1991a, 1995).

Pedicles (Figures 5.2A, 5.2B)

The pedicles bridge the "anterior" (ventral) and "posterior" (dorsal) elements of a vertebra. The anterior consists of the vertebral body, disc and associated ligaments, while the posterior consists of laminae, zygapophyses and associated ligaments (Pal and Routal 1986, Pal 1987; Bogduk and Twomey 1987). By connecting the posterior element to the anterior, the pedicles are positioned to receive forces from the posterior for transmission to the anterior bodies and discs. Pedicles may transmit bending forces resulting from the action of muscles on the spinous and transverse processes. The pedicles may transmit tension from the zygapophyses when the zygapophyses provide resistance to permit the vertebral column from sliding forward (Bogduk and Twomey 1987). Pedicles transmit compressive axial loads from the vertebral body (anterior element) to the laminae (posterior element) (Davis 1961, Pal and Routal 1986).

In view of the above facts, the pedicles should be morphologically affected in size. The increase in the size of the pedicle on the last lumbar vertebra (L5 in human) is associated with the decrease in the caudal surface area of the vertebra (Davis 1961). The explanation for this is that the reduction of the body surface area of L5 indicates that less compressive force is exerted onto the body of this vertebra, than is exerted through the vertebrae above L5. If that is the case then part of the total compressive force to L5 must be transmitted to the region below L5 by a route or mechanism that largely bypasses the caudal surface of the body of L5. The increase in size of the pedicles of L5 therefore implies that the compressive force bypassing the caudal surface of the body of L5 is going through the pedicles of L5 to the caudal region (sacrum). However, the form and function of the pedicles in non-human primates is not yet understood (Sanders 1990; Shapiro 1993a; Ward 1991). If the pedicles are related to the human unique lordosis and bipedal locomotion or posture then their morphology must differ in humans and other primates. Shapiro (1993a) showed that in the lower lumbar region the morphology of the pedicles is not unique to humans. Pedicles exhibit an increase in the cross-sectional area between the penultimate and last lumbar vertebra in a wide range of primates studied by the above two. It was also noted that although humans are not the only primates with large and wide pedicles at L5, humans nevertheless have relatively large pedicles at L5 in relation to their body size. The size and shape of the pedicles, especially at the transitional levels, such as at C-T and T-L transitions, have to be investigated. The features mentioned in the following paragraphs were measured in the study (Shapiro, 1993a; Ward, 1991).

Pedicle Area (Figures 5.2A, 5.2B)

This refers to the cross-sectional area of the mid-coronal plane of a pedicle. Usually measurements are taken on one side of a vertebra. It is given as Pedicle Width x Pedicle Length or (PW x PL, or d x e). (Figures 5.2A, 5.2B). The measurements are respectively, the mediolateral pedicle width and craniocaudal pedicle length (Shapiro 1993a). The pedicle area among hominoids is significantly correlated with the body weight (size) at all vertebral levels (Shapiro 1993a). It changes along the vertebral column in humans and non-human hominoids. In humans, it changes dramatically at the last lumbar because here there is resistance to forward displacement of L5, due to lordosis and the wedge surface at the lumbosacral articulation. This characteristic is present in non-human hominoids as well as *Indri*, *Varecia* and *Papio* (Shapiro 1993a) but is not exaggerated. The pedicle area increases at the last lumbar vertebra even in those primates not characterised by a decrease in body area at the last lumbar e.g., *Ateles* and to a certain degree *Cebus* (Shapiro 1993a). The increased pedicle area at the last lumbar is not entirely dependent on lordosis and bipedalism, although humans are characterised by the most substantial increase in pedicle area at the last lumbar vertebra. It is also evident that this feature is related to body size, because there is a significant difference between humans with very different body sizes (Shapiro, 1993a).

Pedicle ratio

This ratio reflects the relative load passing through the dorsal aspect of the vertebral column relative to the load passing through the ventral aspect of the vertebral column, and is expressed as:

Pedicle area/Vertebral body area (Pal and Routal 1986, Pal 1987).

Articular facets (zygapophyses) and their orientation (Figure 2.8)

Articular facets are orientated in a particular plane depending on the region of the vertebral column and its role in movements, and species. Hominid zygapophyses become increasingly orientated into the coronal plane towards the sacrum. In chimpanzees similar structures become more sagittally orientated in the region towards the sacrum. The articular facets in mordern humans help to resist stress at the lumbosacral joint. This joint is normally oblique since the sacrum must be positioned such that it must leave adequate space in the pelvis for the birth canal. The oblique orientation of lumbosacral joint means that the vertical compression forces in the vertebral column will displace the articulation. The arrangement of the postzygapophyses at the lumbosacral joint, in the coronal plane, helps to resist its displacement. At birth all the zygapophyses in the human lumbar region are orientated in the coronal plane, but by puberty they have come to be in the sagittal plane, except those near the lumbosacral articulation (Roaf, 1971).

DRAWINGS SHOWING MEASUREMENT AND CALCULATION OF THE FACET ANGLE 'a' Modified from Shapiro (1991a)

Figure 5.4 A

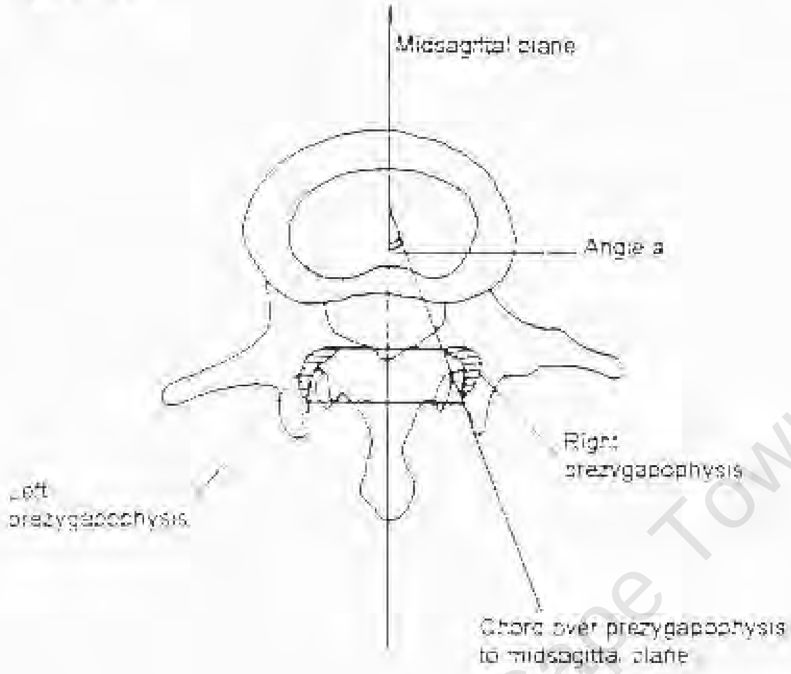
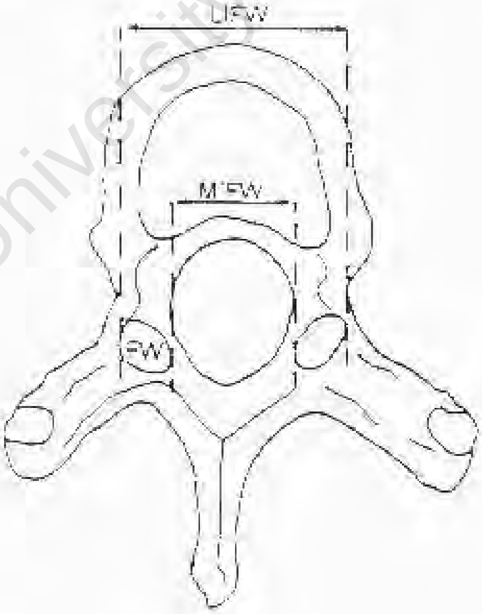


Figure 5.4 B



Refer to key for explanation

DRAWINGS SHOWING MEASUREMENT AND CALCULATION OF THE FACET ANGLE 'a'. Modified from Shapiro (1991a)

Figure 5.4 C

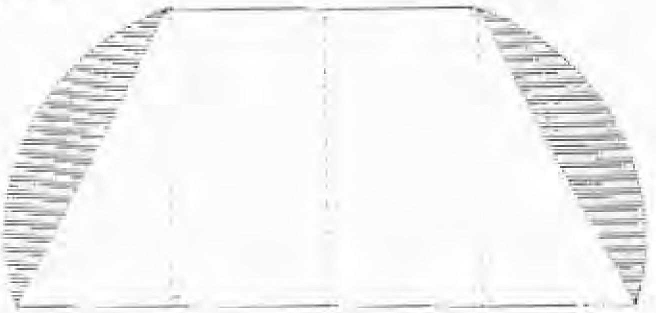
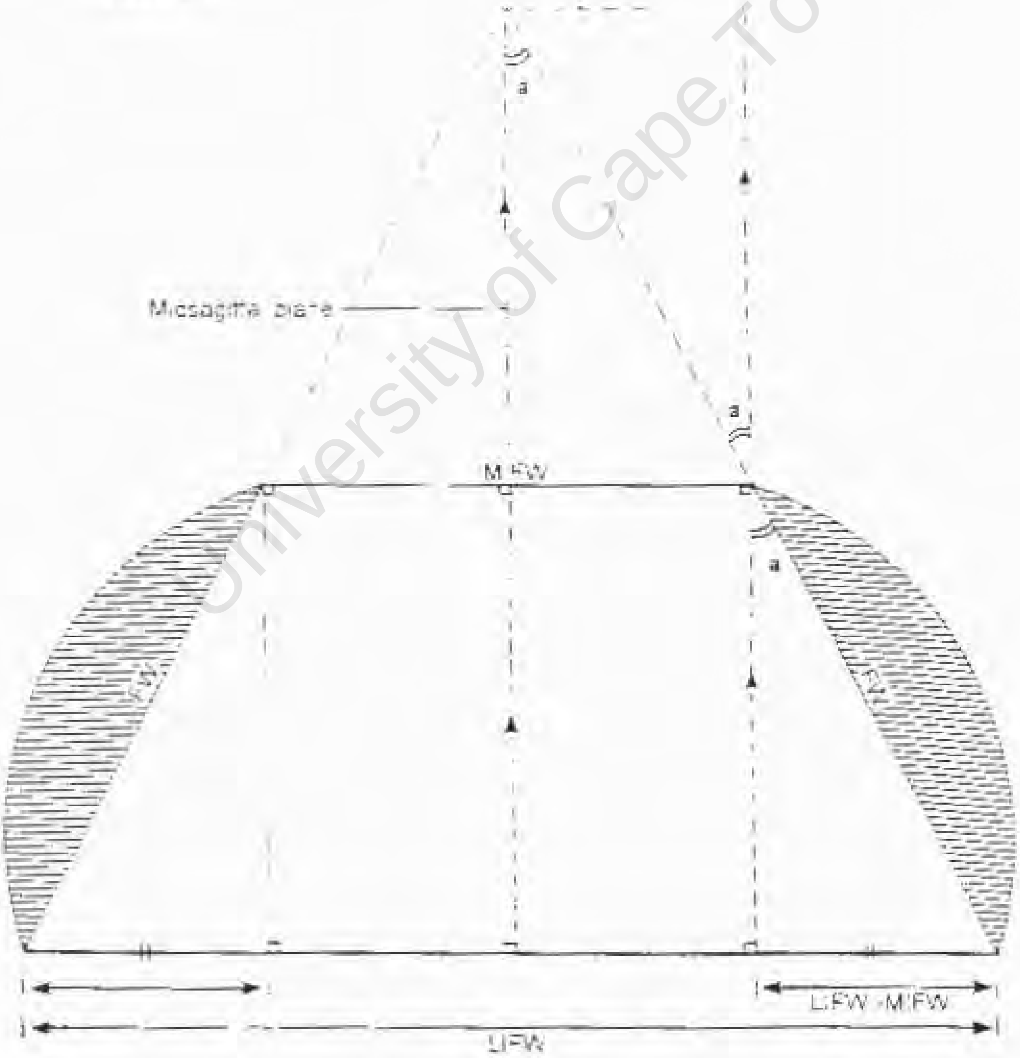


Figure 5.4 D



Refer to key for explanation

KEY to Figure 5.4 A, B, C, D (Formula for Facet Angle 'a')

$$\textbf{Angle } a = \textbf{Sine}\left[\left(\frac{LIFW-MIFW}{2}\right)\right] / FW$$ (Odgers 1933; Shapiro 1991a)

Where LIFW = Lateral interfacet width = m; MIFW = Medial interfacet width = n; and FW = Facet width = p.

Therefore, angle a = $\text{Sine}\left(\frac{m-n}{2}\right) / p$ $\text{Sine}\left(\frac{m-n}{2p}\right)$

The sine is converted to degrees using 'statistica' computer programme or four figure mathematical tables. To get the facet angle for a thoracic vertebra the results (in degrees) obtained from the above formula are sustracted from 180 degrees. From Shapiro (1991a).

The degree of movement at a zygapophyseal joint depends on the angle of inclination of the prezygapophysis or postzygapophysis. The articular facets (zygapophyses) form the joints between adjacent vertebrae. The measurements mentioned below are taken in order to estimate the angle of the zygapophysis in relation to the sagittal plane (For calculation of the angle refer to Figures 2.8; 5.4 A, B, C, D)

(a) Lateral Interfacet Width (LIFW or 'm') is defined as the distance between the lateral (outer) edges of the right and left prezagapophyses of a vertebra.

(b) Medial Interfacet Width (MIFW or 'n') is the distance between the medial (inner) edges of the right and left prezygapophyses, of a vertebra.

(c) Facet width (FW or 'p')

Estimation of the Facet Angle of Inclination:

The angle of inclination of the prezygapophysis or postzygapophysis can be determined from the above measurements, using a trigonometric formula established by Odgers (1933) (Figure 5.4 A, B, C, D).

Thus: The inclination angle of the right prezygapophysis is the angle whose sine = (LIFW - MIFW) / (2 FW) = Sine (m - n) / (2p)

This angle is the angle between the chord of the articular surface of a prezygapophysis and the median sagittal plane of the vertebra (Figure 2.8). When calculated from the formula, 90 degrees indicate an angle that is in the coronal plane, that is, whose articular surface faces dorsally or ventrally, like in some mid-thoracic zygapophyses. The facets whose angles are inclined between zero and 90 degrees are inclined medially and characteristic of the lumbar vertebrae. The facets whose angles are between 90 and 180 degrees are laterally inclined, and are found in some upper thoracic zygapophyses. The lumbar angle is one whose Sine is given as: (m–n) / (p/2)

For the thoracic vertebrae the above results are subtracted from 180 degrees. The Sine has been converted to the degrees, using the Statistica computer programme or mathematical four-figure tables (Odgers, 1933; Shapiro, 1991a).

The surface area of the articular facets

The surface areas of the zygapophyses change along the vertebral column. The incremental change of these areas can be used to compare vertebrae of different species. In humans and fossil hominids such as the Nariokotome *Homo erectus* (KNM-WT 15000) the surface areas of the lumbar and sacral articular facets were found to increase dramatically towards the caudal aspect. In the chimpanzee, there were progressive decreases of corresponding areas (Latimer and Ward, 1993). These authors stated that lordosis causes proportional increases due to loading of the zygapophyses in the lumbar region, where the vertebral elements via the same zygapophyses have to resist the shear stresses that would be imposed in the intervening discs. The zygapophyses towards the sacrum (in the lordotic lumbar region) experience considerable stress, because they are near the inclined lumbosacral junction.

Latimer and Ward (1993), state that the patterns in the increase of zygapophyseal areas along the sequence in the thoracic elements are similar in humans and chimpanzees. This indicates that habitual bipedalism does not result in relative increases in loading of thoracic zygapophyses/posterior elements. The ratio of the zygapophyseal area to the endplate (vertebral body) area can be used to make comparisons among species; in the thoracic region this ratio is smaller in humans and KNM-WT 15000 than in chimpanzees. In the lumbar elements the chimpanzee and hominid ratios converge, but this is probably due to the shrinkage in size of the chimpanzee zygapophyses rather than an increase in the chimpanzee vertebral body areas. The facet area is estimated as the area of an ellipse, by the measurements of the facet width (FW) and facet length (FL) over a large number of facets.

Facet Width (FW or 'p')

This is the maximum (diameter) width of a zygapophysis, on one side of a vertebra (Figure 5.2A).

Facet Length (FL or 'q')

This is the greatest (maximum) length of a zygapophysis in the craniocaudal direction (Figure 5.2 B). FL can also be taken on one side of a vertebra for convenience, as long as this is consistently the same side.

$$\text{Facet Area} = \pi\,(p/2 \times q/2)$$

C) **Statistical methods**

As stated earlier, the sample size for apes and monkeys was low compared to the human sample. This disparity must be remembered when interpreting the results. The small samples were due to constraints of resources especially funds that dictated where to travel for the samples and the time spent at each venue. Particularly, the ape samples were available in small numbers often scattered in several locations, that were hundreds of miles apart (Table 5.1).

The number and locations of specimens are given in Tables 5.1 and 5.2. There were approximately equal numbers of both sexes in the samples, except for the orang-utan where only male specimens were available. The data were first analysed separately as female and male groups. The data consist of two forms, namely the continuous metric variables that are measured directly from the skeletal elements, and the counts of the presacral vertebrae (PSV) consisting of cervical, thoracic and lumbar elements. For the continuous metric variables, the mean, standard deviation, maximum and minimum values are calculated for each measurement and for the computed ratios. Since body size varies widely in the primate sample studied (ranging from vervet to gorilla) it is important that the data is rationalised by taking the average species body-weight into account. The ratios are therefore standardised by using the cube root of the average species body weight, obtained from literature (Table 5.3). Since the ratios are calculated from linear dimensions, rationalisation is needed to 'convert' the body weight to a form that is compatible to these linear ratios. The cube root is applied since the weight is proportional to volume and therefore proportional to length cubed.

Shapiro (1991a), who researched on the lumbar vertebrae applied the formula in similar studies but Henneberg et al., (1989) do not use the cube root. Henneberg writes: "regarding the body weight as being proportional to the third power of linear dimensions may seem logical, but is not true. In all Old World Anthropoidea (monkeys, apes and humans) body weight scales to the exponent of 2 times body length (Henneberg, 1989). This means the weight scales approximately to the square of the body length. Reason: the primate body is elongated, not spherical" (Henneberg's Comment, 16th March 1999).

Despite the above argument by Henneberg it has been decided to use the cube root of body weight for standardisation, as other authorities on body scaling such as Alexander (1985) and Schimidt-Nielsen (1984) advocate its application in similar calculations. "Linear dimension 'l' and 'r' are proportional to *m* "where *m* is the *mass* of the body" (Alexander, 1985).

A comparison between species in this study is not by using magnitude of measurements at each vertebral level. The analysis is in sequential change in the measurement and ratios craniocaudally, along the whole length of the thoracic vertebral column. Although data are presented in accompanying tables, a comparison of each specific vertebra within species and beyond species is beyond the scope of this study.

Male and female data from all the standardised ratios for lengths, areas and angles were compared by means of the Spearman Correlation Co-efficient, and the results are shown in Tables 6.29 to 6.34. None of the data were found to be statistically different and data for both sexes were pooled for futher analyses and comparisons. Comparisons were facilitated by the application of Spearman Correlation Co-efficient (available on the "Statistica" statistical computer package).

The female and male discontinuous (counts) data were subjected to a

Chi-square test which showed that the two samples are closely correlated, and are therefore pooled (Table 6.35). The Spearman Correlation was chosen because it examines sequential patterns rather than paired values sorted by size.

Where the sequential change of measurements, V7 to V12 is proportionately the same (e.g. between V7 – V12) the Spearman Correlation Co-efficient nears 1.0. The smaller the co-efficient the more out of sequence and different the data are. Significance values are assessed from the probability (p-value). Where $p = .05$ or below, the samples are considered to be from the same population and therefore significantly similar. The probabilities (p-values) presented in the tables and are limited to 3 decimal places, and probabilities less than 0.001 appear as '0'.

The interspecies comparisons were presented graphically and in tabular form. The graphic patterns were tested by Spearman Rank Correlation Significance Test. The results of the Spearman Rank Correlation significance tests are found in Tables in 6.2 to 6.28.

Additionally, each comparison was tested by means of Pearson Moment Product Correlation as recommended by one of the examiners. This is an appropriate method for comparison of continuous data, but it is concerned with direct comparison of pairs of vertebra rather than with sequential change along the column. In fact the statistical output of the two techniques is nearly identical, and presentation of the Pearson Correlation Co-efficients and their p-values is unnecessary. Pearson's Correlation data can be presented as Scatter plots, but they provide no more information in this study than the graphs and tables already included. When the Graph profiles are studied side by side with the corresponding tables the characteristics of the species, and the presence of outliers become very clear. In view of the above points it was decided to leave Pearson's plots out of the publication.

The patterns of the discontinuous data, that is the data on vertebral counts, were identified by arranging the data from the most to the least frequent patterns. The patterns of each species were tabulated. The patterns of the presacral vertebrae (PSV) in each vertebral column depend on the position of the thoracolumbar (and sometimes the lumbosacral) transitional vertebral joints. The position of the transitional element depends on the method used to determine the element. The changing facet joints can be used, or the position of the last pair of ribs is conventionally used by anatomists. The two methods have given different results and patterns.

Chapter 6
RESULTS

A) Morphometric Observations

In the following results the correlations reveal similarities or differences across the species with regard to the changes in the morphology along the vertebral column. If the correlation coefficient is significant in comparisons between the species it indicates that the sequential profile pattern is the same between the species in question. Conversely a nonsignificant relationship suggests that the profile patterns being compared are different.

The Absolute Spinous process Ratio

This ratio indicates the relative actual length of the spinous process. The results show that the ratio has two modes of profile patterns (Figure 6.1a. and 6.1b/6.1c). One profile pattern is represented by the curves of the gorilla and orang-utan, and the other pattern is represented by the curves of the baboon, vervet, chimpanzee and human. In the gorilla and orang-utan the relatively longest spinous process is located on V7 (C7), and the lengths gradually decrease caudally towards V19 (T12) (Table 6.1). In the other four hominoids the longest spinous processes are found in the mid-thoracic region on V13/V14 (T6/T7) (Table 6.1). The mid-thoracic region has the relatively longest spinous processes in vervet, baboon, chimpanzee and human. In the chimpanzee and human, the pattern of the profile is similar especially in the mid-thoracic region (V12-V15) (Figure 6.1c). The Spearman correlation coefficient is very close to 1.0 (p = .000) indicating that the two patterns are virtually the same (Table 6.2)

The Spinous process Ratio/Leverage

This ratio indicates the extension leverage of the muscles of the vertebral column, which have attachments on the spinous process. The profile patterns of the ratio exhibit three forms, namely for the gorilla and orang-utan, baboon and vervet, human and chimpanzee (Figure 6.2a, b, c). Though the gorilla and orang-utan profile patterns are visibly similar, we cannot confirm this similarity because the p-value is greater than 0.05 (p-value = 0.068). The baboon profile pattern rises relatively higher through out the thorax than that of the vervet, although the two profile patterns are statistically correlated (p = 0.002) (Table 6.4).

In all the above species, the leverage profiles tend to diverge in the cranial thoracic region and also in the lumbar region. In the thoracic region, profiles remain low and gradual, except in the baboon. The baboon has relatively the highest thoracic spinous leverage, followed by the chimpanzee, vervet, gorilla, orang-utan and human in descending order (Figure 6.2a, b, c; Table 6.3).

In the chimpanzee thoracic region, the profile pattern for the leverage does not change rapidly, that is, it does not fluctuate sharply, but the changes are gradual, giving rise to a relatively gradual curve (Figure 6.2c). However toward the end of the thoracic region, at about V18, the chimpanzee profile pattern rises rapidly, like that of the human. The Spinous Process Leverage in humans rises to a high in the upper thorax at (V10) and falls to its lowest level in the mid-thorax V12/13. It rises again steadily into the lumbar region reaching its highest value on V21 (Figure 6.2c). The gorilla and orang-utan exhibit the highest profile pattern of the Spinous Process Leverages in the upper thoracic region, but these steadily fall to very low values from the mid-thoracic region into the upper lumbar region (Figure 6.2a; Table 6.2).

The negative values (Table 6.4) indicate the inverse properties of the profile patterns, and in this case significance refers to the separate origins of the two samples. In fact the patterns may be regarded as mirror images of each other. For example in Table 6.4, Spearman-R and p-value between human and baboon are -0.779 and 0.001 respectively. A study of the profile patterns clearly indicates that the two patterns (human and baboon) are in fact negatively different. The vervet and baboon profile patterns are inverse to the human and chimpanzee pattern. In some there are negative Spearman-R values, but the p-value in these case shows clearly they are from different samples (not the same).

Lateral Flexion Leverage of the Transverse process or the Lattran Ratio

The ratio indicates the ability to move the trunk laterally, and the ability to counteract lateral flexion, resulting in keeping the trunk straight in the mid-sagittal plane during locomotion.

The lateral flexion leverage is expressed as a ratio in terms of the species body weight, like the other relative ratios. Figure 6.3 and Table 6.5. depict the Lattran ratio in the baboon, vervet, chimpanzee, gorilla, orang-utan and human.
Note, considering only the thoracic region, the baboon has the highest changes in the Lattran ratio. The human and vervet ratios come next, followed by the gorilla, chimpanzee, and orang-utan in that descending order.

After the thoracolumbar transition at V19, the changes in the profile pattern of the ratios rise appreciably. The ratios of the apes and baboon show similar rises in their profiles, starting on V19/V20. However in comparison with the profile pattern of the human Lattran ratios, at that level (the level of the thoracolumbar joint transition) the profile patterns in the apes and the monkeys in the study are lower. In Table 6.5 it can be seen that in humans the ratio at V20 is 0.8 and in the baboon the ratio is 0.6. In the orang-utan and vervet, the profile pattern of the Lattran ratio also begins to rise after V19 and V20 respectively, but does not reach the levels found in the human sample.

Generally, the profile pattern of the Lattran ratio tends to rise in the lumbar region in all the primates in the sample, rising most steeply and to the highest level in humans. Although there are regional differences, the general pattern of the profile pattern of the Lattran ratio throughout the vertebral columns is visibly similar in the above primates (Table 6.6). The orang-utan is different from all the others except humans (p-value = 0.014). This indicates that the orang-utan and humans are correlated in this ratio in spite of their divergent modes of locomotion. Therefore it is not possible to claim orthograde-pronograde dichotomy in the

Lattran ratio of the thoracic region in these primates.

The Ventrodorsal Transverse Tip Ratio or The Vdtran ratio

This ratio indicates the level of the tips of the transverse processes, in relation to the most ventral coronal plane of the vertebral body. The Vdtran ratio has been observed to be above 1.0, in the thoracic region of all the primates studied and does not show general statistical differences between the species. The p-value is less than 0.05 in all species and confirms that the species in the study are all similar in this ratio (Table 6.8). On the other hand, as in the other ratios small visible differences are present at certain levels of the vertebral column profiles (Figure 6.4). For example this ratio is highest in the orthograde humans and semi-orthograde gorilla and chimpanzee where it peaks above 2.2 on V9. (Figure 6.4). There are no differences between the profile patterns of the Vdtran ratio among the humans, chimpanzee and the gorilla. There is therefore no orthograde-pronograde dichotomy in the profile pattern the Vdtran ratio, although the full pronogrades and the suspensory locomotor have relatively low profile patterns for the ratio. The orang-utan, vervet and baboon exhibit the lowest values of the Vdtran ratio, in that order.

The Vdtran ratio reaches its peak generally at V9 in all the primates, after which its profiles decrease steadily through the thoracic region into the lumbar region. Thus, collectively, the extension leverage attributed to the transverse process (through the Vdtran ratio) is highest in the upper thoracic region in all the primates in the study, and lowest towards the lumbar region (Table 6.7). The suspensory locomotor has a small rise in this ratio after V20 (Figure 6.4).

Absolute Facet (Prezygapophyseal) Area

The functional relationship along the vertebral column of this absolute ratio is similar in all the species studied, (p-values are less than 0.05) in all samples (Table 6.10). Because of their massive body the gorillas have the largest absolute facet areas, followed by humans, orang-utan, chimpanzee, baboon and vervet, in that order (Figure 6.5 and Table 6.9). In the gorilla, human and orang-utan, the facet areas are relatively larger at the cervicothoracic (C-T) transitional vertebrae (V7, V8 and V9) than at the mid-thoracic and lower thoracic vertebrae (V10 to 20, depending on species). The absolute thoracic facet areas in the above three species are largest at the C-T transitional vertebrae namely (V8). In the chimpanzee, baboon and vervet, the absolute facet areas between the C-T and the thoracolumbar (T-L) transitions change only gradually.

The absolute facet areas begin to increase at or near the T-L joint and close to last pair of ribs, which is at V20 in baboon and vervet, V19 in human and orang-utan, V20 in gorilla and chimpanzee. The increases are dramatic in humans and apes.

Relative Facet Area or Facet Area Ratio

The relative change in facet areas along the vertebral column is similar ($p \angle 0.05$) (Table 6.12). However, Table 6.11 indicates small specific differences in the values of the ratios at particular levels on the vertebral column, namely at or around the levels of the C-T and T-L transitional joints. For example, the greatest relative change in the ratio of the facet area is located on the C-T transition, on V8 of the gorilla, human and orang-utan (Table 6.11). In the baboon, the greatest change is located on V19 with a reading of 0.310. In humans, vervet and chimpanzee the highest values of the change in the ratio along the vertebral column is found on V20 and are as follows: 0.283, 0.318 and 0.244 respectively (Figure 6.6). These levels of the greatest change in the facet area ratios are at or adjacent to the T-L joint transition. In the gorilla and orang-utan the greatest change in facet area is recorded cranially at C-T transition, specifically at the level of V8. The values are 0.285 and 0.241 respectively in the gorilla and orang-utan (Figure 6.6). Towards the T-L transition, the changes in the facet area ratios dramatically increase in all the primates studied.

Inclination Angle of Facet or Prezygapophyseal Angle

The vervet has relatively the largest thoracic facet angles, followed by the baboon, among the species in this study. Humans also have relatively large thoracic facet angles, closely followed by the chimpanzee. The gorilla and orang-utan have the smallest thoracic facet angles, but of these two the latter generally exhibits the lower values. In the vervet all the thoracic facet angles are above 110 degrees, and in the baboon 9 pairs of thoracic facet angles are above 110 degrees, (Table 6.13; Figure 6.7a). In humans, 6 thoracic vertebrae out of the twelve have facet angles that are 110 degrees and above. In the semi-orthogrades and the suspensory locomotor the thoracic vertebrae having angles that are above 110 degrees are much fewer, than in humans and monkeys. There are 2 pairs of thoracic angles above 110 degrees in the orang-utan, 3 pairs in the gorilla and 4 four in the chimpanzee. In all primates in this study, the relative values of all the facet angles fall dramatically, at and caudal to V20. This drop coincides with the vertebra at or just caudal to the last pair of ribs, that is with the end of the ribs. For example, the facet angles on V19 of the baboon and gorilla are 148 and 110 degrees respectively, while the corresponding angles on V20 in the same animals are 30 and 68 degrees (Table 6.13).

Statistically, according to table 6.14 baboon, vervet, humans and to some extent chimpanzee all have similar profile patterns. The gorilla and orang-utan are statistically different, with p-values that are greater than 0.05 in all comparisons (Figure 6.7b; Table 6.14).

Absolute Cranial Vertebral Body Area

The cranial vertebral body areas increase proportionally craniocaudally towards the lumbar region in all the groups. The profile pattern of the absolute areas of the vervet, from the cranial to the caudal thoracic vertebrae, has relatively the lowest changes in values. The vervet profile pattern is also uniquely separated from the curves of the baboon, human, chimpanzee, gorilla and orang-utan (Figure 6.8, Table 6.15). The profile patterns however are significantly correlated (p-value is less than 0.05 among all the groups).

Relative Cranial Vertebral Body Area

This is the area of the cranial vertebral body surface if the species body weight is taken into account. The profile pattern of the relative area of the cranial surface of the vertebral body still increases craniocaudally in all the species. From the biggest to the smallest profile pattern for the areas recorded, the order is as follows: gorilla, human, orang-utan, chimpanzee, baboon and vervet. Again the vervet stands out alone in having very low relative profile pattern for the vertebral areas (Figure, 6.9, Table 6.17). The profile pattern for the ratio is significantly correlated in all the species in the study. (p-value is less 0.05 throughout) (Table 6.18). However, the profile pattern of the vervet as mentioned above stands out rather low in comparison with the profile patterns of the others.

Relative Caudal Vertebral Body Area

The relative caudal vertebral body area (RCVB area) was measured only over the transitional vertebrae (i.e. C-T and T-L transitions), due to lack of time, because of limited funds. Therefore, the comparison will be made only in the C-T and T-L transitional region. In individual species the RCVB area is relatively higher in the T-L than in the C-T transitional vertebrae in all the primates studied (Figure 6.10 and Table 6.19). The semi-orthogrades (apes) and the orthogrades (humans) have the highest transitional RCVB areas at both the C-T and T-L transitions, compared to the pronogrades (monkeys). The orthogrades have the highest transitional RCVB areas in all the primates studied. The profile patterns for areas are seen to rise caudal to V21 in humans, but in the apes, they fall dramatically at that level. However, the p-value is below 0.05 among all the groups indicating that they are similar for this ratio (Table 6.20).

Pedicle Ratio of the transitional vertebrae

The pedicle measurements were taken in the C-T and T-L transitional regions.

This ratio is the cross-sectional area of the pedicle at mid-transverse level, compared to the area of the cranial surface of the vertebral body, and is highest in the pronogrades. The significance values (Table 6.22) show similarity of the chimpanzee, orang utan and gorilla profile patterns, but most other relationships are not significant. The baboon and vervet share a similar profile pattern but the p-value of 0.72 is just below the significance boundary. It is notable that many of the comparisons are negative, indicating that some of the profile patterns are reversed in relationship to each other, but some of the these negative conditions are significant. In the apes and humans the profile pattern has its highest point at V8 at the C-T transition (Table Figure 6.11b, Table 6.21). This ratio has the lowest profile pattern in the orang-utan.

On the T-L transitional vertebrae the profile patterns dramatically rises in the pronogrades but in the apes and humans the ratio remains low (Figure 6.11a, Table 6.21). The changes in the profile pattern of the pedicle ratio are almost different in each species.

Relative Pedicle Area

This is the cross-sectional area of the pedicle, which increases in a caudal direction in all the primates studied. The increases in the profile pattern are highest at the T-L transition, and again caudally after the T-L transition in all the primates studied. There appears to be only two general profile patterns namely, the profile for the baboon, vervet and human, and the profile for the gorilla, orang-utan and chimpanzee (Figure 6.12). The apes have the lowest profile pattern for relative pedicle areas but not significantly different from the others. The p-value is close to .0 in all, indicating a close correlation of all the species for this characteristic, unlike the pedicle ratio (Table 6.24)

Absolute Vertebral Foramen Area

This is indicates the approximate size of the vertebral foramen and possibly the spinal cord in some parts of the vertebral column. There are no differences between the species in the absolute vertebral foramen area, except in the baboon and orang-utan, as well as the baboon and chimpanzee, where the p-values are 0.164 and 0.136 respectively (Table 6.26). Some small differences in the profile pattern however, can be pointed out from Figure 6.13 and Table 6.25. Whether these differences are functionally important may be debatable. The absolute vertebral foramen area is largest in the gorilla, and decreases consecutively in human, orang-utan, chimpanzee, baboon and vervet (Figure 6.13).

All the profile patterns of the area show large foramen areas at the C-T joint transitional vertebrae, and after that very little change or fluctuation is seen within the thoracic region, until the level of the T-L transition. Apes and humans show relatively higher profile patterns for absolute vertebral foramen areas immediately caudal to their respective T-L transitional joints, than vervets and baboons. The profile patterns near the lumbar region are also notably higher in human and gorilla than in orang-utan, chimpanzee, vervet and baboon (Figure 6.13, Table 6.25).

Relative Vertebral Foramen Area or Vertebral Foramen Area Ratio

There are differences in this profile pattern of the changes in ratio along the vertebral column between the orang-utan and baboon (p-value = 0.164) and between the chimpanzee and baboon (p-value = 0.136). This is one relationship where the absolute and relative patterns are not affected by the weight or body size of the species, because the p-values in both absolute and relative measurements are almost similar. (Tables 6.25 and 6.27). However, when the species weight is taken into account the curves for relative vertebral foramen areas show only two similar but distinctly separate profile patterns, in contrast to the scattered patterns of the absolute measurements (Figures 6.13 and 6.14).

The profile patterns for the vervet, baboon and human form one group near one another, while profiles for the gorilla, chimpanzee and orang-utan also form another group (Figure 6,14). In all the sample dramatically big changes are recorded around the C-T and towards the T-L transitions of each species. These changes correspond to the cervical and lumbar enlargements of the spinal cord. Apart from these changes, and the above grouping of the profile patterns there are no other noticeable differences in the profile patterns of this ratio in the species in the study.

B) Vertebral Counts and Patterns

Each vertebra in the vertebral column was properly identified, using features that have been listed in Chapter 5 (Materials and Methods). The vertebrae of a particular vertebral column were lined in series such that they were properly articulated, as they would be in the body. The presacral vertebrae consisting of the cervical, thoracic and lumbar vertebrae were identified, counted and recorded for each vertebral column. Sacralisation, lumbarisation and thoracolisation can be seen in Table 6.37. Sacralisation occurs when the last lumbar vertebra is fused with the sacrum. Lumbarisation occurs when the first sacral vertebra or the last thoracic vertebra is incorporated into the lumbar vertebrae. A vertebra becomes part of the lumbar region resulting in a longer lumbar region or a short thoracic region. Thoracolisation is a result of inclusion of the first lumbar, or in rare cases, of the seventh cervical vertebra into the thoracic series of vertebrae.

The conventional method of counting vertebrae is by using the articulations of ribs or their absence to identify cervical, thoracic and lumbar regions. In that method a specimen with thirteen pairs of ribs is said to have thirteen thoracic vertebrae, regardless of whether the vertebra carrying the thirteenth rib has lumbar features. A cervical vertebra carrying a cervical rib is classified as thoracic by the method. The shortcomings of the method are clear. In this study therefore the vertebrae were identified by first examining the changes in their zygapophyseal joints (Figures 2.1, 2.2, 2.3). This was preferred to the above mentioned conventional identification because joints are functionally important in the movements of the body, and indeed of the vertebral column. On the other hand, the identification, by use of ribs, was also carried out in order to establish the relationship of the ribs with the thoracolumbar transition.

i) <u>Position of the transitional thoracolumbar vertebral (T-L V) joint</u> (Figure 6.0)

This is a very important point because it demarcates the functional shift from the rotational movements of the cranial region to the extension and flexion movements of the more caudal aspect. In the apes the T-L V always occurs at V19 or V20. This is why the apes have a relatively longer thorax and a shorter lumbar portion than other hominoids (Table 6.39 a, b). In modern human this transition is slightly higher at V18 or V19, which is consistent with the relatively frequent reduction or lumbarisation of the last thoracic vertebra. The T-L joint transition of the baboons and vervets is at a higher level on V17, consistent with their relatively shorter thoracic and longer lumbar setting.

ii) <u>Relations between the transitional T-L V joint and ribs</u> (Figure 6.0)

The use of ribs as a marker of the thoracolumbar transition is quite different from using the change in the movements, at the facet joints. In all the primates in the study except humans, the rib transition occurred at V19-V20 (Figures 6.0 6.38a, b) but humans have much higher rib transitions occurring over a wider range, namely from V17, V18 to V19. In the monkeys the rib transition was located further caudally away from the transitional T-L V joint (Figure 6.0 D, E, F). In apes as well as humans the rib transition was at the T-L V and in some rare cases cranial to the T-L joint transition (Figure 6.0 A, B, C).

Six patterns can be defined when the relationship between ribs and the T-L V joints is considered in the various species, and summarised below (Figure 6.0 A, B, C, D, E, F).

Pattern A (Uncommon pattern): This pattern is the least common in the primates studied. The last pair of ribs is located on the second vertebra cranial to the T-L V.

Pattern B (Ortho and semi-orthograde pattern - humans/apes): The last pair of ribs is located cranial to the T-L V. on the vertebra that is adjacent to the T-L V. This pattern is not found in the monkeys at all.

Pattern C (Again in Ortho and semi-orthogrades): In this pattern the last rib pair is found directly on the T-L V. In the study, it is only found in the apes and humans. It is absent in the vervet and baboon.

Pattern D ('Universal' - found in all): The last pair of ribs is located caudal to the T-L V. on the vertebra that is immediately behind to the T-L V. It is found in all the species studied.

Pattern E (Mainly vervet pattern - arboreal pronogarade): The last pair of ribs is located caudal to the T-L V. on the second vertebra behind the T-L V. This pattern occurs mainly in monkeys, but mainly the usually arboreal vervet.

Pattern F (Mainly baboon, a terrestrial pronograde): The last pair of ribs in this pattern is located caudal to the T-L V, on the third vertebra behind the T-L V. The pattern is exclusively found in the monkeys but dominantly in the terrestrial baboon, not in apes and humans.

iii) Patterns of pre-sacral vertebral (PSV) numbers

The mode of PSV in the vertebral column (Table 6.36) of either humans or chimpanzees is 24. The Gorillas show a high frequency of 24 vertebrae, but individuals with only 23 vertebrae are the most common amongst the gorillas and orang-utans. Vervets and baboons have relatively longer pre-sacral columns most frequently consisting of 26 vertebrae. The increase of the number of pre-sacral vertebrae is at the expense of the number lumbarised, reducing the baboon and monkey sacrum to 3 elements.

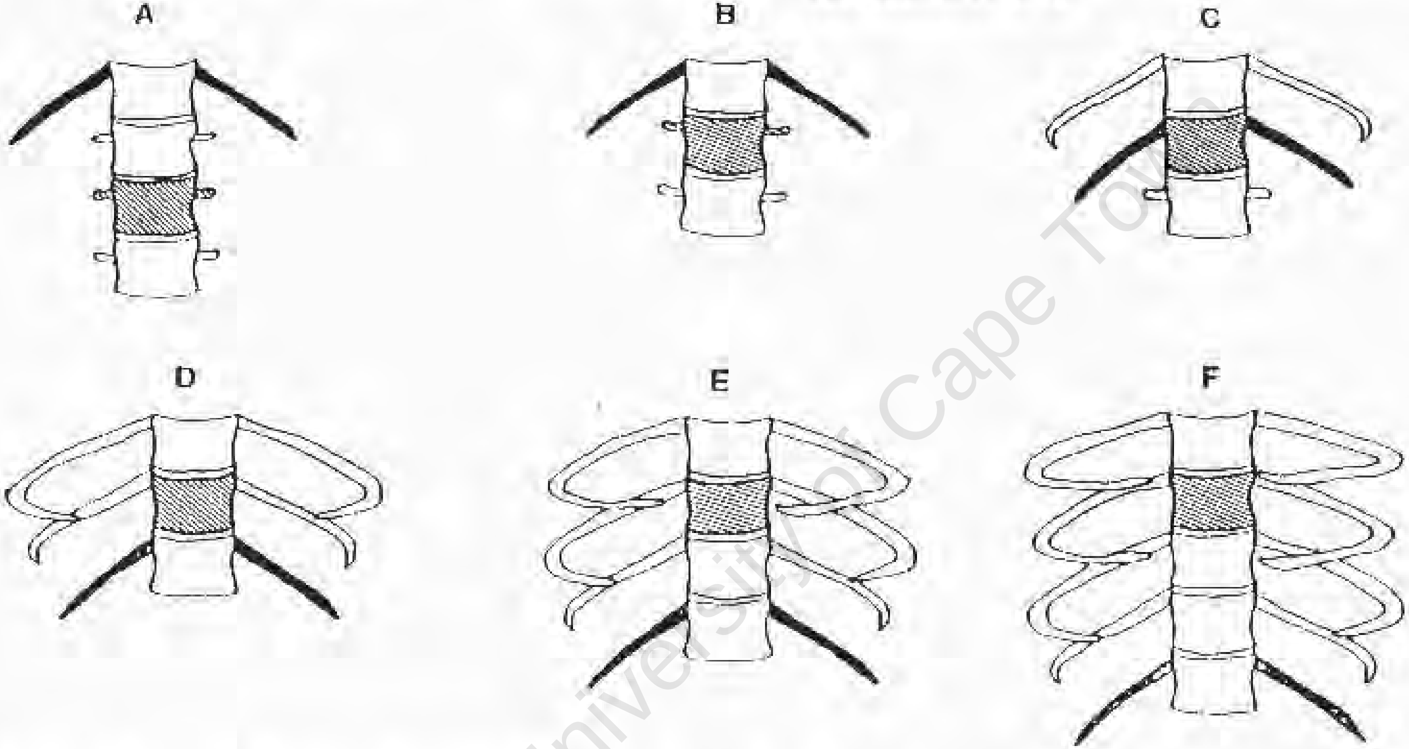
The relationship between the numbers of cervical, thoracic and lumbar vertebrae is represented in Table 6.37. The longest thorax (with 13 vertebrae) and the shortest lumbar region (with 3-4 vertebrae) are found in the chimpanzee, gorilla and orang-utan. Some gorillas (34.6%) have as few as 3 lumbar elements. In contrast the vervet and baboon have relatively fewer thoracic and many lumbar vertebrae.

Humans have more in common with the apes, both species often having 12 thoracic vertebrae. A significant percentage of humans (28.4%) had only 11 thoracic vertebrae. The decrease of the thoracic vertebrae is caused by either the loss of a thoracic element (reduction) or by lumbarisation of T12.

The commonest PSV (C / T / L) patterns and their frequencies can be seen in Table 6.37. The others that are common are C7 T10 L9 (baboon, vervet), C7 T12 L5 (human), C7 T13 L4 (orang-utan), and C7 T13 L3/L4 (gorilla).

Figure 6.0

THE GENERAL POSITION OF THE MOST CAUDAL PAIR OF RIBS IN RELATION TO THE THORACOLUMBAR TRANSITIONAL VERTEBRA (T-L V)



A Last ribs on 2nd vertebra cranial to T-L V. The least common pattern

B Last ribs cranially adjacent to T-L V. Not observed in pronogrades

C Last ribs on T-L V. Exclusively found in apes and humans (semiorthogrades / orthogrades)

D Last ribs caudally adjacent to T-L V. Occurs in all modes of locomotion. But in relatively low numbers.

E Last ribs on 2nd vertebra caudal to T-L V. Dominated by the arboreal pronogrades (vervet)

F Last ribs on 3rd vertebra caudal to T-L V. Exclusively pronogrades (vervet and baboon)

■ Last rib

▨ T-L V

Figure 6.1a

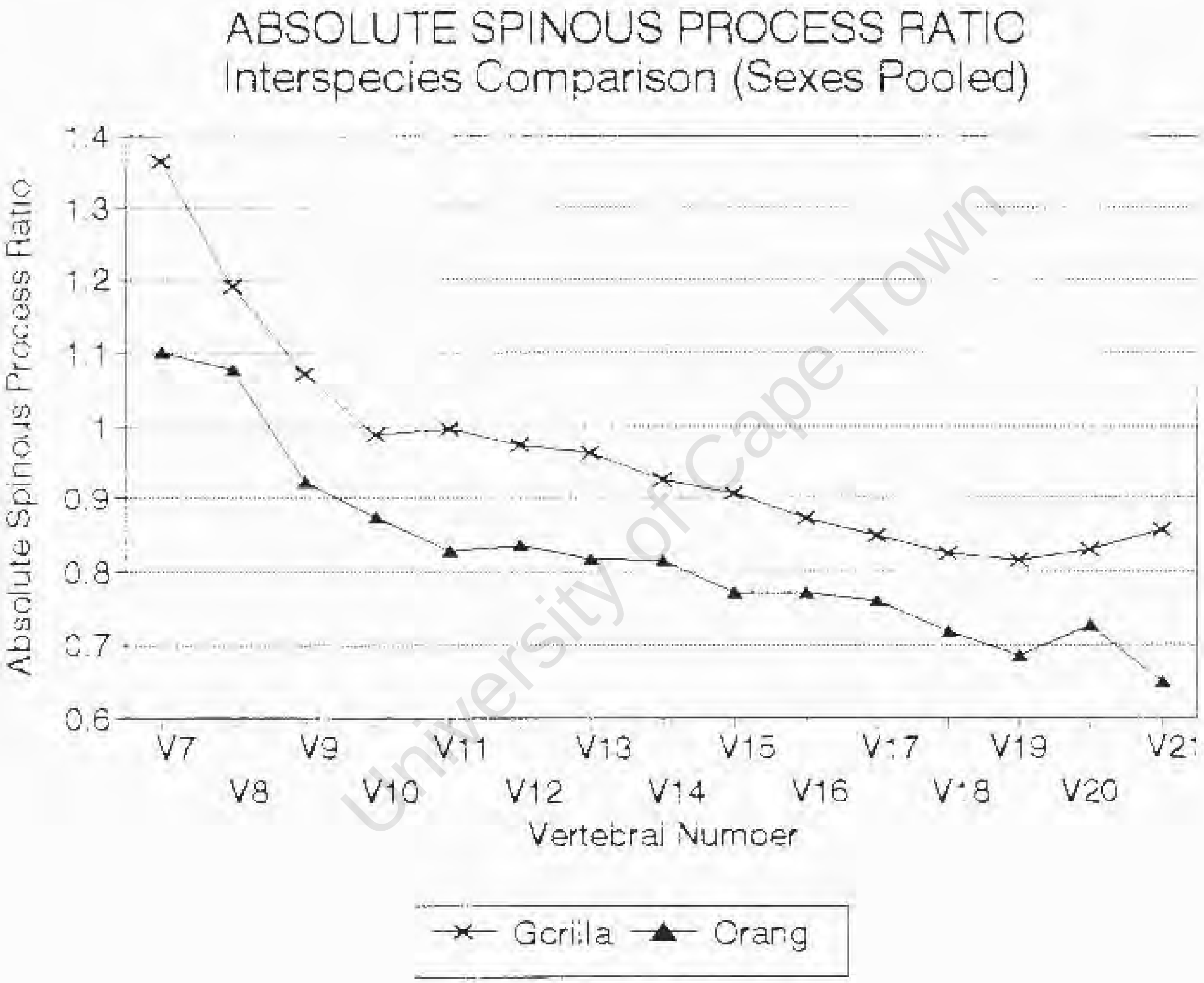

ABSOLUTE SPINOUS PROCESS RATIO
Interspecies Comparison (Sexes Pooled)
Absolute Spinous Process Ratio
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20
V21
Vertebral Number
Gorilla
Orang

Figure 6.1b

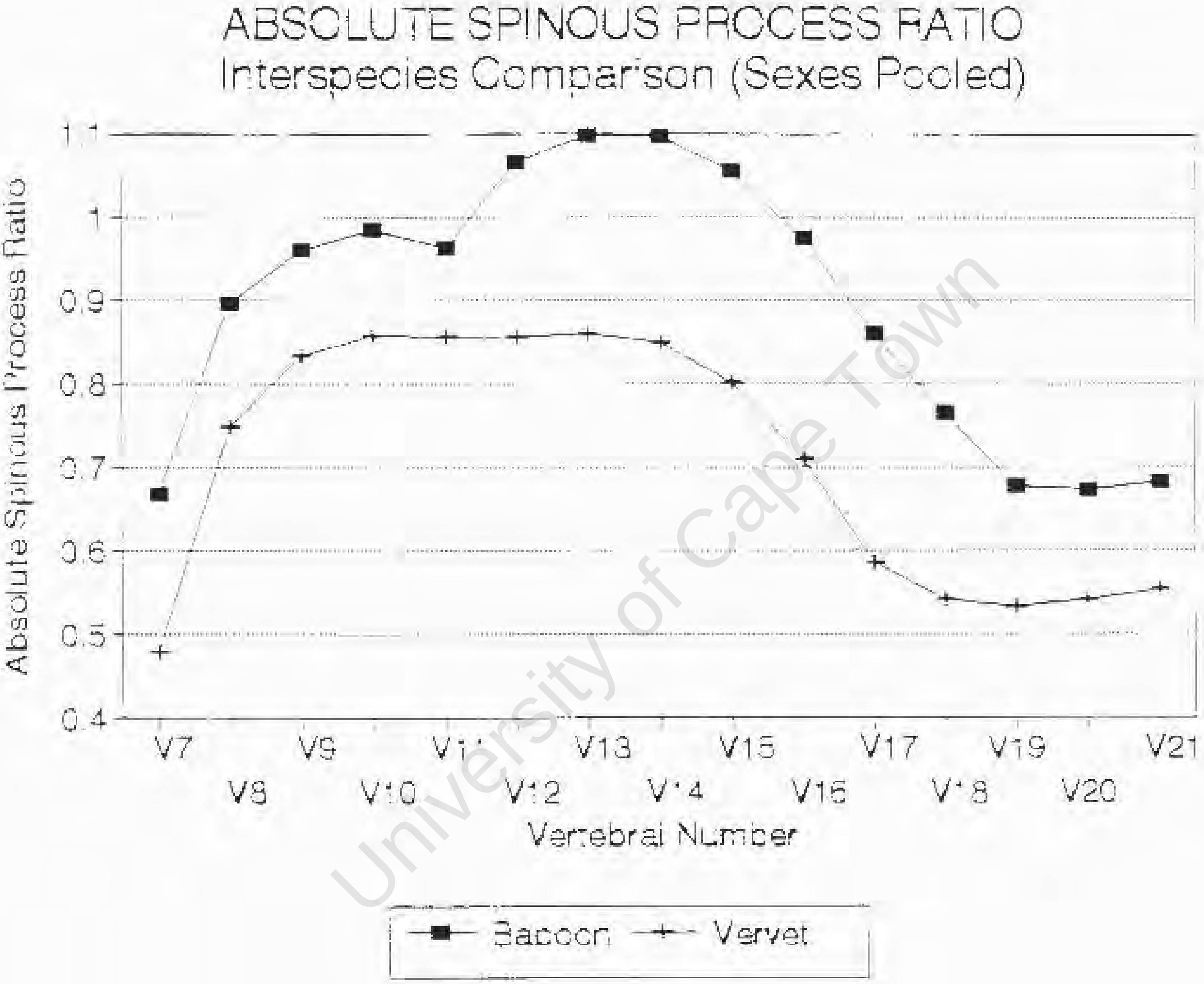

ABSOLUTE SPINOUS PROCESS RATIO
Interspecies Comparison (Sexes Pooled)
Absolute Spinous Process Ratio
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20
V21
Vertebral Number
Baboon
Vervet

Figure 6.1c

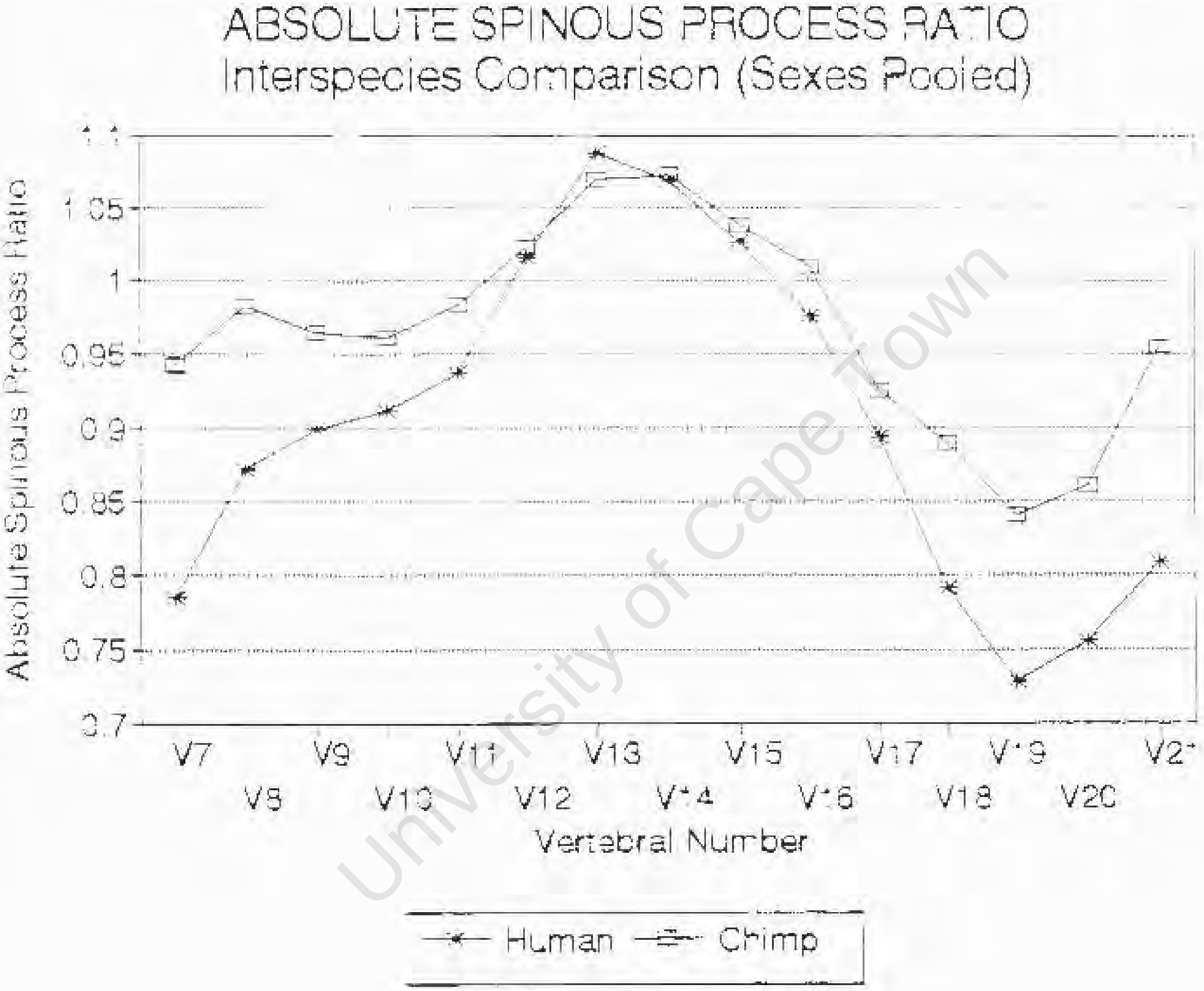

ABSOLUTE SPINOUS PROCESS RATIO
Interspecies Comparison (Sexes Pooled)
Absolute Spinous Process Ratio
1.1
1.05
1
0.95
0.9
0.85
0.8
0.75
0.7
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20
V21
Vertebral Number
Human
Chimp

Figure 6.2a

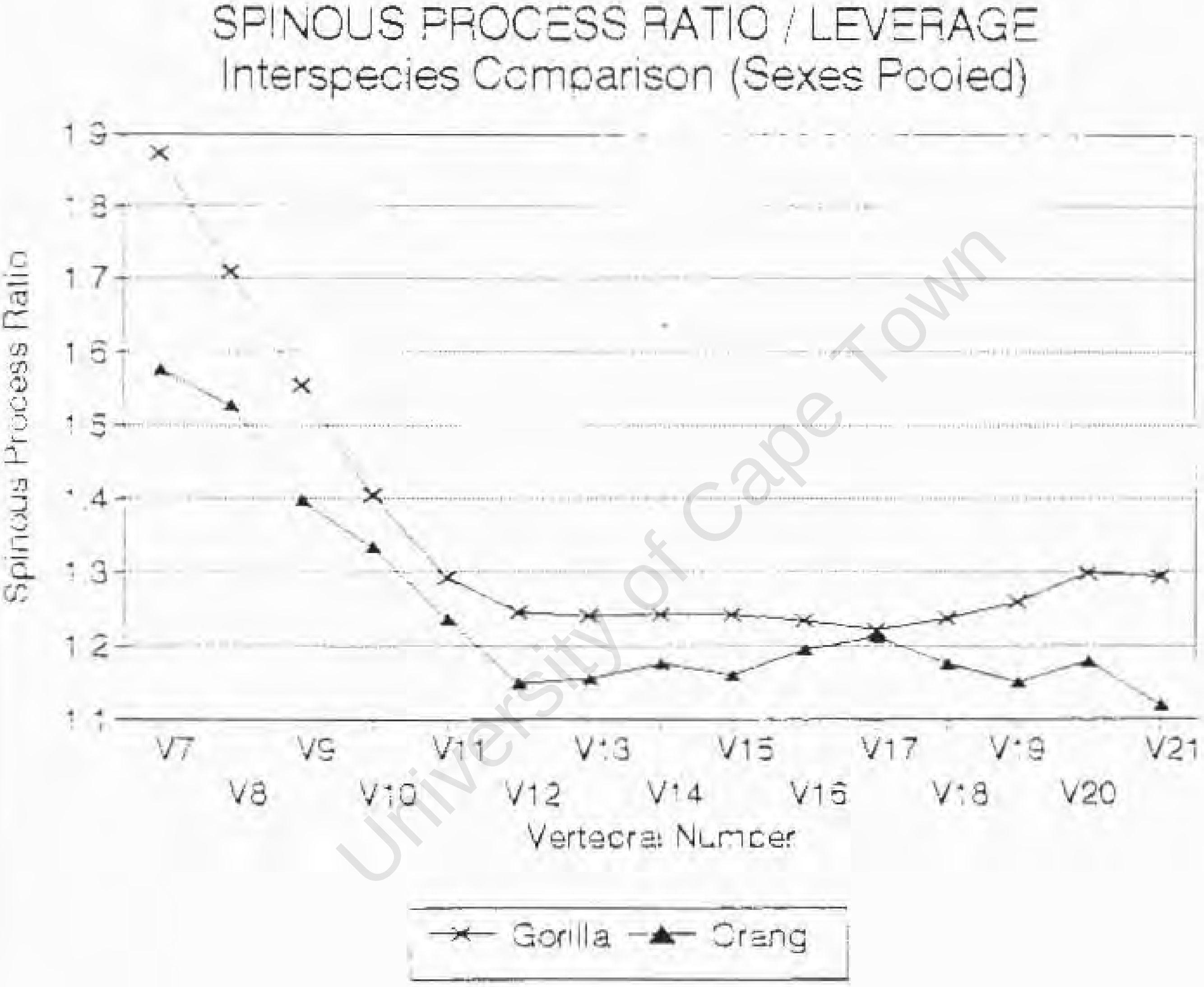

SPINOUS PROCESS RATIO / LEVERAGE
Interspecies Comparison (Sexes Pooled)
Spinous Process Ratio
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20
V21
Vertebral Number
Gorilla
Orang

Figure 6.2b

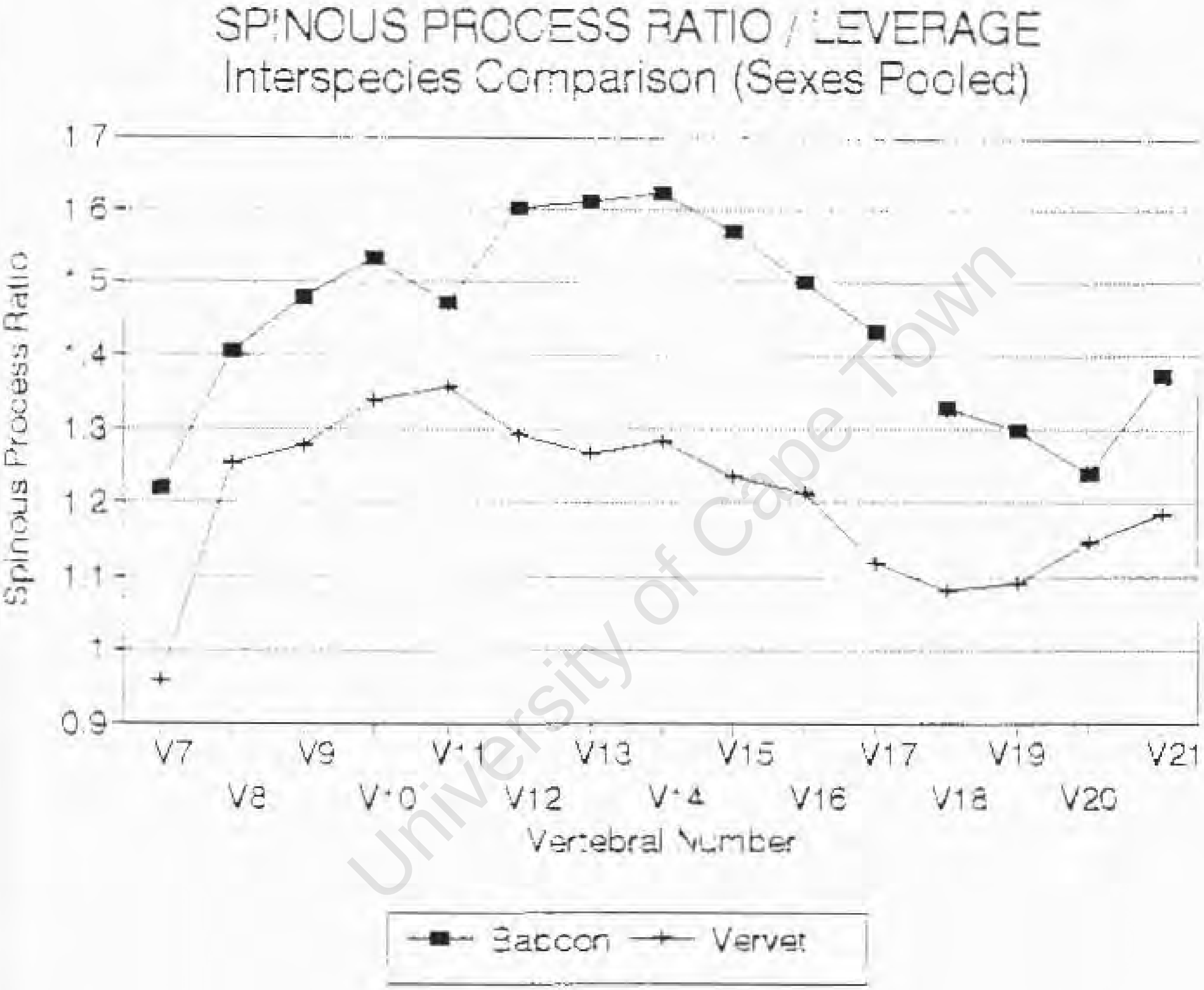

SPINOUS PROCESS RATIO / LEVERAGE
Interspecies Comparison (Sexes Pooled)
Spinous Process Ratio
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1
0.9
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20
V21
Vertebral Number
Baboon
Vervet

Figure 6.2c

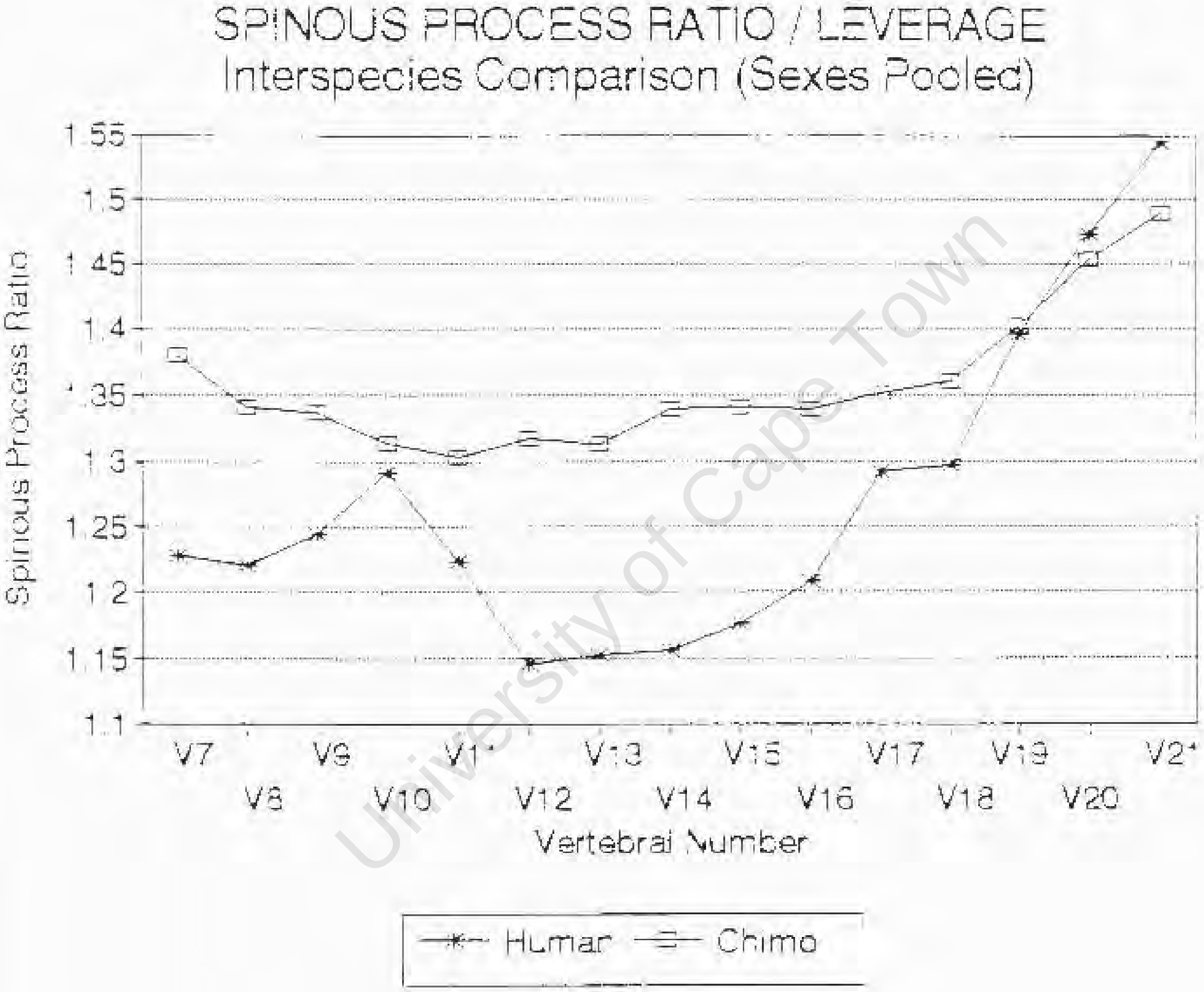

SPINOUS PROCESS RATIO / LEVERAGE
Interspecies Comparison (Sexes Pooled)
Spinous Process Ratio
1.55
1.5
1.45
1.4
1.35
1.3
1.25
1.2
1.15
1.1
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20
V21
Vertebral Number
Human
Chimp

Figure 6.3

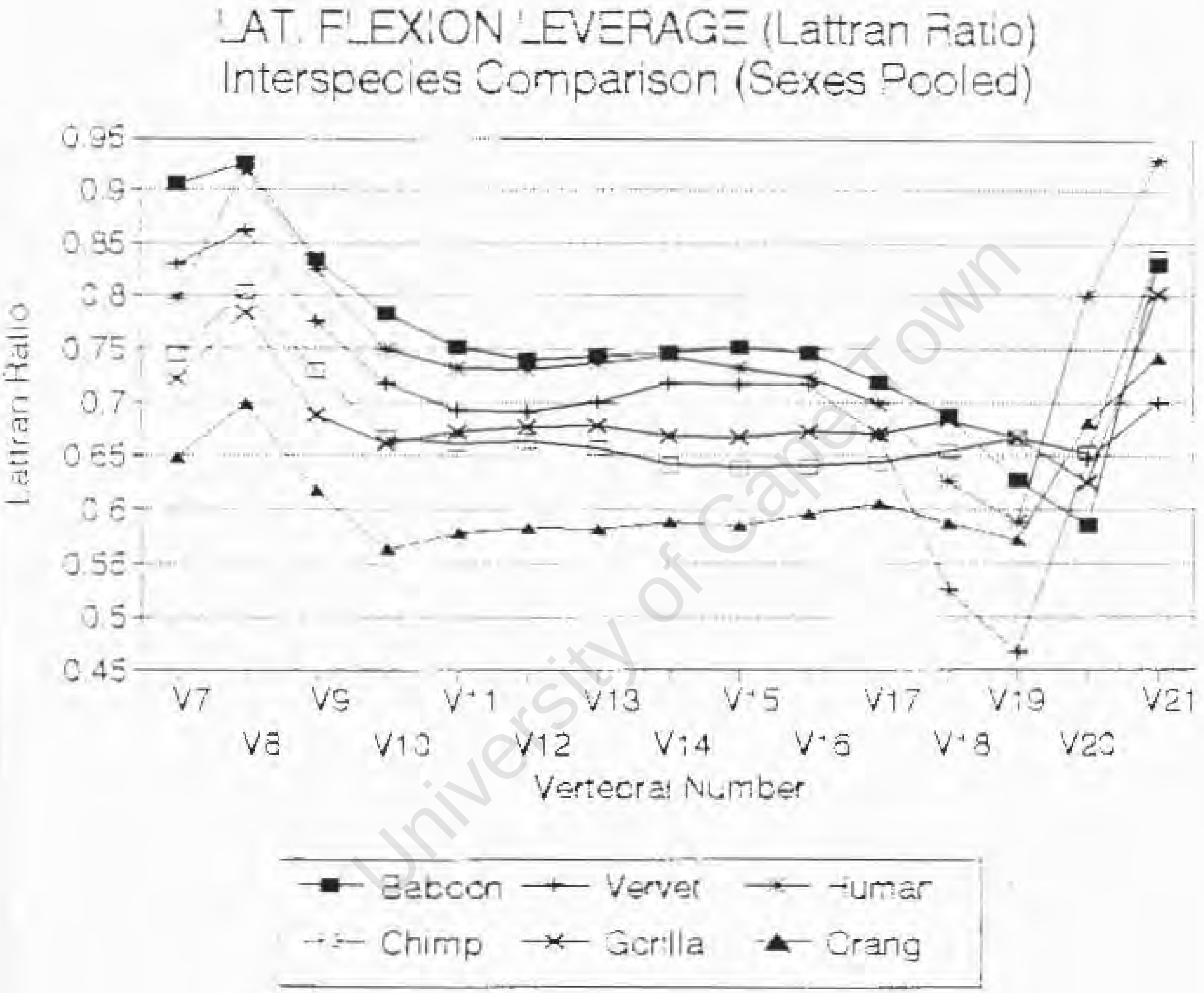

LAT. FLEXION LEVERAGE (Lattran Ratio)
Interspecies Comparison (Sexes Pooled)
Lattran Ratio
0.95
0.9
0.85
0.8
0.75
0.7
0.65
0.6
0.55
0.5
0.45
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20
V21
Vertebral Number
Baboon
Vervet
Human
Chimp
Gorilla
Orang

Figure 6.4

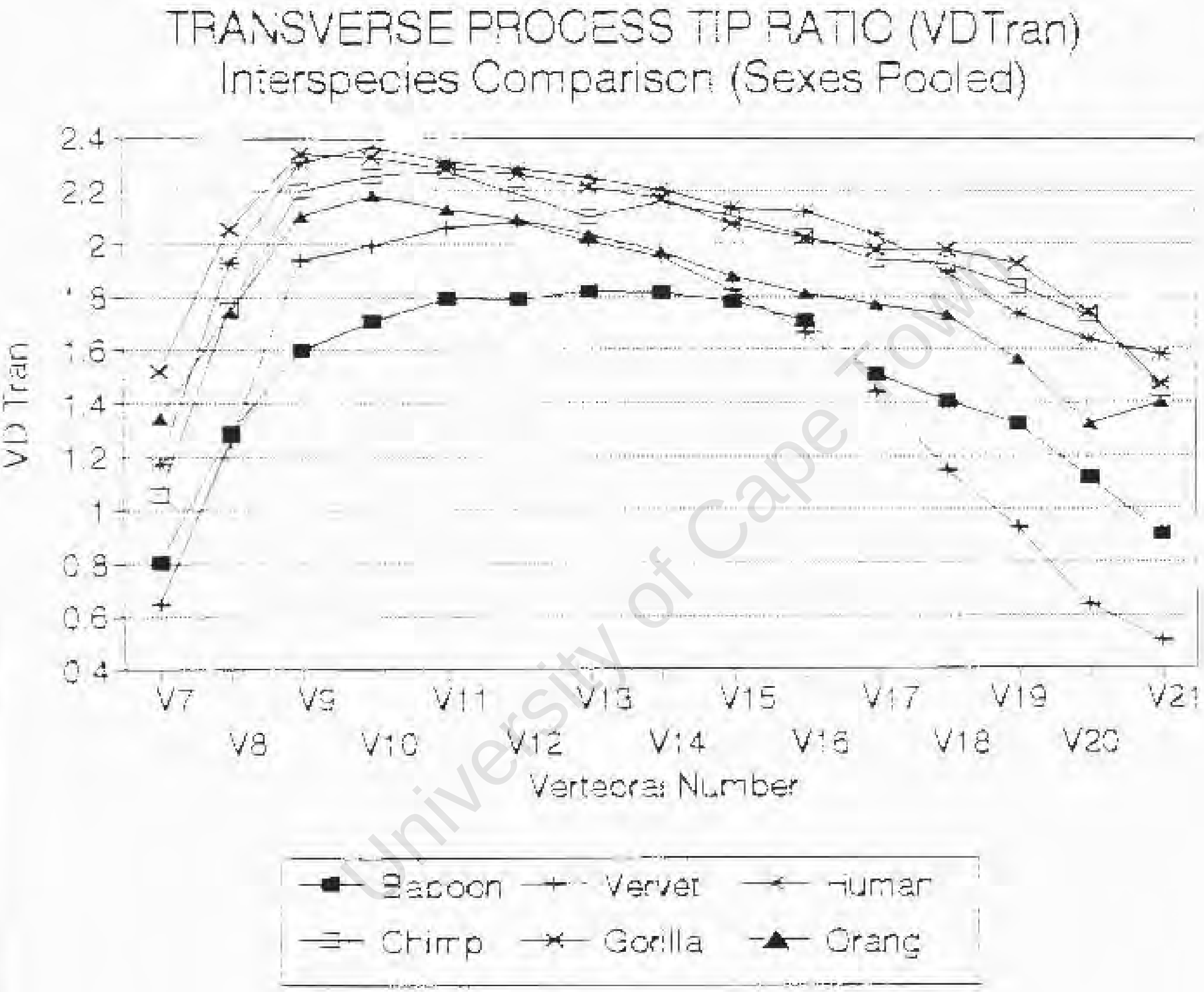

TRANSVERSE PROCESS TIP RATIO (VDTran)
Interspecies Comparison (Sexes Pooled)
VD Tran
2.4
2.2
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20
V21
Vertebral Number
Baboon
Vervet
Human
Chimp
Gorilla
Orang

Figure 5.5

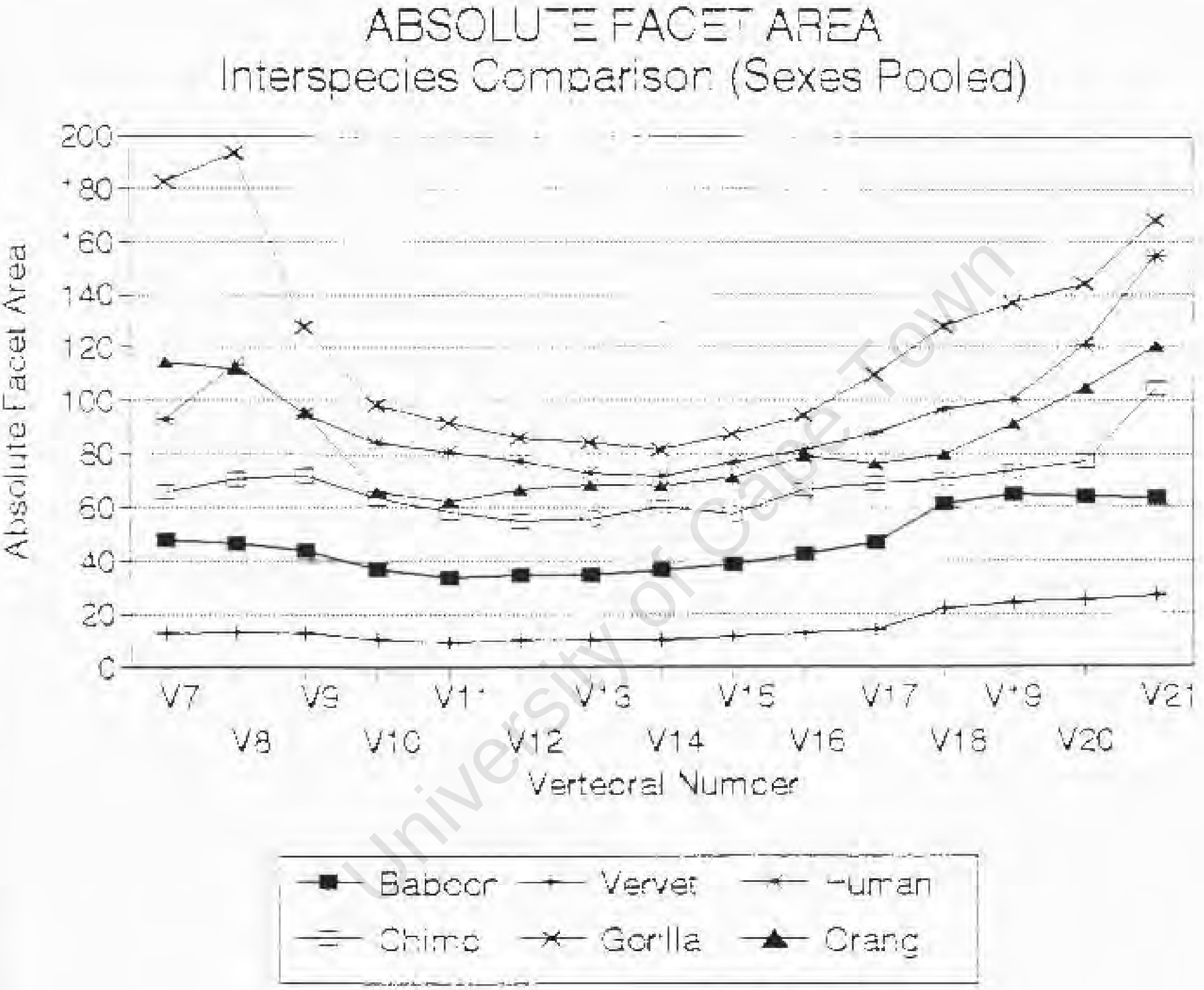

ABSOLUTE FACET AREA
Interspecies Comparison (Sexes Pooled)

Figure 5.3

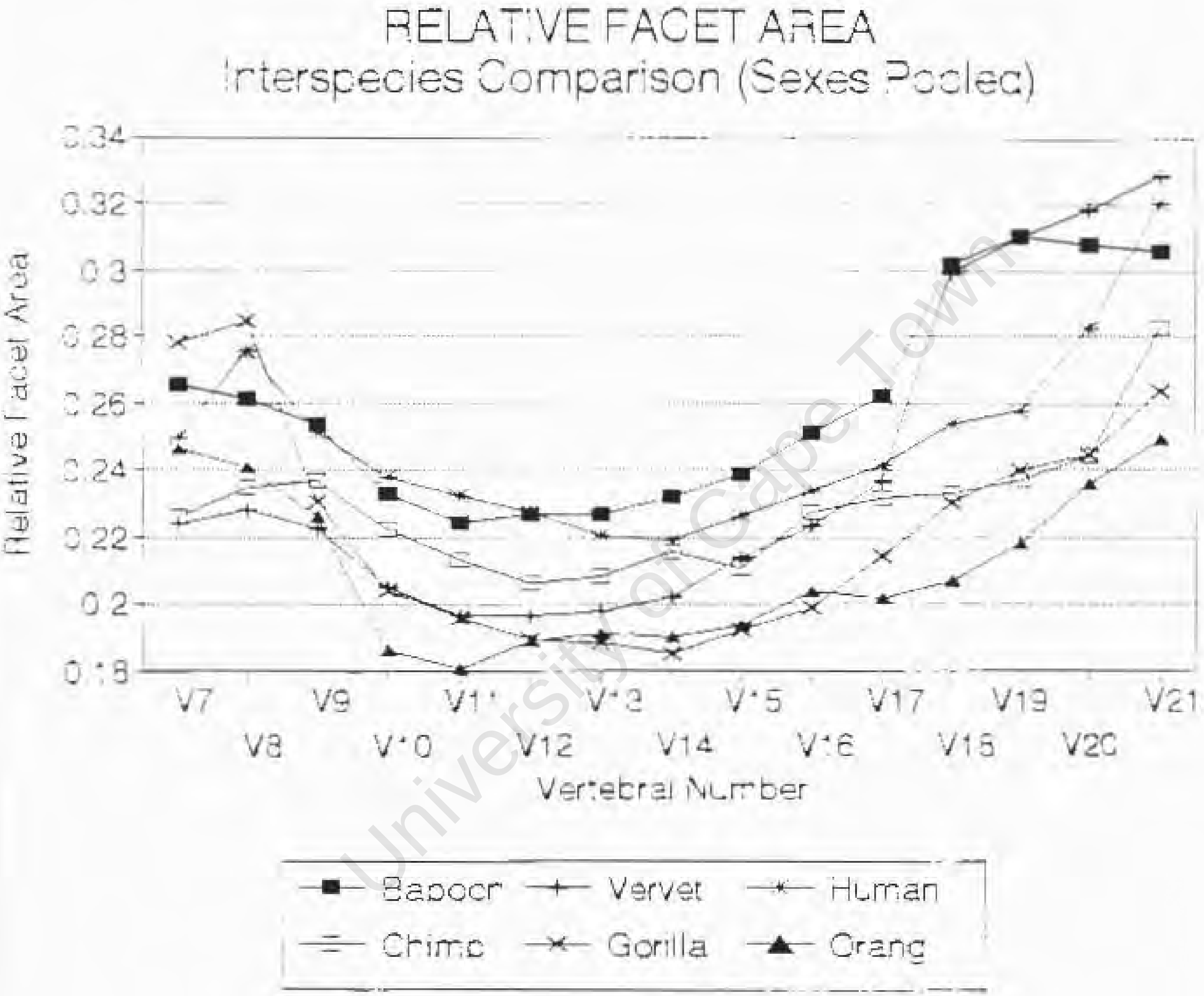

RELATIVE FACET AREA
Interspecies Comparison (Sexes Pooled)
Relative Facet Area
0.34
0.32
0.3
0.28
0.26
0.24
0.22
0.2
0.18
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20
V21
Vertebral Number
Baboon
Vervet
Human
Chimp
Gorilla
Orang

Figure 6.7a

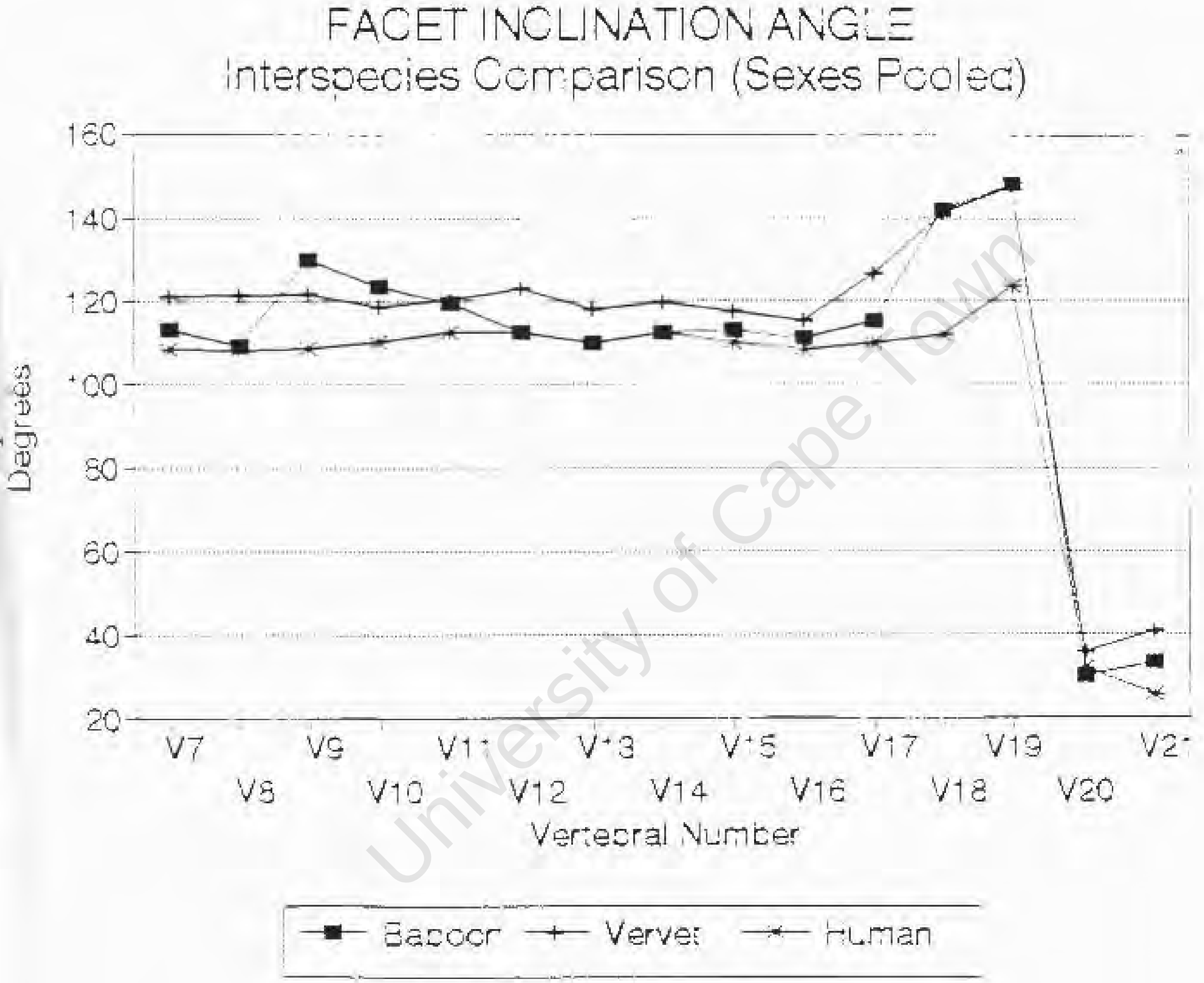

FACET INCLINATION ANGLE
Interspecies Comparison (Sexes Pooled)
160
140
120
100
80
60
40
20
Degrees
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20
V21
Vertebral Number
Baboon
Vervet
Human

Figure 6.7b

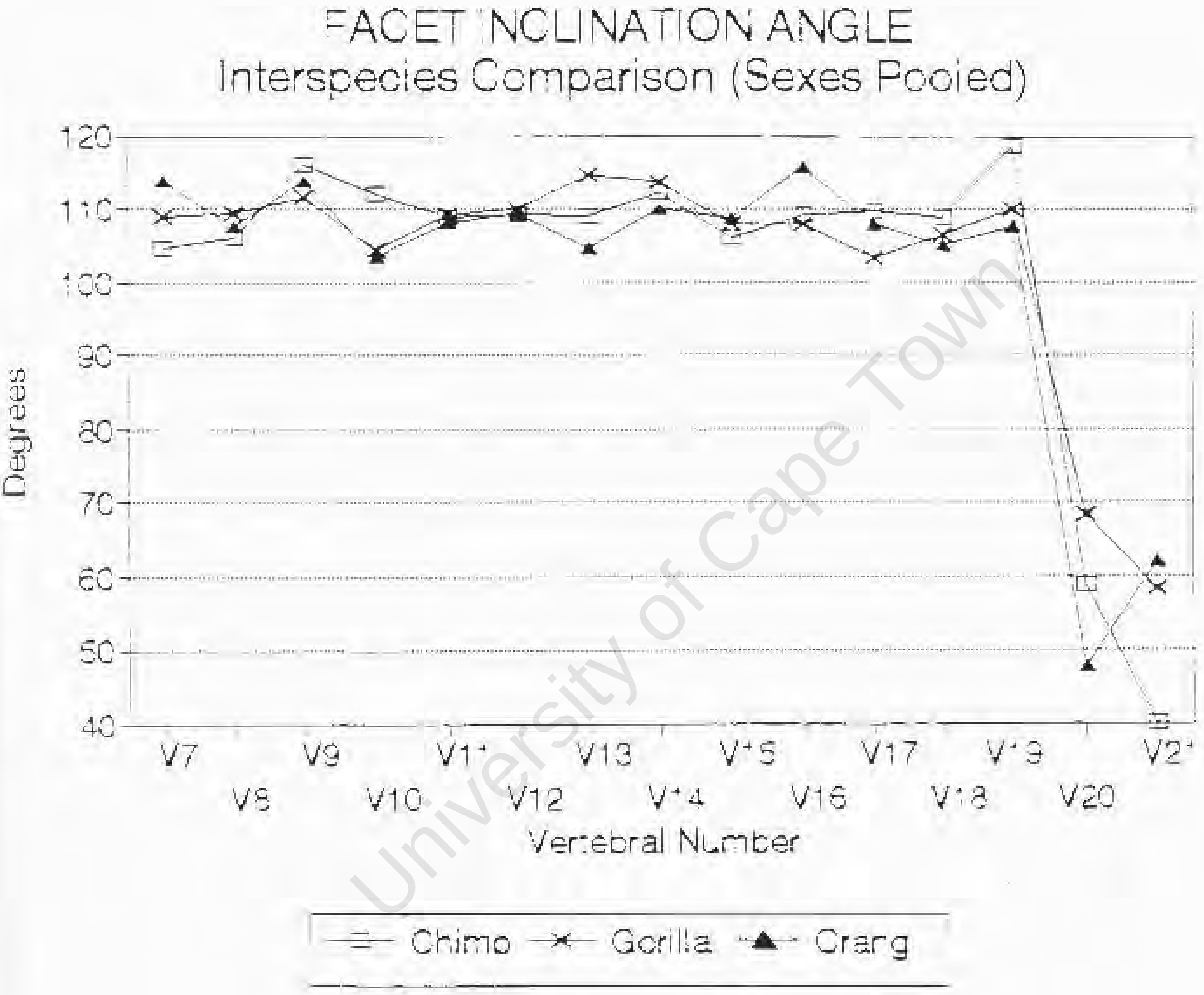

FACET INCLINATION ANGLE
Interspecies Comparison (Sexes Pooled)
120
110
100
90
80
70
60
50
40
Degrees
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20
V21
Vertebral Number
Chimp
Gorilla
Orang

Figure 6.8

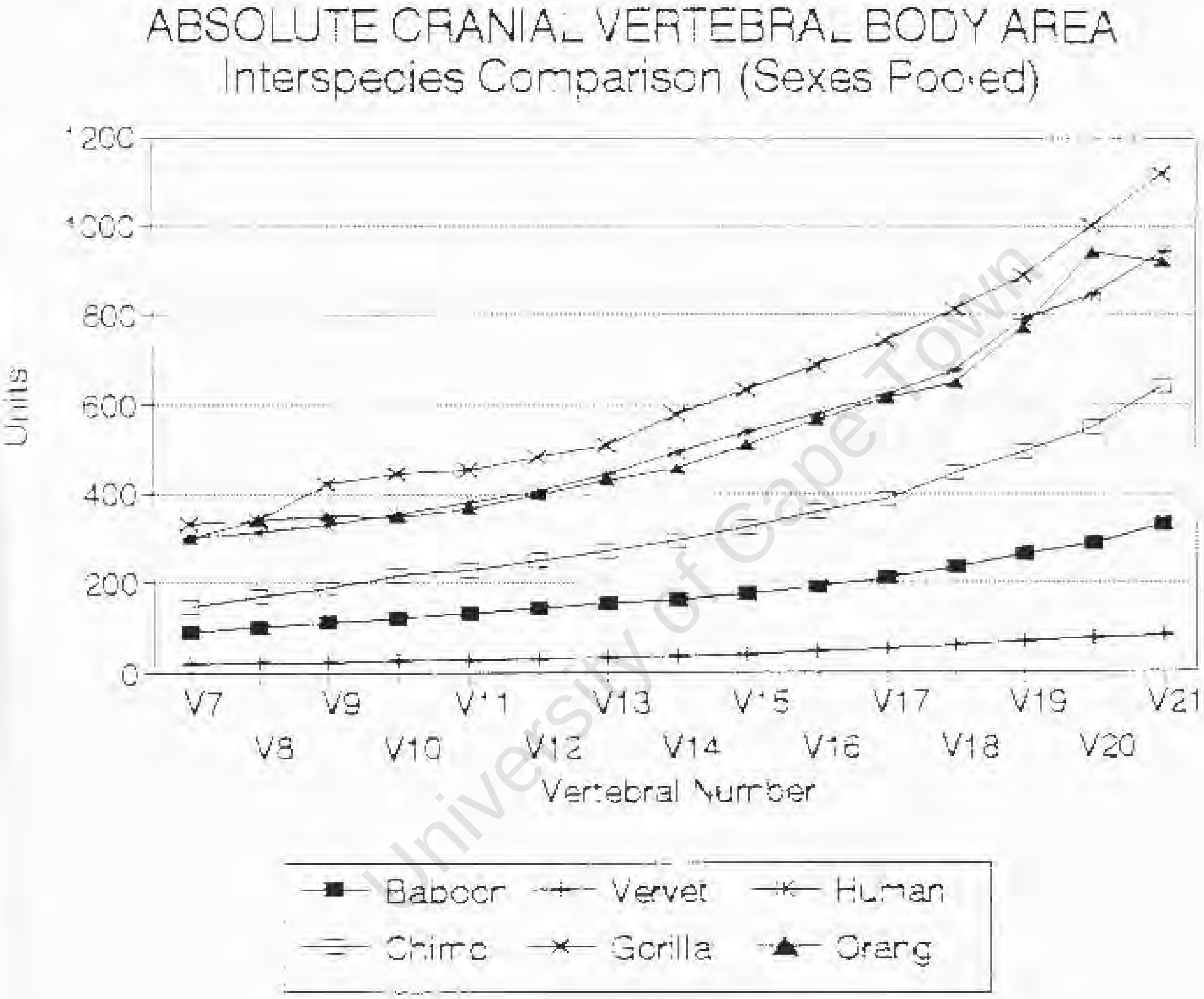

ABSOLUTE CRANIAL VERTEBRAL BODY AREA
Interspecies Comparison (Sexes Pooled)
Units
1200
1000
800
600
400
200
0
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20
V21
Vertebral Number
Baboon
Vervet
Human
Chimp
Gorilla
Orang

Figure 6.9

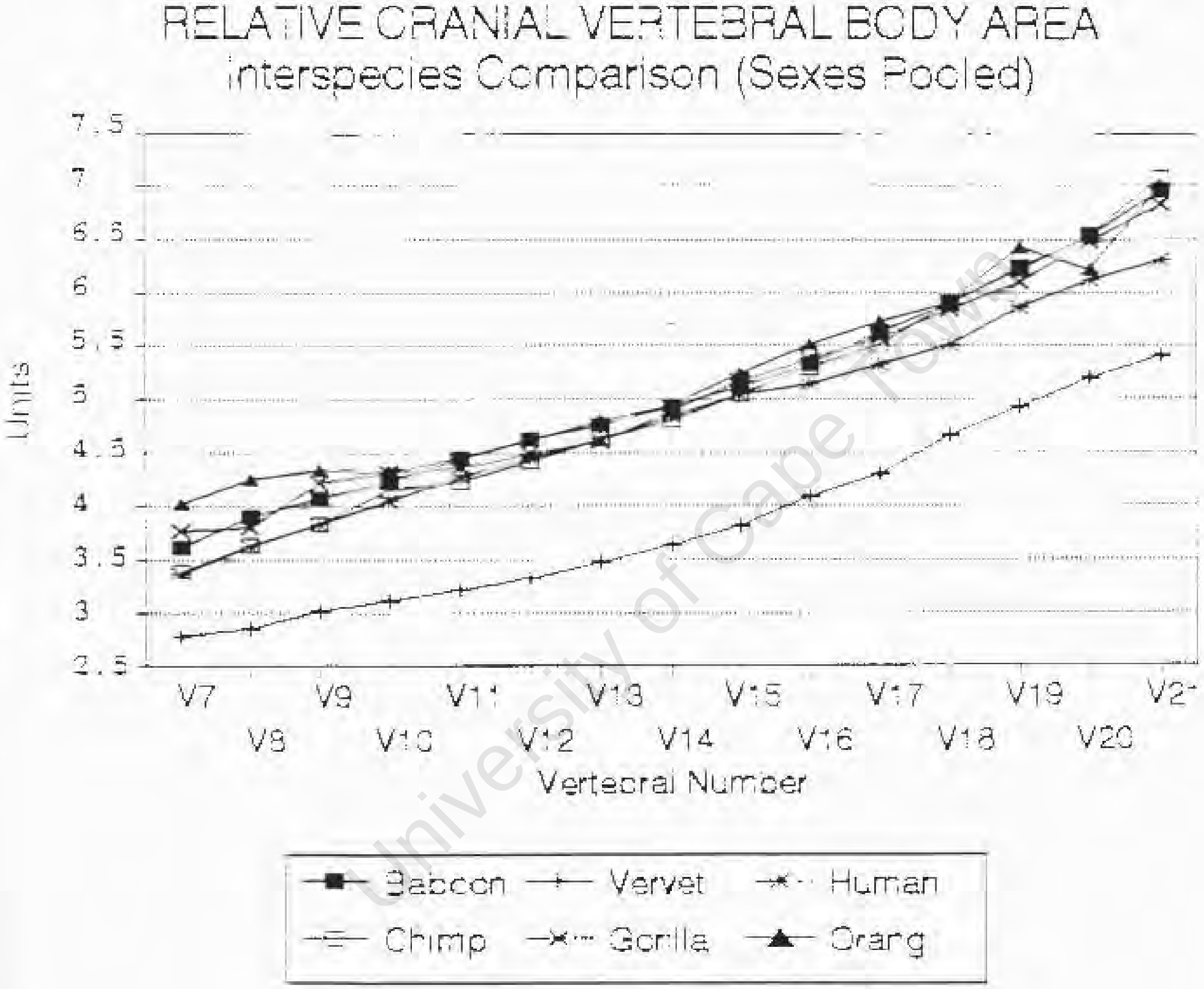

RELATIVE CRANIAL VERTEBRAL BODY AREA
Interspecies Comparison (Sexes Pooled)
Units
7.5
7
6.5
6
5.5
5
4.5
4
3.5
3
2.5
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20
V21
Vertebral Number
Baboon
Vervet
Human
Chimp
Gorilla
Orang

Figure 6.10

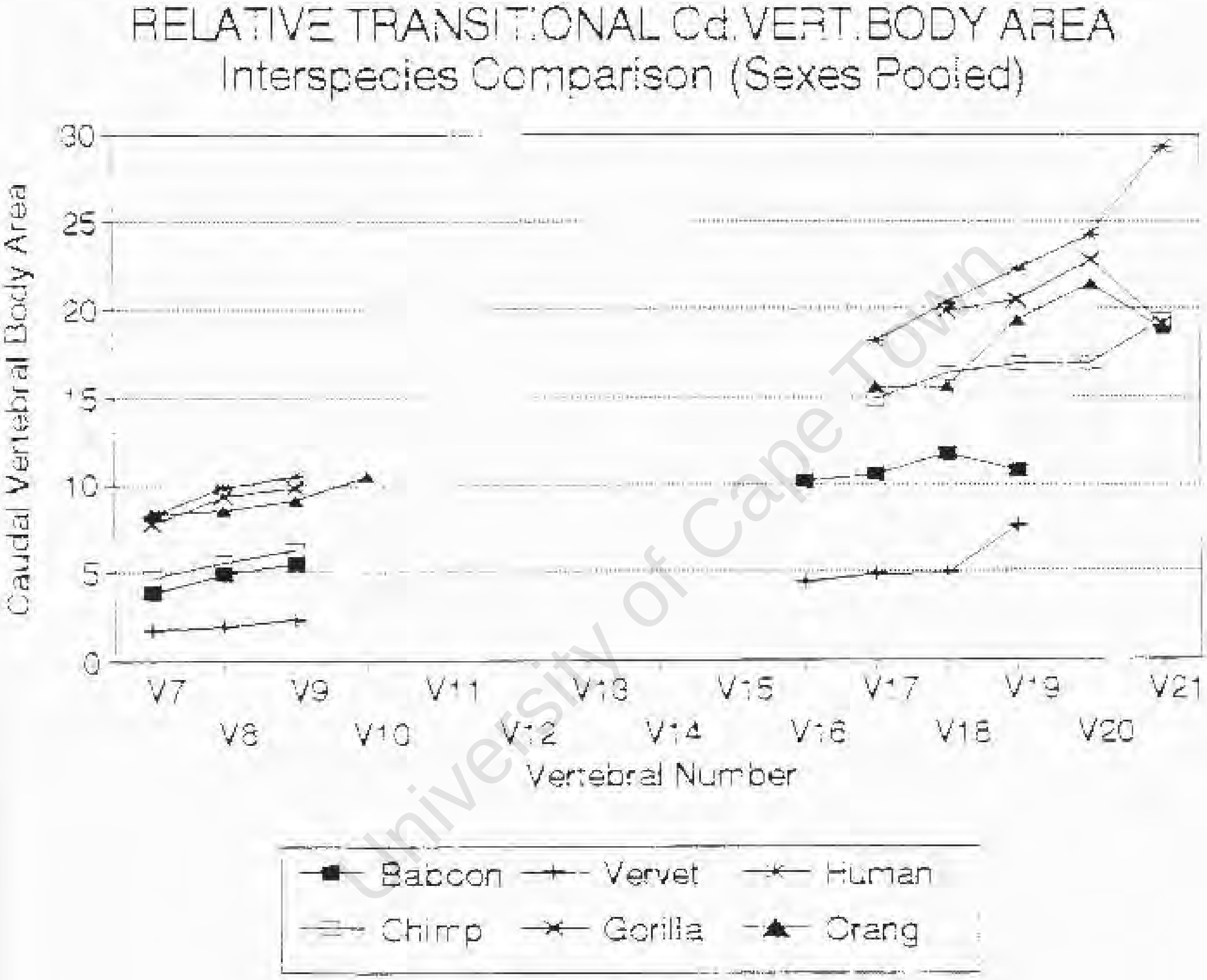

RELATIVE TRANSITIONAL Cd.VERT.BODY AREA
Interspecies Comparison (Sexes Pooled)
Caudal Vertebral Body Area
30
25
20
15
10
5
0
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20
V21
Vertebral Number
Baboon
Vervet
Human
Chimp
Gorilla
Orang

Figure 6.11a

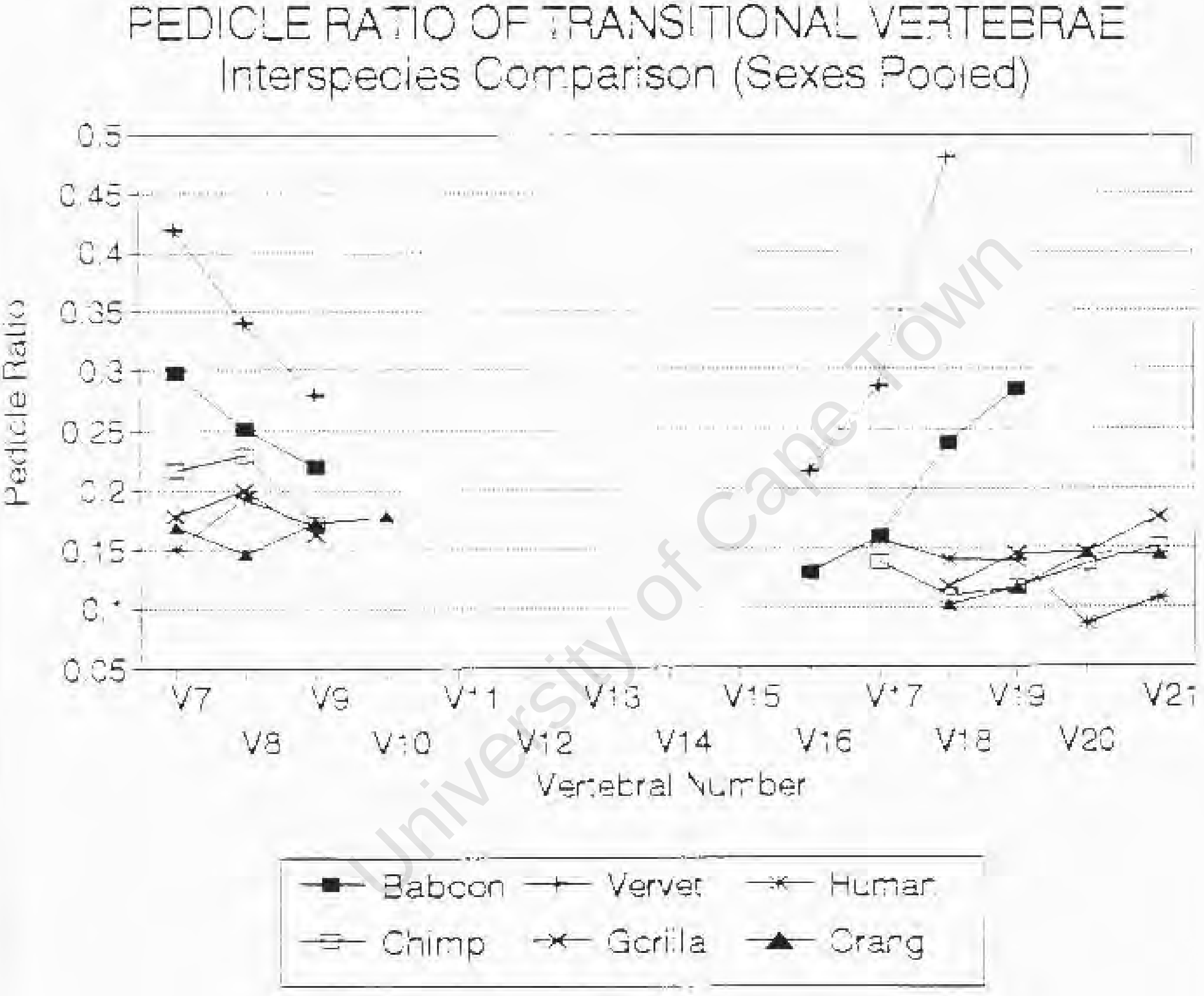

PEDICLE RATIO OF TRANSITIONAL VERTEBRAE
Interspecies Comparison (Sexes Pooled)
Pedicle Ratio
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20
V21
Vertebral Number
Baboon
Vervet
Human
Chimp
Gorilla
Orang

Figure 6.11b

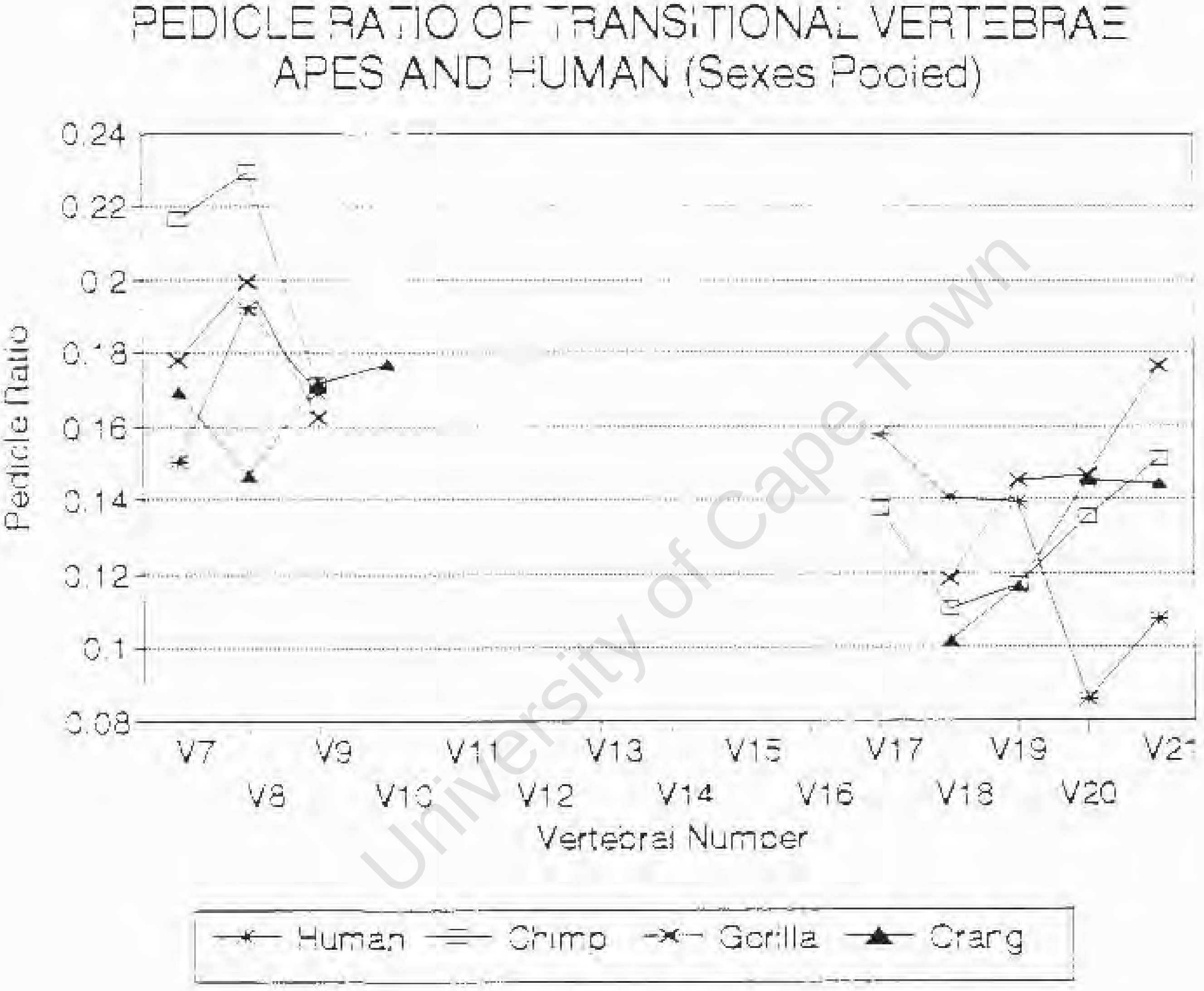
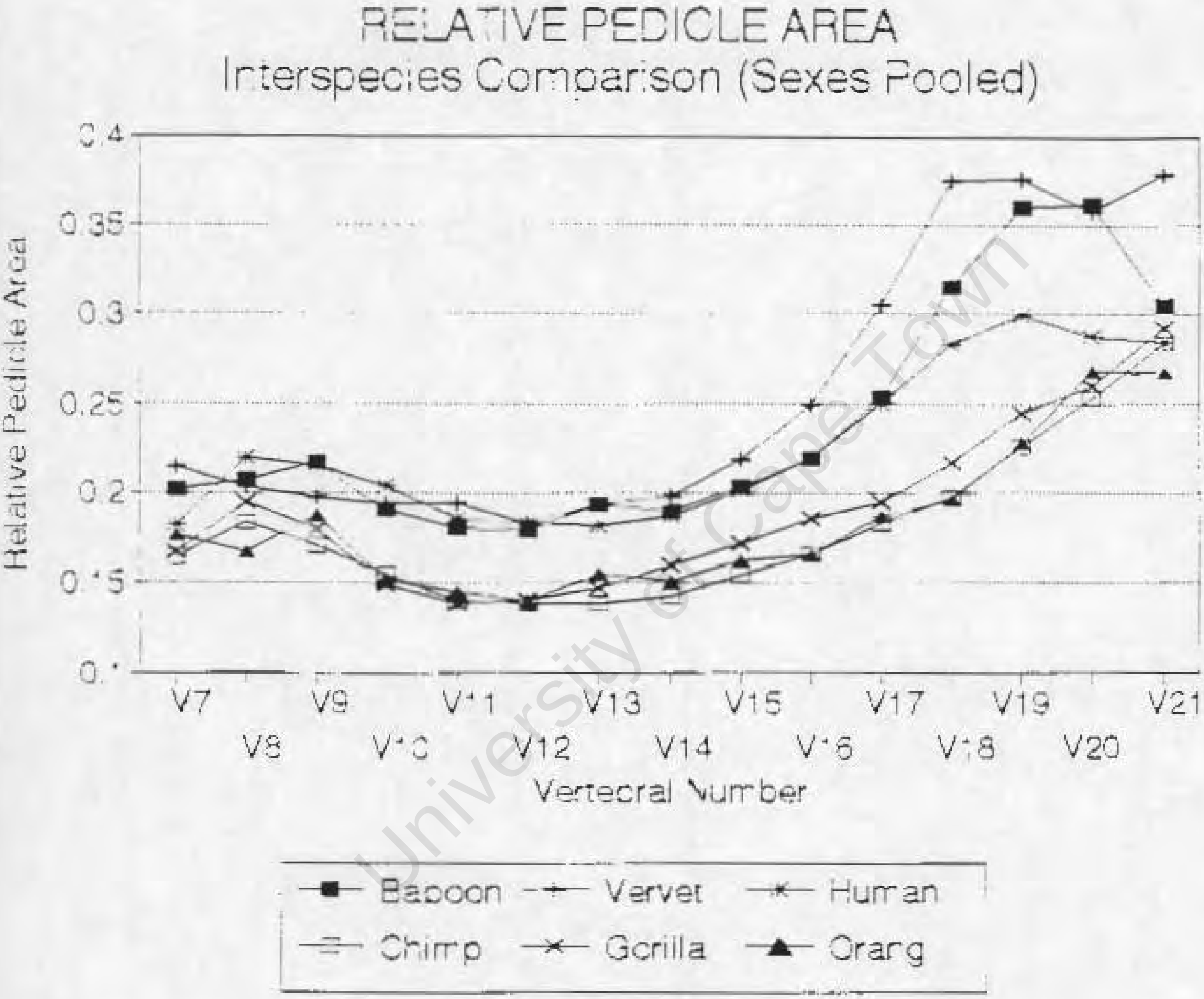

PEDICLE RATIO OF TRANSITIONAL VERTEBRAE
APES AND HUMAN (Sexes Pooled)
0.24
0.22
0.2
0.18
0.16
0.14
0.12
0.1
0.08
Pedicle Ratio
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20
V21
Vertebral Number
Human
Chimp
Gorilla
Orang

Figure 6.12



RELATIVE PEDICLE AREA
Interspecies Comparison (Sexes Pooled)

Figure 6.13

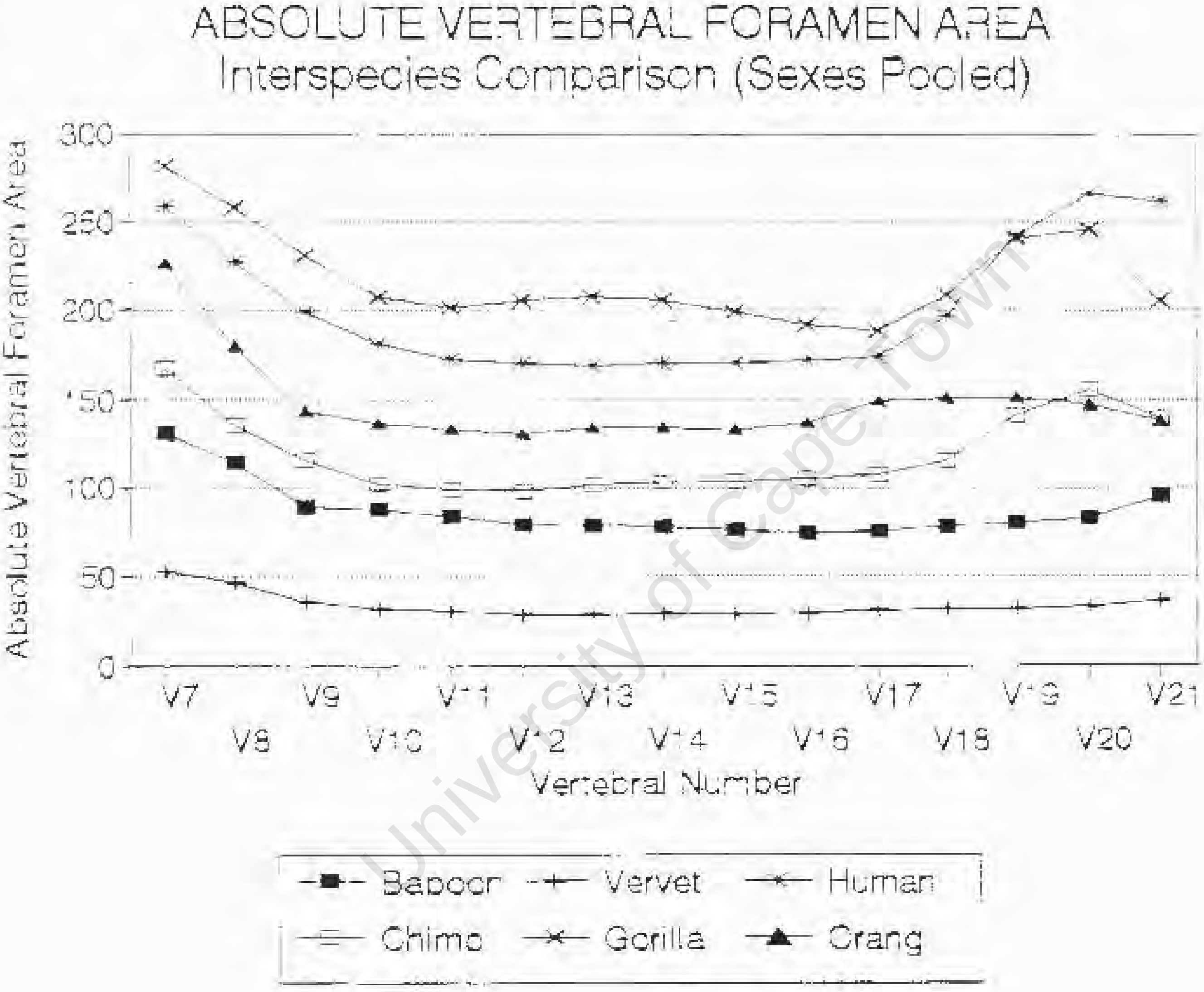

ABSOLUTE VERTEBRAL FORAMEN AREA
Interspecies Comparison (Sexes Pooled)
Absolute Vertebral Foramen Area
300
250
200
150
100
50
0
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20
V21
Vertebral Number
Baboon
Vervet
Human
Chimp
Gorilla
Orang

Figure 6.14

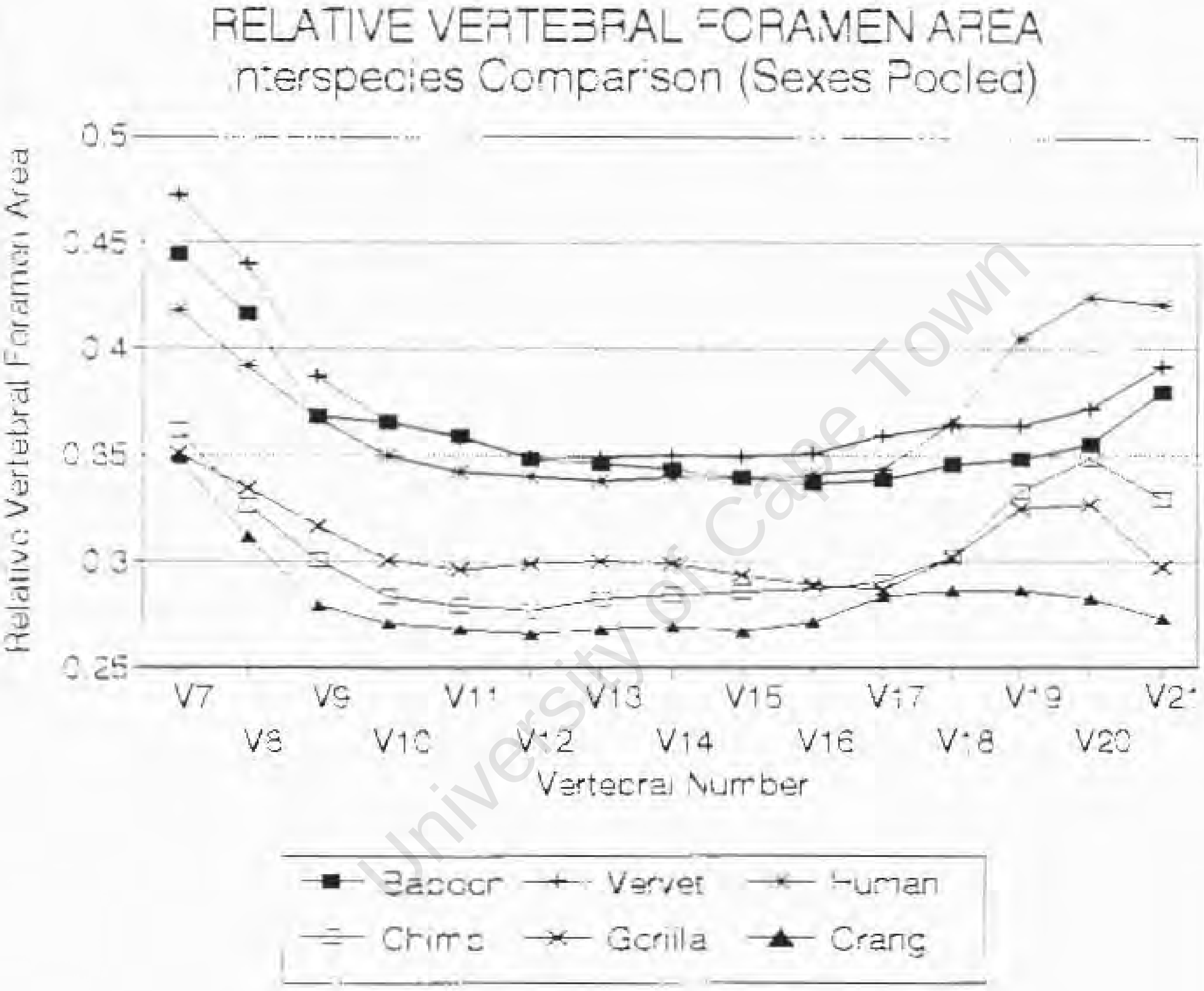

RELATIVE VERTEBRAL FORAMEN AREA
Interspecies Comparison (Sexes Pooled)
Relative Vertebral Foramen Area
0.5
0.45
0.4
0.35
0.3
0.25
V7
V8
V9
V10
V11
V12
V13
V14
V15
V16
V17
V18
V19
V20
V21
Vertebral Number
Baboon
Vervet
Human
Chimp
Gorilla
Orang

Table 6.1

Absolute Spinous Process Ratio
(Sexes Pooled)

	BABOON			VERVET		
	n	mean	std.dev.	n	mean	std.dev.
V7	71	0.668	0.116	61	0.480	0.172
V8	73	0.893	0.137	62	0.748	0.232
V9	74	0.958	0.161	62	0.833	0.225
V10	73	0.984	0.157	62	0.855	0.235
V11	69	0.960	0.161	62	0.854	0.213
V12	74	1.066	0.170	62	0.853	0.221
V13	74	1.097	0.175	62	0.860	0.222
V14	74	1.096	0.178	62	0.847	0.212
V15	74	1.055	0.174	62	0.801	0.202
V16	74	0.974	0.172	62	0.710	0.173
V17	73	0.860	0.153	62	0.585	0.136
V18	73	0.764	0.132	62	0.541	0.123
V19	74	0.677	0.115	61	0.533	0.125
V20	73	0.672	0.106	62	0.541	0.156
V21	73	0.683	0.106	62	0.555	0.143

	CHIMPANZEE			GORILLA		
	n	mean	std.dev.	n	mean	std.dev.
V7	19	0.944	0.112	25	1.362	0.162
V8	18	0.982	0.101	26	1.192	0.173
V9	19	0.964	0.086	25	1.069	0.119
V10	19	0.962	0.096	26	0.988	0.109
V11	18	0.983	0.104	25	0.995	0.096
V12	18	1.024	0.130	26	0.974	0.096
V13	19	1.069	0.122	25	0.964	0.098
V14	19	1.072	0.120	26	0.926	0.097
V15	18	1.039	0.108	26	0.907	0.103
V16	19	1.010	0.114	26	0.871	0.083
V17	19	0.926	0.117	26	0.848	0.084
V18	19	0.890	0.126	26	0.824	0.088
V19	19	0.840	0.110	26	0.814	0.086
V20	19	0.862	0.117	26	0.830	0.199
V21	19	0.96	0.093	26	0.856	0.273

Table 6.1 (continued)

Absolute Spinous Process Ratio
(Sexes Pooled)

	HUMAN			ORANGUTAN		
	n	mean	std.dev.	n	mean	std.dev.
V7	111	0.785	0.097	7	1.101	0.152
V8	112	0.873	0.093	6	1.076	0.085
V9	110	0.900	0.089	7	0.923	0.133
V10	108	0.912	0.101	6	0.872	0.075
V11	111	0.937	0.126	7	0.827	0.119
V12	106	1.015	0.141	7	0.835	0.093
V13	109	1.087	0.159	7	0.816	0.095
V14	108	1.068	0.141	7	0.815	0.071
V15	107	1.025	0.142	7	0.770	0.053
V16	110	0.976	0.131	7	0.770	0.107
V17	108	0.894	0.117	7	0.758	0.134
V18	109	0.792	0.115	7	0.720	0.071
V19	109	0.728	0.110	7	0.684	0.120
V20	112	0.756	0.103	6	0.726	0.072
V21	110	0.809	0.110	7	0.648	0.097

Table 6.2

Spearman Rank Correlation Signficance Test
Absolute Spinous Process Ratio

Spearman-R

Vervet	.889				
Human	.964	.839			
Chimp.	.896	.757	.946		
Gorilla	.250	.439	.300	.443	
Orang.	.264	.414	.275	.382	.950
	Baboon	Vervet	Human	Chimp	Gorilla

p-Value

Vervet	.000				
Human	.000	.000			
Chimp	.000	.001	.000		
Gorilla	.369	.101	.277	.098	
Orangutan	.341	.125	.321	.160	.000
	Baboon	Vervet	Human	Chimp.	Gorilla

Table 6.3

Spinous Process Ratio / Leverage
(Sexes Pooled)

	BABOON			VERVET		
	n	mean	std.dev.	n	mean	std.dev.
V7	71	1.219	0.133	61	0.958	0.182
V8	73	1.405	0.175	62	1.255	0.254
V9	74	1.481	0.192	62	1.279	0.244
V10	73	1.533	0.191	62	1.342	0.270
V11	69	1.472	0.181	62	1.358	0.248
V12	74	1.603	0.197	62	1.294	0.226
V13	74	1.612	0.205	62	1.257	0.260
V14	73	1.525	0.196	62	1.283	0.233
V15	74	1.570	0.198	62	1.235	0.229
V16	74	1.502	0.198	62	1.213	0.216
V17	73	1.433	0.190	62	1.117	0.185
V18	73	1.329	0.164	62	1.082	0.175
V19	74	1.298	0.152	62	1.091	0.190
V20	73	1.240	0.136	62	1.148	0.216
V21	73	1.374	0.150	62	1.185	0.232

	CHIMPANZEE			GORILLA		
	n	mean	std.dev.	n	mean	std.dev.
V7	19	1.380	0.158	25	1.873	0.166
V8	19	1.341	0.140	26	1.710	0.161
V9	19	1.337	0.134	25	1.555	0.132
V10	19	1.314	0.136	26	1.407	0.139
V11	18	1.303	0.116	26	1.293	0.155
V12	18	1.316	0.113	26	1.245	0.148
V13	19	1.313	0.136	26	1.240	0.122
V14	19	1.339	0.135	26	1.241	0.102
V15	19	1.342	0.112	26	1.241	0.106
V16	19	1.339	0.121	25	1.235	0.106
V17	18	1.352	0.108	26	1.221	0.098
V18	19	1.361	0.112	26	1.238	0.115
V19	19	1.403	0.119	26	1.259	0.094
V20	19	1.454	0.129	25	1.299	0.088
V21	19	1.490	0.145	24	1.295	0.144

Table 6.3 (continued)

Spinous Process Ratio / Leverage
(Sexes Pooled)

	HUMAN			ORANGUTAN		
	n	mean	std.dev.	n	mean	std.dev.
V7	109	1.228	0.103	7	1.578	0.166
V8	112	1.220	0.087	6	1.528	0.102
V9	110	1.245	0.109	7	1.399	0.182
V10	107	1.291	0.124	6	1.332	0.099
V11	111	1.224	0.111	7	1.236	0.130
V12	108	1.146	0.109	7	1.149	0.123
V13	109	1.152	0.111	7	1.154	0.109
V14	107	1.156	0.097	7	1.175	0.122
V15	106	1.177	0.111	7	1.159	0.087
V16	107	1.209	0.109	7	1.195	0.130
V17	106	1.292	0.118	7	1.211	0.102
V18	107	1.296	0.106	7	1.175	0.128
V19	108	1.396	0.128	7	1.150	0.110
V20	112	1.473	0.125	6	1.179	0.183
V21	109	1.544	0.138	7	1.118	0.114

Table 6.4

Spearman Rank Correlation Signficance Test
Spinous Process Ratio / Leverage

Spearman-R

Vervet	.743				
Human	-.779	-.539			
Chimp.	-.750	-.850	.696		
Gorilla	-.396	.104	.225	.096	
Orang.	-.245	.043	.023	-.198	.483
	Baboon	Vervet	Human	Chimp.	Gorilla

p-Value

Vervet	.002				
Human	.001	.038			
Chimp.	.001	.000	.004		
Gorilla	.144	.713	.420	.732	
Orang.	.379	.879	.934	.478	.068
	Baboon	Vervet	Human	Chimp.	Gorilla

Table 6.5

Lateral Flexion Leverage (Lattran Ratio)
(Sexes Pooled)

	BABOON			VERVET		
	n	mean	std.dev.	n	mean	std.dev.
V7	70	0.907	0.095	60	0.831	0.129
V8	71	0.926	0.085	61	0.862	0.120
V9	69	0.834	0.070	61	0.775	0.111
V10	71	0.783	0.061	61	0.719	0.102
V11	70	0.752	0.056	61	0.693	0.096
V12	70	0.740	0.059	61	0.692	0.097
V13	71	0.742	0.060	61	0.701	0.101
V14	71	0.747	0.061	61	0.718	0.106
V15	71	0.752	0.064	61	0.717	0.105
V16	71	0.747	0.066	61	0.717	0.101
V17	71	0.719	0.062	61	0.670	0.114
V18	71	0.689	0.075	61	0.525	0.123
V19	71	0.629	0.082	61	0.467	0.057
V20	71	0.585	0.114	61	0.649	0.171
V21	71	0.830	0.121	61	0.700	0.131

	CHIMPANZEE			GORILLA		
	n	mean	std.dev.	n	mean	std.dev.
V7	19	0.745	0.062	25	0.722	0.066
V8	19	0.805	0.060	26	0.785	0.071
V9	19	0.730	0.052	26	0.689	0.058
V10	19	0.667	0.060	25	0.663	0.056
V11	19	0.663	0.060	25	0.674	0.062
V12	18	0.664	0.054	26	0.678	0.062
V13	19	0.657	0.053	26	0.678	0.065
V14	19	0.643	0.053	26	0.669	0.065
V15	19	0.641	0.051	26	0.668	0.062
V16	19	0.641	0.047	26	0.673	0.055
V17	19	0.645	0.046	26	0.670	0.054
V18	19	0.656	0.042	26	0.684	0.060
V19	19	0.667	0.054	26	0.657	0.061
V20	19	0.654	0.103	26	0.626	0.111
V21	19	0.837	0.137	26	0.802	0.137

Table 6.5 (continued)

Lateral Flexion Leverage (Lattran Ratio)
(Sexes Pooled)

	HUMAN			ORANGUTAN		
	n	mean	std.dev.	n	mean	std.dev.
V7	109	0.798	0.090	8	0.649	0.112
V8	110	0.913	0.067	8	0.599	0.045
V9	110	0.825	0.071	8	0.617	0.067
V10	107	0.749	0.098	8	0.564	0.029
V11	109	0.732	0.066	8	0.579	0.019
V12	110	0.731	0.069	8	0.584	0.022
V13	109	0.736	0.066	8	0.582	0.015
V14	110	0.742	0.058	8	0.589	0.018
V15	110	0.733	0.063	8	0.583	0.025
V16	109	0.723	0.050	6	0.597	0.022
V17	108	0.699	0.068	8	0.605	0.036
V18	109	0.627	0.072	6	0.588	0.047
V19	108	0.589	0.090	6	0.571	0.035
V20	108	0.801	0.145	7	0.562	0.081
V21	104	0.929	0.140	6	0.741	0.080

Table 6.6

Spearman Rank Correlation Signficance Test
Lateral Flexion Leverage (Lattran)

Spearman-R

Vervet	.886				
Human	.686	.643			
Chimp	.521	.250	.521		
Gorilla	.571	.369	.389	.607	
Orang.	.332	.300	.618	.261	.511
	Baboon	Vervet	Human	Chimp	Gorilla

p-Value

Vervet	.000				
Human	.005	.010			
Chimp.	.046	.369	.046		
Gorilla	.025	.177	.152	.016	
Orang.	.226	.277	.014	.348	.051
	Baboon	Vervet	Human	Chimp	Gorilla

Table 6.7

Ventrodorsal Transverse Process Tip RatRatio (VDTran)
(Sexes Pooled)

	BABOON n	BABOON mean	BABOON std.dev.	VERVET n	VERVET mean	VERVET std.dev
V7	70	0.832	0.187	59	0.643	0.217
V8	71	1.286	0.235	61	1.253	0.331
V9	70	1.591	0.199	61	1.933	0.203
V10	70	1.732	0.189	61	1.994	0.131
V11	69	1.791	0.141	61	2.062	0.174
V12	70	1.785	0.176	61	2.084	0.156
V13	70	1.818	0.141	61	2.010	0.246
V14	71	1.816	0.145	61	1.952	0.210
V15	71	1.779	0.128	61	1.824	0.189
V16	71	1.703	0.146	61	1.661	0.201
V17	70	1.501	0.142	61	1.435	0.265
V18	71	1.404	0.157	61	1.146	0.313
V19	70	1.319	0.191	61	0.928	0.248
V20	69	1.118	0.230	61	0.636	0.227
V21	70	0.904	0.130	61	0.496	0.253

	CHIMPANZEE n	CHIMPANZEE mean	CHIMPANZEE std.dev.	GORILLA n	GORILLA mean	GORILLA std.dev.
V7	19	1.357	0.333	25	1.577	0.330
V8	19	1.750	0.203	26	2.056	0.217
V9	19	2.196	0.158	26	2.341	0.182
V10	18	2.255	0.087	26	2.323	0.185
V11	19	2.270	0.126	26	2.281	0.224
V12	19	2.187	0.114	26	2.260	0.235
V13	18	2.097	0.170	26	2.214	0.229
V14	19	2.156	0.105	26	2.167	0.300
V15	19	2.103	0.084	26	2.069	0.119
V16	19	2.028	0.097	26	2.019	0.106
V17	18	1.933	0.073	26	1.977	0.120
V18	19	1.921	0.164	26	1.975	0.149
V19	19	1.937	0.073	26	1.924	0.108
V20	19	1.723	0.080	26	1.739	0.122
V21	19	1.446	0.153	26	1.463	0.129

Table 6.7 (continued)

Ventrodorsal Transverse Process Tip RatRatio (VDTran) (Sexes Pooled)

	HUMAN			ORANGUTAN		
	n	mean	std.dev.	n	mean	std.dev.
V7	110	1.172	0.238	8	1.338	0.215
V8	110	1.928	0.253	8	1.741	0.309
V9	110	2.300	0.217	8	2.103	0.203
V10	107	2.366	0.215	8	2.183	0.158
V11	109	2.310	0.177	8	2.128	0.107
V12	110	2.282	0.191	8	2.089	0.087
V13	109	2.245	0.182	8	2.034	0.149
V14	109	2.200	0.178	8	1.968	0.137
V15	110	2.135	0.175	8	1.879	0.111
V16	108	2.120	0.154	8	1.809	0.120
V17	108	2.034	0.167	8	1.768	0.091
V18	108	1.886	0.182	8	1.726	0.090
V19	109	1.729	0.195	8	1.561	0.145
V20	111	1.636	0.232	7	1.318	0.144
V21	110	1.577	0.257	8	1.396	0.179

Table 5.8

Spearman Rank Correlation Signficance Test
Transverse Tip Ratio (Vctran)

Spearman-R

Vervet	.900				
Human	.807	.932			
Chimp.	.814	.907	.975		
Gorilla	.750	.907	.975	.936	
Orang.	.796	.932	.989	.964	.964
	Baboon	Vervet	Human	Chimp	Gorilla

p-Value

Vervet	.000				
Human	.000	.000			
Chimp.	.000	.000	.000		
Gorilla	.001	.000	.000	.000	
Orang.	.000	.000	.000	.000	.000
	Baboon	Vervet	Human	Chimp	Gorilla

Table 6.9

Absolute Facet (Zygopophyseal) Area
(Sexes Pooled)

	BABOON		VERVET		HUMAN	
	n	mean	n	mean	n	mean
V7	72	47.80	61	12.55	112	93.08
V8	74	45.96	62	12.85	112	123.38
V9	74	43.23	62	12.27	112	94.26
V10	74	36.46	62	10.31	110	84.03
V11	73	33.66	62	9.45	111	80.35
V12	74	34.62	62	9.51	110	77.11
V13	74	34.61	62	9.57	111	72.22
V14	74	36.11	62	10.00	110	71.35
V15	74	37.94	62	11.13	110	76.41
V16	74	42.17	62	12.16	110	81.20
V17	74	46.56	62	13.73	110	87.30
V18	74	61.25	61	22.05	112	96.74
V19	74	64.69	62	23.76	112	100.30
V20	74	62.72	62	24.91	112	120.77
V21	73	63.25	62	26.59	109	154.66

	CHIMPANZEE		GORILLA		ORANGUTAN	
	n	mean	n	mean	n	mean
V7	19	65.48	25	182.59	8	114.06
V8	19	70.58	26	193.25	8	111.15
V9	19	71.94	26	127.35	8	95.41
V10	19	63.32	26	98.29	8	65.72
V11	19	58.20	26	91.09	8	61.61
V12	19	54.38	26	85.37	8	66.73
V13	19	55.37	26	83.95	8	68.22
V14	19	59.74	26	81.34	8	67.61
V15	19	57.35	26	87.12	8	70.53
V16	19	66.79	26	93.83	8	73.48
V17	19	68.49	26	109.12	8	76.23
V18	19	70.15	26	127.84	8	79.74
V19	19	73.24	26	136.56	8	90.54
V20	19	76.86	26	143.70	7	104.53
V21	18	103.94	26	168.20	8	120.38

Table 6.10

Spearman Rank Correlation Significance Test
Absolute Facet Area

Spearman-R

Vervet	971				
Human	854	879			
Chimp.	.869	907	919		
Gorilla	807	800	925	796	
Orang.	814	829	800	786	854
	Baboon	Vervet	Human	Chimp	Gorilla

p-Value

Vervet	000				
Human	000	000			
Chimp	000	000	000		
Gorilla	000	000	000	000	
Orang	000	000	000	001	000
	Baboon	Vervet	Human	Chimp	Gorilla

Table 6.11

Relative Facet (Zygopophyseal) Area
(Sexes Pooled)

	BABOON		VERVET		HUMAN	
	n	mean	n	mean	n	mean
V7	72	0.265	61	0.224	112	0.250
V8	74	0.261	62	0.228	112	0.275
V9	74	0.253	62	0.223	112	0.251
V10	74	0.233	62	0.205	110	0.238
V11	73	0.224	62	0.196	111	0.232
V12	74	0.227	62	0.196	110	0.227
V13	74	0.227	62	0.198	111	0.221
V14	74	0.232	62	0.202	110	0.219
V15	74	0.239	61	0.214	110	0.227
V16	73	0.251	62	0.213	110	0.234
V17	74	0.282	62	0.237	110	0.242
V18	74	0.302	62	0.299	112	0.254
V19	74	0.310	62	0.310	112	0.258
V20	74	0.308	62	0.318	112	0.283
V21	73	0.306	62	0.328	109	0.321

	CHIMPANZEE		GORILLA		ORANGUTAN	
	n	mean	n	mean	n	mean
V7	19	0.226	25	0.279	8	0.246
V8	19	0.235	26	0.285	8	0.241
V9	19	0.237	26	0.231	8	0.226
V10	19	0.223	26	0.204	8	0.186
V11	19	0.213	26	0.196	8	0.180
V12	19	0.206	26	0.189	8	0.189
V13	19	0.208	26	0.189	8	0.191
V14	19	0.215	26	0.185	8	0.190
V15	19	0.211	26	0.192	8	0.194
V16	19	0.227	26	0.199	8	0.204
V17	19	0.232	26	0.214	8	0.202
V18	19	0.233	26	0.230	8	0.207
V19	19	0.237	26	0.240	8	0.218
V20	19	0.244	26	0.245	7	0.236
V21	18	0.263	26	0.264	8	0.249

Table 6.12

Spearman Rank Correlation Significance Test
Relative Facet Area

Spearman-R

Vervet	.971				
Human	.846	.864			
Chimp	.871	.893	.916		
Gorilla	.789	.771	.921	.804	
Orang.	.821	.818	.800	.786	.861
	Baboon	Vervet	Human	Chimp	Gorilla

p-Value

Vervet	.000				
HUman	.000	.000			
Chimp	.000	.000	.000		
Gorilla	.001	.001	.000	.000	
Orang	.000	.000	.000	.001	.000
	Baboon	Vervet	Human	Chimp	Gorilla

Table 6.13

Facet (Zygopophyseal) Inclination Angle
(Sexes Pooled)

	BABOON			VERVET		
	n	mean	std.dev.	n	mean	std.dev.
V7	63	112.709	7.587	37	120.914	18.563
V8	49	108.946	7.969	19	121.016	15.240
V9	65	129.729	6.868	29	121.660	13.413
V10	69	123.503	8.825	43	118.630	13.639
V11	59	119.022	12.214	26	120.068	14.182
V12	55	112.167	9.237	18	122.985	20.640
V13	47	109.864	8.022	19	117.911	12.563
V14	43	112.214	10.068	18	119.580	12.238
V15	39	112.891	12.395	17	117.276	15.243
V16	47	110.911	8.923	23	115.068	14.492
V17	45	115.035	10.599	22	126.449	16.718
V18	71	141.881	9.683	57	141.269	12.798
V19	71	148.027	8.264	57	147.531	9.299
V20	71	29.893	6.643	58	35.707	9.293
V21	69	33.189	6.409	58	40.854	10.239

	CHIMPANZEE			GORILLA		
	n	mean	std.dev.	n	mean	std.dev.
V7	7	104.760	5.968	9	108.806	7.144
V8	8	105.908	5.541	16	109.450	7.227
V9	12	116.073	7.929	11	111.585	11.495
V10	16	112.077	6.699	13	104.563	8.089
V11	10	108.800	8.764	17	109.253	7.466
V12	15	109.273	7.489	22	110.093	7.405
V13	12	109.120	6.749	19	114.553	7.074
V14	12	112.379	7.346	14	113.577	14.101
V15	13	106.035	9.242	18	107.837	6.523
V16	13	109.265	11.590	14	107.871	7.533
V17	13	109.580	6.450	12	103.249	5.094
V18	13	108.934	4.586	10	106.504	6.395
V19	9	118.484	13.974	9	110.057	6.768
V20	12	58.805	17.103	11	68.302	12.371
V21	18	40.102	5.707	18	58.394	14.027

Table 6.13 (continued)

Facet (Zygopophyseal) Inclination Angle
(Sexes Pooled)

	HUMAN			ORANGUTAN		
	n	mean	std.dev.	n	mean	std.dev.
V7	38	108.090	8.436	6	113.903	9.424
V8	33	107.733	8.065	1	107.721	0.000
V9	49	108.600	8.450	4	113.734	6.764
V10	55	110.031	12.408	4	103.565	8.501
V11	54	112.074	11.378	2	108.002	2.981
V12	63	112.132	13.189	2	109.499	1.512
V13	63	109.911	9.760	4	124.691	9.107
V14	56	112.015	9.720	4	110.093	6.620
V15	54	109.739	9.334	4	108.601	8.341
V16	52	108.309	9.510	2	115.764	13.976
V17	46	109.794	9.035	4	107.940	6.322
V18	51	111.764	9.751	2	105.105	0.968
V19	70	123.468	21.129	3	107.677	13.182
V20	104	31.729	15.133	4	47.743	6.796
V21	107	25.380	10.781	8	51.968	15.968

Table 6.14

Spearman Rank Correlation Significance Test

Facet Inclination Angle

Spearman-R

Vervet	.689				
Human	.632	.582			
Chimp.	.636	.532	.675		
Gorilla	.136	.325	.479	.504	
Orang.	.189	.211	.121	.291	.457
	Baboon	Vervet	Human	Chimp.	Gorilla

p-Value

Vervet	.004				
Human	.012	.023			
Chimp.	.011	.041	.006		
Gorilla	.630	.237	.071	.056	
Orang.	.499	.451	.666	.289	.086
	Baboon	Vervet	Human	Chimp	Gorilla

Table 6.15

Absolute Cranial Vertebral Body Area
(Sexes Pooled)

	BABOON			VERVET		
	n	mean	std.dev.	n	mean	std.dev.
V7	71	89.039	27.343	61	21.235	6.688
V8	74	102.474	27.817	62	22.426	6.110
V9	74	111.204	28.087	62	24.946	7.027
V10	73	120.162	32.016	62	26.538	6.503
V11	73	132.686	38.434	62	28.180	7.367
V12	73	144.741	43.692	62	30.384	7.404
V13	73	152.545	43.740	62	33.082	8.274
V14	74	163.176	47.320	62	36.425	10.006
V15	74	176.463	52.098	62	40.219	11.453
V16	74	191.480	56.361	62	46.202	14.908
V17	73	213.950	63.892	62	50.924	14.264
V18	74	234.040	69.465	62	59.659	16.513
V19	74	262.561	74.097	62	66.868	18.989
V20	72	287.617	86.445	62	74.323	21.447
V21	73	328.901	99.157	62	80.812	23.592

	CHIMPANZEE			GORILLA		
	n	mean	std.dev.	n	mean	std.dev.
V7	19	147.057	37.527	25	332.614	80.985
V8	19	169.896	48.358	26	339.686	79.367
V9	19	188.892	46.623	26	422.773	109.717
V10	18	219.239	36.054	26	446.086	129.996
V11	19	229.024	40.372	26	453.786	126.294
V12	19	249.844	48.064	26	482.646	128.056
V13	18	271.988	52.547	26	508.458	147.075
V14	19	294.503	56.984	26	575.013	173.769
V15	19	324.565	58.008	26	633.830	168.320
V16	19	357.384	63.133	26	687.976	187.951
V17	18	385.567	61.591	26	743.326	205.584
V18	19	445.868	88.759	26	813.823	229.496
V19	19	494.129	78.310	26	887.800	244.371
V20	19	549.240	95.913	26	1003.037	287.725
V21	19	640.509	112.818	26	1118.646	317.753

Table 6.15 (continued)

Absolute Cranial Vertebral Body Area
(Sexes Pooled)

	HUMAN			ORANGUTAN		
	n	mean	std.dev.	n	mean	std.dev.
V7	112	301.613	49.852	8	301.118	56.970
V8	112	313.189	53.233	8	338.556	71.576
V9	112	329.100	57.339	8	350.951	61.399
V10	111	354.493	55.383	8	349.084	62.402
V11	112	379.705	56.699	8	367.964	65.688
V12	112	407.177	66.594	8	397.989	81.000
V13	112	444.507	75.871	8	430.432	92.575
V14	111	494.098	90.462	8	454.873	61.448
V15	112	539.409	96.955	8	510.546	79.906
V16	111	577.529	102.661	8	564.869	87.686
V17	112	619.254	108.912	8	613.710	109.497
V18	111	676.346	117.531	8	649.891	117.897
V19	112	792.209	180.408	8	771.406	130.647
V20	112	849.235	153.897	7	941.485	187.387
V21	111	944.037	162.200	8	921.154	194.491

Table 6.16

Spearman Rank Correlation Significance Test

Absolute Cranial Vertebral Body Area

Spearman-R

Vervet	1.000				
Human	1.000	1.000			
Chimp	1.000	1.000	1.000		
Gorilla	1.000	1.000	1.000	1.000	
Orang	.993	.993	.993	.993	.993
	Baboon	Vervet	Human	Chimp	Gorilla

p-Value

Vervet	.000				
Human	.000	.000			
Chimp	.000	.000	.000		
Gorilla	.000	.000	.000	.000	
Orang	.000	.000	.000	.000	.000
	Baboon	Vervet	Human	Chimp	Gorilla

Table 6.17

Relative Cranial Vertebral Body Area
(Sexes Pooled)

	BABOON			VERVET		
	n	mean	std.dev.	n	mean	std.dev.
V7	71	3.620	0.380	61	2.770	0.430
V8	74	3.910	0.360	62	2.850	0.400
V9	74	4.080	0.370	62	3.000	0.420
V10	73	4.220	0.350	62	3.110	0.380
V11	73	4.430	0.420	62	3.200	0.420
V12	73	4.630	0.460	62	3.320	0.410
V13	73	4.750	0.450	62	3.470	0.430
V14	74	4.920	0.500	62	3.630	0.500
V15	74	5.120	0.510	62	3.810	0.550
V16	74	5.330	0.530	62	4.080	0.640
V17	73	5.620	0.550	62	4.290	0.600
V18	74	5.890	0.560	62	4.650	0.650
V19	74	6.250	0.590	62	4.920	0.700
V20	72	6.530	0.690	62	5.190	0.740
V21	73	6.970	0.700	62	5.400	0.790

	CHIMPANZEE			GORILLA		
	n	mean		n	mean	std.dev.
V7	19	3.380	0.480	25	3.770	0.360
V8	19	3.630	0.520	26	3.790	0.370
V9	19	3.830	0.490	26	4.220	0.370
V10	18	4.150	0.340	26	4.310	0.390
V11	19	4.230	0.400	26	4.360	0.380
V12	19	4.420	0.450	26	4.500	0.390
V13	18	4.620	0.470	26	4.600	0.480
V14	19	4.800	0.490	26	4.890	0.570
V15	19	5.040	0.470	26	5.160	0.500
V16	19	5.290	0.500	26	5.370	0.510
V17	18	5.500	0.440	26	5.580	0.510
V18	19	5.900	0.600	26	5.830	0.520
V19	19	6.210	0.450	26	6.100	0.540
V20	19	6.550	0.550	26	6.480	0.640
V21	19	7.070	0.580	26	6.840	0.710

Table 6.17 (continued)

Relative Cranial Vertebral Body Area
(Sexes Pooled)

	HUMAN			ORANGUTAN		
	n	mean	std.dev.	n	mean	std.dev.
V7	112	3.360	0.320	8	4.010	0.400
V8	112	3.620	0.330	8	4.250	0.490
V9	112	3.840	0.330	8	4.340	0.390
V10	112	4.050	0.340	8	4.340	0.390
V11	112	4.270	0.350	8	4.440	0.400
V12	112	4.440	0.380	8	4.610	0.480
V13	112	4.630	0.410	8	4.800	0.500
V14	110	4.830	0.410	8	4.950	0.330
V15	112	5.030	0.400	8	5.240	0.400
V16	111	5.130	0.450	8	5.510	0.420
V17	112	5.320	0.480	8	5.740	0.520
V18	111	5.860	0.440	8	5.900	0.550
V19	111	5.860	0.540	8	6.430	0.570
V20	112	6.120	0.510	8	6.210	2.430
V21	111	6.310	0.530	8	7.010	0.780

Table 6.18

Spearman Rank Correlation Signficance Test: Relative Cranial Vertebral Body Area

Spearman-R

Vervet	1.000				
Human	1.000	1.000			
Chimp.	1.000	1.000	1.000		
Gorilla	1.000	1.000	1.000	1.000	
Orang.	.993	.993	.993	.993	.993
	Baboon	Vervet	Human	Chimp	Gorilla

p-Value

Vervet	.000				
Human	.000	.000			
Chimp.	.000	.000	.000		
Gorilla	.000	.000	.000	.000	
Orang.	.000	.000	.000	.000	.000
	Baboon	Vervet	Human	Chimp	Gorilla

Table 6.19

Relative Transitional Caudal Vertebral Body Area (Sexes Pooled)

	BABOON		VERVET		HUMAN	
	n	mean	n	mean	n	mean
V7	15	3.82	11	1.780	17	8.239
V8	17	4.95	11	1.936	17	9.851
V9	17	5.48	11	2.304	16	10.461
V10						
V11						
V12						
V13						
V14						
V15						
V16	17	10.13	11	4.461		
V17	17	10.52	11	4.816	16	18.164
V18	17	11.70	11	4.952	16	20.309
V19	17	10.76	11	7.582	16	22.324
V20					17	24.254
V21					15	29.286

	CHIMPANZEE		GORILLA		ORANGUTAN	
	n	mean	n	mean	n	mean
V7	19	4.659	24	7.730	7	8.339
V8	19	5.552	25	9.294	7	8.497
V9	19	6.252	25	9.808	7	9.135
V10					7	10.470
V11						
V12						
V13						
V14						
V15						
V16						
V17	17	14.828			7	15.520
V18	18	16.292	25	19.858	7	15.526
V19	18	16.892	25	20.566	7	19.403
V20	18	16.956	25	22.888	6	21.429
V21	18	19.347	25	19.153	7	18.790

Table 6.20

Spearman Rank Correlation Significance Test
Relative Transitional Caudal Vertebral Body Area

Spearman-R

Vervet	.964				
Human	.943	1.000			
Chimp.	.943	1.000	1.000		
Gorilla	.900	1.000	.786	.786	
Orang	.943	1.000	.929	.929	.964
	Baboon	Vervet	Human	Chimp.	Gorilla

p-Value

Vervet	.001				
Human	.005	.000			
Chimp.	.005	.000	.000		
Gorilla	.037	.000	.036	.036	
Orang.	.005	.000	.001	.001	.001
	Baboon	Vervet	Human	Chimp.	Gorilla

Table 6.21

Pedicle Ratio of Transitional Vertebrae
(Sexes Pooled)

	BABOON			VERVET		
	n	mean	std.dev.	n	mean	std.dev.
V7	12	0.298	0.057	11	0.419	0.091
V8	12	0.251	0.055	11	0.341	0.050
V9	12	0.219	0.022	11	0.279	0.053
V10						
V11						
V12						
V13						
V14						
V15						
V16	10	0.130	0.030	11	0.214	0.066
V17	10	0.160	0.026	11	0.286	0.112
V18	10	0.238	0.048	11	0.480	0.118
V19	1	0.282				
V20						
V21						

	CHIMPANZEE			GORILLA		
	n	mean	std.dev.	n	mean	std.dev.
V7	19	0.217	0.052	24	0.178	0.043
V8	19	0.229	0.064	25	0.200	0.039
V9	18	0.171	0.046	24	0.162	0.035
V10						
V11						
V12						
V13						
V14						
V15						
V16						
V17						
V18	10	0.110	0.020	7	0.119	0.021
V19	10	0.117	0.030	24	0.145	0.036
V20	10	0.135	0.023	24	0.146	0.026
V21	15	0.151	0.028	19	0.176	0.032

Table 6.21 (continued)

Pedicle Ratio of Transitional Vertebrae
(Sexes Pooled)

	HUMAN			ORANGUTAN		
	n	mean	std.dev.	n	mean	std.dev.
V7	17	0.150	0.036	8	0.169	0.050
V8	17	0.192	0.041	8	0.147	0.061
V9	16	0.169	0.036	7	0.172	0.101
V10				1	0.177	
V11						
V12						
V13						
V14						
V15						
V16						
V17	16	0.157	0.051			
V18	16	0.140	0.036	6	0.102	0.022
V19	16	0.139	0.045	8	0.116	0.030
V20	17	0.086	0.026	7	0.145	0.033
V21	15	0.108	0.020	3	0.144	0.042

Table 6.22

Spearman Rank Correlation Significance Test
Pedicle Ratio of Transitional Vertebrae

Spearman-R

Vervet	.771				
Human	-.371	-.700			
Chimp.	.257	-.200	.619		
Gorilla	.300	-.400	.500	.964	
Orang.	-.100	-.800	.536	.821	.679
	Baboon	Vervet	Human	Chimp.	Gorilla

p-Value

Vervet	.072				
Human	.468	.188			
Chimp	.623	.747	.102		
Gorilla	.624	.600	.253	.000	
Orang	.873	.200	.215	.023	.094
	Baboon	Vervet	Human	Chimp	Gorilla

Table 6.23

Relative Pedicle Area
(Sexes Pooled)

	BABOON		VERVET		HUMAN	
	n	mean	n	mean	n	mean
V7	24	0.182	15	0.201	11	0.214
V8	24	0.220	17	0.207	11	0.203
V9	23	0.215	17	0.216	11	0.196
V10	22	0.204	17	0.190	11	0.193
V11	22	0.185	17	0.180	11	0.193
V12	22	0.182	17	0.178	10	0.183
V13	22	0.181	17	0.192	11	0.193
V14	22	0.186	17	0.189	10	0.197
V15	22	0.201	17	0.203	11	0.218
V16	22	0.219	17	0.219	11	0.249
V17	23	0.250	17	0.253	10	0.305
V18	24	0.282	17	0.315	11	0.375
V19	24	0.299	17	0.360	11	0.376
V20	24	0.288	17	0.362	11	0.357
V21	22	0.284	17	0.305	11	0.378

	CHIMPANZEE		GORILLA		ORANGUTAN	
	n	mean	n	mean	n	mean
V7	19	0.165	24	0.166	8	0.177
V8	19	0.183	25	0.194	8	0.167
V9	19	0.170	25	0.180	8	0.187
V10	19	0.155	25	0.149	8	0.152
V11	19	0.140	25	0.138	8	0.145
V12	18	0.138	25	0.141	8	0.140
V13	18	0.138	25	0.147	7	0.155
V14	18	0.142	25	0.160	8	0.151
V15	18	0.154	25	0.171	8	0.162
V16	18	0.165	25	0.185	8	0.165
V17	18	0.183	25	0.194	8	0.186
V18	18	0.197	25	0.217	8	0.196
V19	18	0.226	25	0.244	8	0.228
V20	18	0.253	25	0.260	7	0.267
V21	18	0.283	25	0.292	8	0.267

Table 6.24

Spearman Rank Correlation Significance Test
<u>Relative Pedicle Area</u>

Spearman-R

Vervet	.889				
Human	.886	.839			
Chimp.	.904	.875	.925		
Gorilla	.950	.929	.914	.961	
Orang.	.946	.843	.804	.921	.929
	Baboon	Vervet	Human	Chimp.	Gorilla

p-Value

Vervet	.000				
Human	.000	.000			
Chimp.	.000	.000	.000		
Gorilla	.000	.000	.000	.000	
Orang.	.000	.000	.000	.000	.000
	Baboon	Vervet	Human	Chimp	Gorilla

Table 6.25

Absolute Vertebral Foramen Area
(Sexes Pooled)

	BABOON			VERVET		
	n	mean	std.dev.	n	mean	std.dev.
V7	72	130.727	21.948	61	53.076	9.362
V8	74	113.992	17.606	62	46.340	9.042
V9	74	89.051	13.216	62	35.751	6.406
V10	74	87.833	12.676	62	31.986	5.260
V11	73	84.464	13.873	62	30.485	5.060
V12	74	79.649	12.796	62	29.156	5.564
V13	74	78.924	13.543	62	29.014	5.024
V14	74	77.635	11.776	62	29.300	6.265
V15	74	75.790	12.408	62	29.096	5.309
V16	73	74.952	12.213	62	29.352	5.013
V17	74	75.502	14.380	62	30.811	5.801
V18	74	78.741	14.042	62	31.608	6.319
V19	74	79.788	13.363	62	31.642	6.501
V20	74	83.130	14.341	62	33.396	9.779
V21	73	95.187	18.473	62	36.791	7.733

	CHIMPANZEE			GORILLA		
	n	mean	std.dev.	n	mean	std.dev.
V7	19	167.112	23.242	25	281.110	46.598
V8	19	135.755	25.316	26	257.810	34.350
V9	19	115.286	18.083	26	231.039	33.881
V10	19	102.475	15.583	26	207.474	30.529
V11	19	98.980	15.065	26	201.517	33.515
V12	19	98.063	15.913	26	205.610	35.561
V13	19	101.479	15.138	26	206.874	35.303
V14	19	102.884	14.222	26	205.820	35.130
V15	19	103.583	16.334	26	198.212	34.647
V16	19	104.749	17.891	26	191.658	32.124
V17	19	107.796	16.382	26	188.489	33.345
V18	19	115.748	15.106	26	208.696	36.976
V19	19	141.251	21.072	26	241.570	40.848
V20	19	155.236	29.168	26	245.919	43.165
V21	19	139.232	24.748	26	205.526	47.037

Table 6.25 (continued)

Absolute Vertebral Foramen Area
(Sexes Pooled)

	HUMAN			ORANGUTAN		
	n	mean	std.dev.	n	mean	std.dev.
V7	112	258.265	40.896	8	225.858	39.772
V8	112	226.624	37.510	8	179.680	21.380
V9	112	198.891	35.315	8	143.629	11.817
V10	112	180.797	29.930	8	136.294	14.745
V11	112	172.415	27.323	8	133.278	17.076
V12	111	170.330	27.254	8	130.407	12.602
V13	112	168.250	27.168	8	133.490	10.264
V14	111	169.916	29.147	8	134.160	12.281
V15	112	169.963	35.003	8	132.193	16.675
V16	112	171.661	29.361	8	136.500	11.231
V17	112	174.146	29.907	8	148.423	9.570
V18	112	196.660	35.673	8	151.567	9.036
V19	111	242.236	42.483	8	151.360	12.226
V20	112	266.273	37.430	7	147.338	10.574
V21	111	261.571	39.871	8	137.885	9.221

Table 6.26

Spearman Rank Correlation Significance Test

Absolute Vertebral Foramen Area

Spearman-R

Vervet	.796				
Human	.661	.904			
Chimp.	.404	.768	.857		
Gorilla	.682	.643	.593	.589	
Orang.	.379	.771	.729	.854	.621
	Baboon	Vervet	Human	Chimp	Gorilla

p-Value

Vervet	.000				
Human	.007	.000			
Chimp.	.136	.001	.000		
Gorilla	.005	.010	.020	.020	
Orang.	.164	.001	.002	.000	.013
	Baboon	Vervet	Human	Chimp.	Gorilla

Table 6.27

Relative Vertebral Foramen Area
(Sexes Pooled)

	BABOON			VERVET		
	n	mean	std.dev.	n	mean	std.dev.
V7	72	0.445	0.037	61	0.472	0.043
V8	74	0.416	0.035	62	0.440	0.041
V9	74	0.368	0.031	62	0.387	0.033
V10	74	0.366	0.029	62	0.366	0.032
V11	73	0.359	0.030	62	0.357	0.031
V12	74	0.348	0.025	62	0.349	0.034
V13	74	0.346	0.027	62	0.348	0.030
V14	74	0.343	0.024	62	0.350	0.035
V15	74	0.339	0.025	62	0.349	0.033
V16	73	0.337	0.026	62	0.351	0.031
V17	74	0.336	0.026	62	0.359	0.036
V18	74	0.345	0.027	62	0.363	0.036
V19	74	0.348	0.028	62	0.363	0.037
V20	74	0.355	0.028	62	0.372	0.046
V21	73	0.379	0.034	62	0.392	0.040

	CHIMPANZEE			GORILLA		
	n	mean	std.dev.	n	mean	std.dev.
V7	19	0.362	0.024	25	0.350	0.040
V8	19	0.326	0.031	26	0.334	0.037
V9	19	0.300	0.023	26	0.316	0.037
V10	19	0.283	0.022	26	0.300	0.040
V11	19	0.278	0.021	26	0.296	0.043
V12	19	0.277	0.023	26	0.299	0.043
V13	19	0.282	0.021	26	0.300	0.043
V14	19	0.284	0.021	26	0.298	0.040
V15	19	0.285	0.024	26	0.293	0.040
V16	19	0.286	0.026	26	0.288	0.041
V17	19	0.291	0.025	26	0.286	0.044
V18	19	0.301	0.023	26	0.301	0.045
V19	19	0.333	0.024	26	0.324	0.049
V20	19	0.348	0.033	26	0.327	0.047
V21	19	0.329	0.026	26	0.297	0.046

Table 6.27 (continued)

Relative Vertebral Foramen Area
(Sexes Pooled)

	HUMAN			ORANGUTAN		
	n	mean	std.dev.	n	mean	std.dev.
V7	112	0.418	0.031	8	0.348	0.029
V8	112	0.392	0.032	8	0.311	0.018
V9	112	0.367	0.031	8	0.278	0.011
V10	112	0.350	0.028	8	0.271	0.014
V11	112	0.342	0.026	8	0.268	0.017
V12	111	0.340	0.026	8	0.265	0.013
V13	112	0.337	0.026	8	0.268	0.010
V14	111	0.339	0.028	8	0.269	0.012
V15	112	0.339	0.033	8	0.267	0.017
V16	112	0.341	0.028	8	0.271	0.011
V17	112	0.343	0.029	8	0.283	0.009
V18	112	0.365	0.032	8	0.286	0.009
V19	111	0.405	0.035	8	0.286	0.011
V20	112	0.425	0.029	7	0.292	0.010
V21	111	0.421	0.031	8	0.273	0.009

Table 6.28

Spearman Rank Correlation Significance Test

Relative Vertebral Foramen Area

Spearman-R

Vervet	.796				
Human	.664	.911			
Chimp.	.404	.768	.854		
Gorilla	.693	.639	.611	.575	
Orang.	.379	.771	.739	.856	.607
	Baboon	Vervet	Human	Chimp.	Gorilla

p-Value

Vervet	.000				
Human	.007	.000			
Chimp.	.136	.001	.000		
Gorilla	.004	.010	.016	.025	
Orang.	.164	.001	.001	.000	.016
	Baboon	Vervet	Human	Chimp.	Gorilla

Table 6.29

Spearman Rank Correlation Test for Female and Male Morphometric Data

a) Absolute Spinous Process Ratio / Leverage

Species	Spearman-R	p-Value Females vs Males
Vervet	.971	.0000
Baboon	.986	.0000
Human	.964	.0000
Chimp.	.904	.0000
Gorilla	.857	.0000

b) Spinous Process Ratio

Species	Spearman-R	p-Value Females vs Males
Vervet	.969	.0000
Baboon	1.000	.0000
Human	.946	.0000
Chimp.	.736	.0000
Gorilla	.689	.0000

Table 6.30

Spearman Rank Correlation Test for Female and Male Morphometric Data

<u>Lateral Flexion Leverage (Lattran Ratio)</u>

Species	Spearman-R	p-Value Females vs Males
Vervet	.975	.0000
Baboon	.993	.0000
Human	.964	.0000
Chimp.	.757	.0010
Gorilla	.607	.0164

Table 6.31

Spearman Rank Correlation Test for Female and Male Morphometric Data

a) Absolute Facet Area

Species	Spearman-R	p-Value Females vs Males
Vervet	.975	.0000
Baboon	.975	.0000
Human	.986	.0000
Chimp.	.879	.0000
Gorilla	.975	.0000

b) Relative Facet Area

Species	Spearman-R	p-Value Females vs Males
Vervet	.979	.0000
Baboon	.971	.0000
Human	.975	.0000
Chimp.	.893	.0000
Gorilla	.986	.0000

c) Facet Inclination Angle

Species	Spearman-R	p-Value Fenmales vs Males
Vervet	.921	.0000
Baboon	.629	.0121
Human	.793	.0004
Chimp.	.546	.0351
Gorilla	.636	.0101

Table 6.32

Spearman Rank Correlation Test for Female and Male Morphometric Data

a) Absolute Vertebral Foramen Area

Species	Spearman-R	p-Value Females vs Males
Vervet	.971	.0000
Baboon	.946	.0000
Human	.929	.0000
Chimp.	.932	.0000
Gorilla	.814	.0002

Table 6.32b

b) Relative Vertebral Foramen Area

Species	Spearman-Rank	p-value Females vs Males
Vervet	.971	.0000
Baboon	.935	.0000
Human	.957	.0000
Chimp	.932	.0000
Gorilla	.829	.0001

Table 6.33

Spearman Rank Correlation Test for Female and Male Morphometric Data

a) Absolute Cranial Vertebral Body Area

Species	Spearman-R	p-Value Females vs Males
Vervet	1.000	.0000
Baboon	1.000	.0000
Human	1.000	.0000
Chimp	1.000	.0000
Gorilla	1.000	.0000

b) Relative Cranial Vertebral Body Area

Species	Spearman-R	p-Value Females vs Males
Vervet	1.000	.0000
Baboon	1.000	.0000
Human	1.000	.0000
Chimp	1.000	.0000
Gorilla	1.000	.0000

Table 6.34

Spearman Rank Correlation Test for Female and Male Morphometric Data

a) Pedicle Ratio

Species	Spearman-R	p-value Female vs Males
Vervet	.943	.0000
Baboon	.875	.0000
Human	.871	.0000
Chimp	.957	.0000
Gorilla	.893	.0000

b) Pedicle Area

Species	Spearman-R	p-Value Females vs Males
Vervet	.779	.0000
Baboon	.743	.0000
Human	.921	.0000
Chimp	.946	.0000
Gorilla	.957	.0000

Explanation of Table 6.35

Table 6.35 indicates the position of the transitional thoracolumbar vertebrae (T-L V) and its relation to the ribs in different primate species. For example, under V17-19 in vervet there are 25 females and 23 males. This means that in the sample there are 25 female and 23 male vervets who have their T-L V at V17 and their last ribs at V19. Under V18 in human the table shows 4 females and 9 males, which means that those individuals have both their T-L V and last ribs on V18. The rest of the table can be interpretted accordingly.

Table 6.35

Chi-square test for position of T-L joint and ribs in females and males

a) Vervet

	V16-18	V16-19	V17-18	V17-19	V17-20	V18-20	Total
Males	0	2	1	23	3	0	29
Females	1	3	2	25	7	0	39
Total	1	5	3	48	10	1	68

Chi-square = 2.806778 df = 5 p= .729745

b) Baboon

	V17-19	V17-20	V18-20	Total
Males	5	27	1	33
Females	2	39	1	42
Total	7	66	2	75

Chi-square = 2.422415 df= 2 p= .297837

c) Chimpanzee

	V19	V19-20	V20	Total
Males	1	0	8	9
Females	0	2	9	11
Totals	1	2	17	20

Chi-square = 2.887701 df= 2 p = .2360172

d) Gorilla

	V18	V18-19	V19-20	V20	Total
Males	0	1	4	8	13
Females	1	0	4	8	13
Total	1	1	8	16	26

Chi-square = 2 df = 3 p =
.5724067

e) Human

	V17	V17-18	V17-19	V18	V18-19	V18-20	V19	V19-20	V20	V20-21	Total
Male	0	0	1	9	40	1	127	16	2	1	197
Female	1	1	0	4	16	2	48	4	1	0	77
Total	1	1	1	13	56	3	175	20	3	1	274

Chi-square = 8.888421 df = 9 p = .4476371

Table 6.36

Frequency of total numbers of primate pre-sacral patterns

	Total	PSV	22	23	24	25	26	27
Species								
Chimpanzee	18	n		1	17			
		%		5.6	94.4			
Gorilla	26	n		13	12	1		
		%		50	46.2	3.8		
Orangutan	14	n	1	8	3	2		
		%	7.1	57.1	21.4	14.3		
Vervet	61	n			1	12	47	1
		%			1.6	19.7	77	1.6
Baboon	72	n				7	63	2
		%				9.7	87.5	2.8
Human	259	n	2	35	200	22		
		%	.8	13.5	77.2	8.6		

Table 6.37

The patterns of the pre-sacral vertebrae and their frequencies

	Baboon		Vervet		Human		Chimp		Gorilla		Orang	
	n	%	n	%	n	%	n	%	n	%	n	%
C / T / L												
6/11/5											1	7.1
6/12/5					2	.8						
6/12/6					1	.4						
7/9/9	3	4.2	8	13.1								
7/10/5					1	.4						
7/10/6					1	4						
7/10/7			1	1.6	1	4						
7/10/8	4	5.6	4	6.6								
7/10/9	61	84,7	46	75,4								
7/10/10	1	1.4	1	1.6								
7/11/4					1	4						
7/11/5					22	8.5	1	5.6				
7/11/6					49	18.9						
7/11/7												
7/11/8	2	2.8	1	1.6								
7/11/9	1	1.4										
7/12/4					10	3,9			4	15,4	8	57.2
7/12/5					142	54.8	1	5.6	3	11,5		
7/12/6					18	6.9					1	7.1
7/13/3									9	34.6		
7/13/4					7	2.7	16	88.8	9	34.6	3	21.4
7/13/5					4	1.5			1	3.8	1	7.1

The processes of reductions/increases of thoracic and lumbar vertebrae through lumbarisation, thoracolisation or otherwise can be seen in the above table.

Table 6.38a

General distribution of last pair of ribs on vertebral column

	N	Level	V16	V17	V18	V19	V20	V21
Vervet	68				4	53	11	
Baboon	77					9	68	
Orangutan	15				2	8	5	
Gorilla	27				1	1	24	1
Chimpanzee	22					1	21	
Human	274		1	14	235	23	1	

Table 6.38b (Percentage Distribution)

	N	Level	V16	V17	V18	V19	V20	V21
			%	%	%	%	%	%
Vervet	68				5.9	77.7	16.2	
Baboon	77					11.7	88.3	
Orangutan	15				13.3	53.3	33.3	
Gorilla	27				3.7	3.7	88.9	3.7
Chimpanzee	22					4.5	95.5	
Human	274			0.4	5.1	85.8	8.4	0.4

Table 6.39a

Species distribution of position of thoracolumbar joint transitional vertebra (T-L V)

	Level	V16	V17	V18	V19	V20	V21	V22
	N							
Vervet	68	6	61	1				
Baboon	77	1	74	2				
Orangutan	15			1	11	3		
Gorilla	27			2	8	16		1
Chimpanzee	22				3	19		
Human	274		3	72	192	7		

Refer to Table 6.39b as well. Note that the general position of the T-L V is V17 for pronogrades, V19 for the suspensory locomotor and orthogrades, and V20 for semiorthogrades. Example: From the above table it can be seen that 61 vervets have their T-L V at V17; 72 humans have their T-L V at V18 and so on.

Table 6.39b

Percentage species distribution of the position of the thoracolumbar joint transitional vertebra (T-L V)

		Level	V16 %	V17 %	V18 %	V19 %	V20 %	V21 %	V22 %
	N								
Vervet	68		8.8	89.7	1.5				
Baboon	77		1.3	96.1	2.6				
Orangutan	15				6.7	73.3	20		
Gorilla	27				7.4	29.6	59.3		3.7
Chimpanzee	22					13.6	86.4		
Human	274			1.1	26.3	70	2.6		

Note: The above table indicates that the T-L V position is often on V17 in over 90% pronogrades, on V19 in over 70% suspensory locomotor and orthogrades, and on V20 in over 60% semi-orthogrades. Table 6.39a should be viewed with this table.

Chapter 7

DISCUSSION

A) Morphometric Functional Structure of the Thoracic Vertebral Column in Primates using different Modes of Locomotion

1) General

The specimens and sample size have been discussed under the 'Statistical Methods'. Under this discussion, it must be remembered that the sample for the great apes and monkeys are relatively smaller than the human sample. The results must be viewed in this light.

The primates in this study practise full pronogrady, orthogrady and semi-orthogrady. The full pronogrades in the study include the usually arboreal vervet monkey and the generally terrestrial baboon. Full pronogrades keep their vertebral column in a position that is horizontal to the ground during locomotion, except when they are climbing.

The orthograde humans keep their vertebral column in a position that is vertical to the ground during locomotion and other activities. The semi-orthograde/semi-pronograde primates in the study are the knuckle-walkers, namely the gorilla and chimpanzee, whose vertebral column is kept in between the horizontal and vertical positions during locomotion. The orang-utan is difficult to place in any of the above locomotive categories, because it practises slow arboreal suspending movements, during which its vertebral column is occasionally kept horizontal and sometimes vertical to the ground. The orang-utan is not often terrestrial in its natural habitat, and of all the great apes it is the least bipedal.

However, it must be remembered that in general primates keep their vertebral column and trunk erect when sitting or climbing. These results, are the morphological analyses of the various aspects of the vertebral column in the primates studied. In this study, it must be pointed out that there were no actual field behavioural observations on the function of the vertebral column. The results are discussed in the light of this background. The discussion refers to postural and locomotive modes that have been mentioned in background literature, as described by various authors cited. The interpretations of these results could possibly be applied to observations in similar studies of fossil vertebral columns, from fossil remains and rare species.

As mentioned earlier, the study of primate vertebrae in relation to locomotion has, in the past concentrated on the lower vertebral region, particularly on the lumbar vertebrae, sacrum, pelvis and limbs. In this study emphasis is placed on the vertebrae of the thoracic region mainly.

In this discussion the various vertebrae are mostly referred to by their serial numbers, in the craniocaudal position, in the vertebral column. For example, V7 refers to the seventh vertebra that is also the seventh cervical vertebra and V19 to the nineteenth vertebra or twelfth thoracic vertebra. This numbering ensures that there is no confusion, when reference is made to a particular vertebra in vertebral columns of any species.

2) **Leverage and Back Muscle Action**

i) The Spinous Process Leverage for back muscles

Vertebral muscles are attached to bony processes that act as levers for the muscles during contraction in order to effect appropriate movements of the vertebral column and trunk. Thus the term leverage of the spinous or transverse processes is used in relation to the muscles and their insertion onto these processes ("levers"). The action of the back muscles on these levers is important in the locomotion of different primates species. The muscles are responsible for various movements of the vertebral column, such as extension, lateral flexion of the trunk and resistance to lateral flexion of the trunk. All these movements occur in pronograde, orthograde and semi-orthograde primates.

When humans and chimpanzees stand in the orthograde (erect) posture, the long back muscles help to resist ventral flexion of the trunk by extending the vertebral column, and the individual avoids bending or falling on the ventral aspect. In quadrupedal running, pronogrades such as monkeys repeatedly flex and extend the back. The muscles concerned with this action, namely the erector spinae and multifidus, have their attachments on the spinous processes, rib-tubercles and tips of the transverse processes. They obtain strong leverages from these points to enable them to act on the vertebral column. The attachments of these muscles to have been explained in chapters three and four. However it must be noted here again that the attachment of the erector spinae onto the ribs affects the movements of the vertebral column, because the ribs are firmly anchored to thoracic vertebrae via the strong costotransverse and costovertebrae ligaments. Firstly, the relationship of the muscles, to the leverage of the spinous process for extension of the back, is discussed here. Secondly, the relationship of the muscles to the leverage of the transverse process is also discussed after.

Shapiro (1991a) notes that the Spinous Process Leverages of the lumbar vertebrae in different species are not related to body-size or weight of the species. For that reason the ratios for the Spinous Process Leverage of the gibbon, which is a relatively small-bodied primate, are not "distinguishable" from the ratios of the relatively large gorilla and orang-utan. Keith (1923) is of the view that there is dichotomy in the Spinous Process Leverage with orthograde primates on one side and pronogrades on the other. Shapiro (1991a) does not agree with this view. This is understandable, in that such categorisation into only two groups of locomotive forms is too limiting. Since primates are divergent, there are bound to be groups that are structurally and functionally transitional between orthogrady and pronogrady. The chimpanzee and human show similarity in the Spinous Process Leverage. The similarity is difficult to explain, except if the chimpanzees and humans are both regarded as orthogrades. If the other primates in this study are regarded to be generally pronogrades, then dichotomy can be said to exist between the orthogrades and the pronogrades as far as the Spinous Process Leverage is concerned. Functional studies on the Spinous Process Leverage still need to be carried out in many other primate species, and on larger sample to provide more information.

Two ratios of the spinous process have been considered. Firstly, the "Absolute Spinous Process Ratio", which gives an indication of the relative length of the spinous process, but is not very important in muscle leverage, (see below). Secondly, the projective "Spinous Process Ratio" or the real Spinous Process Ratio, which indicates the Spinous Process Leverage to muscles of the back, during extension of the vertebral column (Figure 5.1). The Spinous Process Leverage counteracts ventral flexion of the trunk. According to the results, a high Absolute Spinous Process Ratio does not necessarily correspond to a high Spinous Process Ratio, (Figures 6.1a, b, c; 6.2a, b, c; Tables 6.1 and 6.3). In other words, the relatively longest spinous process in a vertebral column is not necessarily the one that provides the greatest leverage to the muscles. This means that it may not necessarily be the most important in extension and other movements of the vertebral column and trunk.

However, Ward (1991) states that the large monkeys, have longer spinous processes, and bigger erectores spinae. Ward states that the "longer spines would improve the movements of the transversospinal muscles". These statements apparently directly relate the absolute length of the spinous process to its leverage and its capability in assisting the muscles to move the vertebral column. According to the present study, the length and leverage of the spinous process are not always directly proportional (Tables 6.1 and 6.3). On the other hand, Shapiro (1991a) and Badoux, (1974) state that it is mainly the angle of inclination of the spinous process to the body of a vertebra that determines the leverage of the spinous process (Figure 2.7). Shapiro (1991a) indicates that the more perpendicular the spinous process is the farther will be the fibres of the erector spinae from the vertebral axis. Since the axis is located near the centre of the disc, the leverage will be greater on a perpendicular spinous process. This implies that a long spinous process making a narrow acute angle with the body of a vertebra imparts less leverage to muscle(s) attached to it, than it would if it made a larger angle (nearer to 90 degrees) (Shapiro 1991a). The more perpendicular a spinous process is to the body of a vertebra, the better is its leverage, regardless of it height (length).

The results in this study also indicate that a high Absolute Spinous

Process Ratio from a relatively long spinous process does not necessarily impart a higher Spinous Process Ratio. A long spinous process does not necessarily provide greater extensor leverage for the back muscles attached to it, if it is angled acutely. For example, in humans and chimpanzees, the study reveals that the greatest Spinous Process Leverage is located on the spine of twentieth first vertebra (V21), which has a relatively short spine, but stands out perpendicular to the body of the vertebra, and is acutely placed to the vertebra. The relatively longest spinous process is located in the mid-thoracic region, on V13 in humans, and on V13/V14 in chimpanzees. (Figure 6.2c; Tables 6.1, 6.3). The mean leverages of these long spines of chimpanzee and human, at the upper and mid-thoracic regions range from 1.15 to 1.34. This range is relatively lower than the leverage of the short spine at V21, are recorded as 1.49 to 1.54.

In the pronogrades such as the baboon and vervet, the relative longest Spinous Process is found in the mid-thoracic and upper thoracic region, on V13/V14 and V10/V13 respectively, (Table 6.1). The vertebrae with greatest Spinous process Leverage are also located in the upper and mid-thoracic region, V11 and V14 respectively (Table 6.2). It must be noted however that the peak of the profile patterns for the two ratios do not exactly occur on the same vertebra in each of the above pronogrades. The peaks for the two ratios do not coincide in their position. Neither do they occur on exactly corresponding vertebrae, as they do in chimpanzee and human. However, the fact that the two peaks occur in the mid-thorax is important to note for pronograde locomotion.

In the gorilla (semi-orthograde) and the orang-utan (slow suspending locomotor), the relatively longest spinous process and the spinous process with the greatest leverage completely coincide on the cervicothoracic transitional vertebra, namely V7 which usually has a vertical spine (Tables 6.1 and 6.2). This means that the longest spinous process provides the greatest leverage in both these modes of locomotion. It is not clear why the longest spinous process and the greatest leverage overlap on the seventh cervical vertebra in these two species having quite different postures and modes of locomotion. The gorilla is clearly a terrestrial semi-orthograde, knuckle-walker, while the orang-utan is an arboreal suspensory quadruped (Mackinnon, 1974, Tuttle and Watts 1985; Tuttle 1986; Ward 1991). However, the following might be an explanation why the leverage overlaps.

Gorillas depend on their fore limbs to support the heavy trunk during knuckle-walking. The orang-utans also actively employ fore limbs in suspension of the trunk, and in limb abduction as they reach out for branches (Mackinnon 1974; Tuttle 1986, Ward 1991). In the gorilla and orang-utan fore limbs are actively engaged in different ways, but for similar purposes, namely postural support and locomotion. The activities of fore limbs make the limb muscles well developed, including those muscles attaching the limb to the trunk. Such muscles include the trapezius and rhomboids, which have their respective origin, on the spinous processes of C7-T12 and C7-T5. It is follows that, the spines of C7 to T5 that give attachments to these two active muscles, are relatively the longest, and have the greatest leverage.

A comparison between the results of this study on the thoracic and some lumbar leverages has been made with Shapiro's study (1991a) of the leverages of the complete lumbar region. In humans and chimpanzees the greatest Spinous Process Leverage of the entire vertebral column is located in the lumbar region, and not in the thoracic region. This confirms Shapiro's work (1991a). It implies that the strain in the lower part of the vertebral column is considerable in orthogrades. Since humans keep their trunk erect most of the time, such strain could have even greater consequences. It remains to be shown by EMG and other studies whether this observation is related to the lower back pain that is common in humans.

The almost overlapping position of the relatively longest spine in the mid-thorax in humans and chimpanzees, and the exactly overlapping position of the greatest spinous leverage on V21, should be analysed. Probably the similarity is because among the primates, the chimpanzee and gibbon can sustain bipedalism. In this regard if the chimpanzee is considered to be a successful orthograde because of its bipedal tendency, then there is orthograde-pronograde dichotomy in the Spinous Process Leverage. The dicotomy is such that the chimpanzee and human are on the one hand and the monkeys on the other. According to comparative anatomist Keith (1923), there is orthograde-pronograde dichotomy in the pattern of the spinous process ratio. The relations of the spinous process are shown in Figures 6.2a, b and c, Table 6.3).

The location of the greatest leverage in the upper and mid-thoracic regions in non-orthograde primates is important (Table 6.3). This is apparently the best position for the greatest leverage in non-orthogrades, because in pronograde and semi-orthograde locomotion it is more important to stabilise the trunk and to keep the body axis from lateral bending and tortion loading (Carrier 1987). Restriction of lateral bending also stabilises the pelvis and thus provides a rigid origin for muscles acting on the hind limb during locomotion (Carlson et al., 1979; English, 1980).

ii) <u>Back muscle action through the Lateral Flexion Leverage of Transverse Processes</u>

It has already been stated that the thoracic vertebrae and their transverse processes are joined to the ribs by strong ligaments. Therefore the action of the back muscles that are attached to the ribs can affect the movements of the vertebral column. The action and leverage of the transverse process should therefore be viewed in this light.

The lever arm of the transverse process determines the unilateral flexion of the trunk. It is described as the Lateral Flexion Leverage or the Lateral Leverage of the Transverse Process. This lever arm is also known as the Lattran Ratio (Shapiro (1991a, 1995). According to Shapiro, early anatomists were of the opinion that there is orthograde-pronograde dichotomy in this ratio. This has not been confirmed by the current study. Neither has it been found that orthograde primates such as humans have the highest Lateral Flexion Leverage of the transverse process. Shapiro (1991a, 1995) made similar observations on the lumbar vertebrae in certain primates.

The highest ratio is in the pronograde baboon, closely followed by the orthograde human, and the pronograde vervet. However the differences between the ratios of the above three are relatively small (Figure 6.3; Table 6.5). The great apes have immovable back ligaments and there is not much room between the last rib (thorax) and the pelvic blades for free much movement (Cartmill and Milton, 1977; Jungers, 1988a). They have the lowest profile patterns for the Lattran ratio. Since there is limited room for lateral movement of the thorax and upper trunk, the apes have no use for long transverse processes that help in lateral movements of the trunk.

Among the three apes, the usually arboreal and only suspensory locomotor, namely the orang-utan has the lowest values of this measurement. This may imply that possibly there is dichotomy in this ratio, between the arboreal suspensory locomotor on the one hand, and the orthograde, semi-orthograde, and pronograde primates in the study on the other hand. The difference in the ratio is certainly not related to size, since the latter three groups consist of primates of varying sizes.

The Spearman Rank Correlation Significance test shows that the Lattran profile pattern for ratio is significantly similar, in baboon, vervet, human and chimpanzee (p-value is less below 0.05) (Table 6.6). This implies that the ratio is equally important in these diverging postures and locomotion of the pronograde, orthograde and semi-orthograde species in the study. The stabilisation of the trunk in the sagittal plane and its restriction by longissimus, iliocostalis and multifidus from lateral bending are important in pronograde, orthograde and semi-orthograde primate locomotion (Carrier, 1987). The Lateral Flexion Leverages on the left and right side of the trunk keep the body in the sagittal plane, and in the anteroposterior axis, by countering one another. The magnitude of the Lattran ratio in all the divergent groups studied indicates that the Lateral Flexion Leverage is important and essential in the locomotion of orthogrades, semi-orthogrades, suspensory locomotors and pronogrades. The leverage is probably less important in the slow suspensory arborealism of the orang-utan, where keeping the trunk in the sagittal plane may not be necessary in moving over and under the branches, (Mackinnon, 1974; Tuttle, 1986). This may explain why in Figure 6.3 the orang-utan profile has the lowest profile pattern for the ratio that is slightly isolated from the rest.

The profile pattern for the Lattran ratio rises sharply in the orthogrades after the 19th vertebra, into the lumbar region, whereby the intensity of the profile pattern is greater than the profile patterns of the pronogrades (Figure

6.3). This could be an indication that in the orthogrades, there are differences between the profile patterns for the ratio in the lumbar because of the lordotic curve that develops along bipedal tendencies. When the above change in the profile pattern occur in apes, it starts at V20.

The results of electromyography (EMG) studies of back muscles by Shapiro and Jungers (1994) reveal similarities in the activity patterns of longissimus, iliocostalis, and multifidus, during quadrupedalism and bipedalism in various primates. The profile patterns for the Lattran ratio are also closely similar in the different locomotive groups. These similarities found in the profile pattern for the Lattran ratio in primates using divergent forms of postures and locomotion, are not surprising in the light of the above EMG findings. The unique suspensory posture and locomotion of the orang-utan may account for the lowest profile pattern for the Lattran ratio in this species. While the relatively active orthograde and pronograde primates need to resist lateral flexion of the trunk during locomotion, the slow suspensory locomotor may require more liberal movements of the trunk and limb abductions to reach out for branches. The suspensory locomotor has no need for a strong lateral flexion leverage.

iii) Back muscle action through the Extensor Leverage of the Transverse Process

The relative position of the roots of the transverse process to the most ventral coronal plane of the vertebral body affects the leverage of the muscles attached to the transverse process during extension of the trunk. According to Shapiro (1991a) this is because the further away the transverse processes are from the ventral aspect of the vertebral body, the greater the leverage of the muscles attached to them. So to some extent the transverse process position should be cautiously equated with effective muscle moments. The position of the transverse process and its relationship with effective muscle moments should be discussed in that light. The general position of the transverse process on a vertebra is known as the Ventrodorsal Transverse Process position and is expressed as a ratio, known as the Vdtran ratio (Shapiro, 1991a).

In the present research, the position of the tips of the transverse process in relation to the most ventral aspect of the vertebral body is examined since it is variable. Unlike in Shapiro's (1991a) and other studies that have focused on the root of the lumbar transverse process this has focussed on the level of the tips of the thoracic transverse processes (Figure 5.3). The reason for this is that the roots and the tips occur at different levels in the primate thorax, and this may affect the function of the back muscles associated with the transverse processes (Moore, 1982). In the semi-orthogrades, orthogrades and the suspensory locomotor, in the current study, the profile patterns for the Vdtran ratio are similar, the p-value is .0 in all groups (Table 6.8). The profile pattern for this ratio for the suspensory locomotor, are the lowest among the above three locomotion groups, due to it unique locomotion probably (Figure 6.4, Table 6.7).

As noted by Halpert et al., (1987) and Shapiro (1991a) again, this ratio is not directly proportional to the species size or body weight. In the current study the profile pattern for this ratio is similar in the apes (except orang utan) and humans (primates of divergent sizes).

In all the primates investigated in this study, the Vdtran ratio is generally shows values above 1.0 for the thoracic region. This is in agreement with the findings in the orthograde the gibbon by Shapiro (1991a). A value above 1.0 in this ratio indicates that the tips of the transverse processes are above the level of the dorsal surface of the vertebral body. A value above one gives rise to sufficient leverage for dorsal extension of the vertebral column and trunk. If the tips are located in the lower position, a value below 1.0 is obtained, resulting in a lower extensor leverage. Primates with a Vdtran ratio value above 1.0 have a better ability to extend their back more unlike primates having values below 1.0. This is very important for primates since the back is characteristically kept in the upright posture when the individual is engaged in various daily activities, such as sitting, grooming, feeding, climbing, etc. The advantage for a primate having the ability to extend the vertebral column is that the individual can effectively counteract the ventral flexors of the trunk, in order to maintain the erect position of vertebral column. In the studies of the lumbar vertebrae of pronogrades by Shapiro (1991a) the Vdtran ratio was found to be below 1.0

and therefore these species were disadvantaged as far as the attaiment of the orthograde posture was concerned.

The orthogrades and semi-orthogrades in this study have a high profile pattern for the thoracic Vdtran ratio, which reaches a peak (above 2.0) in the upper thoracic region. The high profile pattern for the ratio continues into the beginning of the lumbar region (Figure 6.4). The above high profile pattern may be interpreted to mean that these primates are better adapted to extending their vertebral column than the pronograde that exhibit lower values. The low ratio for the Vdtran leverage in the pronogrades negatively influences their potential to practise bipedalism, since they would find it more difficult to maintain the trunk in an erect posture. On the other hand, the relatively high profile pattern for the Vdtran ratio in orthogrades and semi-orthogrades gives them an edge over the other primates in making use of their back extensors, and hence maintaining the erect or semi-erect posture in their locomotion. The fact that the Vdtran ratio in orthograde and semi-orthograde is still high (1.4 to 2.0) towards the lumbar region, implies that the region is important in the extension of the trunk and keeping the trunk erect. In humans and chimpanzees this ties up well with the highest Spinous Process Leverage, being in the lumbar region on V21.

The profile pattern for the Vdtran ratio in the suspensory locomotor and pronogrades are the lowest among the apes. These profiles reflect a poor back extension, resulting in relatively poorer ability at bipedalism or orthogrady, in comparison to the chimpanzees and humans. Generally in all the primates in the study the profile pattern for the Vdtran ratio is highest and probably more effective mostly in the upper part of the vertebral column, (Graph 6.4; Table 6.4). The presence of a high profile pattern for this ratio in the thorax is also advantageous for the trunk must be stabilised in the sagittal plane and prevented from bending ventrally or laterally in all types of locomotion. As pronogrades show lower profile patterns for this ratio, while the orthogrades/semi-orthogrades show relatively higher patterns, it can be claimed that this feature exhibits a degree of orthograde-pronograde dichotomy. This is however still debatable in view of the fact that the differences are not significant (p-value below 0.05 for all the primates). Further investigations would appropriate here.

Summary

The longest spinous process does not necessarily have the greatest leverage, therefore the longest spinous process may not be the most important factor in lifting the trunk and maintaining the erect posture. The position of the greatest leverage in humans is on V21. This is also the position of the greatest leverage in chimpanzees. The similarity in the position of the greatest leverage of the spinous process in the chimpanzee and human is surprising. It could however be explained by regarding the chimpanzee as being more orthograde than the other non-human primates in the study. A degree of orthograde-pronograde dichotomy may then be claimed to exist for the Spinous Process Leverage. The strain on V21 may be considerable during human bipedalism. Whether this contributes to lower-back pain that is a common complaint in humans should be investigated by EMG/clinical studies.

A relative uniformity is present in the lateral flexion leverage and extensor leverage in relation to the transverse process. However, the arboreal suspending locomotor records the lowest profile patterns for the lateral flexion leverage of the transverse process, probably due to unique posture and locomotion of the orang-utan. In this respect the orang-utan is clearly different (though not significantly) from the other primates in the study, which are mainly orthograde and semi-orthograde.

The profile pattern for the Vdtran ratio is highest and hence most effective in the upper thoracic region in all the primates in this study, in spite of their varying modes of posture and locomotion. This is so because, as has been pointed out above, the stability of the trunk in the sagittal plane and anteroposterior axis is necessary in all forms of locomotion and would be best controlled from the upper thorax. The orthograde and semi-orthograde primates in the study have relatively higher profile patterns for the Vdtran ratio than pronogrades, because the former two groups have a postural requirement to keep the back in an erect position.

3) Vertebral Rotational Movements and Prezygapophyseal Angles

The degree and type of movements in the vertebral column at the interfacet joints depend on the angle of inclination of the prezygapophyses and postzygapophyses. Although the differences in these angles between species are small, they may reflect large differences in the locomotive modes of species, because the zygapophyses are lined in a series or 'chain'. Therefore, the cumulative angular differences may be large enough to cause considerable differences in terms of the movements of the vertebral column and the trunk. The size of the facet angles affects the movements because the larger they are the greater is the ability of vertebral column to extend, flex, bend laterally or rotate (MacLarnon, 1993). As already noted in the chapter on Results, pronogrades in the study have the largest prezygapophyseal angles, all the angles being above 110 degrees, except on V8 of the baboon (Table 6.13). Clauser (1980) and Shapiro (1991a) observed prezygapophyseal angles of the same magnitude in different species of monkeys. The larger facet angles of the pronogrades probably give rise to more agile thoracic vertebral columns. Gorilla and orang-utan which, have relatively smaller thoracic prezygapophyseal angles, might not have much agility in their movements. Shapiro (1991a) does not agree that the locomotor and postural differences of primates are reflected in the thoracic prezygapophyseal angles.

In the current research, differences in facet angles have been observed, but they are small differences. It is known that the type of movements generated by joints depend to a certain extent on the angular orientation of the articular surfaces of the joints. It should therefore be expected that movement of the vertebral column is affected by the angular orientation of the vertebral facets. Some differences in postures and locomotion should be expected in primates having different prezygapophyseal angles, even if such differences are relatively small. Much more information from field observations and facet angular measurements on various specimens would be helpful to throw more light on this aspect in the future.

The facet angles in the thoracic region generally increase in magnitude craniocaudally in all the primates in this study, though much less so in the unique orang-utan. Immediately caudal to the last pair of ribs (at the thoracolumbar or T-L transitional vertebra, commonly V19), the facet angles dramatically drop to values below 70 degrees in all the groups of primates investigated (Table 6.13). In the apes and humans the change coincides with the T-L transition. For example, in the semi-orthograde chimpanzee the facet angles drop from 118 to 58 degrees, at V19 and V20 respectively. In the pronograde vervet the change is more dramatic, from 148 to 36 degrees. In the orthograde humans the change is also quite dramatic, from 124 to 26 degrees. The low values of the prezygapophyseal angles generally indicate the beginning of less lateral movements, and possibly more stable joints. The final arrangement gives rise to typical lumbar facet joints that are sagittally orientated, and are structured to resist lateral movements. In contrast the facet joints of thoracic vertebrae are orientated in the coronal plane for lateral movements of the trunk, and resist ventral sliding and sagittal movements.

Six of the twelve thoracic vertebrae in humans have large prezygapophyseal angles, measuring 110 degrees or above. This implies that the flexibility of the human thoracic vertebral column is next to that of pronograde monkeys in the study. In the monkeys in the study, the facet angles are nearly all above 110 degrees. Conversely, the low thoracic facet angles, below 110 degrees, observed in most of the thoracic vertebrae of the semi-orthograde knuckle-walkers and in the suspending locomotor, might imply that thoracic regions are more rigid in these groups. For the arboreal/suspending orang-utan to have low thoracic facet angles, and therefore a relatively less agile vertebral column than the other arboreal pronograde primates, is not surprising. This might partly explain why the orang-utan is slow and cautious in executing its arboreal movements (Mackinnon, 1974; Tuttle, 1986). Quick movements, as those usually seen in the other arboreal monkeys, would require a more agile trunk, facilitated by a great number of larger facet angles in the thorax. Such angles are absent in the orang-utan. As mentioned earlier great apes have immovable backs probably due to tight back ligaments and lack of room between the last pair of ribs and the pelvic girdle blades (Cartmill and Milton, 1977). Large facets for freedom of movements of the zygapophyseal joints would be unnecessary in the apes.

It must be noted that among the apes, the orang-utan has the greatest difficulty in practising orthogrady, an exercise that necessitates intricate balancing of the trunk on two legs and the pelvis (Napier, 1977). Such exercise is difficult if the trunk is rigid due to the presence of small thoracic angles as in the orang-utan.

Clauser (1980) examined thoracic facet angles, and Shapiro (1991a) studied lumbar and a few thoracic facet angles. According to Clauser (1980) most thoracic facet angles of the orthograde human are generally below 110 degrees, like those of the great apes and gibbon. Contrary to Clauser this study shows that six of the twelve pairs of thoracic facet angles in humans are large, and like in the pronograde monkeys measure above 110 degrees or above. It is tempting to suggest that bipedal and pronograde locomotion tend to be facilitated by a *big* number of *large* thoracic facet angles. The larger angles result in freer movements in the thoracic vertebral column and more agility in the upper trunk. Possibly the more the number of the angles above 110 degrees the more flexible or agile the trunk should be. An agile trunk can be more easily manipulated to maintain the centre of gravity and balance in bipedalism (Figures 2.5, 4.2). According to Napier (1977) human bipedalism is a delicate exercise involving striding and rhythmic forward movements of one leg after another, keeping the centre of the body weight between the supporting pedestal or feet. Furthermore, in human walking, there are other complex actions involving other parts of the body, such as balancing the vertebral column on the sacrum, (Conroy, 1997). It is speculated that orthograde walking would be relatively more difficult to perform if the upper trunk had only a few small facet angles, that would result in a rigid trunk, as that found in the lumbar region. Pronograde primates that are usually involved in jumping and leaping would also require a trunk that is relatively flexible. This might explain why the vervet, baboon and human were found to have greater numbers of large facet angles in the thoracic vertebrae, than the apes. Both full pronograde and orthograde primates need a flexible thoracic vertebral column for locomotion.

There are significant differences in the thoracic zygapophyseal angles of the gorilla and orang-utan on the one hand, and vervet, human, chimpanzee and baboon on the other hand (Tables 6.13 and 6.14, Figures 6.7a, b). All the latter four primates have p-values below .05, while the former two have p-value way above .05. However, Shapiro (1991a) suggests that mobility along the thoracic and lumbar column is generally comparable across primates, regardless of differences in their positional behaviour. This current study does not support that view. However, field and laboratory studies are needed on primate facet angles, posture and locomotion, to test the findings of this study and Shapiro's suggestion.

Summary

There are differences in the thoracic facet angles among the primates studied. Although such differences might appear small it may be well to remember that even small changes to the body or environment may bring about the success or failure of a species (Relethford, 1998). Secondly, as the facet angles are lined in series, the functional effect of their sum total should possibly be big enough to bring about noticeable differences in movements of the trunk and in the general locomotion of the different species.

It is believed that the magnitude of the facet angles and its effect on the locomotive behaviour might be related to the size (weight) of the species. For example, the relatively small and agile monkeys having larger angles, while the relatively large apes have smaller angles. However, this is not supported by the fact that the thoracic facet angles in the orthograde human are significantly similar to those of the small sized pronograde monkey rather than to those of the large sized semi-orthograde apes. Investigations of facet angles in terms of body size have not yet been satisfactorily carried out in many forms of primates. Generally, there is still much information that could be learnt from functional field observations of primate locomotion linked to laboratory measurements of the vertebral facet angles (Johnson and Shapiro, 1998).

4) Transitional Vertebrae: Their movements and forces acting on them through the vertebral column

i) Action at the Transitional Facet Areas

The absolute and relative facet areas are significantly similar in all the species in the study since the p-value is below .05 between all the species (Tables 6.10, 6.12; Figures 6.5, 6.6).

Articulations and movements in the vertebral column take place at the facet joints, as well as between the cranial and caudal surfaces of the adjacent vertebral bodies. The articular surface of the facet joints is also important in that compression forces are transmitted from the ventral to the dorsal aspects of the vertebral column and vice versa, through the pedicles and articular facets. Information on the facet areas is therefore useful in the understanding of the part played by the facets in the transmission of compression forces, during the postural and locomotive changes in various modes of primate locomotion.

The thoracic facet areas in the primates studied generally do not show important relative differences. However, in all the primates examined the facet areas at or near the cervicothoracic (C-T) and thoracolumbar (T-L) transitional vertebrae are large both in absolute and relative terms (Tables 6.5 and 6.11; Figures 6.5 and 6.6). Therefore, there is reason to expect that the increased facet areas at the transitional levels of the vertebral column are functionally important. For example, in the orthograde humans and the semi-orthograde apes the transitional vertebra V8 has relatively large facet areas. In comparison to the other spinous processes, V8 also has relatively a more perpendicular spinous process and relatively long transverse processes (Figures 6.2a, b, c; Table 6.3). The aggregate result of these features is a good ability for dorsal extension, lateral flexion and counteracting lateral flexion, as discussed earlier. The large facet areas at this level could therefore be regarded as a prerequisite for extra stability during lateral flexion and counteract lateral flexion movements at the C-T transition.

Vertebrae number 17 and 19/20 are T-L joint transitional vertebrae in, respectively, the pronograde monkeys and orthograde/semi-orthograde locomotors in this study. There are increased facet areas immediately cranial and caudal to these transitional vertebrae in both the above groups. These increases in facet areas should be seen in terms of providing stability at the transitions. Good stabilisation of the transitional vertebrae should be important because different and sometimes opposing movements are taking place cranial and caudal to the transitions. Without proper stabilisation of the transitions, movements of one region could easily be transmitted into the adjacent regions of the vertebral column, creating interference and uncoordinated movements, in the adjacent region of the vertebral column.

Latimer and Ward (1993) do not mention increases in the facet areas in the chimpanzee at the thoracolumbar (T-L) transition. The current study shows that the chimpanzee, human, baboon and vervet register increases in facet areas at or towards their T-L transitions (V17-V19). This emphasises the importance of these areas in the movements of the vertebral column. The largest facets occur at the cervicothoracic (C-T) transition in the gorilla and orang-utan (Tables 6.9 and 6.11). In the gorilla and orang-utan the longest spinous process and the greatest leverage are also found on the C-T transitional vertebra, (V8). This may be due to the strain at the C-T transition, as a result of the attachments of some of the muscles of the fore limb and those supporting the large head. On the other hand the general body size of a group may influence the size of the vertebral parts (Ward, comment 24 March 1999).

The facet areas on the T-L transition and on the lumbar vertebrae are relatively larger than in the upper thoracic region in all the primates studied, thus enhancing stability towards the lumbar region and within the upper lumbar region. In all locomotive modes, a stable lumbar region is important to steady the hind limbs, and this is possibly why the absolute and relative facet areas are increased towards the lumbar region.

It is notable that the pronogrades in this study have generally high profile patterns for facet area ratios especially at the T-L transition (Tables 6.9, 6.10, 6.11and 6.12). Although the relative profile patterns for facet areas of the orthogrades are high at the T-L transition, it is not possible to claim that the size of these facets is responsible for bipedalism, since pronogrades are also endowed with relatively high profile patterns for this ratio. Rather, these large facet areas should be viewed in relation to stabilisation of the transition and the active engagement of the hind limbs that takes place in both orthogracy and pronogracy, which impacts on the facets.

The profile patterns for this ratio of the facet areas are lowest in the slow suspending locomotor and the slow semi-orthograde gorilla. Slow movements can cope with less stability, while fast movements cannot be compromised with instability.

The profile patterns for the relative facet area ratio on the non-transitional vertebrae are relatively low and similar in all the primates in the study (Figure 6.6, Table 6.11). Therefore, as noted by Latimer and Ward (1993), all forces of locomotion and bipedalism have no special effect on the loading, of the posterior vertebral elements via the facets of thoracic vertebrae.

ii) Forces at the transitional Cranial and Caudal Vertebral Body Surfaces

a) Absolute and Relative Areas of the Cranial Vertebral Body Surfaces

There is no significant difference in the absolute and relative areas of the cranial vertebral body surface areas, in all the species in the study. All the results are extremely similar (the p-value is .0 for both ratios between all groups). It is clear therefore that this feature cannot be used to reflect locomotive or other differences in these primates. However, the progressive increases of absolute and profile patterns for the relative areas of the cranial vertebral body, clearly indicates that the vertebral column is functionally geared to bearing the weight of the body and receiving compressive forces in different primate locomotive groups. That is, in the primates considered by the above authors and in the present study, the relative cranial vertebral body surface area does not differ among the species (Figure 6.9 and Tables 6.17, 6.18). Therefore, the cranial areas of the primate vertebral bodies cannot be used as an indicator of size of the body or locomotion differences. For example, the vervet monkey exhibits relatively low profile pattern for this feature than the baboon, which is also a pronograde. The profile pattern for baboon for this ratio is within the range of the profile patterns of the orthogrades and semi-orthogrades (Figure 6.9; Table 6.17). This means that the relative area of the cranial surface of the vertebral body is not influenced by similarities or differences in posture and locomotion. In a recent study, of the lumbar region of atelines and cebines, Johnson and Shapiro (1998) reached a similar conclusion.

b) Compression at the transitional Caudal Vertebral Surface

Unlike the cranial vertebral surface area, the caudal area has some noticeable difference in the various species, due to the different compression forces in some parts of the vertebral column. However, this difference is not statistically significant. The Relative caudal vertebral surface area (RCVS area) at the cervicothoracic (C-T) transitional vertebrae appears to be less affected by the mode of locomotion than the areas at the thoracolumbar (T-L) transitional vertebrae. (Figure 6.10; Table 6.19). The profile patterns for the ratios of the RCVS area at the C-T transition are low in all the primates in this study. At the T-L transition, the profile patterns for the areas are relatively higher than the profile patterns for the areas at the C-T transition, both within species and between species (Figure 6.10 and Table 6.19). This means that the vertebrae at the T-L transition are under relatively greater compression forces in all the primates. In humans in the study, the RCVS areas at the T-L transition show greater divergence. than corresponding areas in other primates. The divergence is possibly due to the unique human posture, which demands special features that help to balance and support the human body in the orthograde posture. One such feature of humans is the increasingly widening caudal diameter of the vertebral body, which should result in relatively larger caudal vertebral surface areas, toward the lumbar region.

iii) Forces at the transitional pedicles

a) The pedicle ratio and the pedicle load

An estimation of the pedicle ratio reflects the relative load passed (shunted) from the ventral aspect of the vertebral column through the pedicles to the dorsal aspect of the vertebral column, and vice versa (Pal and Routal, 1986; Pal, 1987).

In this study, the pedicle ratio and area were considered only at the C-T and T-L transitions, because of lack of time, as explained earlier. That the pronogrades in the study exhibit the highest value of this ratio at both the C-T and T-L transitions indicates that in pronograde locomotion the jumping and running generates relatively greater forces than in orthograde, semi-orthograde and suspensory locomotion. This may be understandable because in full pronograde locomotion there is probably more axial loading (Figure 2.6).

The profile pattern of the pedicle ratio is higher at the C-T than at the T-L transition in all the primates studied (Figure 6.11a; Table 6.21). Another functional explanation for this id by Davis (1961) who noted that the vertebral column is subjected to various forces, that travel forth and back along the vertebral column. Davis noted in humans that at the last lumbar vertebra, (L5) these forces do not pass directly to the sacrum (S1) via the body of the last lumbar. Davis (1961) suggested that, the forces are shunted and reach S1 via the pedicles of L5 (last lumar). This explains why the pedicles of the last lumbar vertebra are relatively large, and the caudal surface of the vertebral body of the last lumbar has a small facet area, in humans and other primates studied by (Shapiro 1991a, 1993).

There are various forces within the cervical region. Axial rotational forces are present due to the freedom of movement in the neck in addition to the other forces generated along the vertebral column. In the apes and humans, there are also compression forces from the relatively heavy head. Among the quadrupeds, especially the monkeys there are impacting forces from the active fore limbs. The limb activities and support for the head impact directly on the C-T transition, via muscles attaching the scapula and the head to the vertebral processes. For example rhomboideus minor has an origin on C7 and T1 (Moore, 1982). Therefore, the effect of the forces acting at the C-T transition cannot be underestimated.

The relatively low profile pattern for the pedicle ratio at V8 in the orang-utan may be a result of lack of active swinging movements in the forearm of this primate.

b) Relative Pedicle Area and the vertebral forces

Relative pedicle area (RP area) gives an indication of the cross-section (size) through the mid-pedicle position. It is therefore an indication of the strength of the forces experienced by the pedicles. The larger the area, the greater are the forces that act on or through the pedicle.

The similarity in the general profile patterns for the RP area, in the primates in this study is probably not surprising. The pedicles serve a similar function in all these species, namely receiving, resisting and possibly later transmitting axial and compression forces from the dorsal to the ventral aspects of the vertebral column, and vice versa. The pedicles must therefore be strong in all types of locomotion.

However, in the study, the profile pattern for RP area of the orthogrades is more closely related to the pattern for RP area of the pronogrades, than to the RP area of the semi-orthogrades (Figure 6.12; Tables 6.23 and 6.24). Under the section on the facet angles, it was argued that in primates full pronogrady and bipedalism share an agile and flexible vertebral column, present in monkeys and humans. The similarity in the profile patterns for RP area between the pronogrades and orthogrades again points to this relationship. This may be an indication that these two species probably experience similar forces passing to and from the pedicles during locomotion.

The dramatic increases in the profile patterns for the RP areas towards the lumbar region in all primates in the study is manifest of the increasing compression forces passing to the pedicles near the lumbar region. The pedicles at the C-T and T-L transitions appear to be well developed in order to deal with the situations at the vertebral column transitions.

Summary

I have speculated that axial forces are probably shunted from the vertebral bodies to the pedicles and vice versa, especially at the transitional junctions. The reason for this is not clear. Perhaps by the forces are buffered or checked by being shunted into the transitional pedicles. This may result in stable and co-ordinated movements of each region. The transitions therefore have well-developed pedicles, with relatively larger pedicles areas and larger pedicle ratios for the job.

The present study concurs with observations on the lumbar pedicles by Sanders (1990), Shapiro (1991a) and Ward (1991). Those authors point out that the functional form of the pedicles in primates is important and complex but not fully understood, and should therefore be researched further.

5) Size of the Vertebral Foramen and Modes of Locomotion

The profile patterns of the absolute and relative sizes of the vertebral foramen, and the approximate size of the spinal cord are similar in the primates studied except in the chimpanzee and baboon (p-value = 0.136), and orang-utan and baboon (p-value = 0.164; Table 6.26). This is one organ where the profile pattern for the absolute ratio is similar to the pattern for relative ratio in most the specimens (Tables 6.27, 6.28). This means that the vertebral foramen is not highly influenced by body size or locomotion or any other condition.

The approximate size of the spinal cord may be determined from the size of the vertebral foramen, except at the atlanto-axial region, where there is a cistern and towards the lower lumbosacral region, where the spinal cord is diminished. It must again be pointed out that the 'size' of the spinal cord referred to here is an estimate. It is a rough estimate because the spinal cord does not extend the full width, height and length of the vertebral canal. Other structures, such as, ligaments, blood vessels, nerve-roots, meninges and cerebral spinofluid also do occupy part of the vertebral canal. Estimates of the spinal cord may be necessary where only the remains of the vertebral column are available, for example, in the case of a fossil excavation or a rare species where only the skeleton is accessible.

The profile patterns for absolute and relative sizes of the vertebral foramen in this study indicate that the vertebral canal and therefore the Spinal cord, have cervical and lumbar enlargements. The canal is of a relatively smaller diameter in the rest of the thoracic region. The enlargements are relatively more sizeable in the orthograde human and the pronograde monkeys, probably because these primates actively engage their fore limbs and hind limbs, in manipulation and locomotion (Figure 6.14 and Table 6.27). To facilitate the activities of the limbs, there are large brachial and lumbar plexuses to provide an efficient nerve supply to the limbs. The roots of these plexuses arise in the regions of the spinal cord enlargements, which are reflected in the vertebral foramen size, at the cervical and lumbar enlargements.

MacLarnon (1987) observes that the size of the vertebral foramen and therefore of the spinal cord relative to body size appears to have little variation among modern primates. However, the profile patterns of the relative vertebral foramen areas in this study show two generally different patterns (Figure 6.14; Table 6.27). There is one pattern for the apes and another pattern for the vervet, baboon and human. The two patterns are not easy to explain in terms of the pronograde and orthograde postures or locomotive modes. The explanation may lie in the evolutionary origin, as Brown et al., (1985) observed. Those researchers noted that the spinal cord evolved to its present size before monkeys and humans separated from a common ancestor. This study, supports that view.

B) THE PRESACRAL VERTEBRAL (PSV) COUNTS AND THEIR PATTERNS

i) Human presacral vertebrae

Studies of vertebral counts and patterns of the human vertebral column by Allbrook (1955), Bornstein and Peterson (1966) and by Kaufman (1974) emphasised sexual, racial, ethnic or tribal and regional (geographical) variations. This was not the aim of this research. Although the sampling consisted of mainly indigenous populations from East, Central and Southern Africa the data are not analysed according to the ethnic background of the groups. The human data are treated as one species of primates and are examined side by side with other primate data. However, for the sake of general interest a summarised comparison with data from the above mentioned earlier studies follows. In the comparison, it must be born in mind that for various reasons statistics from ethnically defined samples cannot fairly be compared with data that encompass a non-ethnic sample. Further, it must be noted that various authors have used different methods in identifying the thoracic and lumbar vertebrae and determining the patterns. While Bornstein and Peterson (1966) used the presence of ribs to define the thoracic vertebrae, Kaufman (1974) and this study have applied changes in the zygapophyseal joints. Allbrook (1955) does not state how the vertebral categories have been defined. Therefore, there are noticeable differences between the results of this and the above studies.

Increases or decreases due to the thoracolisation, lumbarisation and sacralisation are also reported. The incidence of an additional lumbar vertebra was reported to be 6.9% by the current study (Table 6.37) and 4.6% by Allbrook (1955). Sacralisation of the lumbar was present in 3.9% of the study sample and 6.5% in the sample by Allbrook (1955). Reduction of the lumbar vertebrae associated with thoracolisation was observed in 2.7% in the tudy but Allbrook (1955) and Kaufman (1974) do not report on it. Comment on the significance of the differences in the above data cannot be made because the methods used by the different researchers varied, as stated earlier above.

The thoracic vertebrae in humans are sometimes reduced to 11 in association with lumbarisation of T12 to L1, making up six lumbar vertebrae without altering the presacral number of 24. Similar observation was reported in 5% humans by Schultz (1961), Schultz and Starus (1945), and in 18.9% of the human sample in the current study (Figure 6.37). It is not surprising that such a large difference exists between the results by this study and those of Schultz. The explanation for the difference may be in the methodology used. Conventionally the ribs were used to define the thoracic vertebrae and Schultz (1961) used the same method. When facet joints do change at an 11th thoracic vertebra, the vertebra behind it, namely the 12th "thoracic" is still carrying the twelfth pair of ribs, as it should normally. A vertebra of this nature is regarded as thoracic by the conventionalists because of the rib. In the current study, such a vertebra is regarded as a lumbar vertebra, having been lumbarised as L1 although it is carrying a rib, because the changes in the facet joints indicate clearly that it is a lumbar. Hence the difference in the results. This should be a reminder that whenever a reference or a comparison is made in vertebral numbers and patterns the method used should be clearly stated to avoid any misinterpretation that might arise.

ii) **Transitional elements and the presacral (PSV) patterns**

In this study the most common number of the PSV was found to be 23 in the semi-orthograde and suspensory apes, 26 in the pronograde monkeys and 24 in the orthograde human (Figure 6.36). It is important to again point out that the human sample was significantly larger than the samples of the monkeys and individual ape groups. The latter samples, especially the apes sample, were

Figure 7.1

THE POSITION OF THE THORACOLUMBAR TRANSITIONAL JOINT IN PRONOGRADE, ORTHOGRADE AND SEMIORTHOGRADE PRIMATES

Locomotion	Position of joint	Percentage	Species
Pronogrades	**V16**	3.8% Vervet 1.3% Baboon	MONKEYS
Pronogrades	**V17**	89.7% Vervet 96.1% Baboon 1.1% Human	HUMAN
All locomotory modes	**V18**	1.5% Vervet 2.6% Baboon 6.7% Orang 7.4% Gorilla 26.3% Human	MONKEYS APES AND HUMANS
Orthogrades Semiorthogrades and Arboreal suspension	**V19**	13.6% Chimp 29.6% Gorilla 70% Human 73.3% Orang	APES AND HUMANS
Orthogrades Semiorthogrades and Arboreal suspension	**V20**	86.4% Chimp 59.3% Gorilla 2.6% Human 20% Orang	
None	**V21**		NONE
Semiorthograde	**V22**	3.7% Gorilla	APES

small due to reasons beyond control, explained earlier under 'Statistical Methods'. Results should be viewed with this in background. The relative importance of the differences in the number of PSV is not clear. However, the relative length of the vertebral column influences the ability to perform ventrodorsal flexion and extension movements that are important in pronograde running. Pronogrades benefit from dorsiflexion movements of the trunk, during running and leaping.

The position of the cervicothoracic (C-T) joint transition is usually stable in all mammals, on the seventh cervical vertebra, except in matees and sloths (Aiello and Dean, 1990). In this study, only four specimens, (in the human sample), in the total sample of 449 primates demonstrated a PSV pattern where there were less than 7 cervical vertebrae. This indicates that variation in the primate cervical number is probably insignificant in a comparative sense. Variation in the number of thoracic and lumbar vertebrae is controlled both by the level at which the T-L joint is found, and by the relative total number of thoracic and lumbar vertebrae as can be seen in Table 6.37. The different T-L transitions in the primates studied are shown in Figure 7.1. The human orthogrades have the greatest variation in the PSV pattern (13 patterns). However, the large differences in the sample numbers should be taken into account. Otherwise, the multiple PSV patterns in humans could be an indication of a more versatile vertebral column.

In general, pronograde patterns have more lumbar vertebrae with a reduced thoracic set, while the semi-orthograde and the suspensory form reverse this pattern, with a long thoracic sequence and a short lumbar set. This is particularly evident in the gorilla where nearly 35% of the sample has 3 lumbar vertebrae, and another 35% have 4 vertebrae. The thoracic vertebrae are reduced to 8, 9 or 10 in pronograde, and they are 11, 12 or 13 in semi-orthograde and orthograde (Figure 6.37). The lumbar vertebrae are increased to 9, 10 or 11 in pronograde, 3, 4 or 5 in semi-orthograde and 4, 5 or 6 in orthograde.

The position of the T-L joint transition further emphasises this dichotomy (Figures 7.1 and 39 a, b). The pronograde transition is often cranial, at V17, while for the orthograde and the suspensory semi-orthograde, it is mainly at

V19. Although the human orthograde has more patterns, generally the patterns are similar to those of the other semi-orthograde, that often have a transition at V20, and have a slightly shoter lumbar set. An appreciable number of humans (18.9%) have six lumbar vertebrae. Three lumbar vertebrae were never present in the human sample. It may be valuable to investigate clinically the relationship of the increased and decreased lumbar vertebrae (lumbarisation, thoracalisation and sacralisation) to lower back pain in humans.

iii) The ribs, thoracolumbar joint and the stability of the trunk

Various parts of erector spinae insert onto the ribs that are in turn firmly articulated with the bodies and transverse processes of vertebrae via strong costovertebral and costotransverse ligaments. The action of the back muscle attachments on the ribs is usually underrated although it affects the movements of the vertebral column and trunk through these attachments (Figure 3.3). These attachments are therefore iimportant and should not be ignored in vertebral column movements.

The relationship between the T-L V joint and the ribs is also functionally important in the stability of the joint transition, vertebral column and the trunk as a whole by restriction of unnecessary movements. When the transitional T-L V joint occurs more cranial than usual, a rib-carrying "lumbar" vertebra comes in existence. In humans the rib pairs might be reduced to 11 (Figure 6.0 B), or increased to 13 or 14 (Figure 6.0 D, E) which creates an unusual relationship between the ribs and the transitional T-L V joint. (Figure 38 a, b). Stability here means helping to keep the T-L transition joint in place.

The T-L joint transition experiences axial and other forces or movements from the thoracic and lumbar regions concurrently. Although authors like Jenkins (1972) do not agree, general anatomical opinion and researchers such as Kashimoto et al., (1982) claim that in humans maximum sagittal flexion of the back, occurs at the transitional junction. Therefore, it is important that the transition is given as much stability as possible, since in some instances the forces might be considerable and directed in opposing planes or directions. The stability of the trunk and whole body is important in all types of locomotion.

Ribs are inserted onto the body of the sternum, costal arch and into the abdominal wall, and act jointly as the thoracic cage during the movements of the trunk and vertebral column. As such the ribs help to stabilise the vertebral column and the trunk against these forces. The ribs act as girders and anchors for the vertebral column. They also limit thoracic movements where the pelvic blades are high as in apes.

The stability of the vertebral column increases from A to F in Figure 6.0. As more rib-pairs overlap the T-L joint transition, that joint, and therefore the vertebral column, should achieve more stability. The reverse should be true when the last pair of ribs is located on or cranial to the T-L joint transition. The arrangement in 6.0 A is regarded as the most unstable of all the six shown in Figure 6.0, in that the T-L transitional joint is not reinforced by rib-girders, as in Figure 6.0 C to F).

Figure 6.0 F depicts the rib-T-L joint relationship as observed by this study in the terrestrial quadruped (baboon). The terrestrial quadruped (baboon) has possibly developed a comparatively most stable rib-T-L vertebral relationship in primates in this study. It is followed by the arboreal quadruped (vervet) in Figure 6.0 E. The arrangement commonly found in apes and humans in Figures 6.0 C to D is possibly relatively less stable. Thirteen or fourteen pairs of ribs in humans could therefore be advantageous, because they would provide more support to act as girders around the T-L joint transition. The presence of 11 pairs of ribs could be a liability as far as the stability of the human vertebral column is concerned.

The stability is even more important in the quadrupeds since standing or walking on four legs exerts ventrodorsal forces from the ground to the vertebral column (Figure 2.6). Without a strong relationship between the T-L joint transition and ribs, the vertebral column and spinal cord would possibly be in danger of being bent into a severe kyphosis, at the T-L joint. This explains why pattern A was very rare and B was not at all present in the pronogrades studied. The hard terrestrial substrate generates compressive impact forces that are not moderated as happens in the springy tree branches of the arboreal environment. Therefore, pattern F is more common in the terrestrial quadruped (baboon) which walk on hard terrain. The relationship between the T-L joint transition and the ribs is clearly linked to posture and mode of locomotion. Field functional studies were not carried out. Such studies are still necessary on this particular aspect, to backup these morphological observations.

Chapter 8

CONCLUSION

This study has concerned itself with the functional complexity of the vertebral column. It has shown that the thoracic vertebral column is generally and specifically adapted to the various forms of primate posture and locomotion. The adaptations have been observed in the morphometric and in the gross anatomical relations. There were no field observations carried out. The locomotive and postural behaviour is taken from literature. Some of the sample are few, particularly the apes. The results must therefore be seen against this background.

1) Thoracic Morphometric Patterns and Primate Locomotion

a) Pronograde (baboon and vervet) pattern

The maximum Spinous Process Leverage is found in the mid-thoracic region, where it is well placed to keep the trunk in extension. Pronogrades have a higher profile pattern for the Lattran ratio and therefore more lateral flexion or movements of the thoracic area, other anatomical factors allowing. Almost all the thoracic facet angles, in pronogrades, are generally greater than 110, degrees giving the highly active pronogrades a highly flexible vertebral column.

b) Semi-orthograde (gorilla, chimpanzee and orang-utan) pattern

The maximum Spinous Process Leverage and the longest spine coincide on V7/V8 in the gorilla and orang-utan because of the strong muscles attached to the processes of V7/V8, to move the active fore limb and large, heavy heads. The profile patterns for Lattran ratios are low and therefore the column is less flexible. The other primates in the study have fewer pairs of thoracic facet angles in excess of 110 degrees. This implies less flexibility of their thoracic vertebral column. The chimpanzees have a more human-like pattern of Spinous Leverage, probably because they use orthogrady more than the other apes in the study, and hence rely on a flexible vertebral column. The orang-utan is distinctive in having the fewest number of thoracic facets in excess of 110 degrees and low profile patterns for the Lattran ratio. This may explain why the orang-utan is the slowest of the apes.

c) Orthograde (human) pattern

In this pattern there is a clear separation of the position of the longest spinous process, at V13, from the position of the greatest Spinous Leverage, at V21. Therefore, contrary to the general anatomical opinion the longest spinous process does not provide the greatest or highest leverage to muscles. That means that the longest spinous process is always not the most important factor in lifting the trunk and maintaining the erect posture of the trunk. The position of the greatest leverage in the orthograde humans and chimpanzees is at the spinous process of V21 (equivalent to L2 in humans), while the longest spinous process is found on V13 (T6 in both chimpanzees and humans). In the semi-orthograde gorilla and suspensory orang-utan both the greatest leverage and the longest spinous process coincide at V7 (C7) or in terms of the thoracic vertebral column at V8 (T1). In the baboon, a terrestrial pronograde, the longest spinous process and the spinous process with the greatest leverage coincide at V14 (T7). In the vervet monkey that is an arboreal pronograde, the longest spinous process and the spinous process with the greatest leverage do not exactly occur on the same vertebra. However, the two occur on adjacent vertebrae. In the baboon, they are found in the mid-thoracic region.

The position of the greatest leverage on V21 (L2in the human) is probably reflected in the common complaint of lower-back pain. Human EMG studies and other clinical tests would be necessary to throw more light on this matter.

The similarity in the positions of the greatest leverage (V21) and the spinous process (V13) in humans and chimpanzees could possibly be explained by the fact that the chimpanzees use orthogrady more than the other apes in the study.

d) General Morphological Features

In general the profile patterns for the transverse process leverages tend to be similar in all the primates in this study. This means that the lateral flexion leverage (the Lattran ratio) and the extensor leverage (the Vdtran ratio) are equally important in all primate postures and locomotion. The Lattran stabilises the back in the mid-sagittal plane while the Vdtran keeps the back extended. The ability to extend the back is generally necessary for all primates, but it is essential in orthograde and semi-orthograde locomotion. Therefore, the profile pattern for the Lattran ratio is higher in orthogrades and semi-orthogrades than in pronogrades.

However, as far as the transverse process morphometric ratios are concerned the orang-utan tends to have generally lower values, probably because the slow suspensory form of locomotion in this species puts low demand on the vertebral column.

This study has also implied that the greater the number of large thoracic facet angles the more flexible and versatile the vertebral column is probably. Such a flexible vertebral column would be required for orthograde and pronograde locomotion. Thus out of the 12 pairs of thoracic anterior facet (prezygapophyseal) angles, there are respectively 2, 3, 4, 6, 9 and 12 pairs of anterior facet angles that are 110 degrees or above, in the orang-utan, gorilla, chimpanzee, human, baboon and vervet. Among the primates in the study, the orang-utan, with only two pairs of anterior thoracic facet angles above 110 degrees, is renowned for its caution slowness while the vervet, with all the twelve pairs above 110 degrees, is highly agile.

The area of the vertebral foramen in most regions may give a rough estimate of the size of the spinal cord. This is an estimate because the spinal cord does not fill all sides and the length of the vertebral canal. There is no significant difference in this measurement in the species studies. Therefore, the spinal cords are similar in size in the primates in this study. This similarity is difficult to explain. It might however imply that the vertebral column and the spinal cord evolved to reach their present sizes in these species before the species diverged from their common ancestor (Brown, et al., 1985). It is further noted that the relative size of the monkey vertebral foramina (and hence the spinal cord) is closer to the size in humans, than to the size of the other species in the study.

2) **Specific Transitional Morphometric Features**

The area of the cranial vertebral body and therefore the compressive forces increase caudally along the vertebral column in all the primates. The relative cranial area of the vertebral body is not influenced by species posture or locomotion. This means that not much can be concluded from the ratio of the area of the cranial vertebral body surface. The caudal vertebral body area is larger at the T-L transition than at the C-T transition, because the compression forces along the vertebral column increase in the caudal direction.

Among the apes and humans, the relative facet areas at the T-L transition (V19) are largest in humans. This might not be related to the orthograde posture of humans since the pronogrades in the study have much larger facet areas than humans at that particular region of the vertebral column, (Figure 6.6, Table 6.11).

The vertebrae at the transitions have well-developed facets and pedicles. The study proposes that the transitional elements being at crossroads of various opposite movements in the cervical, thoracic and lumbar regions, they must contain and neutralise such forces. For example, if movements were freely allowed to pass unchecked from the thoracic region into the lumbar region, there would be undesirable consequences forcing the lumbar region to behave like the thoracic. The increased facet areas, facet angles, pedicle ratio and pedicle area at the transitional vertebrae indicate that strong actions are taking place at the transitions. These strong actions maintain the stability of the vertebral column, and co-ordinated movements of the column. This means that the structures at the transitions must be well developed.

The facet area, pedicle ratios and pedicle areas are larger at the C-T transition than at the T-L transition. This is difficult explain since it indicates that the strain from the forces on the vertebral column is greater at the C-T than at the T-L transition. This should not be the case. However addition to the normal forces along the vertebral column, there are other forces at the C-T transition. Such forces are a result of the following:

a) Movements of the head and neck

b) Action of the muscles that attach to the processes of the vertebrae at the C-T transition, for the freely swinging hands

c) Impact of the forelimb with the ground that is transmitted to the C-T.

d) The vertebrae at C-T transition have small bodies, therefore the other structures on vertebrae in the C-T area should be well developed to reinforce and compansate for the small bodies.

3) Pre-sacral Vertebral Counts, the T-L Transition and Locomotion

The study has shown that there is a relation between different locomotive modes and the pre-sacral vertebral (PSV) patterns (Tables 6.36, 6.37, 6.38, and Figure 7.1). The pronogrades have relative short thoracic and relatively long lumbar regions. The semi-orthogrades, suspensory locomotor and orthogrades have relatively long thoracic and relatively short lumbar regions. In the apes a short lumbar region is advantageous in swinging by enabling the pelvis to swing forward easily. In the orthograde human, balancing the trunk on a long lumbar region would be difficult.

Ribs are involved in the vertebral column and trunk movements through their strong attachments onto vertebrae via costovertebral and costotransverse ligaments. The insertions of erectores spinae onto the ribs can therefore effectively influence the trunk and vertebral column movements through their attachments to the ribs. The part played by the ribs in the trunk movements should therefore not be underated.

Finally, a very important relation has been noted (in this study) between the pattern of the T-L transition and the ribs, in relation to the stability of the vertebral column, trunk and locomotion generally (Figure 6.0). Figure 6.0 shows that the ribs act as girders to anchor the vertebral column into the body wall. The anchorage and hence stability of the trunk improves, if there are more ribs caudally beyond the T-L transition. The orthograde and semi-orthograde pattern (Figure 6.0 C) is regarded as relatively unstable. The arboreal pronograde and terrestrial pronograde patterns, where the T-L transition has moved cranially into the protection of the ribcage, appear to be the most stable, (Figure 6.0 E, F). The terrestrial pronograde pattern offers the best stability and functionally it should provide maximum stability to the T-L transition.

The patterns seem to be related to both posture and the environment. An unstable T-L transition, as in Figure 6.0 A, would be prone to vertebral dislocation in quadrupedal locomotion because the T-L joint would possibly be protruded dorsally into a severe kyphosis by the impact from the limbs. Terrestrial quadrupeds would need a more stable structure than arboreal quadrupeds because the impact of the feet with the hard ground is greater than the impact on the swinging branches that can provide soft-landing by bending.

In humans moving the T-L transition joint cranially into the ribcage as in Figure 6.0 F would probably reinforce the transitional T-L transition joint. The pattern in Figure 6.0 D is similar to the situation in the human when a 13th rib-pair overlaps T12. Conversely, moving the T-L transition joint caudally outside the ribcage as in Figure 6.0 B, would probably undermine stability of the T-L joint transition and that of the vertebral column. This would be similar to the situation when the ribs are reduced to eleven pairs. Other implications of the above patterns may be clarified by clinical and or field investigations.

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