THORACIC AND LUMBAR VERTEBRAE OF AFRICAN HOMINIDS ANCIENT AND RECENT : MORPHOLOGICAL AND FUNCTIONAL ASPECTS WITH SPECIAL REFERENCE TO UPRIGHT POSTURE

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THORACIC AND LUMBAR VERTEBRAE OF AFRICAN HOMINIDS ANCIENT AND RECENT: MORPHOLOGICAL AND FUNCTIONAL ASPECTS WITH SPECIAL REFERENCE TO UPRIGHT POSTURE

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DECLARATION

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

M.M. Berode
(Name of candidate)

6th day of February, 1990.

ABSTRACT

This is a study of the morphological and functional aspects of *A. africanus* thoracic and lumbar vertebrae in comparison with those of modern human and anthropoid ape vertebrae. The purpose is to determine if any derived features in the morphology of hominids, as distinct from primitive features shared with non-hominids, were present and if so to what stage of attainment of full erectness such features point.

The major results of this study are as follows: (i) There is a difference in the configuration of the lumbar articular facets between pongids, on the one hand, and modern human and *A. africanus*, on the other hand. This difference suggests that similar stresses operate in these regions in the two hominid groups. (ii) Bony adaptation to a developed lumbar lordosis is present in *A. africanus*. (iii) Major agreement has been found in the relative dimensions of modern human and *A. africanus* lumbar vertebrae, in contrast to those of pongid vertebrae. This indicates probable correspondence in the pattern of weight transmission to the pelvis in modern humans and *A. africanus*. (iv) The decrease of inferior lumbar vertebral body area starts at higher levels in Sts 14 (an *A. africanus* partial skeleton) than in modern man, suggesting a longer curved lower lumbar region in *A. africanus*.

From these results it may be concluded that the trunk was probably carried in a fully erect posture in *A. africanus*. The bony adaptation thereto, however, may not have been fully developed as in modern man. It is proposed that, in Sts 14, the last two lumbar vertebrae were carried at an angle relative to each other and to the sacrum, in contrast to the abrupt change in direction between L5 and the sacrum in modern man.

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CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

Introduction

The first known *Australopithecus* fossil, the now famous Taung skull, was discovered in 1924. Since this discovery, the posture and locomotion of these early Plio-Pleistocene hominids have excited the attention of students of human evolution.

The attainment of the human upright posture and striding gait, and their morphological and physiological adaptations, are among the most striking characteristics that distinguish man from the anthropoid apes. The biomechanics of modern human uprightness are functionally correlated with form and proportion. Many of these features affect the skeleton and may be preserved in fossil bones from the body's weight-bearing and locomotor apparatus.

Dart (1925), from his "head-balancing index", inferred that *A. africanus* had assumed "an attitude appeciably more erect than that of modern anthropoids". This means that the hands were being freed from their locomotor function and that greater reliance was being placed upon the feet. Thirteen years later Broom (1938) announced the discovery of a fossil distal femur of *A. africanus* at Sterkfontein. From the morphology of this distal femur he suggested that *A. africanus* was probably a biped.

Today, as more and more australopithecine postcranial fossils become available the overwhelming preponderance of researchers accept that a bipedal form of locomotion was a fundamental part of the australopithecine behaviour (Broom and Robinson 1947; Mednick 1955; Heiple and Lovejoy 1971; Preuschoft 1971; Lovejoy and Heiple 1972; Robinson 1972; Zihlman and Hunter 1972; Leutenegger 1972; McHenry 1978;

Steudel 1978; Latimer *et al.* 1987; Susman and Brain 1988; Latimer and Lovejoy 1989). Controversy has however developed around the stage of evolutionary development of the australopithecine bipedal ability and their gait pattern. Since the upright bipedal posture is accompanied by major changes in the pelvis and lower limbs the studies have concentrated on these parts. Tobias (1982a) stated that uprightness of the modern human body has two aspects to it: erectness of the trunk (posture) and the two-footed or bipedal stance and gait (locomotion). In most of the studies on the pelvis and lower limbs only one aspect of uprightness, the bipedal stance and gait, is addressed. Only a few authors comment on the posture.

Review of Relevant Literature.

The picture of the australopithecine gait portrayed by studies on postcranial elements varies from one which is rather distinct from the gait of modern humans (e.g. Oxnard 1975; Ashton 1981; Stern and Susman 1983; Abitbol 1987a) to one in which the nature of australopithecine bipedality differed in no significant way from that of modern man (e.g. Dart 1958; McHenry 1975; Lovejoy *et al.* 1973).

When we look at the posture of the australopithecines as suggested by the skull, Dart (1925), after the first find of *A. africanus* at Taung, was able to infer that these creatures had assumed a more erect posture than extant apes. He based this on the values of a head-balancing index which expressed the centre of mass of the head in relation to the position of its occipital condyles. The index value in the fossil child skull differed from those in young apes and had moved in a human direction.

Clark (1950) developed Dart's idea and proposed a condylar-position index as an indication of the poise of the head and by inference, of overall bodily posture. This index expressed the length of the skull posterior to the point of maximum convexity of the condyles, as a percentage of the length anterior to this point. He found that the index value of an *A. africanus* adult skull (Sts 5 from Sterkfontein) exceeded the limits of variation in the anthropoid apes and concluded that it was reasonable to infer that the bodily posture of the australopithecines approximated that characteristic of *Homo sapiens*.

Ashton and Zuckerman (1951) remeasured Sts 5 but their method differed slightly from that of Clark (1950), in that they took the lowest point on the condyle as their landmark. They found that the value for the index in the *A. africanus* skull was within the upper end of the range for *Gorilla* skulls and well below that in modern human skulls. This led them to doubt that the position of the condyles in *A. africanus*, by itself, indicated an upright position.

Tobias (1967) discussed the studies of Le Gros Clark (1950) and Ashton and Zuckerman (1951). He concluded that the head-balancing index in *A. boisei* of Olduvai, which is intermediate between those of erect hominines and of obliquely quadrupedal or semi-erect pongids, suggests that the head was not as well balanced in *A. boisei* as in modern man but was better balanced than in pongids.

Adams and Moore (1975) reported that the condylar positional index values of an *A. africanus* (Sts 5) and an *A. boisei* skull casts were intermediate between extant great apes and man. The condylar reference point they used is described as an estimate of the centre of rotation rather than the condyles used in the studies described previously. They also measured the condylar angle, the values of which were within the ranges of modern man and above those for the apes. This angle is viewed as a good indicator of the inclination at which the vertebral column approaches the Frankfurt horizontal of the cranium. They concluded from the condylar angle that *Australopithecus* had an upright posture but that the conditions of head balance were intermediate between those of extant great apes and man and that *Australopithecus* was thus unlike any living members of the Hominoidea.

Conclusions from studies on the australopithecine postcranial skeletal elements are also equivocal. Clark (1955) examined features of the os coxae related to the mechanical requirements of posture and gait. From the total morphological pattern presented by these characters he inferred that the australopithecines had acquired the erect posture and gait distinctive of later Hominidae. However, in some features in which the australopithecine os coxae differ from that of modern man it is more primitive and this led him to conclude that the erect posture in *Australopithecus* had not developed to the degree of perfection found in modern man. Mednick (1955) analyzed the inner form of modern human and *Pan* pelvic bones by the splitline technique. In comparison with these two groups, he found the lack of a well developed iliac tubercle and pillar in the *Australopithecus* os coxae. From this he inferred that their balance was not as good as that of modern man and he came to the same conclusion as Clark (1955), namely: *Australopithecus* was still in process of adapting to orthograde progression.

Preuschoft (1971) examined the shapes of the femur, tibia and foot bones relative to the stresses upon them. From the anteriorly tilted position of the distal tibial joint surface and the distribution of the bony substance in the tibia's cross-section, he inferred that the body's centre of gravity was displaced far to the rear in the upright posture. Associated with the seemingly well developed arms, this led him to suggest that a lumbar lordosis, an indication of the fully developed erect posture, was present in the australopithecines. This is in agreement with the conclusion of Lovejoy *et al.* (1973) in a biomechanical analysis of the australopithecine pelvic and femoral samples available at that time. They stated that the total biomechanical pattern presented by these elements is as fully commensurate with erect striding as is that of modern man. On the other hand, Stern and Susman (1983) suggested a "bent-hip, bent-knee bipedality" for *A. afarensis*, in their extensive study of the postcranial elements of AL 288-1.

In the vertebral column Robinson (1972) confirmed the presence of a lumbar lordosis in *A. africanus* by investigations of the proportions of Sts 14 fossil vertebrae. He concluded that *A. africanus* was habitually erectly bipedal. Abitbol (1987a) measured the lumbosacral angle (LSA) in dogs, non-human primates and modern humans from lateral radiographs to determine the dorsal tilt of the sacrum. This angle is constructed by two lines; one is perpendicular to a line tangential to the body of L3 and the other is perpendicular to a line tangential to the bodies of S1 and S2. A line drawn over the superior body surface of S1 divides the LSA into a lumbar and a sacral angle. He found that when the lower limbs were flexed, these angles contribute equally to the LSA. In extension this angle is increased due to an increase in the lumbar angle. An LSA of thirty degrees is calculated in AL 288-1 from a sacral angle of fifteen degrees cited by personal communication from J. Stern. Abitbol (1987a) concluded that the relatively small LSA confirms the "primitive" nature of the pelvic girdle of *A. afarensis* and suggested an "imperfect" erect posture and "primitive" form of bipedal locomotion.

Pal and Routal (1986, 1987) showed that the lamina area and the distance between the posterior arch and the vertebral body increase in the modern human lumbar vertebrae from above downwards. These results suggest an increase in the load transmitted through the laminae of the lower lumbar vertebrae. They explain this increase by the presence of a lumbar lordosis in modern man. In the present study mensuration of the dimensions which reflect weight-bearing is extended to anthropoid ape and *A. africanus* vertebrae.

Scope and Purpose of Study

As a result of the recent discovery of an *A. africanus* partial vertebral column, and since the evidence of the fossil vertebrae has largely been neglected, the present study focuses on the thoracic and lumbar regions of the vertebral column. It is a comparative study of modern human, anthropoid ape and australopithecine vertebrae. The purposes of this study are to throw some light on the changes that could have occurred in the thoracic and lumbar regions of the vertebral column if man's fully extended stance and his erect striding gait had developed from the flexed oblique position and gait of the great apes; to determine whether any derived features in the morphology of hominid vertebrae, as distinct from primitive features shared in common with non-hominids, were present in the australopithecines; and to ascertain whether any such features of the vertebral column were already fully modern in form in the australopithecines, or at an intermediate stage in the attainment of the modern human pattern.

CHAPTER 2

THE MATERIAL

Contents of Chapter

A. The Modern Human Series

1. Present Study

The modern human material used in the present study comprises Zulu skeletons from the Raymond Dart Collection of African skeletons housed in the Department of Anatomy and Human Biology at the University of the Witwatersrand. This collection is built up from mainly the skeletons of cadavers used in the dissection halls. Since the cadaver material and, thus, the skeletal material are derived from mainly hospital sources, information as to the ethnic group, nationality, tribal group, sex, stated age and cause of death are known from the hospital records.

1.1 Source Population

The Zulu people represent not only South African Negroes, but also modern man in the present study. The Zulus have been chosen because they constitute the largest part of the South African Negro population. According to the 1985 population census, Zulus constitute 35,2% of the South African Negroes. This is 9,6% more than the second largest group, the Sothos, who form 25,6% of the South African Negroes.

1.2 Age and Sex Breakdown of the Series

The age of a patient given in the hospital records is not necessarily correct. Many of the South African Negroes are preliterate and hence uncertain of their date of birth. Further, if the patient is unable to give this information on admission to hospital, age is often estimated by hospital staff.

Three age groups, representing two decades each, are used in the present study. The first age group includes skeletons stated to be between twenty and forty years, the second age group between forty-one and sixty years and the third age group between sixty-one and eighty years.

TABLE 2.1

Distribution by Age and Sex of the Series of 120 Zulu Vertebral Columns examined by Non-metrical Techniques

Age in years	Males		Females		Males & Females	
	n	%	n	%	n	%
20 - 40	25	31,25	13	32,5	38	31,7
41 - 60	35	43,75	17	42,5	52	43,3
61 - 80	20	25,00	10	25,0	30	25,0
	80	100	40	100	120	100

n = Number of vertebral columns examined.

Non-metrical observations are recorded in 120 Zulu vertebral columns. Table 2.1 summarises the sex and stated age distribution of the vertebral columns on which the non-metrical observations and the number of presacral vertebrae are recorded. Of these skeletons 80 (66,7%) are male and 40 (33,3%) are female.

TABLE 2.2

Distribution by Age and Sex of the Series of 60 Zulu Vertebral Columns examined by Metrical Techniques

Age in years	Males n	Males %	Females n	Females %	Males plus Females n	Males plus Females %
20 - 40	10	33,3	12	40,0	22	36,7
41 - 60	10	33,3	11	36,7	21	35,0
61 - 80	10	33,3	7	23,3	17	28,3
	30	99,9	30	100	60	100

n = Number of vertebral columns examined.

Sixty vertebral columns with seven cervical, twelve thoracic and five lumbar vertebrae are examined by metrical techniques (Table 2.2). Thirty of these skeletons are male and thirty female.

2. Comparative Modern Human Series

The studies from which data are used for comparison with the Zulu data of the present study are listed in the next two tables. Many data on variation in the number of presacral vertebrae are available. Those used are listed chronologically in Table 2.3. The populations on which these studies were performed are also mentioned. These studies provide data on a total of 3582 vertebral columns in which the numbers of presacral vertebrae were studied.

TABLE 2.3

The Studies which form the Comparative Modern Human Series for the Variation in the Number of Presacral Vertebrae

Series	Author
French	Topinard (1877)*
German	Steinbach (1889)*
British	Paterson (1892)*
Florentine	Staderini (1894)*
Italian	Bianchi (1895)*
French	Ancel and Sencert (1902)*
American Negroes	Bardeen (1904)
Russian	Adolphi (1905)
Japanese	Hasebe (1913)
Swiss	Frey (1929)
Japanese	Nishi (1928)
Amer. Negroes and Amer. Whites	Lanier (1939)
East African Negroes	Allbrook (1955)
Amer. Negroes, Amer. Whites and Amerind	Bornstein and Peterson (1966)
S.A. Negroes and San	De Beer-Kaufman (1974)

* Cited by Bardeen (1904).

Table 2.4 lists the studies on modern human vertebrae for which comparative data are available on the non-metrical and metrical observations recorded in the present study. These studies are again listed chronologically for each character or set of characters.

TABLE 2.4

The Studies from which Data are used for Comparison with Non-metrical and Metrical Observations of the Present Study.

Observations	Authors
Regional distribution of presacral vertebrae.	Bardeen (1904) Frey (1929) De Beer-Kaufman (1974)
Foramen through the base of the transverse process.	Dwight (1902) Szawlowski (1902) Manner-Smith (1909) Bogduk (1981) Beers *et al.* (1984)
Curvature and orientation of lumbar superior articular facets.	Bogduk and Twomey (1987)
Configuration of lumbar articular facets.	Fawcett (1932)
Absolute and relative dimensions of the vertebral body.	Aeby (1878) Hasebe (1913) Martin (1928) Trotter (1929) Lanier (1939) Allbrook (1956)
Dimensions of the pedicles, transverse processes and vertebral arch in relation to the inferior vertebral body area.	Davis (1955; 1961) Pal and Routal (1986;1987)

B. The African and Asian Great Ape Series

1. Present Study

1.1 Sources

The available pongid skeletons in South Africa are scattered among universities and museums. Most of these skeletons are articulated and are used for display purposes. The Department of Anatomy and Human Biology at the Witwatersrand University houses the largest collection, consisting of nine skeletons. Two of these skeletons are of very young individuals. Articulated skeletons were unsuitable for use in the metrical part of this study since individual vertebrae are measured.

Table 2.5 enumerates the African and Asian great ape skeletons available for examination. A total of twenty skeletons were available for some of the non-metrical observations. Three *Gorilla*, two *Pan* and two *Pongo* skeletons were not articulated. Of these seven skeletons one *Gorilla* (Za 1311) and one *Pongo* (Za 1334) are juvenile, which leaves only five adult vertebral columns available for metrical examination. A third problem is the variation in the number of presacral vertebrae. One of the five unarticulated skeletons, a *Gorilla* (Za 1312) does not present the modal number of presacral vertebrae for these species.

Since the number of anthropoid apes available for metrical study is inadequately small, special methods of treating the samples are adopted to compare the means of small samples. For the purpose of this study, the value of the item in a sample which consists of one item, is regarded as the mean of the sample. Since no dispersion of data occurs in a sample which consists of one item no standard deviation can be calculated. For this reason the z-test, which does not use the standard deviation of the random sample, is designed to compare the mean of a random sample (which may consist of one or more values) with the mean of a population, and is used to determine whether the sample has been drawn from the same population or not (Allan, 1982).

1.2 Age and Sex Breakdown of the Series

The ages at death of the great apes used in the present study are unknown. Vertebral columns with the epiphyseal rings of the vertebrae not fused are regarded as juvenile and are thus excluded from the metrical part of the study.

Only two known female skeletons, one *Pan* and one *Pongo*, are available for the present study.

TABLE 2.5

The African and Asian Great Ape Vertebral Columns used in the Present Study

Catalogue number	Sex	Articulated	PSV	Juvenile
Gorilla gorilla				
Za 1311	Male	No	23	Yes
Za 1312	Male	No	23	No
Za 95	Male	No	24	No
TM$	Male	Yes	24	No
TM 16737	Male	Yes	24	No
ZM 37016	Male	Yes	24	No
Pan troglodytes				
Za 94	Male	No	24	No
Za 1071	Male	No	24	No
TM 16731	Male	Yes	25	No
Z - 159	Male	Yes	24	Yes
822+	Female	Yes	24	No
ZM 37007	Female	Yes	24	No
ZM 37008	Male	Yes	24	No
Pongo pygmaeus				
Za 1334	Male	No	23	Yes
Za 93	Female	No	23	No
TM 16732	Male	Yes	23	No
Z - 158	Male	Yes	23	Yes
DP	Male	Yes	23	No
307+	Male	Yes	23	No
ZM 33590	Male	Yes	23	No

$ No number.
Za = Department of Anatomy and Human Biology at the Witwatersrand University.
TM = Transvaal Museum.
Z = Department of Anatomy at the University of Cape Town.
DP = Zoology Department at the University of Pretoria.
\+ = Zoology Department at the University of the Witwatersrand.
ZM = South African Museum in Cape Town.
PSV = Presacral Vertebrae.

2. Comparative African and Asian Great Ape Series

Data from the literature are used for comparison with the results of the present study and also to enlarge the samples from which conclusions are drawn. The studies used are listed in Table 2.6 in chronological order under the character or set of characters available in each instance.

TABLE 2.6

The Comparative African and Asian Great Ape Series from the Literature.

Observations	Author
Numerical variation	Todd (1922) Schultz (1930) Schultz (1940) Schultz (1941) Randall (1944)
Metrical	Aeby (1878)

C. The Australopithecine Series

1. Present Study

1.1 Sources

Thirty-seven Plio-Pleistocene hominid vertebral elements were available for this study from the sites of Swartkrans and Sterkfontein.

Swartkrans

Four of the vertebral elements come from Swartkrans cave site, namely SK 854, SK 3981a, SK 3981b and SK 853. Robinson (1970, 1972) classified three of them, SK 854, SK 3981a and SK 3981b, as *Australopithecus robustus* vertebrae. (SK 854 is an axis and thus lies outside the field of the present study.) He classified the fourth specimen, SK 853, as a first lumbar vertebra of an immature individual of *Homo erectus*.

Sterkfontein

The other 33 fossil vertebrae have been yielded by Member 4 of the Sterkfontein Formation and emanate from three individuals. The first is Sts 14, a partial vertebral column of fifteen reasonably complete presacral vertebrae. The second individual is represented by Stw 8 which consists of four articulated lumbar vertebrae in different grades of completeness and Stw 41 which consists of two articulated vertebral bodies of the same individual. The third individual is represented *inter alia* by a newly recovered partial vertebral column comprising fifteen vertebral elements. Sts 14 is classified as *Australopithecus africanus* by Robinson (1972) and Tobias (1980). Stw 8 and Stw 41 are also *A. africanus* vertebrae (Tobias, 1980). Morphological study of the newly recovered partial skeleton started recently and no conclusions have been reached yet. Comparison of these new vertebral elements with the earlier discovered fossil vertebrae may lead the author to reach a conclusion as to the classification of the newly recovered specimens.

1.2 Age and Sex Breakdown of the Series

Fused epiphyseal rings indicate an anatomically mature individual. Among the fossil vertebrae described above only SK 853 shows fluted and crenulated margins of the vertebral body, which indicates that the epiphyseal rings were not fused at the time of death. Apart from this specimen the rest of these vertebrae belong to anatomically mature individuals.

A study on the pelvis of Sts 14 by Robinson (1972) provides reasonable grounds for supposing that these skeletal elements belonged to an adult female. The difference in the size of the Sts 14 vertebrae and the fragmentary Sts 73 led Robinson (1972) to suggest that the greater robustness of Sts 73 was a result of its belonging to a male individual. Sts 73 corresponds in size with Stw 8/41. Tobias (1980) points out and illustrates the great variation of vertebral size between the very small vertebrae of the presumptive female Sts 14 and the much larger vertebrae comprising Stw 8/41, which he suggests belonged to a male individual. The resemblance in size between Stw 8/41 and Stw 431 vertebrae suggests that the latter might also have belonged to a male. The newly recovered partial skeleton from Sterkfontein, Stw 431, includes the upper part of the sacrum and a partial os coxae, but they do not articulate to form a partial pelvis. A study of the sacrum and a study on the innominate should provide strong pointers to the sex of this individual and will likely confirm the identification of this partial skeleton as probably a male.

2. Comparative Australopithecine Series

Australopithecus afarensis vertebrae have been recovered from the Hadar Formation in Ethiopia. The AL 288-1 ("Lucy") partial skeleton includes fifteen vertebral elements. This specimen has been described in detail by Johanson *et al.* (1982). The vertebral elements are listed and described individually. Some of the vertebral fragments join to form a total of ten vertebral elements, seven thoracic vertebrae, two lumbar vertebrae and a sacrum. Johanson and White (1979) identified AL 288-1 as a female on the basis of the diminutive size of this partial skeleton. In a study on the pathology in Afar australopithecines, Cook *et al.* (1983) suggest that AL 288-1 (Lucy) was approaching middle age, comparable to the close of the third decade of life or the beginning of the fourth in modern humans. The fused ring epiphyses of the vertebrae, though with their margins still distinct, are among the skeletal age indicators used by these authors.

The AL 333-locality has produced nine isolated vertebrae. Johanson *et al.* (1980) first reported these skeletal elements. Cook *et al.* (1983), in a study on the pathology of the Afar australopithecines, list the vertebral elements of both AL 288 and AL 333. A short description accompanies each element listed. The AL 333 vertebral elements include both small and large specimens. This size difference is in keeping with the marked dimorphism noted by Johanson and White (1979) in other parts of the *A. afarensis* skeleton, and with the marked difference in the size of *A. africanus* vertebral elements yielded by Member 4 of the Sterkfontein formation. The AL 333 vertebral elements include anatomically immature specimens as indicated by incomplete fusion or absence of the ring epiphyses (Cook *et al.*, 1983). Unfortunately these specimens are not detailed in the table on the vertebral body dimensions in AL 333 specimens.

The descriptions of the *A. afarensis* vertebrae in the studies of Johanson *et al.* (1982) and Cook *et al.* (1983) are used for comparison in the non-metrical part of the present study. Both these studies also tabled the results of measurements taken on the fossil vertebrae. These data are used for comparison in the metrical part of the present study.

The comparative *A. afarensis* vertebral elements are listed in Table 2.7.

TABLE 2.7

The *A. afarensis* Vertebrae Recovered from the Hadar Formation in Ethiopia

Catalogue number	Identification by Johanson *et al.* (1982)	Identification by Cook *et al.* (1983)
AL 288		
- 1aa*	L3	L2
- 1ab	?	L3 or L4
- 1ac	T11	T11
- 1ad	T10	T10
- 1ae$	T5 or T6	T6
- 1af	?	T7
- 1ag	T8 or T9	T8
- 1ai	T12	T12
- 1am	T1/T2/T3/T4	T3 or T4
AL 333		
x - 12		T10
w - 8		S1 or L5
w - 14		C5/C6/C7 or T1/T2
51		T7/T8/T9
73		L3
81		T2
83		C1
101		C2
106		C5 or C6

* AK in Cook *et al.* (1983)
$ AH in Cook *et al.* (1983)

CHAPTER 3

METHODOLOGY AND TECHNIQUES

Contents of Chapter

A. Non-metrical Observations

1. Regional Distribution of Presacral Vertebrae

The numbers of vertebrae in the cervical, thoracic and lumbar regions, and the total number of presacral vertebrae, are determined and recorded in 120 Zulu and 20 anthropoid ape vertebral columns. To exclude vertebral columns with missing vertebrae, the vertebrae of each column are articulated serially and the articulations between, and the general conformation of, consecutive vertebrae are scrutinized. Where presacral vertebral elements are fused and the number of clearly complete vertebrae are distinguishable, this number of segments is recorded.

Presacral vertebrae are defined as those between the cranium and the sacrum. Problems of definition and categorisation arise at the craniocervical and, especially, the lumbosacral junctions.

At the craniocervical junction, Bornstein and Peterson (1966) have regarded the assimilation of an atlas as connoting the loss of a presacral vertebral element. In the present study, an atlas which is assimilated to the occipital bone, whether unilaterally or bilaterally, is nevertheless counted as a presacral vertebra. This usage accords with that of De Beer-Kaufman (1974) in her study on variation in the numbers of presacral vertebrae in Southern African Negroes.

An apparently last lumbar vertebra is regarded as sacral if one or both transverse processes are enlarged and developed so as to (i) form part of the sacro-iliac joint and (ii) take part in the formation of a sacral foramen. In the absence of the latter two criteria, simple fusion of the last lumbar and first sacral vertebral bodies is not regarded as complete sacralization and the last lumbar verte a is still classified as presacral. These criteria for a presacral and for a sacralized last lumbar vertebra correspond with those used by Lanier (1939, 1954), Schultz and Straus (1945), Bornstein and Peterson (1966) and De Beer-Kaufman (1974).

There exists a lack of uniformity in the literature concerning the characters which determine the regional allocation of a vertebra. Four different definitions of thoracic vertebrae are used in the literature. Bornstein and Peterson (1966) count a vertebra as thoracic if it bears a costal facet for articulation with a movable rib, unilaterally or bilaterally, and if it articulates with a vertebra which bears costal facets. Following Schultz (1930, 1940, 1941), Schultz and

Straus (1945) have regarded vertebrae at the regional junctional areas with unilateral costal facets as transitional and recorded them as half thoracic and half cervical or lumbar. De Beer-Kaufman (1974) regarded the presence of unilateral or bilateral costal facets, on the vertebral body of an apparently last cervical or first lumbar vertebra, as insufficient evidence to classify a vertebra as thoracic. Washburn and Buettner-Janusch (1952) suggest an alternative method for dividing the vertebrae. This uses the type of articular facets as indicators.

The well known groups of distinguishing characters of each vertebral region are used in the present study to allocate a vertebra to a specific region of the presacral spinal column. The definitions used to allocate a transitional vertebra which shows characters of two adjacent regions correspond with those used by De Beer-Kaufman (1974). Thus, an apparently last cervical or first lumbar vertebra which bears unilateral or bilateral costal facets on the vertebral body is not classified as thoracic. Where comparative data from Schultz's (1930, 1940, 1941) or Schultz's and Straus's (1945) study are used in the present study, transitional vertebrae are counted as cervical or lumbar.

2. Foramina through the Base of Lumbar Transverse Processes

Robinson (1972) explains the presence of a foramen through the base of the left transverse process of L1 in the Sts 14 partial column as due to the lack of complete fusion of the costal and transverse process elements. The lumbar vertebrae in the modern human and great ape samples are scrutinised and the presence, form, size and position of such foramina, are here recorded.

The foramina are classified according to the three groups identified by Manners-Smith (1909).

1. Costotransverse foramen

This foramen is situated between the costal and the transverse elements of the process and is thus bounded medially by the pedicle, anteriorly by the costal element and posteriorly by the transverse element (Fig. 3.1a).

2. Retrotransverse foramen

The foramen is situated close to the superior articular process behind the root of the transverse element. It is bounded posteriorly by a bony bar which passes from the accessory to the mamillary process (Fig. 3.1b).

3. A foramen at the junction of the accessory process and the inferior articular facet (Fig. 1.3c).

3. Curvature and Orientation of Lumbar Superior Articular Facets

Variation in the curvature and in the orientation of the lumbar superior articular facets plays an important role in the biomechanics of the articular facet joints. The shape of the facets in the transverse plane, when viewed from supero-anteriorly, is noted according to the following categories: Flat or planar, slightly curved and markedly curved. The latter group is subdivided into "C-shaped" and "J-shaped" facets according to Bogduk and Twomey (1987). The incidence of the different shapes is recorded at each lumbar level.

The orientation of a lumbar articular facet is defined as the angle made by the average plane of the joint with respect to the sagittal plane (Bogduk and Twomey, 1987). The average plane of a flat articular facet is represented by a line parallel to the facet while a line parallel to the chord of a curved facet represented the average plane of a curved facet.

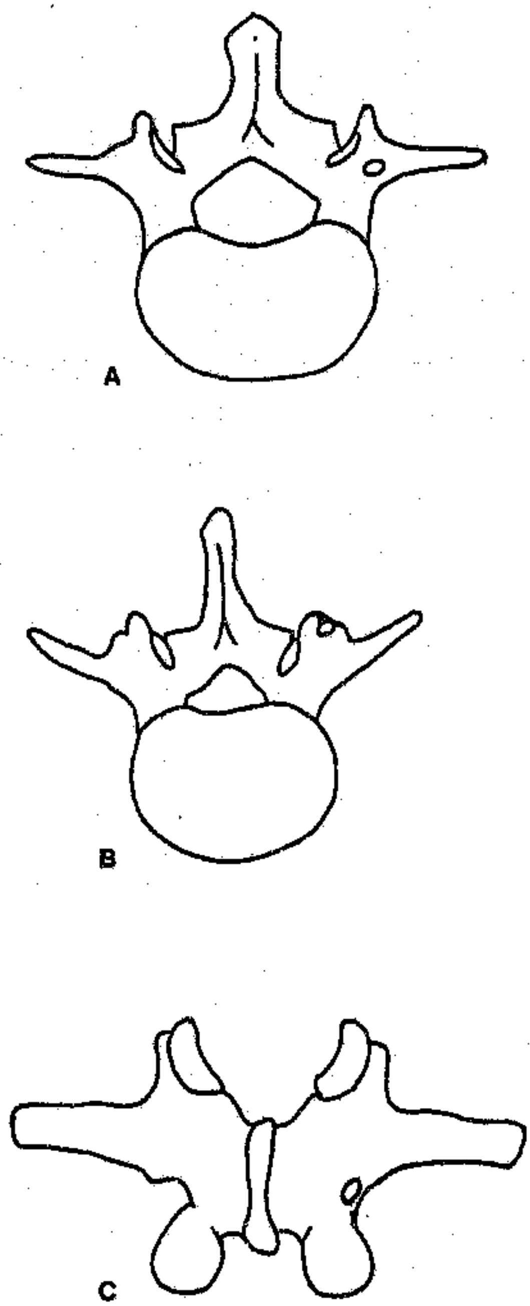

Fig. 3.1 Foramina through the Base of Lumbar Transverse Processes; Costotransverse (A), Retrotransverse (B) and a Foramen at the Junction of the Accessory and the Inferior Articular Facet (C).

The general tendencies of lumbar superior articular facet orientation are recorded in the modern human, pongid and australopithecine series.

4 Configuration of Lumbar Articular Facets

Fawcett (1932) states that in modern man the configuration of the articular facets viewed from posterior is specific for each lumbar vertebra and that, with the exception of the first two, individual lumbar vertebrae can be identified thereby. In the first two lumbar vertebrae the articular processes lie in the angles of a trapezium whose long axis is vertical. In the third these processes lie in the angles of a rectangle whose long sides are vertical and in the fourth the articular processes lie in a square figure. In the fifth lumbar vertebra these processes lie in the [illegible] of a rectangle whose long sides are horizontal; the [illegible]ular processes are however frequently further a[illegible] than the upper ones (Fig. 3.2).

In the present study these features are recorded and used to identify the modern human lumbar vertebrae and to articulate them in sequence. Special attention is paid to columns with six lumbar vertebrae and the configuration of the articular facets in these vertebrae is recorded. These features of the African and Asian great ape and of the australopithecine lumbar vertebrae are recorded and compared with those of modern man.

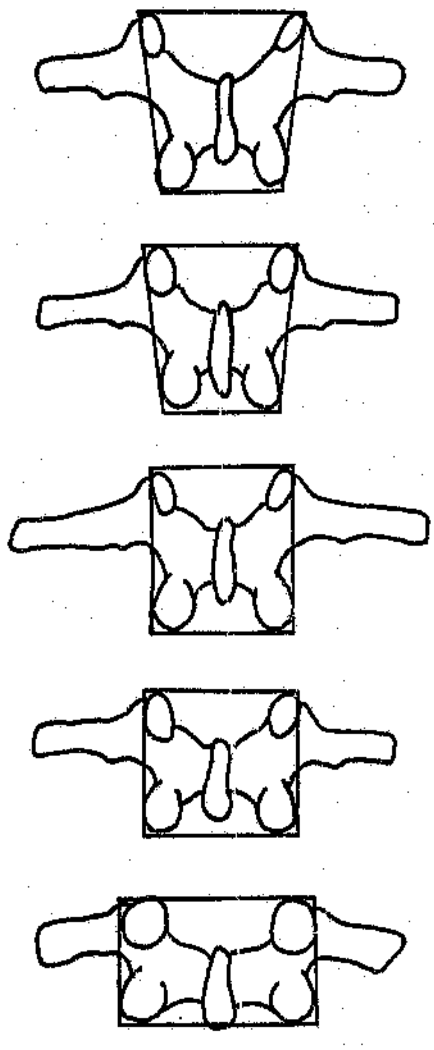

Fig. 3.2 The Configuration of the Articular Facets Viewed from Posterior (after Fawcett, 1932).

B. Metrical Techniques

1. Definitions of Measurements

The techniques used in the present study to measure various dimensions and angles of the thoracic and lumbar vertebrae are described here. In parentheses are abbreviated symbols of the author's devising except for measurements adopted as standard from Martin (1928). The Martin (M) numerical designation is given with these measurements. The names of the measurements as well as the abbreviated symbols are used in the text and tables.

All linear measurements taken by a Vernier caliper are recorded to the nearest tenth of a millimetre, while linear measurements taken by a co-ordinating caliper (which is calibrated in whole millimetres) are recorded to the nearest millimetre. In the text and tables of the comparative series these values are expressed in centimetres, since Pal and Routal (1986, 1987), the only authors who used these measurements (except for those of the pedicles), report their results in centimetres. Linear measurements taken by a spreading caliper calibrated in millimetres are expressed in millimetres, while angular measurements are expressed in degrees.

1.1 Anterior Vertical Height of the Vertebral Body (M1)

The anterior vertical height is measured by a spreading caliper in the midsagittal plane, between the superior and inferior epiphyseal rings, on the anterior aspect of the vertebral body (A in Fig. 3.3). This measurement is adopted as standard from Martin (1928) and is used by Aeby (1878), Hasebe (1913), Lanier (1939), Allbrook (1956), Ericksen (1976) and Berry *et al.* (1987).

The use of a spreading caliper eliminates difficulties which could occur when lipping is present. In the present study spinal columns which present no lipping are arbitrarily chosen for the metrical part of this study, to calculate the inferior surface area accurately.

1.2 Posterior Vertical Height of the Vertebral Body (M2)

The posterior vertical height is measured by a spreading caliper in the midsagittal plane, between the superior and the inferior epiphyseal rings, on the posterior aspect of the vertebral body (B in Fig. 3.3). This measurement is adopted as standard from Martin (1928) and is used by Aeby (1878), Hasebe (1913), Lanier (1939), Allbrook (1956), Ericksen (1976) and Berry *et al.* (1987).

Where erosions produced by the anterior internal vertebral venous plexus occur in the midsagittal plane, the caliper is placed a few millimetres to the side least affected, parallel with the midsagittal plane. Of the authors who have used this measurement, only Lanier (1939) mentions these erosions, but he does not propose how their effect on this measurement may be avoided.

1.3 Inferior Surface Area of the Vertebral Body (ia)

The area of the inferior surface of each thoracic and lumbar vertebral body is obtained by the paper graph method. The outline of the inferior surface is traced on graph paper with a hard pencil. The area is then calculated by counting the number of square millimetres included. Half and larger than half squares included in the outlined area are counted as whole ones while squares smaller than half are disregarded. The results are recorded in square centimetres for purposes of comparison with the data of Pal and Routal (1986, 1987), who have used the same method, and with the data of Davis (1961) who has used an architectural planimeter to measure the inferior surface area.

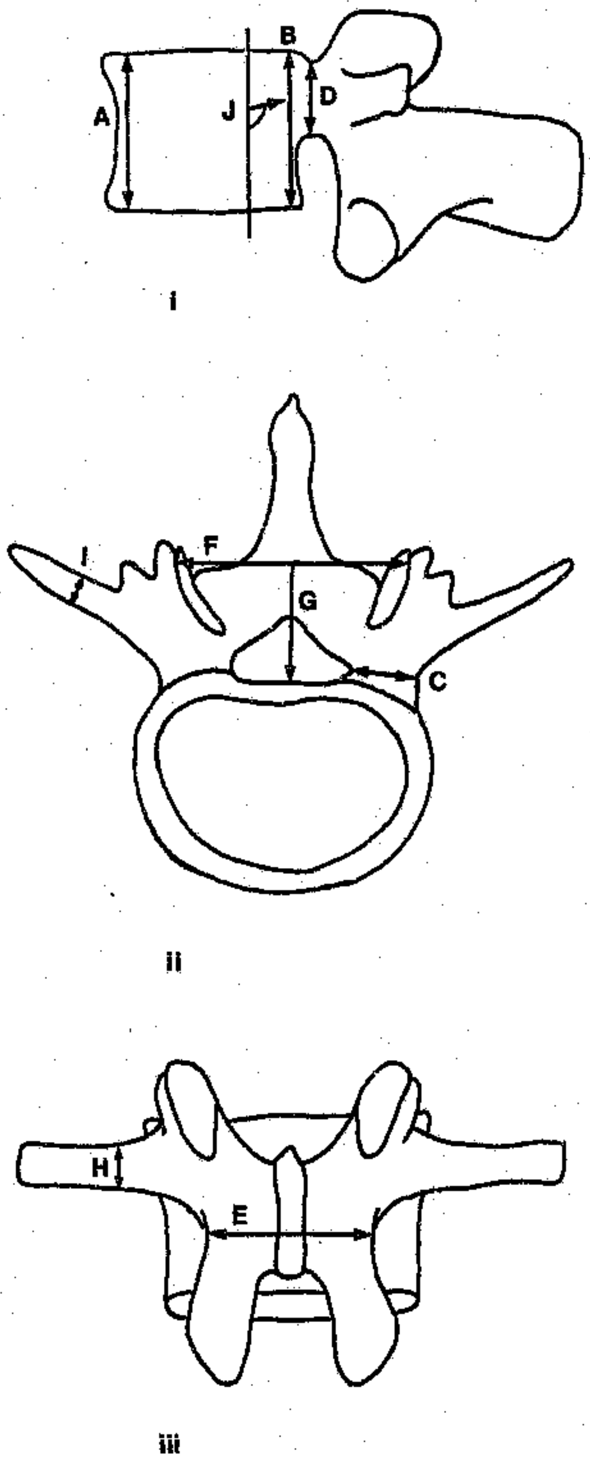

Fig. 3.3 Diagrams demonstrating measurements on (i) lateral, (ii) superior and (iii) posterior aspects of thoracic and lumbar vertebrae

In the australopithecine series it is frequently found that part of the inferior surface area of a fossil vertebra is broken away. In the light of the scantiness of fossil vertebrae it is arbitrarily accepted that, in a vertebra damaged on one side, the two sides would have been equal in size. The midsagittal plane of such a vertebra is placed on a line of the graph paper and the preserved half is traced on the paper. The calculated area of this half is then multiplied by two. The inferior areas of vertebrae calculated in this manner are pointed out in the tables.

The inferior surface is preferred to the superior surface because the former is more representative of compressive force transmission at that level, as each vertebra bears the weight of all that part of the body above it. In the great apes care is taken not to include the costal facet area of thoracic vertebrae in the inferior vertebral body surface area.

1.4 Least Pedicle Diameter (lped)

The least transverse diameter of each pedicle in each thoracic and lumbar vertebra is measured. According to Davis (1955), the diameter is read at the slenderest portion of the pedicle (C in Fig. 3.3). A Vernier caliper is used. Davis (1961), Pal and Routal (1986, 1987), Berry *et al.* (1987) and Zindrick *et al.* (1987) all measured this diameter. Zindrick *et al.* (1987) used computerized tomographic (CT) scans and roentgenograms as material.

1.5 Greatest Pedicle Diameter (gped)

The greatest vertical diameter of each pedicle in each thoracic and lumbar vertebra is measured, according to Davis (1955), at the slenderest portion of the pedicle (D in Fig. 3.3). A Vernier caliper is used. Davis (1961), Pal and Routal (1986, 1987), Berry *et al.* (1987) and Zindrick *et al.*

(1987) all measured this diameter. Zindrick *et al.* (1987) used computerized tomographic (CT) scans and roentgenograms as material.

1.6 Transverse Width of the Lamina (twl)

This diameter (E in Fig 3.3), which is the minimum width, is measured just above the inferior articular facets, as illustrated by Pal and Routal (1986). Care is taken to ensure that the termini of the diameter are in the same horizontal plane. A Vernier caliper is used.

1.7 Thickness of the Lamina (tlam)

The thickness of the lamina is measured in the sagittal plane above the inferior articular facets on both sides of each thoracic and lumbar vertebra. A Vernier caliper is used. Pal and Routal (1987) measured this diameter.

1.8 Maximum Distance between Articular Facets (mfd)

This distance is measured between the lateral borders of the articular facets, both superior and inferior (F in Fig 3.3) as shown by Pal and Routal (1986). Care is taken to ensure that the termini of the diameter are in the same horizontal plane. A Vernier caliper is used.

1.9 Midsagittal Distance between Articular Facets and the Vertebral Body (Mdfb)

This distance is measured by a co-ordinating caliper on the superior and inferior aspects of the vertebral body. The outer legs of the caliper are placed on the termini of the maximum distance between the lateral borders of the articular facets, while the third is extended to the posterior surface of the vertebral body (G in Fig 3.3). Care is taken to ensure that the termini for the diameter are in the same horizontal plane. Pal and Routal (1986) recorded this distance, but gave no description of the method used to obtain it.

1.10 Greatest Diameter of the Transverse Process (gtp)

The greatest vertical diameter of the transverse process, is measured at a point one-third of the distance from the lateral aspect of the superior articular facet to the tip of the transverse process (H in Fig. 3.3). The diameter is read on each of the left and right transverse processes. In the thoracic vertebrae the costal articular facet and most of the muscle attachments lie lateral to this point. In the lumbar vertebrae the buttress for the articular process terminates medial to this point and most of the muscular attachments lie laterally. The dimensions at this point are thus those best suited to mechanical analysis (Davis, 1961). A Vernier caliper is used to record these diameters.

In modern man the morphology of the transverse processes of T11 and T12 differs from that of the rest of the thoracic region. This measurement does not reflect the sizes of these processes in the same manner as in the rest of the thoracic region and is thus not recorded.

1.11 Least Diameter of the Transverse Process (ltp)

For the reasons mentioned above, the least sagittal diameters (I in Fig. 3.3) of both left and right transverse processes are measured at a point one-third of the distance the lateral aspect of the superior articular process to the tip of the transverse process as described by Davis (1961). A Vernier caliper is used to record these diameters.

In modern man the morphology of the transverse processes of T11 and T12 differs from that of the rest of the thoracic region. This measurement does not reflect the sizes of these processes in the same manner as in the rest of the thoracic region and is thus not recorded.

1.12 Body-Pedicle Angle (bpa)

This angle is measured by Pal and Routal (1986, 1987) in some presacral vertebrae. In the present study the body-pedicle angle is measured with a protractor on both sides of the vertebral body. The base line of a protractor is placed along the supero-inferior plane of the body at the base of the pedicle. A shortened reading arm of the protractor is placed along the axis through the midpoint of the pedicle and the angle is recorded in degrees (J in Fig. 3.3). To standardise this measurement the inferior body surface is held against a straight line and the base of the protractor along a line perpendicular to the first line. The last lumbar vertebra presents difficulties in that the inferior surface of this vertebra is frequently wedged anteroposteriorly. Therefore the superior articular surface of the last lumbar vertebra is used to measure this angle.

The fifth lumbar vertebra also presents a difficulty in that the transverse processes arise from the pedicles. Care is taken not to follow the slope of the transverse processes but to record the actual angle of the pedicle in relation to the vertebral body.

2. Definitions of Indices and Other Derived Metrical Characters

Traditionally the formulae for derived metrical characters are as follows:

$$\frac{a+b}{2} = \text{module}$$

$$a \times b = \text{area}$$

$$\frac{a}{b} \times 100 = \text{index}$$

In the light of this, the product represents an area. In the literature, Pal and Routal (1986, 1987) use the product of two means to represent an area but they call it an index (axb = index). They also use the ratio $\frac{\text{index}}{\text{measured area}}$.
In order to facilitate cross referencing I have retained these published usages of Pal and Routal (1986, 1987).

2.1 Vertical Vertebral Index

$$\frac{\text{Posterior Vertical Height (M2)}}{\text{Anterior Vertical Height (M1)}} \times \frac{100}{1}$$

A marked normal lordosis is one of the most distinctive features of the modern human vertebral column. The degree to which the anterior vertical height exceeds the posterior vertical height in several successive vertebrae will obviously be a factor in the formation of such a lordosis. Turner (1886), cited by Lanier (1939), studied the lumbar curve of the spinal column in several races of man. He devised this index, called the lumbar index, and proposed the following categories for purposes of comparison:

x - 97,9 = Kurtorachic (anteriorly convex lumbar column)
98 - 101,9 = Orthorachic (straight lumbar column)
102 - x = Koilorachic (anteriorly concave lumbar column)

In the same year Cunningham (1886), cited by Lanier (1939), used this index in his studies on the lumbar curve in man and apes. It was adopted as a standard by Martin (1928) who called it the "*Anterio-posteriorer Wirbelkörper - Index*". He also summarised the lumbar index values determined by various investigators. Lanier (1939) and Rose (1975) are among the authors who have used this index since.

Trotter (1929) uses the same formula and calculates the indices for the separate presacral regions. She also determines the mean indices for individual lumbar vertebrae in American White and Negro males. Following suit, the writer has calculated the indices of the individual thoracic and lumbar vertebrae in the present study to determine the degree of wedging in these vertebrae. The indices for the thoracic and the lumbar regions are also calculated and compared according to Turner's (1886) categories. Since the thoracic and lumbar vertebrae and both thoracic and lumbar regions are examined, the term "lumbar index" is not appropriate and the term "vertical vertebral index" is used here instead.

2.2 Total Percentage Inferior Surface Area Increase

$$\frac{\text{Inferior area of most caudal free vertebra} - \text{Inferior area of most cranial vertebra}}{\text{Inferior area of most cranial vertebra}} \times \frac{100}{1}$$

The total percentage increase in the inferior surface area is calculated according to this formula for T1 to L4, T1 to T12, and L1 to L4. L4 is used as the most caudal vertebra in the thoracolumbar and the lumbar series, since it is found that inferior surface area increases down to L4 and then decreases from L4 to L5 in modern man.

2.3 Average Percentage Inferior Surface Area Increase between Consecutive Vertebrae

$$\frac{\text{Total percentage inferior surface area increase}}{\text{Number of vertebrae involved}} \times \frac{100}{1}$$

The total percentage increase in a region is divided by the number of vertebrae included in that region to give the average percentage increase of the inferior surface area between consecutive vertebrae. This percentage increase is calculated for the thoracolumbar, the thoracic and the lumbar regions.

2.4 Mean Pedicle Index (lped x gped)

The pedicle index is the product of the greatest and the least pedicle diameters of each pedicle. This is determined as an approximate indicator of the size of the pedicle on both left and right sides. The mean of the index values for the two sides is then calculated to give the mean pedicle index for each vertebra. Davis (1961) and Pal and Routal (1986, 1987) have used this index.

2.5 Pedicle Index/Inferior Surface Area Ratio

There is a progressive increase in the size of the vertebral bodies from the cervical to the pelvic end. Hence, to compare the magnitudes of the pedicle indices at various levels, their ratios to body area are calculated (Pal and Routal, 1986, 1987).

2.6 Mean Lamina Index (twl x tlam)

This is the product of the transverse lamina width and the mean lamina thickness of both sides. The index is determined as an indicator of the cross-sectional area of the lamina which reflects the magnitude of the compressive force transmitted through it.

2.7 Lamina Index/Inferior Surface Area Ratio

There is a progressive increase in the size of the vertebral bodies from above downwards. To compare the magnitudes of the mean lamina index at various levels, their ratios to body area are thus calculated (Pal and Routal, 1986, 1987).

2.8 Mean Arch Index (mfd x mdfb)

The arch index, proposed by Pal and Routal (1986), is the product of the maximum distance between the articular facets and the sagittal distance between these articular facets and the vertebral body. This index indicates approximately the position of the articular facets in relation to the body. The mean of the superior and inferior indicial values is then calculated to give the mean arch index for each vertebra.

2.9 Arch Index/Inferior Area Ratio

The size of the vertebral bodies increases progressively from above downwards. To compare the magnitude of the approximate articular facet positions posterior to the body at various levels, their ratios to the body area are calculated (Pal and Routal, 1986, 1987).

2.10 Mean Transverse Process Index (gtp x ltp)

The transverse process index is the product of the greatest and the smallest diameters of the transverse process. This is determined as an indicator of the transverse process size on both left and right sides. The mean of the indices of the two sides is then calculated to give the mean transverse process index for each vertebra. Davis (1961) used this index.

2.11 Transverse Process Index/Inferior Body Area Ratio

To compare the transverse process index values at various levels, their ratios to the body area are calculated for each vertebra.

2.12 Mean Pedicle-Body Angle

The mean of the pedicle-body angles of the two sides is calculated to give the mean pedicle-body angle for each vertebra.

C. Statistical Methods

1. Metrical Features

The following statistics have been computed from the data for measurements taken on male and on female thoracic and lumbar vertebrae:

$$\text{Mean } (\bar{x}) = \frac{\Sigma x}{n}$$

Range = The difference between the uppermost and lowermost observed values

$$\text{Standard deviation } (s) = \sqrt{\frac{\Sigma(x - \bar{x})^2}{n - 1}}$$

Tests of significance

Student's t-Test is used to determine whether or not a significant difference exists between the means of two samples. The formula used is as follows:

$$t = \frac{\bar{x} - \bar{y}}{SED_{\bar{x} - \bar{y}}} \quad \text{where}$$

standard error of difference between sample means,

$$SED_{\bar{x} - \bar{y}} = \frac{(sx)^2}{\sqrt{\ } n_x} + \frac{(Sy)^2}{n_y}$$

The number of degrees of freedom i' obtained from the formula

$$(n_x - 1) + (n_y - 1)$$

If the calculated t-value occurs with a probability less than 5%, it is accepted that there is probably a significant difference between the means. If the calculated t-value occurs with a probability less than 1%, it is accepted that there is almost certainly a significant difference between the means.

This test is used mainly to compare the means of the Zulu male (n=30) and Zulu female (n=30) samples.

Since the number of anthropoid apes available for metrical study is inadequate, special methods of treating these samples are adopted for comparison. For the purpose of this study, in a sample which consists of one item, the value of that item is regarded as the mean of the sample. Since no dispersion of data occurs in a sample of one item, no standard deviation can be calculated. For this reason the z-test is used. This test is designed to compare the mean of a random sample (which may consist of one or more values) with the mean of a population, to determine whether the samples have been drawn from the same population or not (Allan, 1982).

$$z = \frac{\sqrt{\ } n_x \ (\bar{x} - \bar{y})}{S_x}$$

If the value of z is less than 1,96 it indicates that a significant difference between the sample mean and that of the population is not proved. If the value of z is greater than 1,96, there is probably a significant difference, while a z-value greater than 2,58 indicates an almost certainly significant differénce between the values of the means.

2. Non-Metrical Features

The weighted mean is used where several means which are based on different numbers of observations were to be averaged, to impart relatively more importance to the samples with larger numbers of observations.

A weighted mean is defined by:

$$Y_w = \frac{\Sigma W_i \; Y_i}{\Sigma W_i}$$

The Chi-square test is used to test the significance of intergroup and sex differences of the non-metrical features. The following formula is used:

$$X^2 = \Sigma \frac{(O - E)^2}{E}$$

Where O = Observed frequency

E = Expected frequency

The 1% level of significance ($P<0,01$) is accepted as almost certainly significant. Yates' correction is applied in the calculation of the chi-square test in all cases where the number of degrees of freedom is one, where the frequency in any cell is less than five or where the sample number is fewer than 30.

CHAPTER 4

THE PRELIMINARY DESCRIPTION OF EARLY HOMINID VERTEBRAE FROM STERKFONTEIN AND SWARTKRANS.

A. Sterkfontein

1. Sts 14: The skeletal elements of a partial skeleton which were found in close association are grouped together as Sts 14. These skeletal elements include the proximal part of a femur, ribs, an almost complete pelvis and a partial vertebral column. The vertebrae represent the entire lumbar region and most of the thoracic region in sequence. The descriptions of the Sts 14 fossil vertebrae follow in sequence, as determined by the author.

Robinson (1972) does not use the catalogue numbers in his discussion of the Sts 14 thoracic vertebrae and describes only the last two thoracic vertebrae. He does mention that the thi.d and ninth last thoracic vertebrae are represented by vertebral bodies alone (op.cit., p 106). The sequence as determined by the author differs from the Transvaal Museum catalogue sequence in that Sts 14*l* and Sts 14*i* change places. The vertebrae of Sts 14 are described cranio-caudally.

Sts 14*p* (Fig. 4.1) is a small thoracic vertebral body with the upper part of the left pedicle preserved. This helps to orientate the vertebral body. It is identified as the ninth from the last thoracic vertebra. The inferior epiphyseal ring and a small portion of the superior surface of this vertebral body are missing.

Sts 14*n* (Fig. 4.2) is a small fragile vertebra which follows in sequence and is thus the eighth last thoracic vertebra. Three pieces have been united to form this vertebra. The vertebral body has suffered slight abrasion on the anterior

Fig. 4.1 The Superior Aspect of Sts 14*p*, Identified as an *A. africanus* Ninth Last Thoracic Vertebra (Lifesize)

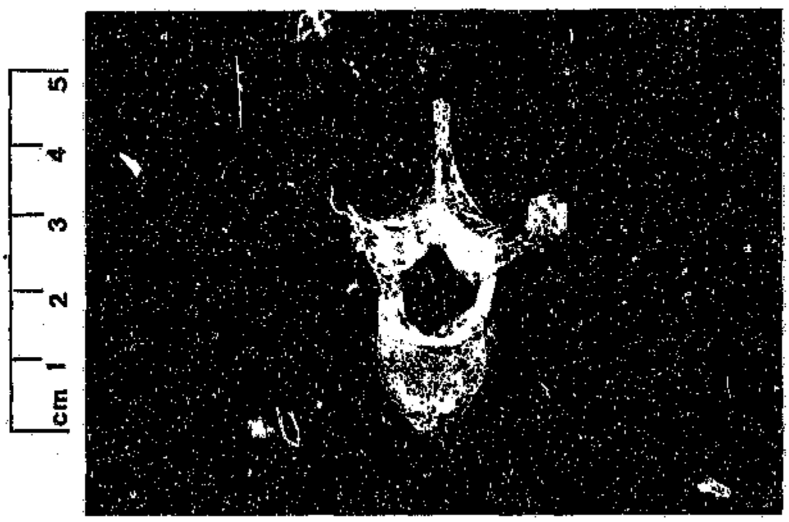

Fig. 4.2 The Superior Aspect of Sts 14*a*, Identified as an *A. africanus* Eighth Last Thoracic Vertebra (Lifesize)

and right side of the inferior surface. The left pedicle is absent and the superior articular facets, as well as the distal part of the spinous process, and right transverse process are broken away. Superior and inferior costal facets are present on the vertebral body. The left transverse process bears a costal facet on the anterior aspect of the distal end: this facet faces upwards and laterally to the process.

Sts 14*m* (Fig. 4.3) is the next thoracic vertebra i.e. the seventh from the last thoracic vertebra. This vertebra is well preserved although the superolateral border of the vertebral body is missing on the left side. The tip of the spinous process and the right transverse process are broken away. The vertebral body and the left transverse process bear costal facets which resemble those described for Sts 14*n*.

Sts 14*i* (Fig. 4.4) is identified by the present author as the next thoracic vertebra i.e. the sixth last. It is an almost complete thoracic vertebra, only the anterior part of the superior epiphyseal ring, the posterior part of the inferior epiphyseal ring, the tip of the right transverse process and the tip of the spinous process being absent. Superior and inferior demifacets are present on both sides of the vertebral body, while the transverse process bears a distinct costal facet which faces anterolaterally.

Sts 14*k* (Fig. 4.5) is the next thoracic vertebra, i.e. the fifth last. This vertebra is well preserved, save only that part of the inferior epiphyseal ring, most of the right transverse process and most of the spinous process are absent. Superior and inferior demifacets are present on the vertebral body and the left transverse process has a costal facet, which faces upwards and lateralwards, on the anterior aspect of the tip of the process.

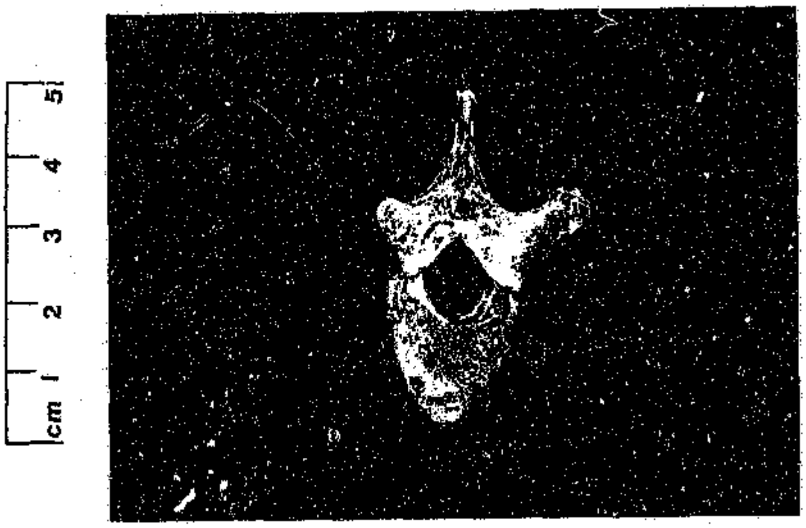

Fig. 4.3 The Superior Aspect of Sts 14*m*, Identified as an *A. africanus* Seventh Last Thoracic Vertebra (Lifesize)

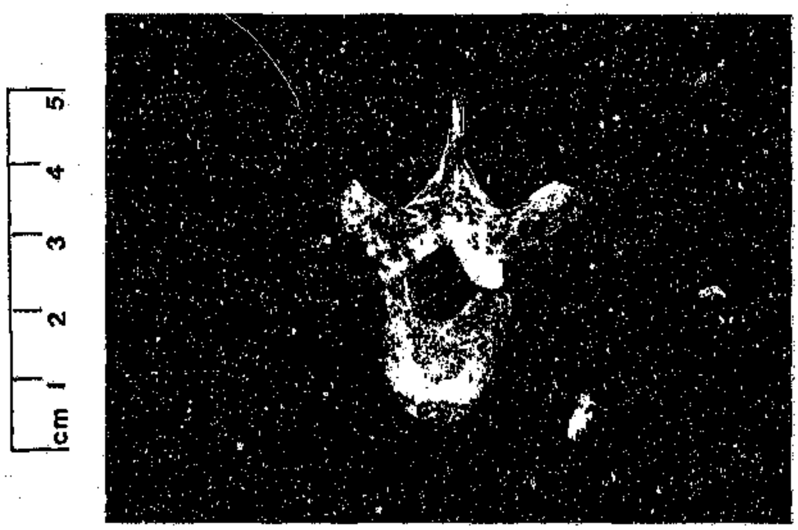

Fig. 4.4 The Superior Aspect of Sts 14*i*, Identified as an *A. africanus* Sixth Last Thoracic Vertebra (Lifesize)

Sts 14*l* (Fig. 4.6) is a nearly complete thoracic vertebra on which the catalogue number is not legible. From the Transvaal Museum catalogue it is evident that it must be Sts 14*l*. The author is of the opinion that this is the next vertebra in sequence i.e. the fourth last thoracic, and that it is thus situated between Sts 14*o* and Sts 14*k*. The posterior and left parts of the superior epiphyseal ring are the only missing parts of this vertebra. The vertebral body bears, on the right side, superior and inferior demifacets. On the left side are a superior demifacet and a very small piece of an inferior costal facet. The transverse processes bear anterolaterally facing costal facets.

Sts 14*o* (Fig. 4.7) is the larger of the two thoracic vertebral bodies and seems to follow on Sts 14*l*, that is, it represents the third last thoracic vertebra. If it is accepted that the inferior surface of the vertebral body is larger than the superior surface, it is possible to determine the superior and inferior surfaces of this vertebral body. The anterior half of the inferior epiphyseal ring is missing.

Sts 14*h* (Fig. 4.8) is the next thoracic vertebra and is identified here as the second last. It is almost complete. The superior and anterior aspects of the vertebral body are damaged and the inferior epiphyseal ring is missing. While the left transverse process is broken away lateral to its base, the right transverse process bears a costal facet on the upper part of its distal end. The costal facet for the tubercle of the rib faces supero-anteriorly. Costal facets for the heads of ribs are placed high on the pedicles and the posterior superolateral aspects of the vertebral body. A whole facet is present on the left side while a superior demifacet is present on the right side.

Sts 14*g* (Fig. 4.9) is an almost complete vertebra which shows all the characteristics of a last thoracic vertebra. The vertebral body has suffered mild abrasion on the anterior

Fig. 4.5 The Superior Aspect of Sts 14*k*, Identified as an *A. africanus* Fifth Last Thoracic Vertebra (Lifesize)

Fig. 4.6 The Superior Aspect of Sts 14*l*, Identified as an *A. africanus* Fourth Last Thoracic Vertebra (Lifesize)

aspect and the anterior parts of the superior and inferior epiphyseal rings are missing. Both pedicles are complete and bear costal facets for the head of a rib. The articular facets, transverse processes, laminae and spinous process are all well preserved.

The superior articular facets are typically thoracic in shape and orientation, while the inferior articular facets are typically lumbar in shape and orientation. The costal facets are placed partly on the pedicles and partly on the vertebral body. On the left side, the costal facet is smaller and is placed higher up on the pedicle than on the right side. These facets face anterolaterally and inferiorly. The transverse processes bear no costal facets and consist of three tubercles each. The left transverse process consists of a superior, an inferior and a small lateral process. On the right is a lateral and an inferior tubercle with a much larger superior tubercle medial to them. The spinous process expands at the tip.

Sts 14f (Figs. 4.10 and 7.1) is the next vertebra. It presents lumbar characteristics and is regarded by Robinson (1972) and by the present author as a first lumbar vertebra, even though it has an articular structure for a lumbar rib on the left side. The inferior surface of the vertebral body is almost complete except for slight abrasion on the right anterolateral aspect. The superior epiphyseal ring has been worn away and the right lateral side of the body has suffered mild abrasion. On the left side the pedicle, superior articular facet and transverse process are complete. Most of the inferior articular facet is reconstructed while the lamina is complete. On the right side the pedicle and superior articular facet are complete. No transverse process is present on this side. Instead, a blunt projection bearing an articular facet occurs on the pedicle, in accordance with the origin of the transverse process on the left side. The oval articular facet faces postero-inferiorly and is convex from posterosuperiorly to antero-inferiorly. Behind this

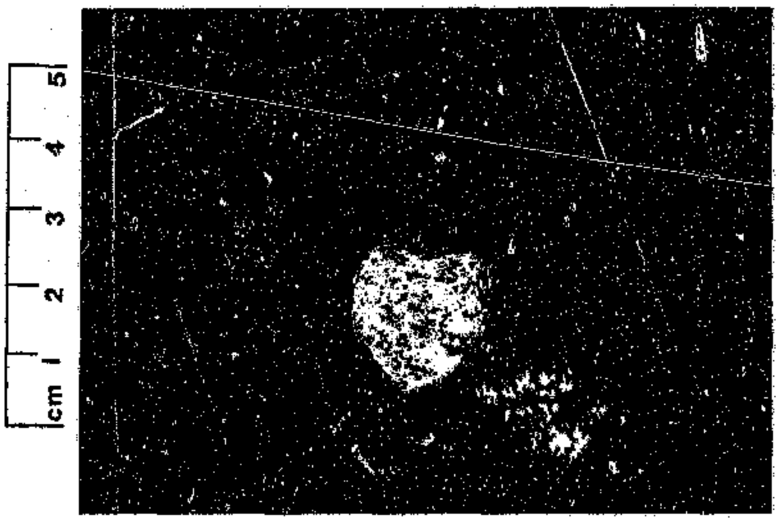

Fig. 4.7 The Superior Aspect of Sts 14*a*, Identified as an *A. africanus* Third Last Thoracic Vertebra (Lifesize)

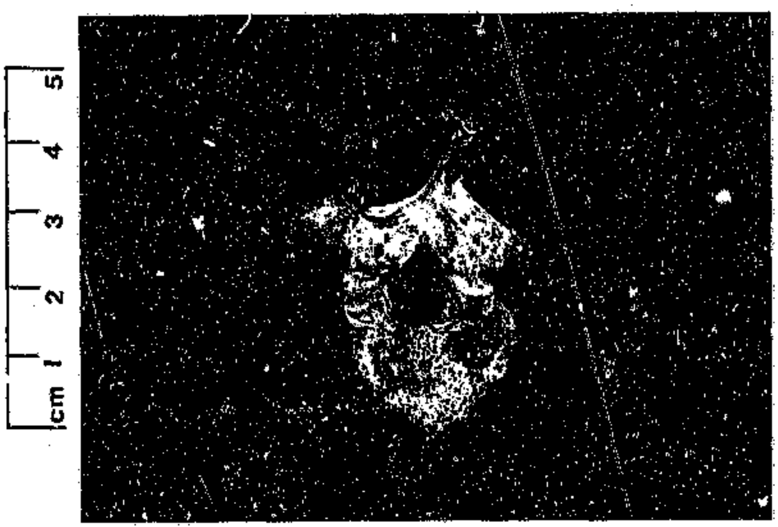

Fig. 4.8 The Superior Aspect of Sts 14*b*, Identified as an *A. africanus* Second Last Thoracic Vertebra (Lifesize)

articular facet-bearing process, another small process projects laterally from the pedicle. The lamina and right inferior articular facet and most of the spinous process are present. Reconstruction has completed the right lamina and the spinous process.

The articular facets are lumbar in shape and position. Viewed from behind, the centroids of the four articular facets connect to form a rectangle. The transverse process is angled more posteriorly than in the rest of the lumbar region and a small foramen runs vertically through the base of the transverse process, just lateral to the pedicle.

Sts 14*e* (Fig. 4.11) is the next lumbar vertebra with the most complete vertebral body thus far. It is classified as a second lumbar vertebra. The vertebral body has suffered only slight abrasion on the right superolateral margin. The pedicles and the right superior articular facet are complete. Only the tip and a small portion at the root of the right transverse process are absent, while part of the left superior articular facet and a part of the root of the left transverse process are missing. These missing parts, as well as the upper portion of the left lamina, the tip and the upper portion of the spinous process, most of the left and a part of the right inferior articular facet have all been reconstructed previously.

The mamillary processes of this vertebra are smaller than those of the previous vertebra but still distinct. Viewed from behind the centroids of the four articular facets connect to form a rectangle. The neural foramen is almost circular.

Sts 14*d* (Fig. 4.12) is the next lumbar vertebra i.e. the third. The vertebral body is complete save for mild abrasion on the right side. The pedicles, superior and inferior articular facets and the laminae are all complete. On the

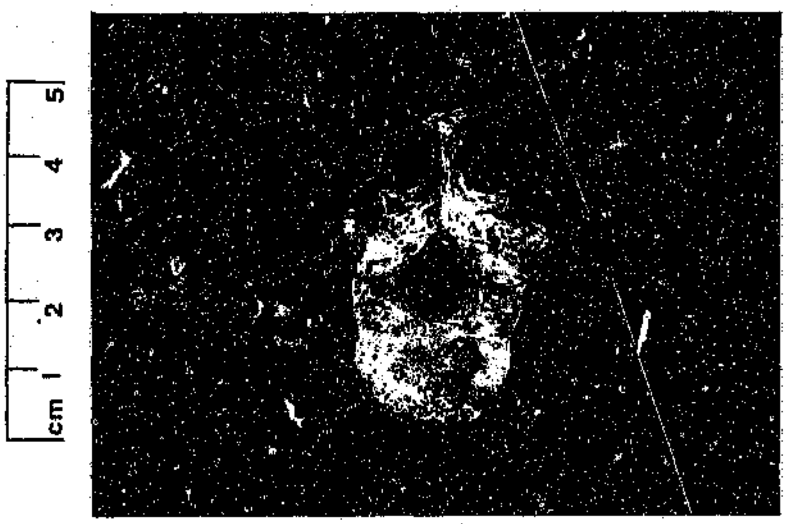

Fig. 4.9 The Superior Aspect of Sts 14*g*, Identified as an *A. africanus* Last Thoracic Vertebra (Lifesize)

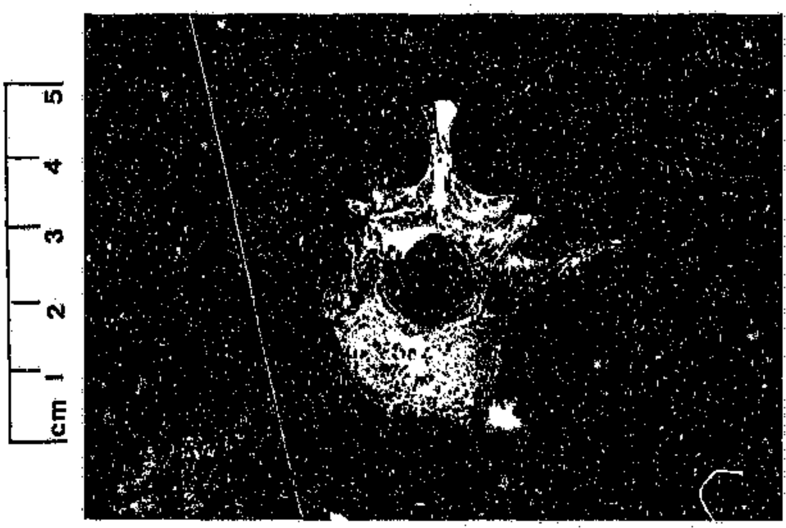

Fig. 4.10 The Superior Aspect of Sts 14*f*, Identified as an *A. africanus* First Lumbar Vertebra (Lifesize)

left projects a long upwards curving transverse process, while the right transverse process is broken away just lateral to its base. The spinous process is complete save for its tip.

This vertebra presents the longest transverse process of the lumbar region. The superior and inferior surfaces of the vertebral body are parallel and the lateral aspects markedly concave. Viewed from behind, the centroids of the four articular facets connect to form an almost perfect square. Clearly distinct mamillary processes project posteriorly from the superior articular facets and an accessory process is present on the left transverse process, near its base.

Sts 14*c* (Fig. 4.13) is the next lumbar vertebra, and is identified as a fourth lumbar. The left side of the vertebral body is preserved and both pedicles are complete. The right transverse process is broken away lateral to its root, while the left transverse process is complete save for its tip. The right superior articular facet, most of the left superior articular facet, the laminae, the root of the spinous process, the right inferior articular facet and most of the left inferior articular facet are preserved. The vertebra's missing parts have been reconstructed.

The left transverse process is long and curves cranially while the neural foramen is almost circular. Viewed from posterior, the centroids of the four articular facets connect to form an almost perfect square. These are all characteristics associated with the second and third last lumbar vertebrae in modern man.

Sts 14*b* (Fig. 4.14) is the second last lumbar vertebra. This vertebra has suffered extensive abrasion on the right side. On this side the vertebral body is weathered away increasingly from superior to inferior, with the result that a large part of the inferior surface is also absent. Most of the pedicle, the transverse process and the inferior articular

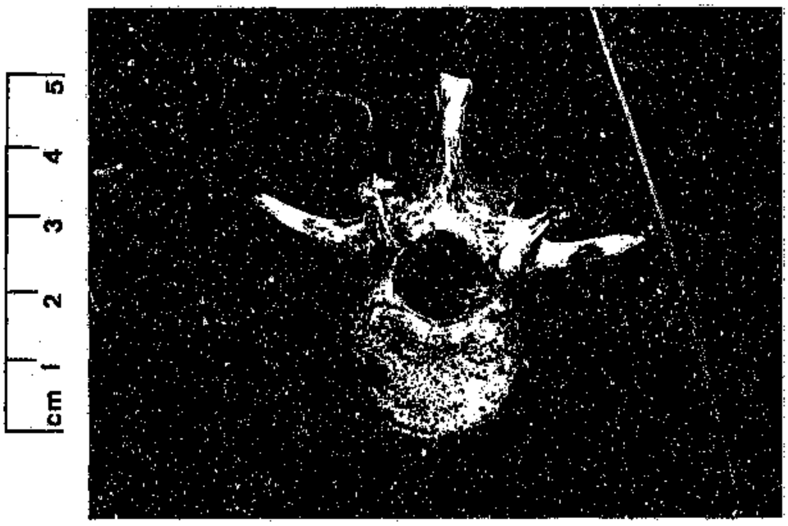

Fig. 4.11 The Superior Aspect of Sts 14*e*, Identified as an *A. africanus* Second Lumbar Vertebra (Lifesize)

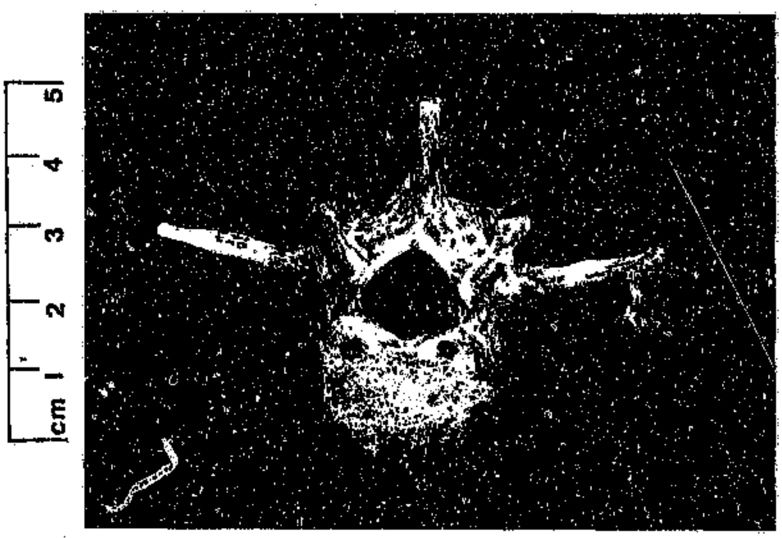

Fig. 4.12 The Superior Aspect of Sts 14*d*, Identified as an *A. africanus* Third Lumbar Vertebra (Lifesize)

facet have been reconstructed. The left side is complete except for the distal part of the transverse process. The upper portions of the laminae and the root of the spinous process are preserved. Distinct mamillary processes project posteriorly from the superior articular facets.

Sts 14*a* (Fig. 4.15) is the last lumbar vertebra. The inferior surface of the vertebral body is complete except for a small part on the right lateral border. Most of the superior surface of the vertebral body has been reconstructed. The right pedicle is almost complete but most of the left pedicle is missing, but has been reconstructed. The superior articular facets and the transverse processes are well preserved, while the rest of the vertebra (the laminae, inferior articular facets and the spinous process) is missing and has been reconstructed. The shape and position of the inferior articular facets have been reconstructed, with the superior articular facets of the sacral piece (Sts 14*g*) as guidelines. These reconstructions have been made previously.

The inferior area of the vertebral body is conspicuously smaller than the superior area. The pedicles are strong and the transverse processes are much more robust than in the rest of the lumbar vertebrae. Near their bases, each of the transverse processes presents a prominent tubercle on the inferior aspect which forms a substantial part of each process. The inferior articular facets are, as in modern man, situated further apart than the superior articular facets.

2. Sts 73 (Fig. 4.16) consists of an isolated, almost complete, vertebral body and parts of both pedicles. The shape of the vertebral body indicates that the vertebra may have been a lower thoracic or an upper lumbar vertebra. The lateral aspects of the body and pedicles are not preserved well enough to claim the presence or absence of costal facets with certainty. The right pedicle presents an ill-defined shallow oval hollow which seems to be an artefact resulting from a missing piece of bone, rather than a costal

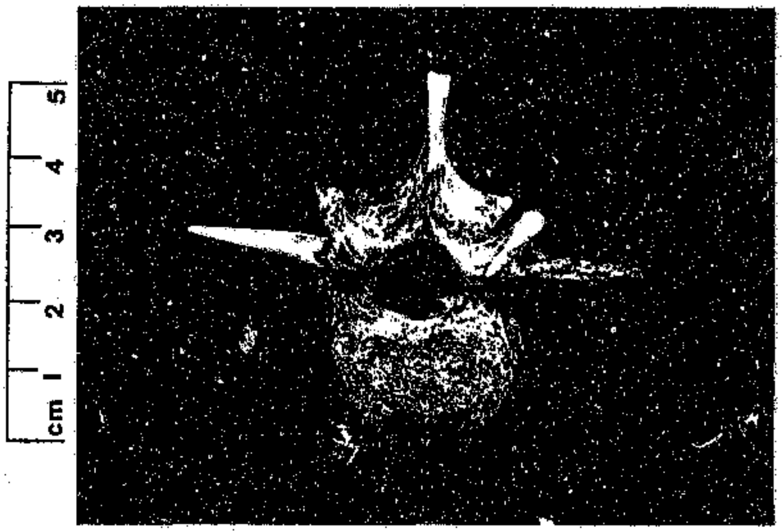

Fig. 4.13 The Superior Aspect of Sts 14*c*, Identified as an *A. africanus* Fou[illegible]bar Vertebra (Lifesize)

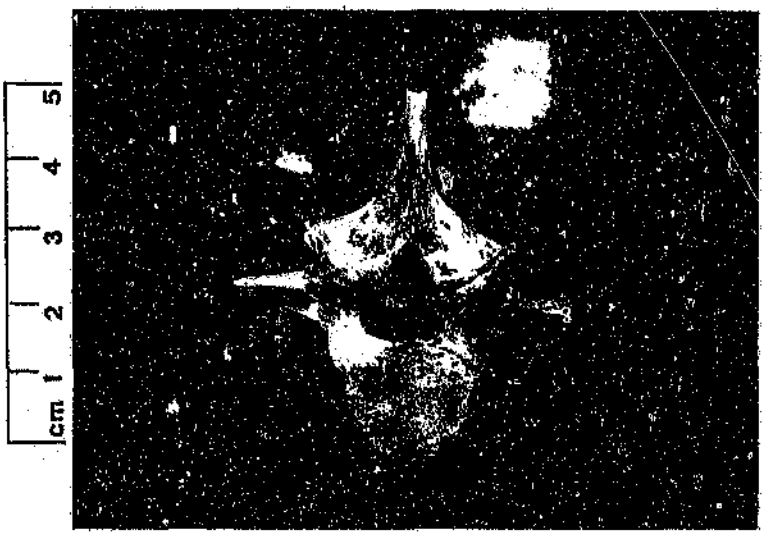

Fig. 4.14 The Superior Aspect of Sts 14*b*, Identified as an *A. africanus* Fift[illegible]bar Vertebra (Lifesize)

facet. The superior surface of the vertebral body is complete except for a small part of the posterior border which is missing in the midline. On the posterior aspect the vertebral body has suffered slight abrasion in the midsagittal plane. Part of the body is broken away on the left side while the inferior surface has suffered mild abrasion which has exposed cancellous bone. The pedicle on the right side is almost complete while the left pedicle is broken away inferiorly. The fragmentary Sts 73 does not appear to belong to the same spinal column as Sts 14 due to the difference in size. The greater robustness of Sts 73 led Robinson (1972) to suggest that it might have belonged to a male individual.

3. Stw 41 (Fig. 4.17) is composed of two consecutive vertebral bodies articulated with each other. The vertebral bodies are well preserved. The superior vertebral body presents a costal facet high up on the right side. The facet seems to be placed at the junction of the vertebral body and the pedicle and to be slightly projecting. It faces superiorly and seems to be complete, although it is placed so high on the vertebra that the head of the rib might have made contact with the vertebral body above. The presence of an inferior demifacet is debatable since this part of the vertebra is damaged.

On the basis of these characteristics the superior vertebral body is identified as one of the last three thoracic vertebrae according to modern hominid features.

The preserved part of the inferior vertebral body does not show costal facets, although one cannot exclude the possibility that they might have been present but had been lost, or that there might have been a facet on the missing pedicle. These two articulating vertebral bodies are thus compatible with having been either two of the last three thoracic vertebrae, or the last thoracic and first lumbar vertebrae.

Fig. 4.15 The Superior Aspect of Sts 14*a*, Identified as an *A. africanus* Sixth Lumbar Vertebra (Lifesize)

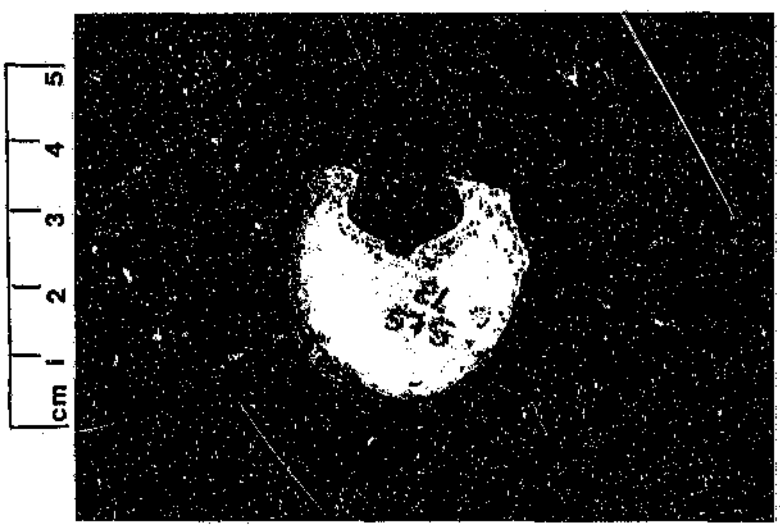

Fig. 4.16 The Superior Aspect of Sts 73, Identified as an *A. africanus* Thoracic Vertebra (Lifesize)

4. Stw 8 (Fig. 4.17) is yielded by the Sterkfontein Lower Breccia and consists of four articulated lumbar vertebral elements. The vertebral bodies are fossilized with breccia between them to form a concavity anteriorly: but this feature is clearly taphonomic and not morphological. The size and shape of the vertebral bodies of Stw 41 match those of the highest vertebra of Stw 8. If one places the two partial vertebral columns together they might easily be from the same individual.

There is matching damage and matching discolouration of the two elements (i.e. the lower of Stw 41 and the highest of Stw 8), providing proof positive that they are not merely compatible, but did belong to one individual (Tobias, 1982a). The two articulating vertebral bodies of Stw 41 are identified above as either two of the last three thoracic or the last thoracic and first lumbar vertebrae. The four articulating lumbar vertebrae of Stw 8 are thus either L1, L2, L3 and L4 or L2, L3, L4 and L5. The four vertebral elements are lettered a, b, c and d from superior to inferior.

Stw 8a has suffered considerable damage. The vertebral body presents no costal facets and the inferior articular facets are lumbar in shape and orientation. It is concluded that this specimen is a lumbar vertebra as stated by Tobias (1973). The vertebral parts present are the vertebral body, the inferior half of the right pedicle, the right inferior articular facet, the inferior part of the right lamina, the root of the spinous process and the medial half of the left inferior articular facet. A small piece above the lateral margin of the right inferior articular facet has been reconstructed. The vertebral body has suffered abrasion on the left side, while the superior third of the posterolateral aspect is broken away on the right side.

Stw 8*b* is the most complete of the four vertebrae and is identified as a second or third lumbar. This vertebra also has suffered mild abrasion on the left side. The lateral

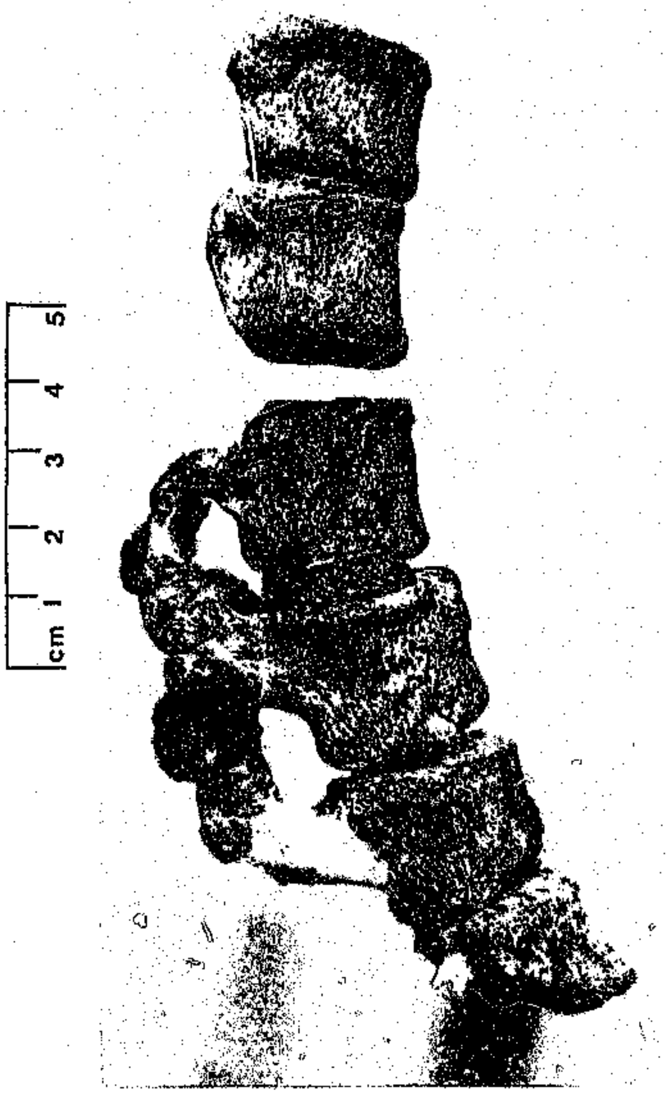

Fig. 4.17 The Right Side of Stw 8/41, Identified as *A. africanus* Thoracic and Lumbar Vertebrae (Lifesize)

half of the pedicle, the transverse process, the left superior articular facet and the inferior articular facet lateral to its root are broken away. The distal end of the spinous process also is missing. The right side of the vertebra is complete except for a small reconstructed part on the superior aspect of the transverse process.

The vertebral body is complete and is deeper posteriorly than anteriorly. The superior articular facet presents a small, indistinct mamillary process, but it is clearly separated from the articular facet proper. The strong transverse process projects laterally but not upwards and there is no accessory process present near the base. A triangular piece of bone is missing from the inferior articular facet, the base of the triangle lying on the inferior border of the facet and the apex along the midline of the facet.

Stw 8*c*: Most of the vertebral body of the next vertebra is well preserved and it is identified as a third or fourth lumbar. Only part of the antero-inferior border of the vertebral body has suffered some abrasion. Most of the right pedicle is reconstructed and the right superior articular facet is fossilized in articulation with the inferior articular facet of the previous vertebra.

Stw 8*d* is a partial vertebral body. The superior surface of the vertebral body, which is in articulation with the inferior surface of the previous vertebra, is complete. The posterior part of the body is broken away, the plane of the break sloping from posterosuperior to nearly antero-inferior.

5. Stw 431. A partial skeleton has recently been recovered almost certainly from Member 4 of the Sterkfontein Formation, the layer which has so far yielded only one hominid, *Australopithecus africanus*. The partial skeleton includes parts of the axial and the appendicular skeletons. Of the axial skeleton we have a small piece of the cranium, fifteen presacral vertebral elements and the upper part of

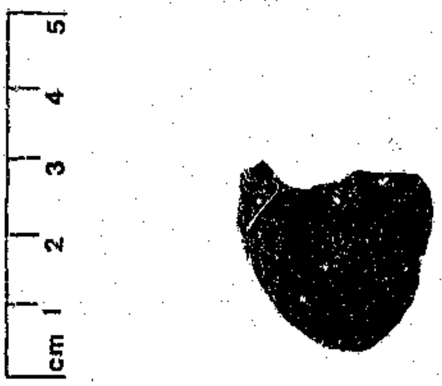

Fig. 4.18 The Superior Aspect of Stw 455, Identified as an *A. africanus* Fourth Last Thoracic Vertebra (Lifesize)

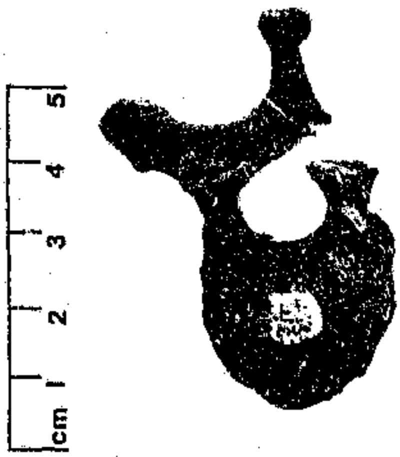

Fig. 4.19 The Superior Aspect of Stw 454a & b, Identified as an *A. africanus* Third Last Thoracic Vertebra (Lifesize)

the sacrum. Among the appendicular skeletal parts is a partial right os coxae; the medial half is unfortunately broken away with the result that the sacrum and ilium cannot be articulated. The following description of the vertebral elements is in sequence cranio-caudally.

Stw 455 (Fig. 4.18) is a thoracic vertebral body. It has suffered damage to the left superior aspect, resulting in the absence of the left superior demifacet. A small piece of the right pedicle root is present. The vertebral body is typically thoracic in shape and bears demifacets for articulation with the rib head.

Stw 454 *a* and *b* (Fig. 4.19): This specimen is composed of two pieces which join in excellent apposition. The joint between the two pieces passes postero-inferior to the right superior articular facet. The parts of this vertebra which are absent are the left transverse process, most of the left lamina and the left inferior articular facet.

The superior margin of the vertebral body is lacking both on the left and the right. On the right side the vertebral body has suffered abrasion from below the superior costal facet, and the inferior costal facet is absent. The costal facets on the vertebral body are demifacets. The right transverse process bears a costal facet which faces laterally and superiorly. The spinous process is long and angled strongly inferiorly. This specimen is the next vertebra in the sequence after Stw 455 and is probably the third last thoracic vertebra. The features set out above are in accordance with this identification.

Stw 453*a* and Stw 453*b* seem to join at the inferomedial aspect of the left pedicle. If, as seems most likely, these two specimens do indeed belong to the same vertebra, the author would classify it as the second last thoracic vertebra.

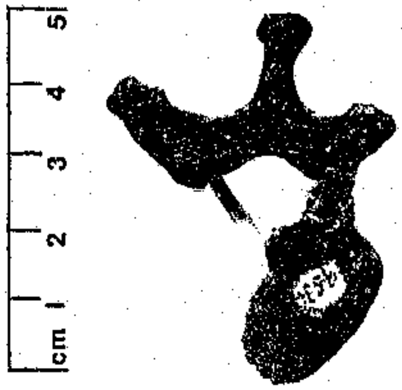

Fig. 4.20 The Superior Aspect of Stw 453a & b, Identified as an *A. africanus* Second Last Thoracic Vertebra (Lifesize)

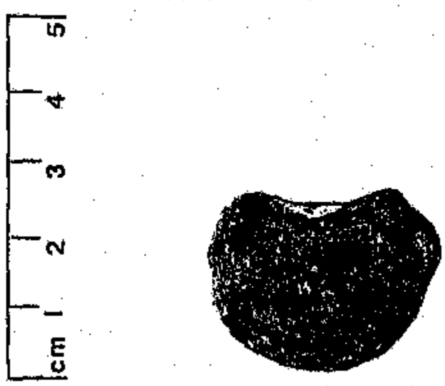

Fig. 4.21 The Inferior Aspect of Stw 457a, Identified as an *A. africanus* Last Thoracic Vertebra (Lifesize)

Stw 453*a* (Fig. 4.20) is the greater part of a vertebral arch. It consists of the spinous process, both inferior articular facets, the laminae and both transverse processes. The tip of the left transverse process and a small piece of the posterior aspect of the right transverse process are missing.

The spinous process, which is complete, is short and expanded at the tip. The angulation of the spinous process is not as inferiorly inclined as in midthoracic vertebrae of modern man. The inferior articular facets are thoracic in shape and orientation and the transverse processes are short. No clear costal facet is present on the right transverse process which is complete. On the basis of these characteristics, this specimen is classified as the second last thoracic vertebra.

Stw 453*b* (Fig. 4.20) is a partial vertebral body with only the left side complete. The root of the left pedicle is present. The left side of the vertebral body presents a large demifacet on the superior margin but no facet on the inferior margin. The demifacet is situated partly on the vertebral body and partly on the pedicle. Owing to the absence of an inferior costal facet on the vertebral body, this specimen conforms to the features of either the second or third last thoracic vertebra.

Stw 457*a* (Fig. 4.21) is part of the next vertebral body. The inferior surface of the body is almost complete, only the left inferior margin being absent. Most of the superior surface and the left side are broken away. The lateral parts of the posterior aspect of the vertebral body are also wanting.

No costal facets are present on the vertebral body but the pedicles which might have borne costal facets are broken away. This partial vertebral body is thus either the last thoracic or the first lumbar vertebra, judged on the body alone.

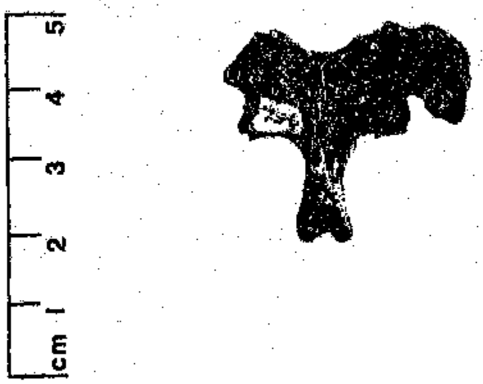

Fig. 4.22 The Posterior Aspect of Stw 452, Identified as an *A. africanus* Last Thoracic Vertebra (Lifesize)

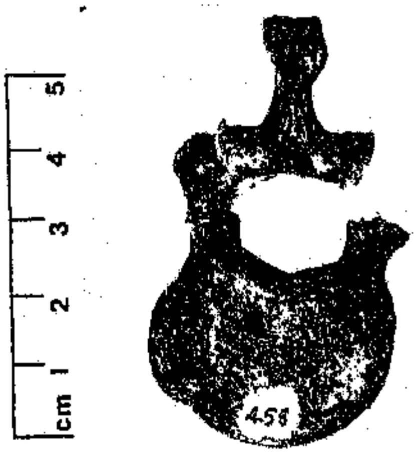

Fig. 4.23 The Inferior Aspect of Stw 458 and Stw 457b, Identified as an *A. africanus* First Lumbar Vertebra (Lifesize)

Stw 452 (Fig. 4.22) consists of a complete spinous process, both inferior articular facets, the laminae and the right transverse process. The transverse process is formed by three distinct tubercles, a superior, inferior and a very small lateral tubercle. The inferior articular facets are transitional in shape and orientation, being more lumbar than thoracic in shape, but orientated more medially than the lumbar inferior articular facets. These atypical or intermediate characteristics correspond with those of a last thoracic vertebra.

Stw 458 (Fig. 4.23) is a well preserved vertebral body, lumbar in shape, with only a small piece of the left inferior margin missing. The roots of both pedicles are present. No costal facets are present on this vertebral body which seems to be the first lumbar vertebra judged on the vertebral body size.

Stw 457*b* (Fig. 4.23) consists of a complete spinous process, both the inferior articular facets, the left lamina, the root of the left superior articular facet and the lateral part of the posterior base of the left pedicle. The spinous process is lumbar in form, projects posteriorly and slopes slightly inferiorly. Both inferior articular facets are lumbar in shape and orientation. This process seems to belong to L1.

Stw 459 (Fig. 4.24) is the most complete vertebra of this partial vertebral column. This specimen is the next lumbar vertebra, that is the second, and only the spinous process and the distal parts of the transverse processes are missing.

The shape of the vertebral body is typically lumbar. The articular facets are situated nearer to the midsagittal line than in the lumbar vertebrae lower down in the column. The orientation of the superior articular facets is more medial and that of the inferior articular facets more lateral. Viewed from posteriorly the four centroids of the articular facets join to form a rectangle. All these characteristics

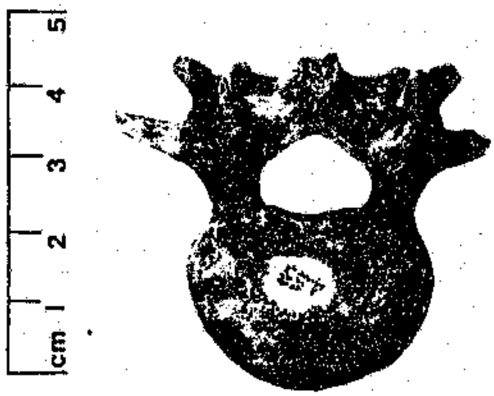

Fig. 4.24 The Superior Aspect of Stw 459, Identified as an *A. africanus* Second Lumbar Vertebra (Later erroneously marked as Stw 453 - Lifesize)

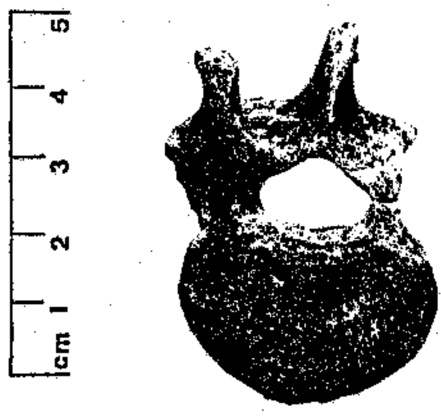

Fig. 4.25 The Superior Aspect of Stw 460, Identified as an *A. africanus* Third Lumbar Vertebra (Lifesize)

are associated with the upper two or three lumbar vertebrae of modern human spinal columns and this specimen has been identified as the second lumbar vertebra. Large, very distinct mamillary processes project posteriorly from the superior articular facets.

Stw 460 (Fig. 4.25) is the next lumbar vertebra i.e. the third. It consists of the vertebral body, the right pedicle, the right superior articular facet, the laminae, the inferior articular facet and the spinous process. The missing parts of this vertebra are most of the left pedicle, the left transverse process and the left superior articular facet. The right transverse process is broken away lateral to its root and the tip of the spinous process is missing.

The vertebral body is typically lumbar in shape and the vertebral canal almost circular. Although the left superior articular facet is missing, the right superior articular facet bears a distinct mamillary process.

Stw 461 (Fig. 4.26) is part of the second last lumbar vertebra, to which also Stw 462 belongs. This part consists of the vertebral body, the root of the left pedicle, the right pedicle, right superior articular facet and the transverse process. The latter process is broken obliquely from superior to inferior, lateral to the root of the process.

A crack runs through the vertebral body but no distortion of the dimension has taken place. On the anterior aspect and the antero-inferior margin, some bone is missing in the crack. The superior surface of the vertebral body is complete, while the postero-inferior part of the vertebral body has suffered abrasion. A few short bony spurs occur on the anterior aspect of the vertebral body and lipping of the inferolateral margins occur.

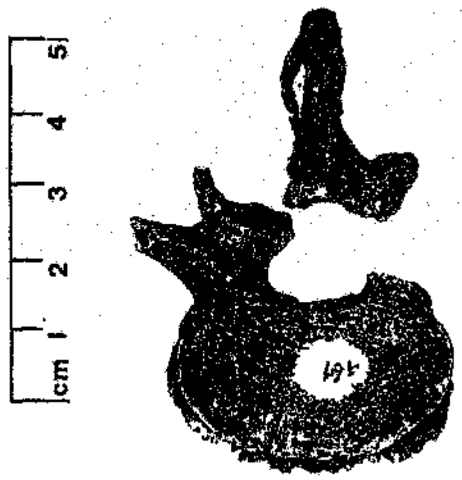

Fig. 4.26 The Superior Aspect of Stw 461 and Stw 462, Identified as an *A. africanus* Fourth Lumbar Vertebra (Lifesize)

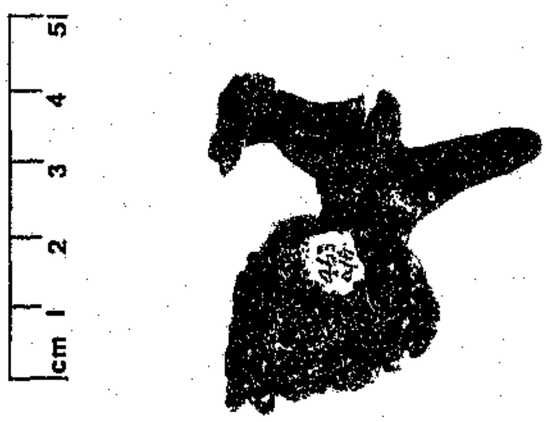

Fig. 4.27 The Superior Aspect of Stw 463a & b Identified as an *A. africanus* Fifth Lumbar Vertebra (Lifesize)

Stw 462 (Fig. 4.26) is another part of the second last lumbar vertebra (L4) which consists of the complete spinous process and the left inferior articular facet. The spinous process is broad and strong and it slopes slightly inferiorly. The inferior articular facet is complete and fits well with the superior articular facet of Stw 463a and b.

Although Stw 461 and Stw 462 make no bony contact with each other, articulation of these vertebral elements with the respective parts of Stw 463*a* and *b* show that they belong to the same vertebra, namely the second last lumbar vertebra, in this case the fourth lumbar vertebra.

Stw 463*a* and *b* (Fig. 4.27) fit together in exellent apposition by means of the left pedicle to form the left side of the last lumbar vertebra (L5). This specimen consists of the partial vertebral body, the left pedicle, transverse process, superior and inferior articular facets and the left lamina. The root of the spinous process and the posterior part of the right lamina also are preserved to complete the left half of the vertebral foramen. The right side of the vertebra is broken away.

Stw 463*a* and *b* are classified as the last lumbar vertebra (in this case the fifth) on the basis of the following characteristics:

1. Though broken, the vertebral body gives the impression that the area of the superior surface was larger than the area of the inferior surface.

2. The inferior surface area of the vertebral body of Sts 462 is too big to articulate with th. first sacral piece.

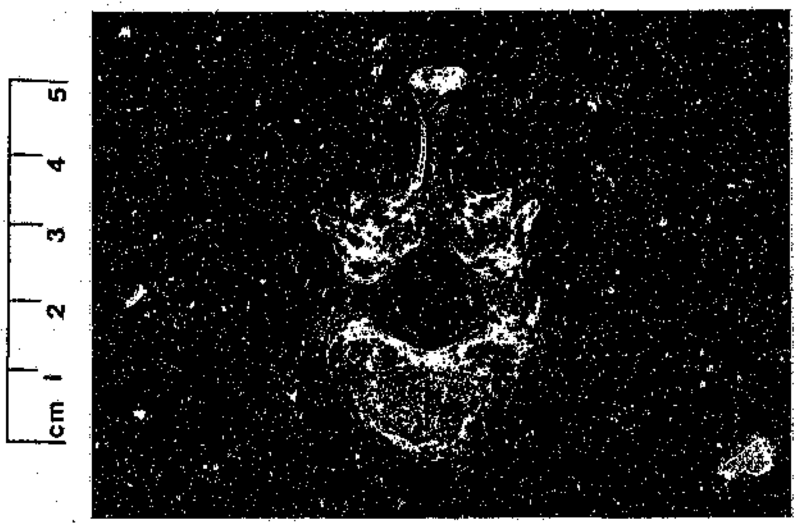

Fig. 4.28 The Superior Aspect of SK 3981a, Identified as an *A. robustus* Last Thoracic Vertebra (Lifesize)

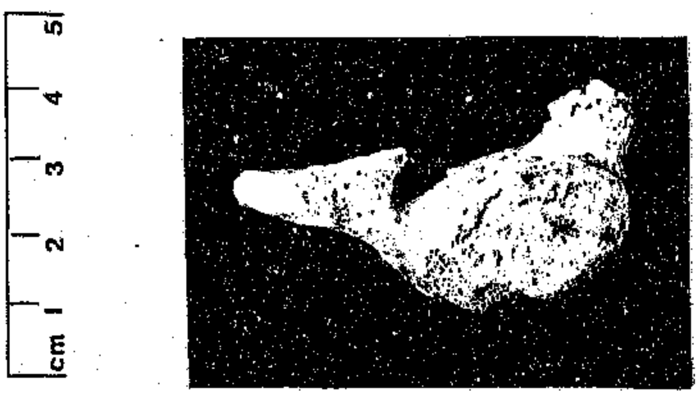

Fig. 4.29 The Inferior Aspect of SK 3981b, Identified as an *A. robustus* Last Lumbar Vertebra (Lifesize)

3. The left side of the partial vertebral body of Stw 463 and the left inferior articular facet articulate well with the corresponding superior parts of the first sacral piece.

4. The strong pedicle and the shape of the vertebral foramen are also characteristic of a last lumbar vertebra.

The features of the vertebrae of the 1987 partial vertebral column correspond with the features of Sts 14 mentioned earlier, except for the size of these vertebrae which are larger than those of Sts 14. (See 1.2. The Age and Sex Breakdown of the Fossil Hominid Series in Chapter 2). Unlike Sts 14, the new Sterkfontein skeleton possesses five lumbar vertebrae.

6. Sts 65 is a Sterkfontein fossil vertebral element described by Robinson (1972) which was not available for the present study. It consists of the posterior surface of a vertebral body and the bases of the pedicles. Robinson (1972) reports that this specimen is too fragmentary for him to be certain that it belongs to *Australopithecus africanus* though he thought it likely. In view of the size of the specimen Robinson (1972) identifies Sts 65 as a vertebra from low down in the spinal column.

B. Swartkrans

SK 3981a (Fig. 4.28) is probably a last thoracic vertebra because, firstly, it has superior articular facets which are typically thoracic and inferior articular facets which are typically lumbar in shape and orientation. Secondly, the vertebra bears complete costal facets for the capitula of the ribs bilaterally. The costal facets are placed partly on the pedicles and partly on the vertebral body, they are slightly protuberant and face posteriorly and caudally. SK 3981a is a well-preserved vertebra, only a small part of the inferior

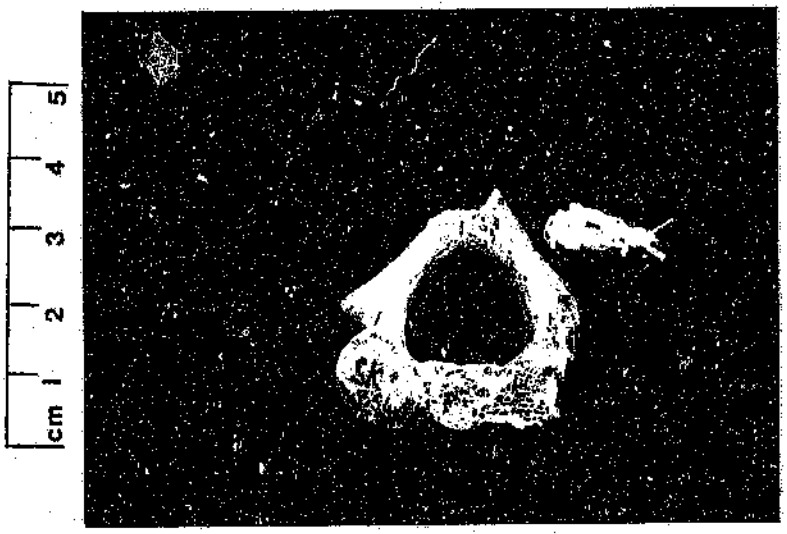

Fig. 4.30 The Superior Aspect of SK 854, Identified as an *A. robustus* Axis (Lifesize)

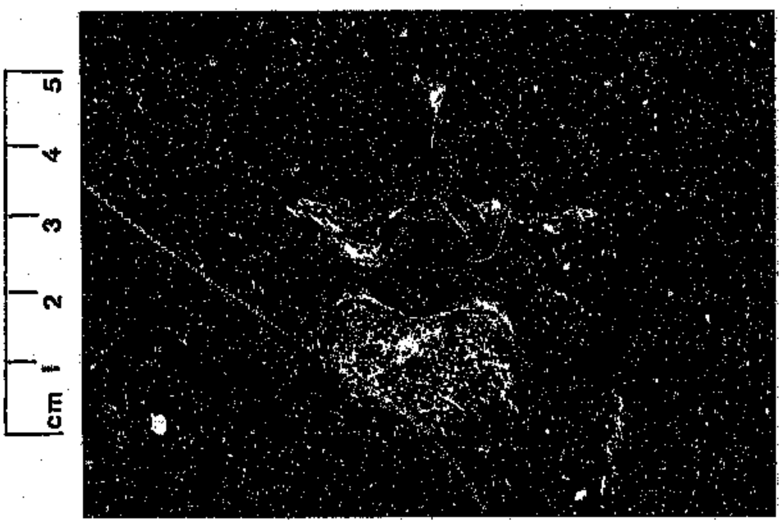

Fig. 4.31 The Superior Aspect of SK 853, Identified as a *H. erectus* Lumbar Vertebra (Lifesize)

surface of the vertebral body being broken away on the right side. The vertebral foramen is proportionately large which gives rise to wide inferior notches. The homologue of the mamillary process is well developed and resembles a small transverse process. The accessory process is a small tubercle well below the latter. A relatively long, complete spinous process projects posteriorly approximately at a right angle to the supero-inferior axis of the vertebra.

SK 3981*b* (Fig. 4.29) is an incomplete last lumbar vertebra. It consists of a vertebral body, both pedicles and most of the left transverse process. The inferior surface of the vertebral body is damaged on the left side and the right pedicle has suffered slight abrasion on the medial aspect. The vertebral body is deeper anteriorly than posteriorly and the superior surface is larger than the inferior surface in cross-section.

The pedicles are strong and, on the left side, give rise to a large, strong transverse process which projects supero-laterally. A small tubercle is situated on the inferior aspect of the transverse process near its base.

The fused epiphyseal rings of the two vertebrae described above indicate that both were adult specimens. They probably belonged to the same individual as the vertebrae were found in the same block of breccia. Their relative sizes also correspond.

SK 854 (Fig. 4.30) is an axis with the dens broken away. It is distinctly hominid in general appearance, but does not closely resemble the modern human equivalent which led Robinson (1972) to classify it as an *A. robustus* vertebra. Since the present study is confined to the thoracolumbar region, this vertebra is not included in the metrical and non-metrical analysis but is mentioned here for the sake of completeness.

SK 853 (Fig. 4.31) is the fourth vertebra from Swartkrans. This has been identified as a well preserved lumbar vertebra of an immature *Homo erectus* individual (Robinson, 1972), a view supported by the author. The epiphyseal rings of this vertebra were not fused at the time of death and are missing. This leaves the margins of the vertebral body fluted and crenulated. This vertebra is almost complete, missing only the tip of the right transverse process and a part of the right superior articular facet. The spinous process is broad from superior to inferior but not enlarged at the tip.

CHAPTER 5

VARIATION IN THE NUMBERS OF PRESACRAL VERTEBRAE IN VARIOUS HOMINOIDS

Contents of Chapter

Introduction

While this is a study of the thoracic and lumbar regions of the vertebral column, the writer holds that an adequate study of these regions requires that they be considered as part of the entire spinal column, at least cranial to the sacrum.

Accordingly, the numbers of presacral vertebrae were determined. The term presacral vertebrae (PSV) is used often in the text and tables.

Variation in the number of PSV has been the subject of much study and speculation in the past century. It appears that Topinard in 1877 was the first to have taken up a statistical study of the frequency of numerical variation in modern human vertebrae (Bardeen, 1904).

Variations in the number of PSV may be in the form of a plus-variation or a minus-variation. The plus-variation indicates an increase in the number of presacral vertebrae (25 PSV) over the modal number (24 PSV), while a minus-variation indicates a reduction in the number of presacral vertebrae (23 PSV). The sum of the plus- and minus-variates forms the total number of numerical variates (23 PSV plus 25 PSV). The regions of the spinal column most affected by variations are the thoracic and lumbar regions. The cervical region is found to be remarkably stable in primates (Todd, 1922; Schultz, 1930).

The definitions used to determine the regional allocation of a vertebra are described in Chapter 3. A seemingly last lumbar vertebra is counted as sacral if one or both transverse processes are enlarged and developed so as to form part of the sacro-iliac joint and to contribute to the formation of a sacral foramen.

A. Numbers of Presacral Vertebrae in Modern Human Series

1. Zulu Series

In Table 5.1 the numbers of PSV in males and females of the Zulu vertebral columns are compared.

TABLE 5.1

The Numbers of Presacral Vertebrae (PSV) in Zulu Spinal Columns

PSV	Males		Females		Males plus Females	
	n	%	n	%	n	%
23	7	8,8	5	12,5	12	10,0
24	62	77,5	33	82,5	95	79,2
25	11	13,8	2	5,0	13	10,8
	80		40		120	

The decreased number of 23 PSV and the increased number of 25 PSV are noted in 10,0% and 10,8% of the skeletons respectively. The females, with an incidence of 12.5%, present a higher frequency of 23 PSV than the males (8,8%). In contrast the males (13,8%) show a higher frequency of 25 PSV than the females (5%). Total variates (23 PSV plus 25 PSV) occur in 25 of the 120 skeletons (20,8%) in this series, the male group presenting a higher percentage of total variates (22,5%) than the female group (17,5%).

2. Other Modern Human Populations

2.1 Sources of Data

The Southern African Negro (S.A. Negro) data used for comparison are those of De Beer-Kaufman (1974). Her series were made up from four major tribal groups in Southern Africa: 137 Natal Nguni (Zulu and Swazi males and females), 12 Cape Nguni males and females, 143 Sotho males and females and 60 Shangaan males.

The San series of De Beer-Kaufman's (1974) study, 16 male and 12 female vertebral columns, were also used for comparison in the present study.

The North American Negro (Amer. Negro) series are compiled from the data of Bardeen (1904) on 34 male and 20 female columns, Bornstein and Peterson (1966) on 248 male and 269 female columns and Lanier (1939) on 100 male vertebral columns.

Allbrook (1955) reported on combined male and female East African Negro vertebral columns only, but his data are included in Table 5.7.

The Mongoloid data include those for Japanese male and female vertebral columns (Hasebe, 1913; Nishi, 1928). These two sources provide a total of 322 Japanese vertebral columns. The other Mongoloid data are from 234 Eskimo plus Indian vertebral columns (Bornstein and Peterson, 1966).

The Caucasoid data are compiled from works on North American Whites and Eur-Asian Whites. The data on North American Whites are taken from the works of Bornstein and Peterson (1966) on 263 males and 225 females, and of Lanier (1939) on 100 males. The Eur-Asian data are from Steinbach (1889) on 83 German skeletons, from Bianchi (1895) on 130 Italian skeletons (both cited by Bardeen, 1904) and from Adolphi (1905) on 83 Russian vertebral columns. The data of Frey (1929) on 150 Swiss vertebral columns are also included. These authors reported the number of PSV in males and females separately and the data are included in Tables 5.3 and 5.5. The studies of Topinard (1877) on 350 French skeletons, Paterson (1892) on 132 British skeletons, Staderini (1894) on 100 Florence skeletons and of Ancel and Sencert (1902) on 43 French skeletons, all cited by Bardeen (1904), reported on combined male and female vertebral columns and are included in Table 5.7.

Studies of other workers were consulted but no other reports were found which were suitable for comparison of PSV. A total of 217 excavated Eskimo skeletons, 107 males 96 females and 14 vertebral columns of unknown sex, were examined by Stewart (1932). As he reported no case of 23 PSV his data are not included in the present study. He ascribed the lack of skeletons presenting 23 PSV to the sorting process of excavated material. During the sorting process skeletons with fewer than 24 PSV might have been considered incomplete and thus not been included in his sample. Jonck (1959) reported on the number of thoracolumbar vertebrae but not of PSV of S.A. Negroes

The frequency of the specific variants (23 PSV, and 25 PSV) and the frequency of total variates (23 PSV plus 25 PSV) among the different population groups are considered in the following section.

3. Intergroup Comparisons of Presacral Vertebrae

To compare the frequencies of specific variations (23 PSV, and 25 PSV) and total variation (23 PSV plus 25 PSV) in the various population groups, the data in Tables 5.2, 5.3, 5.5 and 5.7 were analysed. When the actual number of skeletons departing from the modal number of PSV was known, the chi-square test was used. The 1% level of significance ($P<0.01$) is accepted as almost certainly significant for this test. Yates's correction for continuity was applied to the chi-square test when any cell frequency was less than five. The z-test for percentage is used for values expressed as a percentage, such as the weighted mean. The same level of significance ($P<0.01$) as for the chi-square test was accepted as almost certainly significant. Both these tests are fully described in Chapter 3.

3.1 Intragroup Comparisons among S.A. Negro Series

The Zulu series of the present study and the S.A. Negro series of De Beer-Kaufman's (1974) study are now compared (Table 5.2). When one looks at the males of the two samples the Zulu males present a higher frequency of 23 PSV (8,8%) than the S.A. Negro males (4,9%). This difference proves not significant (chi-square = 1,73; P<0,25). In De Beer-Kaufman's S.A. Negro sample, Natal Nguni males (a subsample which consists of Zulu and Swazi males) have the highest frequency of 23 PSV (8,3%) and Shangaan males the lowest (1,7%). The frequencies of 23 PSV in Zulu (8,8%) and Natal Nguni (8,3%) males correspond. Comparison of the frequencies of 23 PSV among the tribes showed no significant difference (chi-square = 3.51; P<0,50 with four degrees of freedom).

Comparison of the frequencies of 25 PSV among the tribes also showed no significant difference (chi-square = 1,81; P<0,9 with four degrees of freedom). This is expected from the small range of 25 PSV frequencies among the males of the different tribes. The frequencies of this specific variant range between 10,0% in Shangaan males and 17,6% in Cape Nguni males. There is a difference of only 0,7% between the Zulu and Natal Nguni males.

The frequencies of total variates (23 PSV plus 25 PSV) range from 11,7% in Shangaan males to 23,5% in Cape Nguni males. Comparison of these frequencies among the males of the tribes showed no significant difference (chi-square = 4,11; P<0,50 with four degrees of freedom).

In the female series Zulu females present the highest frequency of 23 PSV (12,5%) and Sotho females the lowest (4,5%). Statistical comparison among the females of the tribes shows no significant difference in the frequencies of 23 PSV (chi-square = 1,37; P<0,75 with three degrees of freedom). The same applies to the frequencies of 25 PSV (chi-square = 1,42;

P<0,75 with three degrees of freedom) and the frequencies of total variates (chi-square = 3,25; P<0,50 with three degrees of freedom).

When the sexes are considered together (Table 5.2) the Zulus present the highest frequency of 23 PSV (10,0%) and the Sotho males plus females the lowest (3,5%). Comparison of the frequencies of 23 PSV among the tribes showed no significant differences (chi-square = 4,79; P<0,25 with three degrees of freedom). The difference between the frequencies of this variant in the Zulu and De Beer-Kaufman's S.A. Negro males plus females is not significant (chi-square = 1,71; P<0,25).

Comparison of the frequencies of 25 PSV among the tribes also showed no significant difference (chi-square = 2,08; P<0,75). The Cape Nguni males plus females present the highest frequency of 25 PSV (13,9%). The same applies to the frequencies of total variates; no significant differences are found among the tribes (chi-square = 5,39; P<0,25 with three degrees of freedom) and the Cape Nguni males plus females present the highest frequency of total variates.

De Beer-Kaufman (1974) found no significant intertribal differences in the frequencies of total variates for males or females and the series were therefore treated as a sample of a single S.A. Negro population. This is in accordance with the findings of a craniological study by De Villiers (1968) which showed no major intertribal differences in either metrical or non-metrical features of the skull. No differences in the frequencies of the specific variants or of total variates are found between De Beer-Kaufman's S.A. Negro sample and the present Zulu series for males, females and the sexes considered together. The two samples are thus pooled to form a combined S.A. Negro sample.

TABLE 5.2

The Numbers of Presacral Vertebrae (PSV) in South African Negroes.

Tribal group	n	24 PSV n	24 PSV %	23 PSV n	23 PSV %	25 PSV n	25 PSV %	23 & 25 PSV n	23 & 25 PSV %	Reference
1. MALES										
Zulu	80	62	77,5	7	8,8	11	13,8	18	22,5	Present Study
Natal Nguni	84	66	78,6	7	8,3	11	13,1	18	21,4	De Beer-Kaufman (1974)
Cape Nguni	85	65	76,5	5	5,9	15	17,6	20	23,5	De Beer-Kaufman (1974)
Sotho	76	63	83,0	2	2,6	11	14,5	13	17,0	De Beer-Kaufman (1974)
Shangaan	60	53	88,3	1	1,7	6	10,0	7	11,7	De Beer-Kaufman (1974)
Total	305	247	81,0	15	4,9	43	14,1	58	19,0	
Pooled S.A. Negro	385	309	80,3	22	5,7	54	14,0	76	19,7	
2. FEMALES										
Zulu	40	33	82,5	5	12,5	2	5,0	7	17,5	Present Study
Natal Nguni	53	44	83,1	5	9,4	4	7,5	9	16,9	De Beer-Kaufman (1974)
Cape Nguni	37	31	83,8	4	10,8	2	5,4	6	16,2	De Beer-Kaufman (1974)
Sotho	67	63	94,0	3	4,5	1	1,5	4	6,0	De Beer-Kaufman (1974)
Total	157	138	88,0	12	7,6	7	4,5	19	12,1	
Pooled S.A. Negro	197	171	86,8	17	8,6	9	4,6	26	13,2	
3. Males plus Females										
Zulu	120	95	79,2	12	10,0	13	10,8	25	20,8	Present Study
Natal Nguni	137	110	80,3	12	8,8	15	10,9	27	19,7	De Beer-Kaufman (1974)
Cape Nguni	122	96	78,7	9	7,4	17	13,9	26	21,3	De Beer-Kaufman (1974)
Sotho	143	126	88,1	5	3,5	12	8,4	17	11,9	De Beer-Kaufman (1974)
Total	402	332	82,6	26	6,5	44	10,9	70	17,4	
Pooled S.A. Negro	522	427	81,8	38	7,3	57	10,9	95	18,2	

3.2 Intragroup Comparison among Subsets of Other Population Groups

Intragroup comparisons revealed no significant differences in the frequencies of 23 PSV, 24 PSV or 25 PSV among the subsets of each population group, for either sexes and for the sexes combined. The data on the subsets of each major racial constellation have thus been pooled, to provide combined unweighted and weighted mean values for each of the groups (S.A. Negro, American Negro, Caucasoid and Mongoloid) within the categories males, females and males plus females.

3.3 Intergroup Comparisons among Males

Table 5.3 summarises the numbers of PSV in the males of various population groups. The differences among the males of the major racial constellations with respect to the frequency of 23 PSV were not significant (chi-square = 1,61; P<0,90 with four degrees of freedom). This is expected when one looks at the small range of frequencies of 23 PSV among the males of the various population groups. The frequencies of this specific variant range between 3,6% in the Mongoloid sample and 5,7% in the S.A. Negro sample and 6,2% in the San. This low incidence of 23 PSV in the Mongoloid sample is based largely upon the low frequency in the Eskimo plus Indian sample (2,9%). Comparison of the weighted means of S.A. Negroes, American Negroes, Mongoloids and Caucasoids showed that, as suggested by the chi-square test among the major population groups, no significant differences in the frequencies of 23 PSV were found among the males of these major population groups.

The differences in the frequencies of 25 PSV among the males of different population groups were highly significant (chi-square = 28,65, P<0,001 with four degrees of freedom). If one looks at the frequencies of 25 PSV in various population groups, the exceptionally high frequencies of 25% in San and 14,0% in S.A. Negro males stand out. In the Mongoloid series

TABLE 5.3

The Numbers of Presacral Vertebrae (PSV) in Males of Various Population Groups

Population group	n	24 PSV		23 PSV		25 PSV		23 + 25 PSV		Reference
		n	%	n	%	n	%	n	%	
S.A. Negro:										
Zulu	80	62	77,5	7	8,8	11	13,8	18	22,5	Present Study
Natal Nguni	84	66	78,6	7	8,3	11	13,1	18	21,4	De Beer-Kaufman (1974)
Cape Nguni	85	65	76,5	5	5,9	15	17,6	20	23,5	De Beer-Kaufman (1974)
Sotho	76	63	83,0	2	2,6	11	14,5	13	17,0	De Beer-Kaufman (1974)
Shangaan	60	53	88,3	1	1,7	6	10,0	7	11,7	De Beer-Kaufman (1974)
Pooled S.A. Negro	385	309	80,3	22	5,7	54	14,0	76	19,7	
San:	16	11	68,8	1	6,2	4	25,0	5	31,2	De Beer-Kaufman (1974)
Amer. Negro:										
	34	28	82,3	3	8,8	3	8,8	6	17,6	Bardeen (1904)
	248	225	90,7	12	4,8	11	4,4	23	9,3	Bornstein & Peterson (1966)
	100	88	88,0	5	5,0	7	7,0	12	12,0	Lanier (1939)
Pooled Amer. Negro	382	341	89,3	20	5,2	21	5,5	41	10,7	
Mongoloid:										
Japanese	122	110	90,2	5	4,1	7	5,7	12	9,8	Hasebe (1913)
Japanese	105	97	92,1	4	3,8	4	3,8	8	7,6	Nishi (1928)
Total Japanese	227	207	91,2	9	4,0	11	4,8	20	8,8	
Eskimo & Amerind	136	116	85,3	4	2,9	16	11,8	20	14,7	Bornstein & Peterson (1966)
Pooled Mongoloids	363	323	89,0	13	3,6	27	7,4	40	11,0	
Caucasoid:										
Amer. Whites	100	95	95,0	3	3,0	2	2,0	5	5.0	L[illegible]39)
Amer. Whites	263	235	89,4	11	4,2	17	6,5	28	10,6	Bo[illegible] Peterson (1966)
German	48	40	83,3	2	4,2	6	12,5	8	16,7	Steinbach (1889)*
Italian	60	50	83,3	7	11,7	3	5,0	10	16,7	Bianchi (189[illegible])**
Russian	48	43	89,6	3	6,3	2	4,2	5	10,4	Adolphi (1905)
Swiss	92	83	90,0	3	3,0	6	7,0	9	10,0	Frey (1929)
Pooled Caucasoids	611	546	89,4	29	4,7	36	5,9	65	10,6	

* Cited by Bardeen (1904).

** Cited by Bardeen (1904) as 1895 and by Bornstein and Peterson (1966) as 1894.

the Eskimo plus Indian subset presents a frequency of 11,8% to the 4,8% of the Japanese. This difference proved probably significant (chi-square = 5,91; P<0,025). The high frequency of 25 PSV (11,8%) in the Eskimo plus Indians also proved probably significantly different from the frequencies in American Negro and Caucasoid males. The 14,0% frequency of 25 PSV in S.A. Negro males also proved to be significantly higher than the 5,5% in American Negro males, the 7,4% in Mongoloid males and the 5,9% in Caucasoid males (Table 5.4). The differences in the frequencies of 25 PSV between San males and firstly Mongoloid males and secondly Caucasoid males are probably significant (P<0,05), while the difference between San and American Negro males is almost certainly significant (P<0,01).

The differences in the frequencies of total variation (23 PSV plus 25 PSV) were highly significant (chi-square = 26,31; P<0,001 with four degrees of freedom) among the males of the different population groups. The frequencies of total variation range from 10,6% in Caucasoid males to 19,7% in S.A. Negroid males and 31,2% in San males. The difference in the high frequency of total variates (23 PSV plus 25 PSV) in S.A. Negro males proved almost certainly significantly different from those in the American Negro males, the Caucasoid males and the Mongoloid males (Table 5.4). Comparison of the weighted means corroborated these findings.

TABLE 5.4

The Chi-square Values for the Differences of the Frequencies of the Specific Variant (25 PSV) and the Total Variates between Males of Various Population Groups.

Population groups	25 PSV χ^2	25 PSV P<	23 PSV + 25 PSV χ^2	23 PSV + 25 PSV P<
1. S.A. Negro v.				
San	2,51$	0,25	0,65$	0,90
Amer. Negro	15,81	0,001	12,03	0,001
Mongoloid	6,40	0,005	10,84	0,001
Caucasoid	19,01	0,001	16,10	0,001
2. San v.				
Amer. Negro	6,89$	0,01	4,48$	0,05+
Mongoloid	4,17$	0,05+	5,99	0,025+
Caucasoid	6,60$	0,025+	6,68	0,01
3. Amer. Negro v.				
Mongoloid	1,16	0,50	0,02	0,90
Caucasoid	0,07	0,90	2,21	0,25
4. Mongoloid v.				
Caucasoid	0,90	0,90	0,03	0,90

$ = Yates's correction for small samples applied.
+ = Probably significant.
Underlined = Almost certainly and highly significant.

3.4 Intergroup Comparisons among Females

Table 5.5 summarises the numbers of PSV in the females of various population groups. The differences in the frequencies of 23 PSV among the females of the population groups are probably significant (chi-square = 11,37, P<0,025 with four degrees of freedom). This implies the probability of a significant difference between specific population groups. Chi-square tests of the differences in the frequencies of 23 PSV between American Negro females and Mongoloid females (chi-square = 7,87; P<0,01) as well as Caucasoid females

TABLE 5.5

The Numbers of Presacral Vertebrae (PSV) in Females of Various Population Groups

Population group	n	24 PSV n	24 PSV %	23 PSV n	23 PSV %	25 PSV n	25 PSV %	23 + 25 PSV n	23 + 25 PSV %	Reference
Negroid:										
S.A. Negro:										
Zulu	40	33	82,5	5	12,5	2	5,0	7	17,5	Present Study
Natal Nguni	53	44	83,1	5	9,4	4	7,5	9	16,9	De Beer-Kaufman (1974)
Cape Nguni	37	31	83,8	4	10,8	2	5,4	6	16,2	De Beer-Kaufman (1974)
Sotho	67	63	94,0	3	4,5	1	1,5	4	6,0	De Beer-Kaufman (1974)
Pooled S.A. Negro	197	171	86,8	17	8,6	9	4,6	26	13,2	
San:	12	10	83,3	1	8,3	1	8,3	2	16,7	De Beer-Kaufman (1974)
Amer. Negro:	20	16	80,0	2	10,0	2	10,0	4	20,0	Bardeen (1904)
	269	233	86,6	31	11,5	5	1,9	36	13,4	Bornstein & Peterson (1966)
Pooled Amer. Negro	289	249	86,2	33	11,4	7	2,4	40	13,8	
Mongoloid:										
Japanese	59	53	89,8	4	6,8	2	3,4	6	10,2	Hasebe (1913)
Japanese	36	32	88,9	1	2,8	3	2,8	4	11,1	Nishi (1928)
Total Japanese	95	85	89,5	5	5,3	5	5,3	10	10,5	
Eskimo & Amerind	98	91	92,9	3	3,1	4	4,1	7	7,1	Bornstein & Peterson (1966)
Pooled Mongoloids	193	176	91,2	8	4,1	9	4,7	17	8,8	
Caucasoid:										
Amer. Whites	225	203	90,2	13	5,8	9	4,0	22	9,8	Bornstein & Peterson (1966)
German	35	34	97,1	1	2,8	-	-	1	2,8	Steinbach (1889)*
Italian	70	65	92,9	5	7,1	-	-	5	7,1	Bianchi (1894)**
Russian	35	34	97,1	-	-	1	2,9	1	2,9	Adolphi (1905)
Swiss	58	52	90,0	4	7,0	2	3,0	6	10,3	Frey (1929)
Pooled Caucasoids	423	388	91,7	23	5,4	12	2,8	35	8,3	

* Cited by Bardeen (1904).
** Cited by Bardeen (1904) as 1895 and by Bornstein and Peterson (1966) as 1894.

(chi-square = 8,48; P<0,005) proved to be significant (Table 5.6). This difference is produced mainly by the high incidence of 23 PSV in American Negro females (11,4%) and the low incidences in Mongoloid females (4,1%) and Caucasoid females (5,4%). When the weighted means are compared by the z-test for percentages a significant difference in the frequency of 23 PSV is found between American Negro females and Mongoloid females (z = 2,67; P<0,01). The difference between American Negro and Caucasoid females is probably significant (z = 2,41; P<0,05).

TABLE 5.6

The Chi-square Values of the Differences in the Frequencies of 23 Presacral Vertebrae between Females of Various Population Groups.

Population groups	23 PSV X^2	P<
1. S.A. Negro v.		
San	0,24*	0,75
Amer. Negro	0,99	0,50
Mongoloid	3,29	0,10
Caucasoid	2,27	0,25
2. San v.		
Amer. Negro	0,02*	0,90
Mongoloid	0,002*	0,95
Caucasoid	0,04*	0,90
3. Amer. Negro v.		
Mongoloid	7,87	<u>0,01</u>
Caucasoid	8,48	<u>0,005</u>
4. Mongoloid v.		
Caucasoid	0,46	0,50

* = Yates's correction for small samples.
Underlined = Almost certainly and highly significant.

Among the females of the various population groups, no significant differences in the frequencies of 25 PSV were found (chi-square = 1,94; P<0,75 with four degrees of freedom). The frequencies of 25 PSV in females range between 2,4% in the American Negro series and 8,3% in the San. As suggested by the chi-square test among the females of the population groups, comparison among the weighted means of the groups by the z-test showed no significant differences among the females.

The differences in the frequencies of total variates (23 PSV plus 25 PSV) among the females of the population groups were not significant (chi-square = 6,60; P<0,25 with four degrees of freedom). The frequencies of total variates range from 8,3% in combined Caucasoid females to 16,7% in San females. Due to the high incidence of 23 PSV, the American Negro females present the second highest frequency of total variation (13,8%). As the chi-square test for the frequencies of total variates among the population groups suggested, no significant differences among the population groups were found. When the weighted means of the population groups were compared, a probably significant (P<0,05) difference in the frequency of total variates was found only between American Negro and Caucasoid females.

3.5 Intergroup Comparisons among Combined Sex Samples

Table 5.7 summarises the number of PSV in the combined sex samples of the various population groups. The differences in the frequencies of 23 PSV in males plus females among the various population groups were highly significant (chi-square = 16,7; P<0,005 with five degrees of freedom). The high frequency of 23 PSV in American Negro males plus females (8,4%) proved to be significantly different from that in Mongoloid and Caucasoid males plus females (Table 5.8). The difference in the frequency of 23 PSV between S.A. Negroes and Mongoloids and between American Negroes and East African Negroes proved to be probably significant.

Among the females of the various population groups, no significant differences in the frequencies of 25 PSV were found (chi-square = 1,94; P<0,75 with four degrees of freedom). The frequencies of 25 PSV in females range between 2,4% in the American Negro series and 8;3% in the San. As suggested by the chi-square test among the females of the population groups, comparison among the weighted means of the groups by the z-test showed no significant differences among the females.

The differences in the frequencies of total variates (23 PSV plus 25 PSV) among the females of the population groups were not significant (chi-square = 6,60; P<0,25 with four degrees of freedom). The frequencies of total variates range from 8,3% in combined Caucasoid females to 16,7% in San females. Due to the high incidence of 23 PSV, the American Negro females present the second highest frequency of total variation (13,8%). As the chi-square test for the frequencies of total variates among the population groups suggested, no significant differences among the population groups were found. When the weighted means of the population groups were compared, a probably significant (P<0,05) difference in the frequency of total variates was found only between American Negro and Caucasoid females.

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TABLE 5.7

The Numbers of Presacral Vertebrae (PSV) in Combined Sex Samples of Various Population Groups

Population group	n	24 PSV n	24 PSV %	23 PSV n	23 PSV %	25 PSV n	25 PSV %	23 + 25 PSV n	23 + 25 PSV %	Reference
Negroid:										
S.A. Negro										
Zulu	120	95	79,2	12	10,0	13	10,8	25	20,8	Present Study
S.A. Negro	462	385	83,3	27	5,8	50	10,8	77	16,7	De Beer-Kaufman (1974)
Pooled S.A. Negro	582	480	82,5	39	6,7	63	10,8	102	17,5	
San:	28	21	75,0	2	7,1	5	17,9	7	25,0	De Beer-Kaufman (1974)
Amer. Negro:	54	44	81,5	5	9,3	5	9,2	10	18,5	Bardeen (1904)
	517	458	88,6	43	8,3	16	3,1	59	11,4	Bornstein & Peterson (1966)
Pooled Amer. Negro	571	502	87,9	48	8,4	21	3,7	69	12,1	
East African Negro:	206	175	84,9	7	3,4	24	11,7	31	15,1	Allbrook (1955)
Mongoloid:										
Japanese	181	163	90,1	9	5,0	9	5,0	18	9,9	Hasebe (1913)
Japanese	141	129	91,5	5	3,5	7	5,0	12	8,5	Nishi (1928)
Total Japanese	322	292	90,7	14	4,3	16	5,0	30	9,3	
Eskimo & Amerind	234	207	88,5	7	3,0	20	8,5	27	11,5	Bornstein & Peterson (1966)
Pooled Mongoloids	556	499	89,7	21	3,8	36	6.5	57	10,3	
Caucasoid:										
Amer. Whites	408	438	89,8	24	4,9	26	5,3	50	10,2	Bornstein & Peterson (1966)
French	350	332	94,9	8	2,3	10	2,9	18	5,1	Topinard (1877)*
French	43	39	90,7	1	2,3	3	7,0	4	9,3	Ancel & Sencert (1902)*
German	83	74	89,1	3	3,6	6	7,2	9	10,8	Steinbach (1889)*
British	132	118	89,4	7	5,3	7	5,3	14	10,6	Paterson (1892)*
Florence	100	89	89,0	7	7,0	4	4,0	11	11,0	Staderini (1894)*
Italian	130	115	88,5	12	9,2	3	2,3	15	11,5	Bianchi (1894)**
Russian	83	77	92,8	3	3,6	3	3,6	6	7,2	Adolphi (1905)
Swiss	150	135	90,0	7	4,7	8	5,3	15	10,0	Frey (1929)
Pooled Caucasoids	1559	1417	90,9	72	4,6	70	4,5	142	9,1	

* Cited by Bardeen (1904).
** Cited by Bardeen (1904) as 1895 and by Bornstein and Peterson (1966) as 1894.

The differences among the frequencies of 25 PSV in the males plus females of the population groups are highly significant (chi-square = 52,19; P<0,001 with five degrees of freedom). San present the highest frequency (17,9%) of 25 PSV and the East African Negroes the second highest (11,7%). American Negroes present the lowest frequency (3,7%). Comparison of the means of the different population groups (Table 5.8) revealed highly significant differences in the frequencies of 25 PSV between S.A. Negroes and, firstly, American Negroes (chi-square = 21,8; P<0,001), secondly Caucasoids (chi-square = 21,19; P<0,001) and thirdly Mongoloids (chi-square = 6,77; P<0,01). The frequencies of 25 PSV in San were significantly different from those in the American Negro, Caucasoid and Japanese while the difference between San and Mongoloid males plus females is probably significant (chi-square = 5,29; P<0,025). The American Negroes differ highly significantly from the East African Negroids (chi-square = P<0,001), and from the Eskimo plus Indians. The latter two groups are also significantly different from the Caucasoids.

The frequencies of total variates in the males plus females among the various population groups were found to differ *inter se* highly significantly (chi-square = 37,63 P<0,001 with five degrees of freedom). The frequencies of total variates range from 9,1% in the Caucasoids to 25,0% in the San series. Comparison of the means of the different population groups revealed a highly significant difference in the frequencies of total variates (Table 5.8) between S.A. Negroes and, firstly, American Negroes (chi-square = 6,76, P<0,01), secondly, Mongoloids (chi-square = 12,52, P<0,001) and thirdly Caucasoids (chi-square = 29,74; P<0,001). San differ highly significantly from Caucasoids (chi-square = 8,17, P<0,005) and probably significantly from American Negroes and Mongoloids. The difference between East African Negro and Caucasoid males plus females proves to be significant (chi-square = 7,26, P<0,01). The results of the z-test for percentages on the weighed means of S.A. Negroes, American Negroes, Mongoloids and Caucasoids correspond to the results of the chi-square test.

TABLE 5.8

The Chi-square Values of the Differences in the Frequencies of the Specific Variants and the Total Variates between Combined Sexes of Various Population Groups.

Population groups	23 PSV		25 PSV		23 & 25 PSV	
	X^2	P<	X^2	P<	X^2	P<
1. S.A. Negro v.						
San	0,09\$	0,90	1,33	0,25	1,02	0,50
East African Negro	1,20	0,25	0,11	0,75	0,67	0,50
Amer. Negro	3,02	0,10	21,80	0,001	6,76	0,01
Mongoloid	4,87	0,05+	6,77	0,01	12,52	0,001
Caucasoid	3,74	0,10	29,19	0,001	29,74	0,001
2. San v.						
East African Negro	0,20\$	0,75	0,87	0,50	1,79	0,25
Amer. Negro	0,01\$	0,90	12,92	0,001	4,02	0,05+
Mongoloid	0,16\$	0,75	5,29	0,025+	5,94	0,025+
Caucasoid	0,03\$	0,90	10,92	0,001	8,17	0,005
3. East African Negro v.						
Amer Negro	5,77	0,025+	17,64	0,001	1,19	0,50
Mongoloid	0,06	0,90	5,55	0,025+	3,39	0,10
Caucasoid	0,63	0,50	18,50	0,001	7,26	0,01
4. Amer. Negro v.						
Mongoloid	10,50	0,005	4,59	0,05+	0,95	0,50
Caucasoid	11,28	0,001	0,67	0,50	4,15	0,05+
5. Mongoloid v.						
Caucasoid	0,69	0,50	3,39	0,10	0,63	0,50

\$ = Yates's correction for small samples applied.
+ = Probably significant.
Underlined = Almost certainly and highly significant.

4. Sexual Differences in Numbers of Presacral Vertebrae

The numbers of PSV in males (Table 5.3) and females (Table 5.5) are now compared.

There is a tendency to a greater frequency of 23 PSV in the females than in the males of a population group. The difference in the frequency of 23 PSV is largest between American Negro males (5,2%) and females (11,4%). This difference is highly significant (chi-square = 8,64; P<0,005) and is the only significant difference between males and females with respect to the frequency of 23 PSV (Table 5.9).

TABLE 5.9

The Chi-square Values for the Differences in the Frequencies of 23 PSV, 25 PSV and Total Variates (23 PSV plus 25 PSV) between the Males and Females of Various Population Groups

Population Groups	23 PSV		25 PSV		23 PSV + 25 PSV	
	X^2	P<	X^2	P<	X^2	P<
Zulu (Present Series)	0,42	0,75	1,30	0,50	0,40	0,75
Natal Nguni (De Beer-Kaufman, 1974)	[illegible]	0,90	0,54*	0,50	0,41	0,75
Cape Nguni (De Beer-Kaufman, 1974)	0,34*	0,75	2,28*	0,25	0,82	0,50
Sotho (De Beer-Kaufman, 1974)	0,02*	0,90	6,21*	0,025+	3,22*	0,10
S.A. Negro (De Beer-Kaufman, 1974)	1,40	0,25	9,98*	0,005	3,57	0,10
Pooled S.A. Negro	1,77	0,25	12,08	0,001	3,86	0,05+
San	0,28*	0,75	0,41*	0,50	0,19*	0,75
Pooled American Negro	8,64	0,005	3,89	0,05+	1,50	0,25
Pooled Caucasoid	0,25	0,75	5,27	0,025+	1,60	0,25
Pooled Mongoloid	0,11	0,75	1,60	0,25	0,67	0,50
Japanese (Hasebe, 1913; Nishi, 1928)	0,27	0,75	0,02	0,90	0,23	0,75
Eskimo & Indian (Bornstein and Peterson, 1966)	0,11*	0,75	3,37	0,10	3,19	0,10

$ = Yates's correction for small samples applied
+ = Probably significant

An increased presacral vertebral number of 25 PSV is present much more commonly in males than in females. The highest frequency (25%) of 25 PSV is presented by San males. In the Zulu series no significant u... .erence in the frequencies of 25 PSV is present between sexes. This is in accordance with the difference between Natal Nguni males and females of De

Beer-Kaufman's (1974) study. Her S.A. Negro series show a highly significant difference (chi-square = 9,98; P<0,005) in the frequencies of 25 PSV between sexes. Of her study's sub-samples the difference between only Sotho males and females is probably significant (chi-square = 6,21; P<0,025).

In the pooled S.A. Negro sample the difference between sexes is highly significant (chi-square = 12,08; P<0,001). The American Negro, Caucasoid and Mongoloid males also outnumber their females in the incidence of 25 PSV. The differences between American Negro males and females (chi-square 3,89; P<0,05) and between Caucasoid males and females (chi-square = 5,27; P<0,025) are probably significant (Table 5.9).

Total variates (23 PSV plus 25 PSV) occur more frequently in males than in females of all population groups except American Negroes. In the American Negro series the females (13,8%) present a higher frequency of total variates than the males (10,7%), due especially to the high frequency of 23 PSV in the females. When the chi-square test was applied to the data in Tables 5.3 and 5.5, it was found that the differences in total variates between males and females within each population group were not significant (Table 5.9). The difference between only the pooled S.A. Negro males and females is probably significant (chi-square = 3,86; P<0,05).

The differences between the sexes with respect to the frequencies of specific variants (23 PSV v. 25 PSV) were highly significant in the pooled S.A. Negro (chi-square = 10,89; P<0,001) and in American Negro (chi-square = 10,18; P<0,01) samples and probably significant in the Caucasoid (chi-square = 4,06; P<0,05) sample (Table 5.10). This difference between the sexes in the pooled S.A. Negro sample is in accordance with the finding of De Beer-Kaufman (1974) while Bornstein and Peterson (1966) report the same result in their American Negro sample. From Tables 5.3 and 5.5 it is evident that these differences arise from different trends. In S.A. Negroes the high frequency of 25 PSV in the males gives rise to this difference while, in the American Negroes, it is produced mainly by the high frequency of 23 PSV in the females. The Caucasoid females present a low frequency of 23 PSV. The absence of significant differences in the frequencies of specific variants (23 PSV v. 25 PSV) between the sexes of the other population groups (Table 5.10) is corroborated by the absence of significant differences between the sexes for each of the specific variants (23 PSV; 25 PSV) on its own (Table 5.9).

TABLE 5.10

The Chi-square Values for the Differences between the Sexes with respect to the Frequencies of Specific Numerical Variations in Presacral Vertebrae (23 PSV vs 25 PSV)

Population group	Chi-square value	P<
Zulu* (Present study)	1,03	0,50
Natal Nguni* (De Beer-Kaufman, 1974)	0,17	0,75
Cape Nguni* (De Beer-Kaufman, 1974)	1,94	0,25
Sotho* (De Beer-Kaufman, 1974)	2,76	0,10
S.A. Negro (De Beer-Kaufman; 1974)	8,74	0,005
Pooled S.A. Negro	10,89	0,001
San*	0,02	0,90
American Negro	10,18	0,01
Caucasoid	4,06	0,05+
Mongoloid	1,09	0,50
Japanese	0,07	0,90
Eskimo + Indian*	0,47	0,[illegible]

$ = Yates' correction for small samples applied.
+ = Probably significant.
Underlined = Highly significant.

When data for firstly all males and secondly all females of all population groups are pooled, the degree of sexual difference with respect to the numbers of PSV in *Homo sapiens* can be derived from the combined weighted means. These results confirm that males tend to have an increased number of PSV (9,8%, n = 1757) as compared with females (3,7%, n = 1114). This difference between the sexes is highly significant ($z = 6,72$; $P < 0,001$). Conversely females (8,4%, n = 1114) have a greater tendency towards shortening of the vertebral column than males (4,95%, n = 1757). The difference between the sexes with respect to 23 PSV is highly significant (z = 3,52; P<0,001).

Thus, there is a tendency towards an increase in the number of PSV in males and towards a decrease in females. This association of sex with specific variations in the number of presacral vertebrae, as demonstrated in this study, has been suggested by Trotter (1929) and Danforth (1930) on the basis of small samples. Bornstein and Peterson (1966) and De Beer-Kaufman (1974) report, on large samples, similar findings which confirm this association. This led Bornstein and Peterson (1966) to suggest that variation in presacral vertebral number may be a sex dependent characteristic, females being more likely to have a shorter presacral column and males a longer presacral column.

B. The Numbers of Presacral Vertebrae in African and Asian Great Apes

1. Present Study

Problems in the obtaining of great ape material in South Africa are discussed in Chapter 3. For this part of the study articulated material could be used and the findings are reported in Table 5.11.

In these small series, it seems that the modal number in *Gorilla gorilla* may be 24 PSV and that there is a tendency to the reduction of the thoracic vertebrae resulting in 23 PSV. Among the seven *Pan troglodytes* specimens one has 25 PSV. This is the only individual in this ape series with 25 PSV.

The modal number in *Pan troglodytes* seems to be 24 PSV. The seven *Pongo pygmaeus* vertebral columns all present 23 PSV - which is a possible indication of the reduction of the modal number to 23 PSV in this Asian great ape species.

TABLE 5.11

The Numbers of Presacral Vertebrae (PSV) in African and Asian Great Apes

Catalogue number	Sex	PSV pattern	PSV
Gorilla gorilla			
Za 1311	Male	C7 T12 L4	23
Za 1312	Male	C7 T12 L4	23
Za 95	Male	C7 T13 L4	24
*TM	Male	C7 T13 L4	24
TM 16737	Male	C7 T13 L4	24
ZM 37016	Male	C7 T14 L3	24
Pan troglodytes			
Za 94	Male	C7 T13 L4	24
Za 1071	Male	C7 T14 L3	24
Z - 159	Male	C7 T13 L4	24
822 (W)	Female	C7 T13 L4	24
ZM 37007	Female	C7 T13 L4	24
ZM 37008	Male	C7 T13 L4	24
TM 16731	Male	C7 T14 L4	25
Pongo pygmaeus			
Za 1334	Male	C7 T11 L5	23
Z- 158	Male	C7 T11 L5	23
Za 93	Female	C7 T12 L4	23
TM 16732	Male	C7 T12 L4	23
UP	Male	C7 T12 L4	23
307 (W)	Male	C7 T12 L4	23
ZM 33590	Male	C7 T13 L3	23

* No number
Za = Raymond Dart Collection at the Department of Anatomy and Human Biology of the University of the Witwatersrand
TM = Transvaal Museum
UP = Zoology Department at the University of Pretoria
Z = Anatomy Department at the University of Cape Town
(W) = Zoology Department at the University of the Witwatersrand
ZM = South African Museum

2. Other African and Asian Great Ape Groups

2.1 Sources of Data

Although many studies have been made on the numerical variability of the great ape vertebral column, only a *few* permit statistical comparison of the numbers of PSV and even fewer permit statistical comparison between males and females of the great ape groups.

Todd (1922) reports the number of thoracolumbar vertebrae in 45 *Pan*, 33 *Gorilla* and 50 *Pongo* vertebral columns. He states that in mammals the number of cervical vertebrae generally is seven.

> "Hence, if we know the total of presacrals, we can readily ascertain the number of vertebrae comprising the thoracic and lumbar series together."
> (op.cit., p 263).

The opposite reasoning is used in the present study. If we know the number of thoracolumbar vertebrae, we can readily ascertain the number of presacral vertebrae for the number of cervical vertebrae generally is seven. The numbers of PSV are thus calculated from Todd's (1922) data and used in the present study. The sex of the vertebral columns is not reported and it is taken that the data are for males and females together.

Schultz (1930) also reports the numbers of thoracolumbar vertebrae in vertebral columns of all three great ape groups. He states that no case with a deviation in the normal number of seven cervical vertebrae was encountered. It is thus again possible to calculate the numbers of PSV in the 63 *Pan*, 86 *Gorilla* and 83 *Pongo* vertebral columns and to use Schultz's (1930) data in the present study. These data are not reported by sex and it is again taken as male plus female data.

Schultz (1940) reports the numbers of thoracolumbar vertebrae in 78 *Pan* vertebral columns. He also mentions that each of the vertebral columns has seven cervical vertebrae. It is thus again possible to calculate the numbers of PSV in these vertebral columns and to include these data in the present study. According to the definitions used by Schultz (1940), vertebrae presenting unilateral sacralization are counted half lumbar and half sacral. In the present study such vertebrae are counted as sacral with the result that in the 4% columns, reported by Schultz (1940), with thirteen thoracic and three and a half lumbar vertebrae the transitional vertebra is reported as sacral in the present study. The sex of the vertebral columns is again not mentioned and the data are taken as for males plus females.

The 78 *Pan* vertebral columns reported in Schultz's (1940) study may include sixteen of the 63 *Pan* vertebral columns reported by Schultz in 1930. In view of the scantiness of data on the great apes, the results of both studies are included in the present study.

Schultz (1941) reports the number of thoracic plus lumbar vertebrae in 107 *Pongo* vertebral columns. In three of these vertebral columns the seventh vertebra bears ribs that reach the manubrium, in two cases bilaterally. The precise definitions of the different types of vertebrae are not noted but according to definitions of a previous study (Schultz, 1930) these vertebrae are probably counted as thoracic. Unfortunately the numbers of thoracolumbar vertebrae of these three vertebral columns are not mentioned; hence they cannot be excluded from the rest of the vertebral columns. It is thus not possible to calculate the numbers of PSV in these vertebral columns with certainty. The data on 107 *Pongo* vertebral columns are thus not used in the present study. In another part of the Schultz (1941) study, the numbers of thoracolumbar vertebrae in 24 male and 24 female *Pongo* vertebral columns are mentioned. No comment as to the number of cervical vertebrae accompanies these results, but since only three vertebral columns out of a total of 107 vertebral columns (2,8%) show deviation from the normal number of seven cervical vertebrae, the author is of opinion that the number of cervical vertebrae in the 48 vertebral columns were almost certainly seven. The numbers of PSV in these 48 vertebral columns are thus calculated and included in the present study. These data are important for they are the only data on males and females separately thus far.

It is not possible to include the extensive study by Randall (1944) on *Gorilla* vertebral columns in this part of the present study. Although he states that seven cervical vertebrae were present in all the vertebral columns, he reports the number of thoracic vertebrae and the number of lumbar vertebrae separately which make it impossible to calculate the numbers of PSV in these vertebral columns as was done with the results of the previously mentioned studies. This is indeed unfortunate because all his data are recorded according to sex. Randall's (1944) study is, however, used fruitfully in the next chapter where the regional distribution of the PSV are discussed.

From the sources mentioned above the numbers of PSV in 186 *Pan*, 119 *Gorilla* and 181 *Pongo* vertebral columns are available for comparison. The results of the present study and the data available from the literature are summarised in Table 5.12. Only the 24 male and 24 female *Pongo* vertebral columns reported by Schultz (1941) permit comparison between males and females.

With an incidence of 71,5% it is evident that the modal number of PSV in the pooled *Pan* (males plus females) series is 24. The sets of data on *Pan* are contrasting in the sense that Schultz (1930; 1940) reports a high incidence of 24 PSV (74,6% and 76,0% respectively) indicating a fairly stable condition, while the incidence of 57,8% reported by Todd (1922) reflects a much more unstable condition. The difference between their results lies in the high frequency of

25 PSV (17,8%) reported by Todd (1922), while Schultz (1930) reports an incidence of 4,8% and Schultz (1940) reports no incidence of 25 PSV. The *Pan* specimen housed in the Transvaal Museum in Pretoria, one out of seven *Pan* columns examined by the author, presents 25 PSV. The frequency of 25 PSV in the pooled *Pan* series is 6,2%.

Both Todd (1922) and Schultz (1930; 1940) report a high tendency to reduction of the number of PSV in the chimpanzee. The minus-variations, 23 PSV and 22 PSV, occur in 21,2% and 1% of the pooled vertebral columns respectively. None of the seven vertebral columns examined by the author presents fewer than 24 PSV.

The difference between the frequencies of 23 PSV and 25 PSV (23 PSV v. 25 PSV) in the pooled *Pan* series is highly significant (chi-square = 17,15; P<0,001). This significantly higher incidence of 23 PSV shows a definite tendency towards shortening of the vertebral column in the pooled *Pan* (males plus females) series.

In the *Gorilla* series the modal number of PSV is also 24 but the relatively low incidence of 57,6% indicates a greater tendency towards variation. Only one vertebral column (0,8%) with 25 PSV is recorded. The frequency of 23 PSV in the pooled *Gorilla* series is 39,2%, while 22 PSV occurs in 2,4% of the vertebral columns. Although only six *Gorilla* vertebral columns have been examined by the author, their variability in the number of PSV did not differ from that of the rest of the *Gorilla* vertebral columns summarised in Table 5.12.

The difference between the frequencies of 25 PSV and 23 PSV in the pooled *Gorilla* series is highly significant (chi-square = 55,23; P<0,001). This significantly higher frequency of 23 PSV indicates an even more striking tendency towards shortening (i.e. affecting 41,6%) than is apparent in *Pan* (22,2% affected).

TABLE 5.12

The Numbers of Presacral Vertebrae in a Comparative African and Asian Great Ape Series

Great Ape Taxon	n	Sex	22 PSV		23 PSV		24 PSV		25 PSV		Reference
			n	%	n	%	n	%	n	%	
Pan	45	M+F	1	2,2	10	22,2	26	57,8	8	17,8	Todd (1922)
	63	M+F	1	1,6	12	19,0	47	74,6	3	4,8	Schultz (1930)
	78	M+F	-	-	19	24,0	59	76,0	-	-	Schultz (1940)
	5	M	-	-	-	-	4	66,7	1	33,3	Present Study
	2	F	-	-	-	-	2	100	-	-	Present Study
	193	M+F	2	1,0	41	21,2	138	71,5	12	6,2	
Gorilla	33	M+F	2	6,1	13	39,4	18	54,5	-	-	Todd (1922)
	86	M+F	1	1,2	34	39,5	50	58,1	1	1,2	Schultz (1930)
	6	M	-	-	2	33,3	4	66,7	-	-	Present Study
	125	M+F	3	2,4	49	39,2	72	57,6	1	0,8	
Pongo	50	M+F	3	6,0	39	78,0	8	16,0	-	-	Todd (1922)
	83	M+F	12	14,5	63	75,9	8	9,6	-	-	Schultz (1930)
	24	M	4	16,7	18	75,0	2	8,3	-	-	Schultz (1941)
	24	F	4	16,7	17	70,8	3	12,5	-	-	Schultz (1941)
	6	M	-	-	6	100	-	-	-	-	Present Study
	1	F	-	-	1	100	-	-	-	-	Present Study
	188	M+F	23	12,2	144	76,6	21	11,2	-	-	

In the pooled *Pongo* series (males plus females), 76,6% of the vertebral columns present 23 PSV; i.e. the modal number of PSV is 23. This high frequency of the modal number indicates a fairly stable condition with a low tendency to variation. No vertebral column with 25 PSV is recorded. The frequency of 24 PSV is 11,2%, while 22 PSV occurs in 12,2% of the pooled *Pongo* vertebral columns. The difference between the frequencies of 22 PSV and 24 PSV is not significant (chi-square = 0,03; P<0,75), which shows a symmetrical distribution of the tendency to variation. No deviation from the modal number of 23 PSV occurs in the seven *Pongo* vertebral columns examined by the author.

3. Intergroup Comparisons of the Presacral Vertebrae

When the African great apes are compared the frequencies of 24 PSV are the highest. The modal number of PSV is 24 in both *Pan* and *Gorilla* vertebral columns. The frequency of 24 PSV is however much higher in the pooled *Pan* vertebral columns (71,5%) than in the pooled *Gorilla* vertebral columns (57,6%). This difference between the frequencies of 24 PSV in the African great ape vertebral columns is significant (chi-square = 5,93; P<0,25), which indicates a more stable condition in *Pan* vertebral columns.

The tendency to the plus-variation is lower than the tendency to the minus-variation in both *Pan* and *Gorilla* vertebral columns. The pooled *Pan* vertebral columns (n = 193), however, present a higher frequency of 25 PSV (6,2%) than the pooled *Gorilla* vertebral columns (n = 125) in which only one vertebral column (0,8%) has 25 PSV. The difference between the frequencies of 25 PSV in the African great apes is probably significant (chi-square = 4,27; P<0,05).

The minus-variations, 23 PSV and 22 PSV, occur more frequently in the pooled *Gorilla* vertebral columns than in the pooled *Pan* vertebral columns. The frequency of 23 PSV in *Gorilla* vertebral columns, 39,2%, and the frequency of 23 PSV in *Pan* vertebral columns, 21,2%, are highly significantly different (chi-square = 11,19; P<0,001). The difference in the frequencies of 22 PSV between the African great ape vertebral columns is not significant (chi-square = 0,24; P<0,75).

Variation in the numbers of PSV in both *Pan* and *Gorilla* vertebral columns show a greater tendency towards shortening of the vertebral column than towards lengthening. The tendency towards shortening of the vertebral column is highly significantly greater in *Gorilla* vertebral columns than in *Pan* vertebral columns. A tendency towards lengthening of the vertebral column is very small in both genera, but is probably significantly greater in *Pan* vertebral columns than in *Gorilla* vertebral columns.

The most important difference between the African and Asian great ape vertebral columns is that the modal number of PSV is 23 in *Pongo* and 24 in *Pan* and *Gorilla* vertebral columns. The high incidence (76,6%) of the modal number of PSV in *Pongo* vertebral columns seems to indicate a more stable condition in the numbers of PSV in *Pongo* than in *Pan* and *Gorilla* vertebral columns. The chi-square test, however, shows no significant difference (chi-square = 1,03; P<0,50) between the frequencies of the modal numbers of PSV in *Pongo* and *Pan* vertebral columns. The difference between the frequencies of the modal number of PSV in *Pongo* and *Gorilla* vertebral columns is highly significant (chi-square = 11,80; P<0,001).

The tendency to the plus-variation is greater in the *Pongo* vertebral columns (11,2%) than in either *Pan* (6,2%) or *Gorilla* (0.8%) vertebral columns. The difference in the frequencies of the plus-variation between *Pongo* and *Pan* vertebral columns is not significant (chi-square = 2,36; P<0,25). The difference in the frequencies of the plus-variation between *Pongo* and *Gorilla* vertebral columns is, however, highly significant (chi-square = 10,82; P<0,005).

In comparison with the African great ape vertebral columns, *Pongo* vertebral columns present a lower tendency towards the reduction of the modal number of PSV (minus-variation). The frequencies of the minus-variation in *Pongo* and in *Pan* vertebral columns are probably significantly different (chi-square = 5,65; P<0,025). The difference between the frequency of the minus-variation in the *Pongo* (12,2%) and the frequency of 23 PSV in *Gorilla* vertebral columns (39,2%) is highly significant (chi-square = 29,32; P<0,001).

Comparison of the numbers of PSV in African and Asian great ape vertebral columns shows firstly that the modal number of PSV is 23 in *Pongo* and 24 in *Pan* and *Gorilla* vertebral columns. Secondly the frequencies of the modal number, the plus-variation and the minus-variation are highly significantly different between the *Pongo* and the *Gorilla* vertebral columns. This highly significant difference may be owing to the unstable condition in the numbers of PSV in *Gorilla* vertebral columns associated with a high tendency towards reduction of the number of PSV in the vertebral columns. Thirdly, the frequencies of the modal number of PSV and the plus-variation between *Pongo* and *Pan* vertebral columns are not significantly different, while the difference in the frequencies of the minus-variation between *Pongo* and *Pan* vertebral columns is probably significant. These results may be ascribed to the high frequencies of the modal number of PSV in both great ape groups which indicates a fairly stable condition. The difference between *Pongo* and *Pan* vertebral columns lies in the fact that the modal number of PSV is different and that *Pan* vertebral columns present a probably significantly higher tendency towards reduction of the modal number of PSV while the tendency towards variation is distributed equally between plus-variation and minus-variation in the *Pongo* vertebral columns.

4. Sexual Differences in Numbers of Presacral Vertebrae

The only data which permit comparison between males and females are the 24 male and 24 female *Pongo* vertebral columns reported by Schultz (1941). The male and female vertebral columns present an equal tendency towards reduction of the modal number of PSV. The frequency of the modal number of PSV is higher in the males (75,0%) than in the females (70,8%). This difference is however, caused by the fact that the females present three vertebral columns with 24 PSV to the two male vertebral columns with 24 PSV.

Only one *Pan* and one *Pongo* female are included in the present study. From these data a difference in the number of PSV between males and females of African and Asian great apes can not be derived although there may be such a difference.

C. The Numbers of Presacral Vertebrae in Australopithecinae

There are as yet no complete vertebral columns among the many *Australopithecus* fossils discovered. The partial vertebral column of Sts 14 from Member 4 of the Sterkfontein Formation, which presents the lower fifteen presacral vertebrae, is the most complete discovered yet.

Sts 14 partial vertebral column appears to represent the entire lumbar region and most of the thoracic region in sequence. Robinson (1972) classifies these vertebrae as six lumbar and nine thoracic vertebrae. The author supports Robinson's (1972) classification as is explained in Chapter 6 of the present study where the regional distribution of the presacral vertebrae is discussed.

The newly recovered Sterkfontein partial vertebral column (Stw 431) appears to represent the entire lumbar region of five vertebrae and the last four thoracic vertebrae of the same individual. Since the upper part of the thoracic region and at least the last cervical vertebra are not preserved in either of the partial skeletons, it is not possible to number the existing thoracic vertebrae with certainty.

The rest of the *Australopithecus africanus* fossil vertebrae are either single vertebrae (Sts 73, Sts 65) or parts of a vertebral column (Stw 8 + Stw 41) and thus not informative as to the number of presacral vertebrae. The same applies to the three individual *Australopithecus robustus* vertebrae (SK 3981a; SK 3981b; SK 853) from Swartkrans, each representing a different vertebral region.

It is also not possible to derive the segmentation or the number of presacral vertebrae of *Australopithecus afarensis* from the vertebrae yielded by the Hadar formation in Ethiopia, for they are either isolated vertebrae of different individuals, or from the same partial column but do not follow in sequence. The nine isolated vertebrae of different individuals are yielded by the AL-333 locality of the Hadar formation (Cook *et al.*, 1983). The partial vertebral column AL-288 (Lucy), from the same formation, presents ten vertebrae but they do not follow in sequence (Johanson, *et al.*, 1982).

There is thus as yet no evidence as to what number of total presacral vertebrae occurred in *Australopithecus*.

D. Discussion of the Numbers of Presacral Vertebrae

Most of the contributions, at the turn of the century, to the subject of the variations in the number of PSV in Man resolved themselves into a discussion of mainly two groups of hypotheses. The first group sought to explain numerical variation in human vertebrae as phylogenetic shortening or lengthening, while the second group saw these variations as expressions of inherent variability.

The two names usually associated with the first group of hypotheses are those of Rosenberg (1876) and Welcker (1878). Rosenberg (1876) contended that the vertebral column had undergone the phylogenetic and ontogenetic shortening by cranial movement of the pelvis. Simultaneously, the thorax had shortened by the loss of ribs. In contrast to this view, where the movement of the pelvis plays an important role, Welcker (1878) emphasized the importance of the 'vertebra fulcralis' (the vertebra which contributes most largely to the auricular surface of the sacrum) as a fixed point. Variations in the number of PSV occur by intercalation or excalation of parts cranial to this point.

Paterson (1892), a supporter of the second hypothesis, discarded Welcker's (1878) theory and argued that the hypothesis of inherent variability fully explains the cases of individual variation. In contrast to Rosenberg (1876), Bardeen (1904) showed that the supposed vestigial ribs probably do not exist in the human embryo and that ontogenetically the pelvis moves caudally instead of cranially. He concluded:

> "Regional variation in the vertebral column is an inherited condition which makes itself manifest early in embryonic development". (op.cit., p 513)

This view is corroborated by the family and twin studies of Kühn (1932, 1936) in which he showed that variability in vertebral number is an inherited trait. He noted also differences in vertebral number in different human races which he attributed to variations in gene frequency.

Studies of hereditary variation in the axial skeleton of the rabbit by Sawin (1937) argued against the possibility of a single mendelian gene with only dominant and recessive alleles. In a later study, Sawin and Trask (1965) provided evidence that, by the transfer of a specific gene to a different genome, the tendency to shift the thoracolumbar and lumbosacral vertebral junctions cephalad can be enhanced or inhibited. Sawin, Gow and Muehlke (1967) showed that in the rabbit several minor modifying genes with one major gene, influence the variations in the vertebral junction areas.

Danforth (1930, on modern humans) and Sawin (1937, on rabbits) suggested that one of the factors influencing the expression of numerical variation is associated with sex. Bornstein and Peterson (1966) presented evidence that race and sex must be considered to influence the expression of the genes for numerical variation in man. They found their American Negro group to differ from the Caucasoid and Mongoloid groups with respect to the distribution of specific vertebral variants. This led to the hypothesis:

> "The total incidence of variation in the number of presacral vertebrae appears to be a specific characteristic of any particular population group studied." (op.cit., p 145)

In the present study the frequency of total variation in S.A. Negro (males plus females) differs almost certainly significantly from American Negroes, Caucasoids and Mongoloids, but not from San or East African Negroids. This tends to confirm that total variation in the number of PSV in males plus females appears to be a specific characteristic of each major racial group. With respect to the specific variant, 23 PSV, the American Negroes differ highly significantly from Mongoloids and Caucasoids. This difference is based mainly on the high frequency of 23 PSV and the low frequency of 25 PSV in American Negroes. The low frequency of 25 PSV in American Negroids may be compared with the low frequency of 25 PSV in Caucasoids, in which respect these two groups differ highly significantly from the S.A. Negroes, San and East African Negroes. If the numerical variations are genetically determined, a possible explanation for the similarity of the Caucasoid and American Negroids may lie in the genetic composition of American Negroids. Glass and Li (1953), using data on Rh_o frequency, estimate that the amount of Caucasoid admixture in North American Negroids is 30,57%. A revision of this (Glass, 1955) estimates admixture to be 21,6%. Si .larly Roberts (1955), who uses five discriminating characters, estimates the amount of admixture to be 20%. Reed (1969) reviews evidence and estimates the amount of admixture to be 21,95%, using Fy^a frequencies. Such a large degree of hybridisation may account for the low incidence of 25 PSV in American Negroids, in contrast with the higher incidence in African Negroids.

The results of the present study agree with De Beer-Kaufman's (1974) results. She suggested that racial differences in presacral vertebral variation may be more readily recognised when males and females are considered separately, for sexual differences may mask racial differences. In the present study this was found partly true, for the difference in total variates in the male category revealed racial differences (Table 5.4) more readily than in the male plus female category (Table 5.8). When data for the male plus female category and for the female category were compared, the males plus females proved to show racial differences more readily. For each of the specific variants, 23 PSV and 25 PSV, the data for males plus females (Table 5.8) also more readily show racial differences than does either the male category (Table 5.4) or the female category (Table 5.6).

Bornstein and Peterson (1966) hypothesized further that within each group the frequency of the trend towards lengthening (25 PSV) of the column appears to be a characteristic associated more with sex than with race. They were led to this conclusion by the fact that a higher incidence of 23 PSV in females and of 25 PSV in males have been reported by several investigators (Bardeen, 1904; Danforth, 1930; Trotter, 1929), and by similar findings in their own study. The findings of De Beer-Kaufman (1974) and of the present study support the higher incidence of 23 PSV in females and of 25 PSV in males.

The high frequency of total variation in both males and females found in the present study supports the finding of De Beer-Kaufman (1974). She reported an extremely high incidence of vertebral variants in the Nguni and Sotho tribal groups in contrast to the Shangaan. The San series was the only group to exceed this high frequency of variation.

It has been suggested that the number of PSV may be a genetically determined variant influenced by race and sex. The following discussion on the relationship of the different population groups is based on this supposition.

No significant difference in the frequencies of numerical variation was found between the Zulu sample of the present study and any of De Beer-Kaufman's (1974) sub samples (tribal groups). This has led the author to pool the tribal samples to form a S.A. Negro series. When the combined sexes of the S.A. Negro sample and of Allbrook's (1955) sample of East Africans are compared, no significant differences in the frequencies of total variates or specific variants are found. Tobias (1972) listed sub-Saharan African genotypes and showed the genetic unity of sub-Saharan negriform peoples. (This means that the sub-Saharan Negroes belong to the same major gene constellation or geographical race.) The absence of differences in numerical variation between S.A. Negroes and East African Negroes thus supports the view that the number of PSV may be a genetically determined variant.

No significant differences in the frequencies of numerical variation were found between San and S.A. Negroes when the sexes were considered apart or combined. The same is true for San and East African Negro males plus females. Tobias (1972) has reviewed genetic studies and has shown the general sub-Saharan African affinities of the Khoisan, in spite of the numerous morphological characteristics in which San differ appreciably from Southern African Negroes. He has postulated that early proto-negriform Africans split into two major branches, the Khoisans and the Negroes, from a basically Khoisan-like ancestral genome. This split was followed by a fairly lengthy period of geographical isolation, with the Khoisans mainly in eastern and southern Africa and the Negroes in tropical Africa. During this period of isolation certain genetic divergences arose in both populations, but not so striking as to obliterate their basically similar genetic makeup. Later there occurred expansion of the Negroes and hybridization between them and the San.

The absence from African peoples of significant differences in numerical variations of the vertebral column is due mainly to the agreement of San, S.A. Negroes and East African

Negroes in having high frequencies of an increase of PSV. The findings of this presumed genetic trait tend to support the evidence that Khoisans and Southern African Negroes sprang from the same ancestral proto-negrifo.. stock.

The exceptionally high frequency of an increased number of PSV (17,9% in the sexes combined, 25% in the males and 8,3% in the females) in De Beer-Kaufman's (1974) small San sample provides slight further evidence of the trend noted by Tobias (1966) that the San tend to show extreme values for a number of genetic markers and some somatic traits. Such extreme values might be explained by Tobias's (1972) postulate that the recent Khoisan have departed relatively little from the inferred ancestral genotype, here characterised by a tendency towards an increased number of presacral vertebrae.

Tobias (1972) noted further that during later regional expansion some of the Negroes encountered Khoisan populations and hybridised with them.

> "There is little doubt from skeletal, serological, anthropometric and anthroposcopic evidence that hybridization occurred in varying degrees between southern African Negroes and Khoisans".
> (op.cit., p 128).

On the basis of the frequency of the serum protein allele $Gm^{1,13}$, which attains a high value in Khoisan, Jenkins, Zoutendyk and Steinberg (1970) estimate the amount of San admixture in Southern African populations as 60% admixture in Xhosa (Cape Nguni), 45% in Zulu (Natal Nguni), 29% in Sotho and 15% in Shangana-Tsonga. This is supported by the exceptionally high frequency of 25 PSV in San and in the Cape Nguni sample. De Beer-Kaufman (1974) reports that the analysis of precoccygeal vertebral variation supports the evidence of a relatively closer relationship between San and Cape

Nguni than between San and Sotho, San and Natal Nguni or San and Shangaan. De Villiers (1975) shows the same relationship through cranial metrical traits, blood groups and serum factors.

The relationship among African Negroes, American Negroes and Caucasoids is discussed earlier. Hybridisation, to the extent of approximately 21% Caucasoid admixture, may account for the low incidence of 25 PSV in American Negroes (which is in accordance with the low incidence of 25 PSV in Caucasoids), in contrast with the high incidence of 25 PSV in African Negroes.

Comparison of the numbers of PSV in the giant anthropoids reveals a closer relationship between the African great apes, for both *Pan* and *Gorilla* vertebral columns present a modal number of 24 PSV, in contrast with the modal number of 23 PSV in *Pongo* vertebral columns. The frequencies of variations in the number of PSV show that the African great apes have a higher tendency to 23 PSV (minus-variation) than to 25 PSV (plus-variation), though *Pan* has a definitely stronger tendency to 25 PSV than does *Gorilla* (Table 5.12). In *Pongo* there is no significant difference between the frequencies of the plus-variation and the minus-variation.

When we compare man with the African and Asian great apes we see that the modal number in man, *Gorilla* and *Pan* is 24 PSV. *Gorilla* and *Pan*, however, show a much higher tendency to departures from the mode than does man. *Gorilla* presents the highest frequency of variation. In contrast with man who shows a higher tendency to 25 PSV than to 23 PSV, both African great apes have a higher tendency to 23 PSV than to 25 PSV. *Pan* however has a definitely stronger tendency to 25 PSV than does *Gorilla*. From this evidence of the variations in the numbers of PSV, the difference in the modal number between *Pongo* and the African great apes plus man suggests that the African great apes are more closely related to man than

Pongo is related to man. The higher frequency of 25 PSV in *Pan* than in *Gorilla* suggests that *Pan* in its spinal column is phylogenetically nearer to man than is *Gorilla*.

Andrews and Cronin (1982) use the morphology of the lower face to show that many of the characters shared by man, chimpanzee, gorilla and gibbons are not present in the orang-utan. They indicate that man and the African apes share the derived condition. They also review molecular data and conclude:

> "The conclusion, therefore, is that, in so far as the molecular evidence reveals phylogenetic relationships, the orang-utan is removed from unique association with the African apes and is the sister group to the clade comprising the African apes and man" (op.cit., p 542).

Goodman *et al.* (1983), by using α- and β-haemoglobin amino acid sequences with other known haemoglobin sequences in phylogenetically reconstructions present evidence which cladistically joins *Pan* and *Gorilla* to *Homo* in Homininae rather than to *Pongo* in Ponginae. Evidence from the amino acid sequence data hints also at the possibility that *Pan* is more closely related to *Homo* than to *Gorilla*.

Todd (1922), who studied the number of thoracolumbar vertebrae in the Primates, concluded that the number of thoracolumbar vertebrae bears an interesting relationship to the degree of specialization of the genus. Phylogenetic shortening of the vertebral column by evolutionary migration of the pelvis in a cephalic direction has gone distinctly further in the giant anthropoids than in Man. *Pongo* has gone furthest in this dispensation and so has become most specialised in this respect.

The study of the numbers of PSV shows thus that variations in the numbers of PSV in modern humans are influenced by race and sex. The frequencies of variations may be accepted as additional evidence indicating the relationships among different races. The frequencies of variation show also a tendency towards lengthening in male vertebral columns and a tendency towards shortening of the vertebral column in females. In the great ape series the modal numbers show that *Pan* and *Gorilla* may be more closely associated. It shows also a closer association between man and the African great apes than between man and *Pongo*. The greater tendency towards lengthening of the vertebral column in *Pan* than in *Gorilla* vertebral columns is in keeping with a closer association between *Pan* and *Homo* than between *Gorilla* and *Homo*.

E. Summary and Conclusions

1. The variation in the number of PSV in the Zulu sample of the present study corresponds with the results of earlier studies on S.A. Negro vertebral columns. No significant difference was found in the frequencies of specific numerical variants or of total variates between the Zulu sample and De Beer-Kaufman's (1974) subsamples or tribal groups in the categories males, females and males plus females. The data for the tribal groups have thus been pooled to form a representative S.A. Negro sample.

2. The results of the present study on the frequencies of the specific variants (23 PSV; 25 PSV) further support the evidence that the variation in the number of presacral vertebrae appears to be a specific characteristic of each major racial group.

3. Within each group the frequency of the tendency towards lengthening or shortening of the vertebral column is associated more with sex than with race. The tendency towards an increase in the number of presacral vertebrae

in males and towards a decrease in females found in this study accords with findings in previous studies. When the population groups are pooled to form a sample of *Homo sapiens* the difference between the sexes with respect to the specific variants proved highly significant.

4. The author's data support the suggestion that the number of presacral vertebrae may be a genetically determined variant influenced by race and sex. Based on this supposition the number of presacral vertebrae provides further support for the inferred genetic relationships of the sub-Saharan African Negroes, that between San and sub-Saharan African Negroes, the specific relationship between San and Southern African Negroes and that between African and American Negroes with specific reference to Caucasoid admixture in the latter.

5. Comparison of the numbers of PSV in the African great apes shows that the modal number is 24 PSV in both *Pan* and *Gorilla* vertebral columns. The significant difference between the frequencies of 24 PSV indicates a lower tendency to variation in *Pan* vertebral columns than in *Gorilla* vertebral columns. Variations in the numbers of PSV in both *Pan* and *Gorilla* vertebral columns show a greater tendency towards shortening of the vertebral column than towards lengthening, though *Pan* has a definitely stronger tendency towards 25 PSV (i.e. lengthening) than does *Gorilla*.

6. When the numbers of PSV in African and Asian great ape vertebral columns are compared, the outstanding difference is the modal number. *Pongo* vertebral columns present a modal number of 23 PSV, in contrast with the modal number of 24 PSV in *Pan* and *Gorilla* (and in human) vertebral columns. *Pongo* vertebral columns also present an almost equal (no significant difference) tendency towards lengthening and shortening of the vertebral

column about the mode of 23 PSV, whereas both *Pan* and *Gorilla* vertebral columns show a significantly greater tendency towards shortening of the vertebral column.

7. Comparison of the numbers of PSV in the African and Asian great apes and man show a difference in the modal number of PSV between *Pongo* (23 PSV) and *Homo*, *Pan* and *Gorilla* (24 PSV), which suggests a closer relationship between man and the African great apes than between man and *Pongo*. *Gorilla* and *Pan*, however, show a higher tendency to departures from the mode than man. In the frequencies of variations man shows a higher tendency to 25 PSV than to 23 PSV. In contrast both the African great apes have a higher tendency to 23 PSV than to 25 PSV. *Pan*, however, has a definitely stronger tendency to 25 PSV than *Gorilla* which might be an indication of a position phylogenetically nearer to man than that of *Gorilla*.

8. The numbers of PSV bear an interesting relationship to the degree of specialization of the genus. Phylogenetic shortening of the vertebral column by evolutionary migration of the pelvis in a cephalic direction has gone distinctly further in the Asian great apes than in African great apes and in man. *Pongo* has gone furthest and so become most specialised in this respect.

9. The modal numbers of PSV and the variations in the number of PSV in man and the giant anthorpoids support the current opinion on the branching sequence or cladistic relationships of the living apes and man as shown by morphological and molecular studies. The evolution of hominoids involved first the divergence of the gibbons, followed by the orang-utans, followed by a split between hominids, chimpanzees and gorillas. Evidence as to the order of the last divergence is at present equivocal.

The higher frequency of 25 PSV in *Pan* than in *Gorilla* vertebral columns supports evidence from the amino acid sequence data which hints at the possibility that *Pan* is more closely related to *Homo* than to *Gorilla*.

CHAPTER 6

THE NUMBERS OF THORACIC AND LUMBAR VERTEBRAE IN VARIOUS HOMINOIDS

Contents of Chapter

Introduction

The total numbers of presacral vertebrae (PSV), as discussed in the previous chapter, give no necessary indication of variation in the regional distribution of presacral vertebrae. The absolute numbers of vertebrae, and the numerical variability in the cervical, thoracic and lumbar regions of the vertebral column are recorded in a modern human sample (120 Zulu vertebral columns) and in an African and Asian great ape sample of 20 available vertebral columns, and the numbers of vertebrae in the fossil partial vertebral columns are then appraised in the light of these results.

Criteria concerning the characteristic features which determine the regional allocation of a vertebra are described in Chapter 3. An apparently last cervical or first lumbar vertebra with costal facets, unilateral or bilateral, is not classified as thoracic. A seemingly last lumbar vertebra is counted as sacral if one or both transverse processes are enlarged and developed so as to form part of the sacro-iliac joint and to contribute to the formation of a sacral foramen.

Yates's correction is applied in the calculation of chi-square in all cases where the number of degrees of freedom is one, where the frequency in any cell is less than five and if the sample numbers are fewer than 30.

A. The Numbers of Thoracic and Lumbar Vertebrae in Modern Human Series

1. Zulu Series

No variation in the numbers of cervical vertebrae is found in the 120 Zulu vertebral columns examined. The regional distribution of presacral vertebrae (PSV) may be classified into seven regional patterns (Table 6.1). Vertebral columns of combined sex with the modal number of 24 PSV present three patterns of regional distribution: the typical regional formula C7, T12, L5 observed in 77,50% of the vertebral columns; C7, T11, L6 observed in one column (0,83%); and C7, T13, L4 found in one column (0,83%).

TABLE 6.1

The Regional Distribution of Presacral Vertebrae in Zulu Spinal Columns

PSV	Regional Pattern	Males n	Males %	Females n	Females %	Total n	Total %
23	C7 T11 L5	3	3,75	2	5,0	5	4,17
23	C7 T12 L4	4	5,00	3	7,5	7	5,83
24	C7 T11 L6	1	1,25	0	0	1	0,83
24	C7 T12 L5	60	75,00	33	82,5	93	77,50
24	C7 T13 L4	1	1,25	0	0	1	0,83
25	C7 T12 L6	8	10,00	2	5,0	10	8,33
25	C7 T13 L5	3	3,75	0	0	3	2,50
Total		80	100	40	100	120	100

Two patterns of regional distribution are noted among the twelve vertebral columns with 23 PSV. Seven (5,83%) of these columns have the regional formula C7, T12, L4, while the formula C7, T11, L5 is observed in five (4,17%).

The thirteen vertebral columns with 25 PSV show two patterns of regional distribution: ten (8,33%) with the formula C7, T12, L6, and three (2,50%) with C7, T13, L5.

In the male vertebral columns (n = 80), the regional formula with the second highest frequency (10,00%) is C7, T12, L6 (25 PSV). C7, T12, L4 occurs in four (5%) of the male columns while there is an equal distribution (3,75%) of the regional formulae C7, T11, L5 (23 PSV) and C7, T13, L5 (25 PSV). From these results it seems as if a small tendency to increase the number of PSV and of lumbar vertebrae marks the male vertebral columns.

The female vertebral columns (n = 40) present only four different patterns of regional distribution and the frequency of the modal formula, C7, T12, L5, is higher in the female columns (82,5%) than in the male columns (75,0%). The regional formula with the second highest frequency (7,5%) is C7, T12, L4 (23 PSV), while there is an equal distribution (5,0%) of the regional formulae C7, T11, L5 (23 PSV) and C7, T12, L6 (25 PSV). From these results it seems as if there is a tendency to reduction of the number of PSV and of the thoracic or lumbar vertebrae in the female vertebral columns.

When the numbers of vertebrae in the thoracic and lumbar regions are considered separately, the numbers of thoracic vertebrae in the Zulu vertebral columns (Table 6.2) range between eleven and thirteen, with twelve the modal number in both male and female columns. When the sexes are considered together, two more cases of eleven than of thirteen thoracic vertebrae are presented. The male vertebral columns show a greater tendency to thirteen thoracic vertebrae than do the female columns.

TABLE 6.2

The Numbers of Thoracic Vertebrae in Zulu Spinal Columns

	n	11		12		13	
		n	%	n	%	n	%
Males	80	4	5,0	72	90,0	4	5,0
Females	40	2	5,0	38	95,0	0	0,0
Total	120	6	5,0	110	91,7	4	3,3

Of the six vertebral columns (four male and two female) with eleven thoracic vertebrae, five have 23 PSV while the sixth column, which belongs to a male skeleton, has 24 PSV. Three of the four male columns with thirteen thoracic vertebrae present 25 PSV and the remaining column 24 PSV.

The numbers of lumbar vertebrae in the Zulu vertebral columns (Table 6.3) range between four and six, with five the modal number. The frequency of the modal number is 84,17% in the sexes combined. The females show a slightly higher frequency (87,5%) of the modal number than the males (82,5), which again suggests a lower tendency to variation in the female columns. In the frequencies of variants from the modal number, male columns have a higher tendency to an increased number, and female columns to a decreased number, of lumbar vertebrae. The differences between the frequencies of four and six lumbar vertebrae prove not significant in the male (chi-square = 0,70; P<0,50), female (chi-square = 0,21; P<0,75) and male-plus-female (chi-square = 0,06; P<0,90) series.

TABLE 6.3

The Numbers of Lumbar Vertebrae in Zulu Spinal Columns

	n	4		5		6	
		n	%	n	%	n	%
Males	80	5	6,25	66	82,50	9	1,25
Females	40	3	7,50	35	87,50	2	5,00
Total	120	8	6,67	101	84,17	11	9,16

In the Zulu sample, the lumbar vertebrae present a greater tendency to variation than the thoracic in all three categories: males, females and the sexes considered together. The chi-square tests, however, show no significant differences between the frequencies of variation in the thoracic and lumbar regions in all three categories.

2. Other Modern Human Populations

2.1 Sources of Data

In Chapter 4 on variations in the numbers of PSV in various population groups, the results of authors on series drawn from the same population group, which show no significant differences *inter se*, are pooled. Results from the same studies are considered here, provided firstly the regional distribution of PSV is available and, secondly, the criteria used to allocate a vertebra to a specific region agree with those used in the present study.

Comparative S.A. Negro data are provided by the study of De Beer-Kaufman (1974). She reports the regional distribution of PSV in 305 male and 157 female vertebral columns. She notes also the regional distribution of PSV in 28 San vertebral columns (16 male and 12 female) which data are also included in the present study.

Data on American Negro males and females are noted by Bardeen (1904) in 34 male and in 20 female vertebral columns.

The data on regional distribution of PSV in Caucasoids are taken from the studies of Steinbach 1389) on 83 German vertebral columns, Bianchi (1894) on 130 Italian vertebral columns, both cited by Bardeen (1904), and of Frey (1929) on 150 Swiss vertebral columns. Together these studies provide data on 363 Caucasoid vertebral columns, 200 male and 163 female.

The results of Bornstein and Peterson (1966) on 248 male and 269 female vertebral columns of American Negroes and on 488 American White vertebral columns (263 males and 225 females) are not suitable for comparison with those of the present study, since different definitions are used to allocate a vertebra to the thoracic region. In contrast to the present study, they count cervical and lumbar vertebrae which bear costal facets as thoracic vertebrae (See Chapter 3). The same holds for their data on 234 Mongoloid vertebral columns.

The data used for comparison with the results of the present study are listed in Tables 6.4, 6.5, 6.6, 6.7, 6.8 and 6.9.

3. Intergroup Comparisons of the Numbers of Thoracic Vertebrae.

3.1 Intergroup Comparisons among Males

In the males of each population group, twelve is the modal number and no significant difference between the frequencies of eleven and thirteen thoracic vertebrae is found.

Comparisons among the males of various population groups (Table 6.4) reveal firstly no significant differences among the populations in the frequencies of eleven, twelve and thirteen thoracic vertebrae (chi-square = 1,39; P<0,975 with six degrees of freedom). Secondly, the tendencies to variation and thirdly, the frequency of eleven thoracic vertebrae versus that of thirteen thoracic vertebrae show no significant differences among the population groups (P<0,75; with three degrees of freedom).

TABLE 6.4

The Numbers of Thoracic Vertebrae in the Males [illegible] Various Population Groups

Population group	n	11		12		13		Mean	References
		n	%	n	%	n	%		
S.A. Negro:									
Zulu	80	4	5,00	72	90,00	4	5,00	12,00	Present Study
	305	11	3,61	281	92,13	13	4,26	12,01	De Beer-Kaufman (1974)
Pooled	385	15	3,90	353	91,68	17	4,42	12,01	
Amer. Negro:	34	2	5,88	31	91,18	1	2,94	11,97	Bardeen (1904)
San:	16	-	-	15	93,75	1	6,25	12,06	De Beer-Kaufman (1974)
Caucasoid:									
German	48	-	-	45	93,75	3	6,25	12,06	Steinbach* (1889)
Italian	60	2	3,33	58	96,67	-	-	11,97	Bianchi$ (1894)
Swiss	92	4	4,35	86	93,48	2	2,17	11,98	Frey (1929)
Pooled	200	6	3,00	189	94,50	5	2,50	12,00	
Total:	635	23	3,62	588	92,60	24	3,78	12,00	

* Cited by Bardeen (1904)

$ Italian columns from the province Siena reported by Bianchi (1894) erroneously cited by Bardeen (1904) as Scienese skeletons and as from a 1895 study.

3.2 Intergroup Comparisons among Females

The numbers of thoracic vertebrae in female vertebral columns (Table 6.5) show no significant differences among population groups in respect of the frequencies of eleven, twelve and thirteen thoracic vertebrae (chi-square = 7,90; P<0,25 with six degrees of freedom), the frequencies of variants (chi-square = 3.17; P<0,5 with three degrees of freedom) and the frequency of eleven thoracic vertebrae (chi-square = 2,77; P<0,50 with three degrees of freedom).

TABLE 6.5

The Numbers of Thoracic Vertebrae in Females of Various Population Groups

Population Group	n	11		12		13		Mean	Reference
		n	%	n	%	n	%		
S.A. Negro:									
Zulu	40	2	5,00	38	95,00	-	-	11,95	Present Study
	157	19	12,10	137	87,26	1	0,64	11,89	De Beer-Kaufman (1974)
Pooled	197	21	10,66	175	88,83	1	0,51	11,90	
Amer. Negro:	20	1	5,00	18	90,00	1	5,00	12,00	Bardeen (1904)
San:	12	1	8,33	11	91,67	-	-	11,92	De Beer-Kaufman (1974)
Caucasoid:									
German	35	-	-	35	100,00	-	-	12,00	Steinbach* (1889)
Italian	70	3	4,29	67	95,71	-	-	11,96	Bianchi$ (1894)
Swiss	58	6	10,34	52	89,66	-	-	11,90	Frey (1929)
Pooled	163	9	5,52	154	94,48	-	-	11,94	
Total:	392	32	8,16	358	91,33	2	0,51	11,92	

* Cited by Bardeen (1904)

$ Italian columns from the province Siena reported by Bianchi (1894) erroneouly cited by Bardeen (1904) as Scienese skeletons and as from a 1985 study

Twelve is the modal number of thoracic vertebrae in female vertebral columns. When one looks at the deviations from the modal number, a greater tendency to eleven thoracic vertebrae than to thirteen is noted. The S.A. Negro female columns present a highly significantly greater frequency of eleven than thirteen thoracic vertebrae (chi-square = 15,60; P<0,005). The same difference is probably significant in the Caucasoid female vertebral columns (chi-square = 5,60; P<0,025). The mean numbers of thoracic vertebrae range between 11,90 in S.A. Negro female vertebral columns and 12,00 in American Negro female vertebral columns.

3.3 Intergroup Comparisons among Combined Sex Samples

When the sexes are considered together (Table 6.6), the numbers of thoracic vertebrae show no significant differences among population groups in comparisons of firstly the frequencies of eleven, twelve and thirteen vertebrae (chi-square = 3,84; P<0,75 with six degrees of freedom) and secondly the frequency of eleven versus that of thirteen thoracic vertebrae (chi-square = 0,25; P<0,975 with three degrees of freedom). The differences in the frequencies of variation from the modal number of thoracic vertebrae among population groups prove to be not significant (chi-square = 3,93; P<0,50 with three degrees of freedom).

TABLE 6.6

The Numbers of Thoracic Vertebrae in the Combined Sexes of Various Population Groups

Population Group	n	11		12		13		Mean	Reference
		n	%	n	%	n	%		
S.A. Negro:									
Zulu	120	6	5,00	110	91,67	4	3,33	11,98	Present Study
	462	30	6,49	418	90,48	14	3,03	11,97	De Beer-Kaufman (1974)
Pooled	582	36	6,19	528	90,72	18	3,09	11,97	
Amer. Negro:	54	3	5,55	49	90,74	2	3,70	11,98	Bardeen (1904)
San:	28	1	3,57	26	92,86	1	3,57	12,00	De Beer-Kaufman (1974)
Caucasoid:									
German	83	-	-	80	96,39	3	3,61	12,04	Steinbach* (1889)
Italian	130	5	3,85	125	96,15	-	-	11,96	Bianchi$(1894)
Swiss	150	10	6,67	138	92,00	2	1,33	11,95	Frey (1929)
Pooled	363	15	4,13	343	94,49	5	1,38	11,97	
Total:	1 027	55	5,36	946	92,11	26	2,53	11,97	

* Cited by Bardeen (1904)

$ Italian columns from the province Siena reported by Bianchi (1894) erroneously cited by Bardeen (1904) as Scienese skeletons and as from a 1895 study

The variant, eleven thoracic vertebrae, occurs more frequently than does thirteen thoracic vertebrae in the female columns of all population groups compared except the San. The frequencies of eleven thoracic vertebrae are, however, not significantly different among the population groups. Within the population groups, the frequency of eleven thoracic vertebrae proves to be probably significantly greater than the frequency of thirteen thoracic vertebrae in S.A. Negro (chi-square = 4,97; P<0,05) vertebral columns. No significant difference is found in American Negro and Caucasoid columns while equal frequencies are presented by the San vertebral columns.

4. Intergroup Comparisons of the Numbers of Lumbar Vertebrae

4.1 Intergroup Comparisons Among Males

The numbers of lumbar vertebrae in male vertebral columns (Table 6.7) show no significant differences in the frequencies of variation among the population groups (chi-square = 4,08; P<0,50 with three degrees of freedom).

The differences in the frequencies of four, five and six lumbar vertebrae prove not significant (chi-square = 5,06; P<0,75 with six degrees of freedom) among the males of various population groups. Although the frequency of six lumbar vertebrae is much higher in San males than in the males of the remaining population groups, no significant difference in the frequencies of six lumbar vertebrae is found among the population groups (chi-square = 4,88; P<0,25 with three degrees of freedom).

TABLE 6.7

The Numbers of Lumbar Vertebrae in Males of Various Population Groups

Population Group	n	4		5		6		Mean	Reference
		n	%	n	%	n	%		
S.A. Negro:									
Zulu	80	5	6,25	66	82,50	9	11,25	5,05	Present Study
	305	12	3,93	255	83,61	38	12,46	5,09	De Beer-Kaufman (1974)
Pooled	385	17	4,42	321	83,38	47	12,20	5,08	
Amer. Negro:	34	1	2,94	31	91 "	2	5,88	5,03	Bardeen (1904)
San:	16	1	6,25	12	75,00	3	18,75	5,13	De Beer-Kaufman (1974)
Caucasoid:									
German	48	2	4,17	43	89,58	3	6,25	5,02	Steinbach* (1889)
Italian	60	5	8,33	52	86,67	3	5,00	4,97	Bianchi* (1894)
Swiss	92	2	2,17	83	90,22	7	7,61	4,79	Frey (1929)
Pooled	200	9	4,5	178	89,00	13	6,50	5,02	
Total:	635	28	4,41	542	85,35	65	10,24	5,06	

*Cited by Bardeen (1904)

The frequency of six lumbar vertebrae compared with the frequency of four lumbar vertebrae in each population group shows a highly significantly greater frequency of six lumbar vertebrae in S.A. Negro males. No significant differences between the frequencies of four and six lumbar vertebrae are found in the American Negro, San and Caucasoid male vertebral columns.

The differences in the frequencies of four versus those of six lumbar vertebrae are not significant among the population groups (chi-square = 1,35; P<0,75 with three degrees of freedom).

4.2 Intergroup Comparisons among the Females

The numbers of lumbar vertebrae in female vertebral columns of various population groups are summarised in Table 6.8. The modal number of lumbar vertebrae is five in all population groups compared. The tendency to variation from this mode proved to be not significantly different among females of various population groups (chi-square = 5,72; P<0,25 with three degrees of freedom). No significant differences (chi-square = 5,47; P< 0,50 with six degrees of freedom) in the frequencies of four, five and six lumbar vertebrae are found among the female columns of various population groups.

TABLE 6.8

The Numbers of Lumbar Vertebrae in Females of Various Population Groups

Population Group	n	4		5		6		Mean	Reference
		n	%	n	%	n	%		
S.A. Negro:									
Zulu	40	3	7,50	35	87,50	2	5,00	4,98	Present Study
	157	3	1,91	138	87,90	16	10,19	5,08	De Beer-Kaufman (1974)
Pooled	197	6	3,05	173	87,82	18	9,14	5,06	
Amer. Negro:	20	1	5,00	18	90,00	1	5,00	5,00	Bardeen (1904)
San:	12	1	8,33	9	75,00	2	16,67	5,08	De Beer-Kaufman (1974)
Caucasoid:									
German	35	1	2,86	34	97,14	-	-	4,97	Steinbach* (1889)
Italian	70	2	2,86	68	97,14	-	-	4,97	Bianchi* (1894)
Swiss	58	1	1,72	52	89,66	5	8,62	5,07	Frey (1929)
Pooled	163	4	2,45	154	94,48	5	3,07	5,01	
Total:	392	12	3,06	354	90,31	26	6,63	5,04	

* Cited by Bardeen (1904)

Except for the American Negro female columns which show an equal tendency to four and six lumbar vertebrae, the S.A. Negro, San and Caucasoid female vertebral columns all show a greater tendency to six lumbar vertebrae than to four lumbar vertebrae. The differences in the relative frequencies of four and six lumbar vertebrae are not significant (chi-square = 1,33; P< 0,75 with three degrees of freedom) among population groups. S.A. Negro females show a probably significantly (chi-square = 4,44; P<0,05) greater frequency of six lumbar vertebrae than of four.

4.3 Intergroup Comparisons among Combined Sex Samples

The modal number of lumbar vertebrae is five in all population groups compared (Table 6.9). The difference in the frequencies of four, five and six lumbar vertebrae is probably significant (chi-square = 12,72; P<0,05 with six degrees of freedom) among the population groups.

In accordance with this result, the differences in the frequencies of variation from the modal number are highly significant (chi-square = 12,85; P<0,005 with three degrees of freedom) among the population groups. These differences may be owing to the almost certainly significant differences among the population groups in the frequencies of six lumbar vertebrae (chi-square = 12,12; P<0,01 with three degrees of freedom). The high frequency of six lumbar vertebrae in S.A. Negro vertebral columns is strongly significantly (chi-square = 9,27; P<0,005) higher than in Caucasoid vertebral columns. San vertebral columns present a probably significant (chi-square = 3,85; P<0,05) higher frequency of six lumbar vertebrae than Caucasoid columns.

The differences between the relative frequencies of four and six lumbar vertebrae are highly significant in S.A. Negro (chi-square = 19,67; P<0,005) vertebral columns. A comparison of these differences (four lumbar versus six lumbar vertebrae) among population groups shows no significant differences (chi-square = 2,10; P<0,75 with three degrees of freedom).

TABLE 6.9

The Numbers of Lumbar Vertebrae in Combined Sexes of Various Population Groups

Population Group	n	4		5		6		Mean	Reference
		n	%	n	%	n	%		
S.A. Negro:									
Zulu	120	8	6,66	101	84,17	11	9,17	5,03	Present study
	462	15	3,25	393	85,06	54	11,69	5,08	De Beer-Kaufman (1974)
Pooled	582	23	3,95	494	84,88	65	11,17	5,07	
Amer. Negro:	54	2	3,70	49	90,74	3	5,56	5,02	Bardeen (1904)
San :	28	2	7,14	21	75,00	5	17,86	5,11	De Beer-Kaufman (1974)
Caucasoid:									
German	83	3	3,61	77	92,77	3	3,61	5,00	Steinbach* (1889)
Italian	130	7	5,38	120	92,31	3	2,31	4,97	Bianchi* (1894)
Swiss	150	3	2,00	135	90,00	12	8,00	5,06	Frey (1929)
Pooled	363	13	3,58	332	91,46	18	4,96	5,01	
Total:	1027	40	3,89	896	87,24	91	8,86	5,05	

* Cited by Bardeen (1904)

5. Sexual Differences in the Numbers of Thoracic and Lumbar Vertebrae

There is a greater tendency to eleven than to thirteen thoracic vertebrae in females of various populations with San females the only exception. They present an equal tendency to eleven and thirteen thoracic vertebrae. The male columns present an almost equal tendency to eleven and thirteen thoracic vertebrae. American Negro males show a higher frequency of eleven thoracic vertebrae, while no San male columns with eleven thoracic vertebrae are reported.

The frequencies of eleven thoracic vertebrae are higher in female vertebral columns than in male vertebral columns. Comparison of the differences in the frequencies of eleven thoracic vertebrae betwe.. males (Table 6.4) and females (Table 6.5) of each population group reveals a highly significant difference (chi-square = 8,07; P<0,005) between S.A. Negro males and females. No significant differences in the frequencies of eleven thoracic vertebrae are found between the sexes of the remaining population groups.

The frequencies of thirteen thoracic vertebrae are higher in S.A. Negro, San and Caucasoid male series than in female vertebral columns. American Negro females present a higher frequency of thirteen thoracic vertebrae than American Negro males. This difference between American Negro male and female vertebral columns is highly significant (chi-square = 12,22; P<0,005). S.A. Negro males present a probably significantly (chi-square = 4,30; P<0,05) higher frequency of thirteen thoracic vertebrae than S.A. Negro females.

There are no significant sex differences in the incidence of variations in the numbers of lumbar vertebrae (Tables 6.7 and 6.8). The tendency to variation, the absolute frequency of four lumbar vertebrae, the absolute frequency of six lumbar vertebrae and the relative frequencies of four and six lumbar vertebrae between the males and females of each population group are determined.

The pooling of data for all males of all population groups, and similarly for all females enables the degree of sexual dimorphism in respect of the numbers of thoracic vertebrae and of the numbers of lumbar vertebrae in *Homo sapiens* to be derived from the means. Comparison of the means of the numbers of thoracic vertebrae between the sexes confirms that the frequency of thirteen thoracic vertebrae is significantly higher (chi-square = 8,02; P<0,005) in males (3,78%) than in females (0,51%), while the frequency of eleven thoracic vertebrae is significantly higher (chi-square = 8,15;

P<0,005) in females (8,16%) than in males (3,62%). Comparison of the means of the numbers of lumbar vertebrae between the sexes reveals no significant differences in the frequencies of four and six lumbar vertebrae, while a probably significant (chi-square = 4,49; P<0,05) difference in the frequencies of L5 occurs between the sexes. From these results it seems as if the tendency to lengthening of the vertebral column in males and of shortening in females, as shown in Chapter 5, affects the thoracic region more than the lumbar region.

B. The Numbers of Thoracic and Lumbar Vertebrae in African and Asian Great Apes

1. Present Study

The African and Asian great ape vertebral columns used in this part of the present study (Table 6.10) are from the osteological collections housed in the following institutions, with the catalogue classification used by some:

1. Department of Anatomy and Human Biology at the Witwatersrand University -Za
2. Department of Anatomy at the University of Cape Town -Z
3. Department of Zoology at the Witwatersrand University
4. Department of Zoology at the University of Pretoria
5. The Transvaal Museum in Pretoria - TM
6. The South African Museum in Cape Town - ZM

In six male *Gorilla gorilla* skeletons three different patterns of regional distribution are observed. One column presents the regional formula C7, T14, L3; one column has the regional formula C7, T12, L4 and four columns the formula C7, T13, L4. The seven *Pan troglodytes* vertebral columns consist of five male and two female columns. Two different patterns of regional distribution of PSV are observed: six columns, which include the two female columns, present the formula C7, T13, L4 and one column shows the formula C7, T14, L4.

TABLE 6.10

The Regional Distribution of Presacral Vertebrae in African and Asian Great Apes

Species and catalogue number	Sex	Regional pattern	PSV
Gorilla gorilla			
Za 1311	Male	C7 T12 L4	23
Za 1312	Male	C7 T12 L4	23
Za 95	Male	C7 T13 L4	24
TM*	Male	C7 T13 L4	24
TM 16737	Male	C7 T13 L4	24
ZM 37016	Male	C7 T14 L3	24.
Pan troglodytes			
Za 1071	Male	C7 T13 L4	24
Za 94	Male	C7 T13 L4	24
Z - 159	Male	C7 T13 L4	24
ZM 37007	Female	C7 T13 L4	24
ZM 37008	Male	C7 T13 L4	24
822#	Female	C7 T13 L4	24
TM 16731	Male	C7 T14 L4	25
Pongo pygmaeus			
Za 1334	Male	C7 T11 L5	23
Z - 158	Male	C7 T11 L5	23
Za 93	Female	C7 T12 L4	23
TM 16732	Male	C7 T12 L4	23
UP•	Male	C7 T12 L4	23
307#	Male	C7 T12 L4	23
ZM 33590	Male	C7 T13 L3	23

* No catalogue number
\# In the Department of Zoology of the Witwatersrand University
• In the Department of Zoology of the University of Pretoria

The seven *Pongo pygmaeus* vertebral columns are drawn from six males and one female. Though no deviation in the modal number of 23 PSV is observed, three different patterns of regional distribution are recorded. One female and three male columns present the regional formula C7, T12, L4, two columns show the formula C7, T11, L5 and one column has the formula C7, T13, L3.

TABLE 6.11

The Numbers of Thoracic Vertebrae in African and Asian Great Apes

Genus and Species	n	11		12		13		14		Mean
		n	%	n	%	n	%	n	%	
Gorilla gorilla	6	-	-	1	16,7	4	66,7	1	16,7	13,0
Pan troglodytes	7	-	-	-	-	6	85,7	1	14,3	13,1
Pongo pygmaeus	7	2	28,6	4	57,1	1	14,3	-	-	11,9

Tables 6.11 and 6.12 list the numbers of thoracic and of lumbar vertebrae respectively in the 20 great ape skeletons studied. Though the number of vertebral columns in each group is too small to allow one to draw any secure conclusions on variations in the numbers of thoracic and of lumbar vertebrae, the mean number of vertebrae in each region may be confirmed by larger samples.

TABLE 6.12

The Numbers of Lumbar Vertebrae in African and Asian Great Apes

Genus and Species	n	3		4		5		Mean
		n	%	n	%	n	%	
Gorilla gorilla	6	1	16,7	5	83,3	-	-	3,8
Pan troglodytes	7	-	-	7	100,0	-	-	4,0
Pongo pygmaeus	7	1	14,3	4	57,1	2	28,6	4,1

2. Other African and Asian Great Apes

2.1 Sources of Data

The numbers of thoracic and the numbers of lumbar vertebrae in African and Asian great apes are reported by various authors but only Randall (1944) reports on the sexes separately in his study on *Gorilla* vertebral columns. In all the studies from which data are used for comparison the authors noted vertebrae with a unilateral rib as half thoracic and half cervical or half lumbar, as the case may be. Lumbar vertebrae which present unilateral sacralization are recorded as half lumbar and half sacral. In the present study, a typical last cervical or first lumbar vertebra which bears costal facets unilaterally or bilaterally is not classified as thoracic. The thoracic vertebrae noted as half in the comparative studies are thus not recorded as a thoracic vertebra in the present study. A vertebra with unilateral sacralization is counted as sacral in the present study. Last lumbar vertebrae noted as half in comparative studies due to unilateral sacralization are thus not recorded as lumbar in the present study.

The studies from which comparative data on the numbers of thoracic (Table 6.13) and of lumbar (Table 6.14) vertebrae are used, are listed below:

1. Fick (1933) cited by Schultz (1941) on the number of thoracic vertebrae in 35 *Pongo* vertebral columns.

2. Randall (1944) on the numbers of thoracic vertebrae in 109 male and 62 female and the numbers of lumbar vertebrae in 112 male and 63 female *Gorilla* vertebral columns.

3. Schultz and Straus (1945) on 93 *Pan*, 58 *Gorilla* and 121 *Pongo* vertebral columns.

As the study of Schultz and Straus (1945) is based on material included in several previous reports (Schultz, 1930, 1940, 1941), the data cited in these earlier studies of Schultz are thus not listed separately here.

Abitbol (1987b) gives regional vertebral numbers of all spinal regions in 29 *Pongo*, 14 *Pan* and 39 *Gorilla* vertebral columns. He does however not report on the criteria used for the definition of a thoracic vertebra and the criteria used for the definition of sacralization differ from those used in the present study. The classical criteria for sacralization used in the present study are enlargement and fusion of one or both transverse processes of a seemingly last lumbar vertebra to take part in the sacro-iliac joint and in the formation of a sacral foramen. Opposed to this Abitbol (1987b) recorded four stages of sacralization. The first three stages include vertebrae of which (i) a transverse process articulates with the most medial part of the iliac crest, (ii) a transverse process is enlarged to form an isolated "sacral wing" that articulates separately with the ilium and (iii) the vertebral body is fused with that of S1. While these vertebrae are counted as sacral in his study, they are recorded as lumbar in the present study. Data from Abitbol (1987b) are thus not included for comparison.

3. Intergroup Comparison of the Numbers of Thoracic Vertebrae

From the results of the present study and the sources listed above, the numbers of thoracic vertebrae in 100 *Pan*, 235 *Gorilla* and 163 *Pongo* vertebral columns are available for comparison. These data are listed in Table 6.13.

With an incidence of 83% it is evident that the modal number of thoracic vertebrae in the pooled *Pan* (male plus female) vertebral columns is thirteen. Twelve thoracic vertebrae, the minus-variant, occur in 1% of the vertebral columns in contrast to 16% with the plus-variant, namely fourteen thoracic vertebrae. The relative frequencies of twelve and fourteen thoracic vertebrae in *Pan* vertebral columns prove to be highly significant (chi-square = 10,86; P<0,005). This significant difference suggests a significantly greater tendency to an increase in the number of thoracic vertebrae than to a decrease. The mean number of thoracic vertebrae presented by the *Pan* columns is 13,2.

TABLE 6.13

The Numbers of Thoracic Vertebrae in African and Asian Great Apes

Reference	Sex	n	11		12		13		14		Mean
			n	%	n	%	n	%	n	%	
1. *Pan troglodytes*:											
Schultz & Straus (1945)	M + F	93			1	1,0	77	83,0	15	16,0	13,2
Present study	M	5					4	80,0	1	20,0	13,2
	F	2					2	100			13,0
	M + F	100			1	1,0	83	83,0	16	16,0	13,2
2. *Gorilla gorilla*:											
Randall (1944)	M	109			8	7,3	91	83,5	10	9,2	13,0
	F	62			5	8,0	53	85,5	4	6,5	13,0
Schultz & Straus (1945)	M + F	58			8	13,0	48	83,0	2	4,0	12,9
Present study	M	6			1	16,7	4	66,7	1	16,7	12,8
	M + F	235			22	9,4	196	83,4	17	7,2	13,0
3. *Pongo pygmaeus*:											
Pick (1933)	M + F	35	3	8,6	26	74,3	6	17,1			12,1
Schultz & Straus (1945)	M + F	121	24	20,0	92	76,0	5	4,0			11,8
Present Study	M	6	2	33,3	3	50,0	1	16,7			11,8
	F	1			1	100,0					12,0
	M + F	163	29	17,8	122	74,8	12	7,4			11,9

In the pooled *Gorilla* series (males plus females) the modal number of thoracic vertebrae is thirteen (83,4%). The mean number of thoracic vertebrae is thirteen, the incidences of twelve and of fourteen thoracic vertebrae being not significantly different (chi-square = 0,25; P<0,75).

The pooled *Pongo* series (male plus female) presents a mode of twelve thoracic vertebrae, this number occurring in 74,8% of the columns. Variations from the modal number of thoracic vertebrae show a greater tendency to reduction (17,8%) than to an increase (7,4%) in the number of thoracic vertebrae. This difference between the frequencies of eleven and thirteen thoracic vertebrae in *Pongo* vertebral columns proves probably significant (chi-square = 6,28; P<0,025). No *Pongo* vertebral column with fourteen thoracic vertebrae has yet been recorded according to the data available to the author. The mean number of thoracic vertebrae in *Pongo* vertebral columns is 11,9.

When the numbers of thoracic vertebrae in African and Asian great ape vertebral columns are compared, the most important difference is in the modal number. The modal number of thoracic vertebrae is thirteen in the African great apes, *Pan* and *Gorilla*, but twelve in the Asian ape *Pongo*. The differences among the frequencies of the modal numbers of thoracic vertebrae are highly significant (chi-square = 14,64; P<0,005 with two degrees of freedom). This significant difference results from the relatively lower frequency of the modal number of thoracic vertebrae in *Pongo* (74,8%) than in *Pan* (83,0%) and in *Gorilla* (83,4%) vertebral columns.

Pan vertebral columns present a high frequency (16,0%) of the plus-variant in contrast with 7,2% in *Gorilla* and 7,4% in *Pongo* vertebral columns. These differences in the frequencies of the plus-variant prove probably significant among the great ape groups (chi-square = 7,38; <0,025 with two degrees of freedom). The high frequency (16,0%) of the plus-variant in *Pan* vertebral columns is probably significantly greater (chi-square = 4,26; P<0,05) than the frequency in *Gorilla* columns (7,2%). The differences between *Pongo* and *Gorilla*, and between *Pongo* and *Pan* vertebral columns are not significant.

The frequencies of the minus-variant show a highly significant difference (chi-square = 17,38; P<0,005 with two degrees of freedom) among the great ape groups. The low frequency in *Pan* columns (1,0%) differs probably significantly (chi-square = 5,28; P<0,005) from the frequency in *Gorilla* columns (9,4%). The high frequency in *Pongo* columns (17,8%) differs highly significantly (chi-square = 14,13; P<0,005) from the frequency in *Pan* columns (1%) and probably significantly (chi-square = 4,71; P<0,05) frc the frequency in *Gorilla* columns (9,4%).

Intergroup comparisons of African and Asian great apes show thus a modal number of thirteen thoracic vertebrae in African great apes and of twelve thoracic vertebrae in *Pongo*. The comparison also reveals the greater tendency to an increased number of thoracic vertebrae in *Pan*, the almost equal dis ribution of + and - variants in *Gorilla* and the greater tendency to a decreased number of thoracic vertebrae in *Pongo* columns.

4. Intergroup Comparisons of the Numbers of Lumbar Vertebrae

The classification of the lumbar vertebrae reported as half lumbar is problematic since not only the presence of lumbar ribs but also unilateral sacralization of the last lumbar vertebra must be taken into account. Schultz and Straus (1945) report three half thoracic and six half lumbar vertebrae in 93 *Pan* vertebral columns. Three vertebrae are thus recorded as half thoracic and half lumbar and are reported as lumbar in the present study. The remaining three are reported sacral in the present study for it is assumed that these vertebrae are recorded half lumbar and half sacral. All the data on transitional vertebrae are treated as this example shows.

No transitional vertebra is reported among the numbers of thoracic vertebrae in 35 *Pongo* columns noted by Fick 1933 (cited by Schultz, 1941). Among the numbers of lumbar vertebrae in 37 *Pongo* columns two transitional vertebrae are reported. Since it is unknown if these vertebrae bear unilateral ribs or are unilaterally sacralised, it is not possible to calculate the exact number of lumbar vertebrae according to the criteria used in the present study. These data are thus not included in the present study.

Four lumbar vertebrae, with an incidence of 62,0%, are the modal number in *Pan* vertebral columns (Table 6.14). Variations from the modal number of lumbar vertebrae show a great tendency to a decrease in the number of lumbar vertebrae. The frequency of three lumbar vertebrae is 38,0%. The average number of lumbar vertebrae in *Pan* vertebral columns is thus only 3,6.

With an incidence of 69,9%, four lumbar vertebrae provide the modal number also in *Gorilla* vertebral columns (Table 6.14). Randall (1944) records one vertebral column (0,4%) with two lumbar vertebrae while the frequency of three lumbar vertebrae in *Gorilla* vertebral columns is 29,7%. With no instance of five lumbar vertebrae, there is thus a definite tendency to a decreased number of lumbar vertebrae in *Gorilla* vertebral columns which is reflected also in the average number of 3,7 lumbar vertebrae.

The frequency of the modal four lumbar vertebrae in *Pongo* vertebral columns is 81,1% (Table 6.14). Though the tendency to the plus-variant is higher than the tendency to the minus-variant, the difference between the respective frequencies of three and five lumbar vertebrae is not significant (chi-square = 0,74; P<0,50).

TABLE 6.14

The Numbers of Lumbar Vertebrae in African and Asian Great Apes

Reference	Sex	n	2		3		4		5		Mean
			n	%	n	%	n	%	n	%	
1. *Pan troglodytes*:											
Schultz & Straus (1945)	M + F	93			38	41,0	55	59,0			3,6
Present Study	M	5					5	100,0			4,0
	F	2					2	100,0			4,0
	M + F	100			38	38,0	62	62,0			3,6
2. *Gorilla gorilla*:											
Randall (1944)	M	112	1	0,9	32	28,6	79	70,5			3,7
	F	63			21	33,2	42	66,8			3,7
Schultz & Straus (1945)	M + F	58			17	29,0	41	71,0			3,7
Present Study	M	6			1	16,7	5	83,3			3,8
	M + F	239	1	0,4	71	29,7	167	69,9			3,7
3. *Pongo pygmaeus*:											
Schultz & Straus (1945)	M + F	120			8	7,0	99	82,0	13	11,0	4,0
Present Study	M	6			1	16,7	3	50,0	2	33,3	4,2
	F	1					1	100,0			4,0
	M + F	127			9	7,1	103	81,1	15	11,8	4,0

Intergroup comparison reveals no significant differences in the frequencies of three (chi-square = 1,53; P<0,25), or four (chi-square = 1,34; P<0,25) lumbar vertebrae in African great apes. No case of an increased number of five lumbar vertebrae is recorded in either group. *Pan* and *Gorilla* vertebral columns present thus a modal number of four lumbar vertebrae and both groups show a great tendency to a reduction in the number of lumbar vertebrae.

When the African and Asian great apes are compared four lumbar vertebrae are found to be the modal number in all three groups. The chi-square test reveals a significant difference (chi-square = 10,41; P<0,01 with two degrees of freedom) in the frequencies of four lumbar vertebrae among the great apes. The high frequency of four lumbar vertebrae in *Pongo* vertebral columns (81,1%) is highly significantly (chi-square = 8,45; P<0,005) greater than the frequency in *Pan* vertebral columns (62,0%) and probably significantly higher (chi-square = 4,30; P<0,05) than in *Gorilla* vertebral columns (69,9%). The higher frequency of four lumbar vertebrae in *Pongo* vertebral columns indicates thus a definitely lower tendency to variation in the number of lumbar vertebrae in *Pongo* than in the African great apes.

The frequencies of three lumbar vertebrae are significantly higher in *Pan* (chi-square = 28,91; P<0,005) and in *Gorilla* (chi-square = 20,63; P<0,005) vertebral columns than in *Pongo* vertebral columns. These results indicate a significantly greater tendency to reduction in the number of lumbar vertebrae in the African great apes than in *Pongo*. On the other hand, *Pongo* shows a greater tendency to an increase in the number of lumbar vertebrae than the African great apes. The frequency of five lumbar vertebrae in *Pongo* vertebral columns is 11,8%.

5. Sexual Differences in the Numbers of Thoracic and of Lumbar Vertebrae

Apart from the author's scanty data, only the data from Randall (1944) on the numbers of thoracic and of lumbar vertebrae in *Gorilla* allow comparison of the sexes. The chi-square tests on the differences in the frequencies of twelve, thirteen and fourteen thoracic vertebrae and on the differences in the frequencies of three and four lumbar vertebrae show no significant differences between *Gorilla* males and females (Table 6.15).

TABLE 6.15

The Chi-square Values of the Differences in the Frequencies of Thoracic and Lumbar Vertebrae in *Gorilla* Males and Females

Number of vertebrae	Chi-square value	P(
12 Thoracic	0,183	0,75
13 Thoracic	0,008	0,95
14 Thoracic	0,002	0,95
3 Lumbar	0,099	0,90
4 Lumbar	0,036	0,90

C. The Numbers of Thoracic and Lumbar Vertebrae in Australopithecinae

The *Australopithecus* fossil vertebrae available for study are described in Chapter 2. Among these specimens only the two partial vertebral columns, Sts 14, and Stw 431, may throw some light on the regional distribution of presacral vertebrae in Australopithecinae. The partial vertebral columns have been recovered from Member 4 of the Sterkfontein Formation. This layer has so far yielded only one generally accepted taxon of hominid, *Australopithecus africanus*.

The Sts 14 vertebrae are classified as six lumbar and nine thoracic vertebrae. The first lumbar vertebra shows a riblike articular structure on the right side. When this vertebra is scrutinised closely a convex articular facet on a short process projecting from the pedicle, instead of the normal shallow depression that receives the complete head of the last rib, is found. The form of the facet for the tuberculum of the rib is rudimentary and it is positioned almost directly behind the costal facet for the head of the rib. A lumbar rib most probably articulated at the right side of this vertebra while a transverse process is present on the left side. This is thus a thoracolumbar transitional vertebra but is, according to the criteria used in the present study, noted as a lumbar vertebra (Fig. 7.1).

The second Sterkfontein partial vertebral column presents, in the author's opinion, five lumbar and the lower four thoracic vertebrae as described in Chapter 4.

The fact that one out of two partial vertebral columns present six lumbar vertebrae suggests that a large percentage of the *A. africanus* population might have had six lumbar vertebrae. On the other hand, Sts 14 presents the lower nine thoracic vertebrae and the newly recovered partial vertebral column the lower four thoracic vertebrae. Since the upper part of the thoracic region and at least the last cervical vertebra are not preserved in either of the partial vertebral columns, it is not possible to determine the number of thoracic vertebrae in these two specimens of *A. africanus*.

The most complete early hominid (*Homo erectus*) skeleton ever found was discovered in 1984 at Nariokotome III, west Lake Turkana, Kenya. The skeletal parts include vertebral elements; a last cervical vertebra, eight thoracic and five lumbar vertebrae (Brown *et al.*, 1985).

D. Discussion

In 120 Zulu (male and female) vertebral columns seven patterns of regional distribution of presacral vertebrae (PSV) are observed. Vertebral columns with 24 PSV present three regional formulae, while two patterns each are noted among columns with 23 PSV and with 25 PSV.

The male vertebral columns also present seven patterns while the female columns show four patterns of regional distribution with the modal formula C7, T12, L5 in both groups. Bornstein and Peterson (1966) report fourteen patterns of regional distribution of PSV in a total of 1 239 modern human vertebral columns. These fourteen patterns include two regional patterns with assimilation of the atlas. No case of assimilation of an atlas is encountered in the present study.

The results on the regional distribution of presacral vertebrae suggest that the tendency to an increased number of PSV in modern human males, noted in the previous chapter, marks the lumbar region. In modern human female columns the tendency to a decreased number of PSV, reported in the previous chapter, seems to mark both regions.

The differences in the frequencies of the specific thoracic variants among the males, among the females and among the combined sexes of various population groups prove to be not significant. The frequencies of the specific variants show a tendency to a decreased number of thoracic vertebrae in the females of various population groups, while the males present almost equal frequencies of eleven and thirteen thoracic vertebrae. Within each population group, the tendency to eleven thoracic vertebrae is significantly greater than the tendency to thirteen in S.A. Negro female vertebral columns and probably significantly greater in Caucasoid female columns. When the sexes are combined, this difference (T11 v. T13) is probably significant in S.A. Negro vertebral columns.

Both males and females present a definitely greater tendency to six lumbar vertebrae than to four. The relative difference between four and six lumbar vertebrae is however significant only in S.A. Negro males, females and the sexes combined.

The chi-square tests on the frequencies of the numbers of lumbar vertebrae among the males and among the females of various population groups show no significant differences in (i) the frequencies of four, five and six lumbar vertebrae,

(ii) frequencies of total variation and (iii) the relative frequencies of four and six lumbar vertebrae. However, when the sexes are combined, a probably significant difference in the frequencies of four, five and six lumbar vertebrae is found among the population groups. A highly significant difference in the tendency to variation is also found among the males-plus-females of the various population groups. These differences may be the result of the significant difference i the frequencies of six lumbar vertebrae among the population groups. The frequency of six lumbar vertebrae in Caucasoid vertebral columns is significantly smaller than the frequency in S.A. Negro columns and probably significantly smaller than in San vertebral columns.

The differences between the sexes with respect to the frequencies of thoracic vertebrae show a highly significantly greater frequency of eleven thoracic vertebrae in S.A. Negro females than in males. The male columns, on the other hand, present probably significantly higher frequencies of thirteen thoracic vertebrae than S.A. Negro female columns. American Negro female columns show a definitely higher incidence of thirteen thoracic vertebrae than the male columns. The differences between the sexes with respect to the frequencies of firstly total variation, secondly the plus-variant and thirdly the minus-variant in the numbers of lumbar vertebrae prove not significant in any of the population groups.

The numbers of thoracic vertebrae in African great apes range between twelve and fourteen with thirteen the modal number. Intragroup comparison of the frequencies of the specific variants shows a definite tendency towards lengthening of the thoracic region in *Pan* vertebral columns. *Gorilla* vertebral columns have an almost equal distribution of the plus- and minus-variants. The numbers of thoracic vertebrae in *Pongo* vertebral columns range between eleven and thirteen thoracic vertebrae with twelve the modal number. The frequency of eleven thoracic vertebrae is significantly greater than the frequency of thirteen thoracic vertebrae.

Among the hominoids twelve thoracic vertebrae form the modal number in man and *Pongo*, while thirteen thoracic vertebrae is the rule in African great apes. The frequencies of the modal numbers of thoracic vertebrae is 92,1% in man, 83,4% in *Gorilla*, 83,0% in *Pan and* 74,8% in *Pongo*. The percentage frequencies of the variations within the series of hominoids may be considered to express the relative stability of each group. Man on this basis is the most stable form in regard to variations in the numbers of thoracic vertebrae.

If the relative distribution of variants in the number of thoracic vertebrae shows the direction of phylogenetic trends, *Pan* (with a modal number of thirteen thoracic vertebrae) presents a stronger tendency to an increase in the number of thoracic vertebrae. *Gorilla*, also with a modal number of thirteen thoracic vertebrae, shows an almost equal distribution of plus- and minus-variants. Man and *Pongo*, with a modal number of twelve thoracic vertebrae, present a greater tendency to a decrease in the number of thoracic vertebrae.

On the basis of data on the numbers of thoracic vertebrae in various primates, including platyrrhine and catarrhine monkeys and higher primates, Schultz (1930) suggests that at least fourteen or fifteen thoracic vertebrae may represent the primitive condition. In that event, the occurrence of only eleven thoracic vertebrae may be viewed as a marked specialization or derived feature.

The upper part of the thoracic region and at least the last cervical vertebra are not preserved in either of the *A. africanus* partial vertebral columns, Sts 14 and Stw 431. It is thus not yet possible to determine the number of thoracic vertebrae in this taxon. In this chapter it is seen that the average number of thoracic vertebrae is 11,97 in man, 11,9 in *Pongo*, 13,0 in *Gorilla* and 13,2 in *Pan* vertebral columns. The modal number of thoracic vertebrae in *Australopithecus* is thus likely to have been either twelve or thirteen.

The numbers of lumbar vertebrae in African great apes range between three and five and in Asian great apes between two and four, with four the modal number. Intragroup comparisons of the frequencies of the specific variants show a strong tendency to shortening of the lumbar region in the African great apes studied. *Pongo* presents a greater, though not significantly so, incidence of five than of three lumbar vertebrae.

Comparison of the numbers of lumbar vertebrae among the extant hominoids shows a modal number of four lumbar vertebrae in the anthropoid apes and of five in modern man. The relatively higher incidence of the modal number of lumbar vertebrae in modern man points to relatively greater stability in modern man in regard to the numbers of lumbar vertebrae.

The apparent direction of the phylogenetic trend, as suggested by the numbers of lumbar vertebrae, is towards shortening of the lumbar region in all extant hominoids. Schultz and Straus (1945) in a study on the numbers of vertebrae in various primates, state:

> "The great apes, or Ponginae, are the only primates showing the extreme individual reductions to only three lumbar vertebrae" (op.cit., p 610).

The lowest average number of lumbar vertebrae (3,6) occurs in the *Pan* series. In *Gorilla*, in *Pongo* and in modern man the average numbers of lumbar vertebrae are 3,7, 4,0 and 5,05 respectively. Schultz (1930) concluded that these extreme reductions in the numbers of lumbar vertebrae in the anthropoid apes are marked specializations. It may be inferred that specialization, in the form of reduction of the numbers of lumbar vertebrae, has gone distinctly further in African and Asian great apes than in man. Schultz and Straus (1945) suggest that the common ancestor of all primates possibly possessed seven cervical, thirteen thoracic and six lumbar vertebrae. The long lumbar region may be judged as the primitive condition in primates for the more simply designed primates, which are judged to have retained primitive features, present long lumbar regions (Clark, 1962). A character state from which transformation starts is called the plesiomorphous state (Hennig, 1966). The loss of one or more lumbar vertebrae, suggested by Schultz (1930) to be a specialization, presents a derived or apomorphous character state. Among the recent hominoids surveyed here, six lumbar vertebrae occur only in modern man. The presence of six lumbar vertebrae in one of the two *A. africanus* partial vertebral columns may suggest a relatively high frequency of this number of lumbar vertebrae in the *A. africanus* population. It suggests also that, in the number of elements, the lumbar spine of *A. africanus* is even less specialized than the minimally specialized lumbar spine of modern man. The longer lumbar region in *A. africanus* and modern man presents the plesiomorphous "primitive" extreme, while the shortened lumbar region in *Pan* presents a strongly apomorphous "derived" extreme.

From a phylogenetic point of view, the more primitive or plesiomorphic trends in *A. africanus* and in modern humans tend to link these two groups closer together than to the anthropoid apes. The apomorphic trend to shortening seems to link the African apes, the *Gorilla* and *Pan*, closer together.

E. Summary and Conclusions

1. In 120 Zulu (male and female) vertebral columns the regional distribution of PSV falls into seven patterns. The modal regional formula is C7, T12, L5 and the regional formula with the second highest frequency is C7, T12, L6. When the sexes are considered separately the male vertebral columns present the same trends as the sexes combined. The female vertebral columns, however,

present only four patterns of regional distribution of PSV. The typical regional formula is C7, T12, L5 and the regional formula with the second highest frequency is C7, T12, L4.

2. No variation in the number of cervical vertebrae is observed in 120 Zulu vertebral columns.

3. The numbers of thoracic vertebrae in modern man range between eleven and thirteen thoracic vertebrae with twelve the modal number. The differences in the frequencies of the specific variants among the males, among the females and among the combined sexes of various population groups prove to be not significant. Female columns present a greater tendency towards shortening, while male columns tend towards lengthening of the thoracic region.

4. Both male and female columns of all modern human population groups present a greater tendency towards lengthening of the lumbar region. The differences in the frequencies of six lumbar vertebrae prove significant among the various population groups. The low frequency of six lumbar vertebrae in Caucasoid columns is significantly smaller than the frequency in S.A. Negro columns and probably significantly smaller than the frequency in San vertebral columns.

5. In *Pan* and in *Gorilla* the numbers of thoracic vertebrae range between twelve and fourteen with thirteen the modal number. *Pan* presents a tendency to an increase in the number of thoracic vertebrae to fourteen while *Gorilla* shows an almost equal distribution of the plus- and minus-variants. In *Pongo* and in modern man the numbers of thoracic vertebrae range between eleven and thirteen with twelve the modal number. *Pongo* and modern man show a tendency to a decreased number (eleven) of thoracic vertebrae.

6. The number of thoracic vertebrae in *A. africanus* is unknown, since the thoracic regions of the recovered two partial vertebral columns are not complete. In this chapter it is seen that the average numbers of thoracic vertebrae in extant hominoids are: 13,2 in *Pan*, 13,0 in *Gorilla*, 11,97 in man and 11,9 in *Pongo* vertebral columns. The average number of thoracic vertebrae in *A. africanus* vertebral columns is thus likely to have been either twelve or thirteen.

7. In modern human vertebral columns the numbers of lumbar vertebrae range between three and six, with five the modal number. In African and Asian great apes, the numbers of lumbar vertebrae range between two and five with four the modal number. Man is the most stable of extant hominoids surveyed, in respect of the variations in the numbers of lumbar vertebrae.

8. The relative frequencies of departures from the modal number suggest the direction of phylogenetic trends. The African great apes show a definite tendency towards fewer lumbar vertebrae. *Pongo* shows a similar but lesser tendency, and it manifests a higher frequency of five lumbar vertebrae than the African great apes studied. Modern man presents a tendency to an increased number of six lumbar vertebrae. The direction of phylogenetic change, as suggested by the numbers of vertebrae, is towards shortening of the lumbar region in existing hominoids. This reduction in the number of lumbar vertebrae has gone distinctly further in the great apes than in man.

9. The six lumbar vertebrae observed in one of the two *A. africanus* partial vertebral columns fall within the range of numbers of lumbar vertebrae in man only. If these two vertebral columns are typical of *A. africanus*, or, at least, reflect a high frequency of six lumbar vertebrae in the species, it would follow that the postulated

tendency towards a reduction in the lumbar vertebrae in hominoids has occurred to a lesser degree in *A. africanus* than in the extant hominoids.

CHAPTER 7

NON-METRICAL OBSERVATIONS ON HOMINOID THORACIC AND LUMBAR VERTEBRAE

Contents of Chapter

A. Foramina through the Base of Lumbar Transverse Processes

A foramen through the base of the transverse process of a modern human last lumbar vertebra was first described by Szawlowski (1902). Following this description Dwight (1902) reported another such case. Manners-Smith (1909), in a study on the variability of the human last lumbar vertebra, identified three types of foramina through the transverse processes, according to the position of the foramen. The first type of foramen is called costotransverse and runs vertically through the medial part of the transverse process. The second type is the retrotransverse foramen which is situated at the bases of the transverse and superior articular facets. It is bound posteriorly by a bony bar which passes from the mamillary to the accessory process. This bar is not always complete and an open groove is then seen. The third type is a foramen through the transverse process at the junction of the accessory and inferior articular processes (Fig. 3.1).

1. Results

1.1 Modern Human Series

When Manners-Smith's (1909) classification is used, a total of 31 costotransverse foramina are recorded in the modern human (Zulu) series of the present study. These foramina are noted in one or more of the upper four lumbar vertebrae. No costotransverse foramen has been observed on a last lumbar vertebra. Among 40 female spinal columns four individuals with eleven affected vertebrae are found. Nine of these vertebrae present bilateral costotransverse foramina (Table 7.1). Seven male individuals out of 80, with nine affected vertebrae, are noted. Only two of these vertebrae show bilateral costotransverse foramina while six present the foramen on the right side. The highest incidence of costotransverse foramina occurs at the level of L1 in both males and females.

TABLE 7.1

The Costotransverse Foramina in Male and Female Zulu Lumbar Vertebrae

Vertebra	Male					Female				
	Absent	Present Unilateral		Present	n	Absent	Present Unilateral		Present	n
		Left	Right	Bilateral			Left	Right	Bilateral	
L1	76	0	2	2	80	36		1	3	40
L2	78	1	1	0	80	37		1	2	40
L3	78	0	2	0	80	38	0	0	2	40
L4	79	0	1	0	80	38	0	0	2	40
L5	80	0	0	0	80	40	0	0	0	40
		1	6	2			0	2	9	

Far fewer retrotransverse foramina are recorded. In 120 Zulu spinal columns six individuals with seven affected vertebrae are noted. Four out of 40 female individuals present two vertebrae with bilateral retrotransverse foramina, two vertebrae with foramina on the left and one with a foramen on the right side (Table 7.2). In 80 male columns only two retrotransverse foramina in two vertebrae of different individuals are noted. The highest incidence of retrotransverse foramina occurs at the level of L5. An open groove is found in seven instances, five in male and two in female Zulu columns.

TABLE 7.2

The Retrotransverse Foramina in Male and Female Zulu Lumbar Vertebrae

Vertebra	Male					Female				
	Absent	Present Unilateral		Present	n	Absent	Present Unilateral		Present	n
		Left	Right	Bilateral			Left	Right	Bilateral	
L1	80	0	0	0	80	40	0	0	0	40
L2	80	0	0	0	80	40	0	0	0	40
L3	80	0	0	0	80	40	0	0	0	40
L4	80	0	0	0	80	38	0	1	1	40
L5	79	1	0	0	80	37	2	0	1	40
L6	79	0	1	0	80					
		1	1	0			2	1	2	

No foramen through the transverse process between the accessory process and the inferior articular facet is recorded in the modern human series of the present study.

Comparative series: Manners-Smith (1909) studied the variability of the last lumbar vertebra in an unknown number of mostly Egyptian vertebral columns. He reported costotransverse foramina in two adult vertebrae and in two spines of young people. He found retrotransverse foramina in 14 specimens, bilateral in four, on the right in six and on the left side in four specimens. In five specimens a groove instead of a foramen is noted. One foramen formed by the junction of the accessory with the inferior articular processes is also reported. Beers *et al.* (1984) report three costotransverse and one retrotransverse foramen in L5 seen during routine computed tomography (CT) of the lower lumbar spine in an unknown number of patients with backache and sciatica.

1.2 African and Asian Great Ape Series

In the African and Asian great ape series of the present study, no foramen through the base of a lumbar transverse process is recorded. Two interesting features are however observed. One *Gorilla* column presents deep grooves between the costal and transverse elements of the L1 transverse processes. One *Pan* L1 vertebra presents no transverse process on the right side; only the accessory process is present. On the left side the accessory process is also present, but from the pedicle projects a small rib-like structure.

1.3 Australopithecine Series

L1 of Sts 14 presents a very small costotransverse foramen on the left side (Fig. 7.1). It runs vertically through the base of the transverse process, just lateral to the pedicle. On the right side no transverse process is present. Instead a blunt process, with a convex facet on top projects from the pedicle. This process is accompanied by a smaller process situated a little further back. The distance between these projections is somewhat larger than the diameter of the foramen on the left side which seems to represent part of the space that exists on the right side.

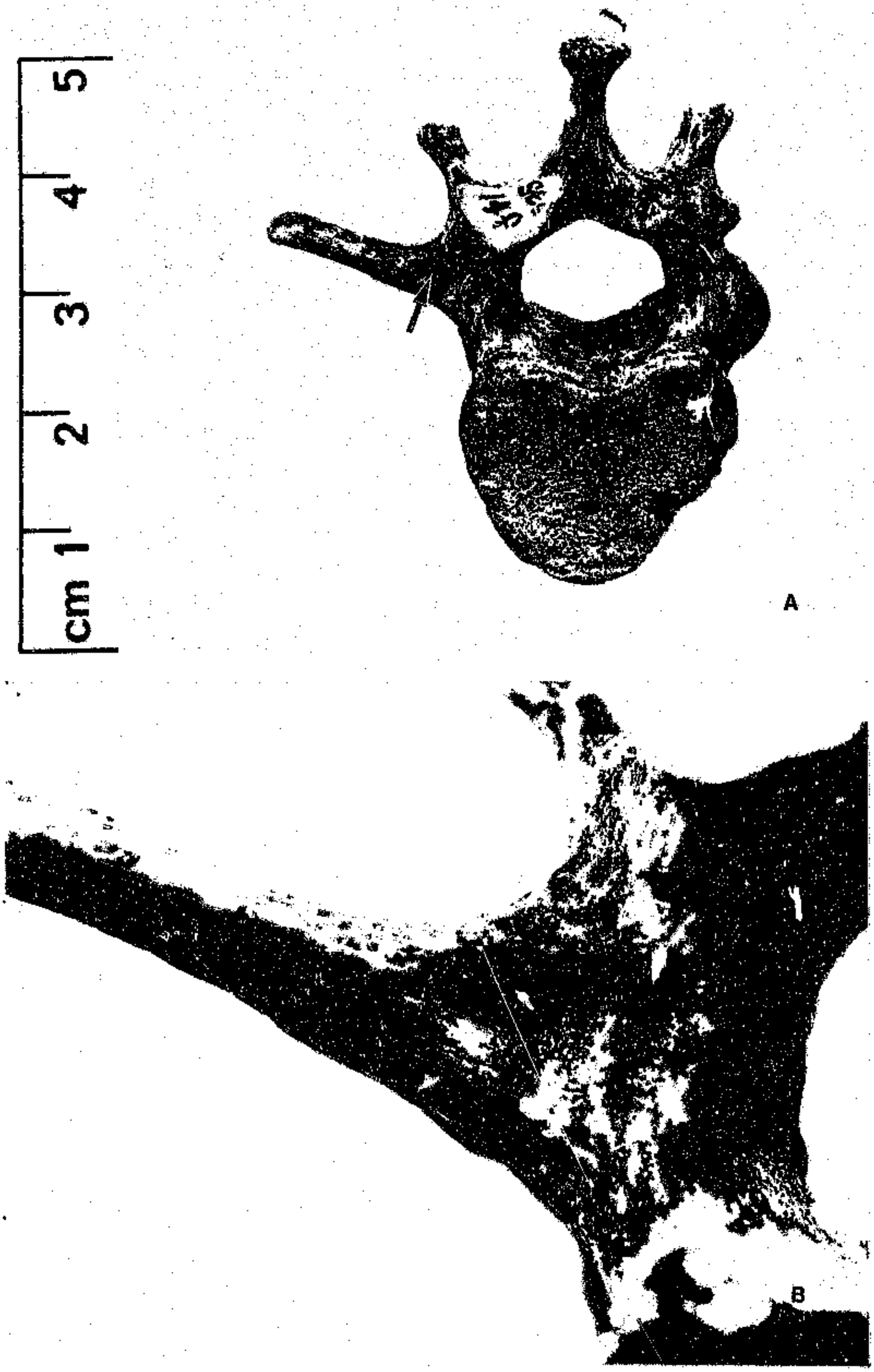


Fig. 7.1 L1 of Sts 14 with a very small costotransverse foramen through the base of the left transverse process (a) and a magnification of the foramen (b).

2 Discussion

2.1 Costotransverse Foramina

To explain the formation of the costotransverse foramina a brief review of the development of the transverse processes is necessary. Warwick and Williams (1980) stated that in the second stage of development of the vertebral column, dorsal extensions of the sclerotomes form the primitive neural arch and, later, its processes. The ventrolateral extensions of the sclerotomes foreshadow the costal elements. In the thoracic region the costal elements develop distally to form the ribs, while the transverse elements form the transverse processes. In the cervical and lumbar regions, the costal elements do not develop to form separate ribs, but constitute part of the transverse processes. The costal element of a cervical transverse process, which corresponds to the head and neck of a rib, forms the part ventrolateral to the foramen of the transverse process, while the transverse element limits the foramen posteriorly. (The vertebral arteries run through the foramina of the upper six vertebrae.) In the lumbar region the costal elements give rise to the largest part of the transverse processes, while a smaller medial and posterior part, which includes the accessory process, arises from the transverse process element.

The costotransverse foramina through the medial part of the transverse process root are situated between the costal and transverse elements. These foramina are probably instances of incomplete fusion of the costal and transverse elements. Manners-Smith (1909) states:

> "There is little doubt that this foramen is truly costo-transverse, is homologous with the cervical foramen and like it is vascular. It is probably for an enlarged retro-costal anastomosis ..."
> (op.cit., p 148).

From the results of the present study it is evident that costotransverse foramina, or variations in the fusion of the costal and transverse elements, occur most frequently at the level of L1. Of the costotransverse foramina noted in the modern human series 43,3% occur at L1. In Sts 14, the small costotransverse foramen is also present at the level of L1.

In the *Pan* column (Za 1071), with a small rib-like structure projecting from the left pedicle of L1, it seems as if the costal and transverse elements had not fused, the costal element forming instead a small rib-like structure which is fused with the pedicle.

2.2 Retrotransverse Foramina

The retrotransverse foramina at the bases of the transverse and superior articular processes are probably formed through the ossification of the mamillo-accessory ligaments described by Bogduk (1981). These ligaments bridge between the mamillary and accessory processes of each lumbar vertebra to convert the notch between them into a foramen or short canal. Bogduk (1981) finds these foramina to be better developed and more typical in form at upper lumbar levels. Ossification of these ligaments is however confined to the lower lumbar vertebrae and it occurs most frequently at L5. Manners-Smith (1909) proposes the transmission of small vessels which form a retrotransverse anastomosis. Bogduk (1981), in a series of dissections, finds that the retrotransverse foramina transmit the medial branch of the dorsal ramus of the spinal nerve, exiting at the intervertebral space immediately above.

B. The Curvature and Orientation of the Lumbar Superior Articular Facets

Variations in the shape and in the orientation of the lumbar articular facets, when viewed from above, play an important rôle in the biomechanics of the articular facet joints. The normal function of these joints is to stabilize the motion segment (two consecutive vertebrae with an intervening disc) and to control its movements.

1 Results

1.1 Modern Human Series

In the modern human (Zulu) series wide variation in the curvature and orientation of the articular surfaces of the superior articular facets is found. The curvature of these facets ranges from flat to markedly concave and is recorded in the categories; flat, slightly curved and markedly curved. Marked curvatures are classified according to the categories used by Bogduk and Twomey (1987) into subdivisions: "J-shaped" or "C-shaped" when viewed from superior and anterior (Table 7.3).

The incidence of marked C-shaped superior articular facets is the highest in both male and female Zulu vertebral columns with five lumbar vertebrae. In the eight male columns with six lumbar vertebrae, the J-shaped curve occurs in five (62,5%) of the columns at L1. From L2 to L6 the C-shaped curvature is the commonest.

The orientation of the superior articular facets in modern human subjects is found to vary from the coronal to the sagittal plane. The modal pattern of orientation seems to be inwards at L1, sloping more from above downwards. At the level of the last lumbar vertebra the facets face posteriorly as much as medially.

TABLE 7.3

The Curvature of Lumbar Superior Articular Facets of Male and Female Zulu Spines

Vertebra	Males (n=66) Flat	Curved Slightly	Markedly C-shaped	Markedly J-shaped	Females (n=35) Flat	Curved Slightly	Markedly C-shaped	Markedly J-shaped
L1: n	10,00	9,00	27,00	20,00	8,00	4,00	19,00	4,00
%	15,15	13,64	40,91	30,30	22,86	11,43	54,29	11,42
L2: n	7,00	10,00	28,00	21,00	2,00	6,00	20,00	7,00
%	10,61	15,15	42,42	31,82	5,71	17,14	57,14	20,00
L3: n	2,00	12,00	22,00	30,00	3,00	4,00	20,00	8,00
%	3,03	18,18	33,33	45,45	8,57	11,43	57,14	22,86
L4: n	4,00	9,00	32,00	21,00	2,00	2,00	21,00	10,00
%	6,06	13,64	48,48	31,82	5,71	5,71	60,00	28,57
L5: n	6,00	21,00	30,00	9,00	5,00	8,00	20,00	2,00
%	9,09	31,82	45,45	13,64	14,29	22,86	57,14	5,71

1.2 African and Asian Great Ape Series

In comparison with the modern human series, the general pattern of orientation of the superior articular facets is reversed in the pongid series. The facets face progressively more medial from the first to the last lumbar vertebra. The concavity of the ape facets is conspicuously less than that of modern human facets, those of the *Pan* vertebral columns showing the greatest curvatures (Table 7.4).

TABLE 7.4

The Curvature of Pongid Lumbar Superior Articular Facets

Column	L1	L2	L3	L4
Gorilla:				
Za 95	S	F	F	F
Za 1311	F	F	F	F
Za 1312	F	F	S	F
Pan:				
Za 94	C	C	C	C
Za 1071	S	J	S	C
Pongo:				
Za 93	F	S	S	F
Za 1334	S	S	S	

F = Flat or, planar facets
S= Slightly curved facets
J = 'J-shaped' curvature
C = 'C-shaped' curvature

1.3 Australopithecine Series

The concavity of the lumbar superior articular facets is fairly shallow in both Sts 14 and Stw 431 (Table 7.5). These facets are orientated more medially in the superior lumbar vertebrae and progressively laterally downwards. In the last lumbar vertebrae the superior articular facets face more backwards than medially. The same tendency is noted in the modern human columns, while the pongid columns present superior articular facets that face progressively more medially from L1 to L4.

TABLE 7.5

The Curvature of *A. africanus* Lumbar Superior Articular Facets

Column	L1	L2	L3	L4	L5	L6
Sts 14	F	F	S	S* C$	S	S
Stw 431	-	J	C$	S$	C*	-
Stw 8	S	-	-	-	-	-

F = Flat or planar facets
S = Slightly curved facets
J = "J-shaped" curvature
C = "C-shaped" curvature
* = Left side only
$ = Right side only

2. Discussion

The normal function of articular facet joints is to prevent forward displacement of the vertebra above and to control its rotary movements. These functions are influenced by both the curvature and the orientation of the articular facets. The biomechanics of the superior articular facets are explained by Bogduk and Twomey (1987).

Flat or planar superior articular facets which face inwards afford no resistance to forward displacement of the vertebra above. The inferior articular facets of the vertebra above are able to slide past the superior facets of the vertebra immediately below. These joints on the other hand strongly resist rotation (Fig. 7.2a).

In a joint with planar superior articular facets which are orientated obiquely, the facets face backwards and medially. These facets are able to prevent forward displacement due to their partly posterior orientation. The partly medial orien-

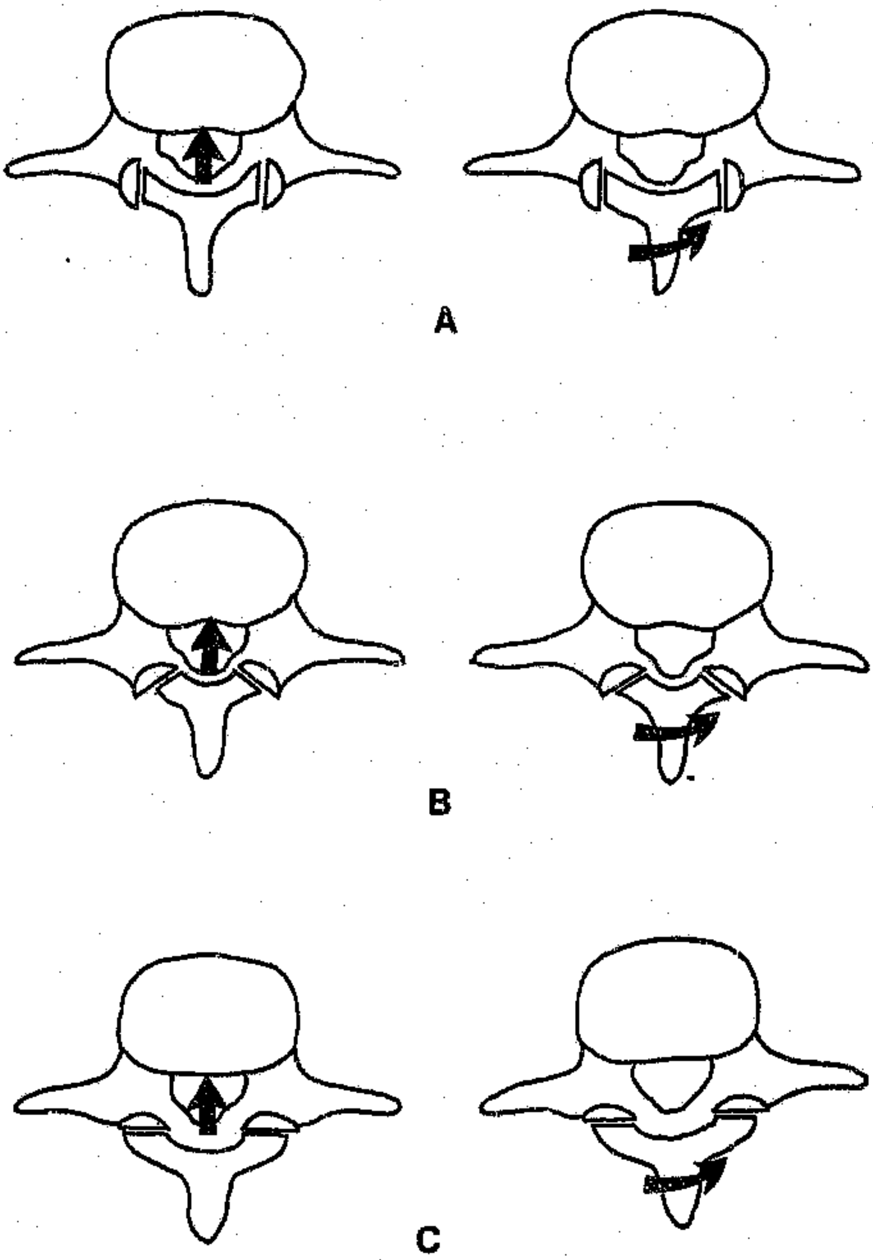


Fig. 7.2 The Mechanics of Flat Lumbar Articular Facets Orientated Medially (A), Obliquely (B) and Posteriorly (C).

= Rotation

= Forward Displacement

tation resists rotation since the inferior facets of the preceding vertebra will impact against the superior articular faces of the succeeding vertebra during rotation (Fig. 7.2b).

In joints with flat superior articular facets which face backwards, maximum resistance to forward displacement occurs, since the entire articular surface directly opposes forward movement. These facets do not resist rotation effectively. During rotation the inferior articular facets of the vertebra above impact against the superior articular facets of the vertebra below at an angle and are able to glance off the superior facets (Fig. 7.2c).

In joints with curved articular facets, the anteromedial parts resist forward displacement of the preceding vertebra. The C-shaped curvature thus provides better resistance than the J-shaped curve with a smaller anteromedial part. Rotation is well resisted by curved articular facets since almost the entire articular surface is brought into contact by this movement (Fig. 7.3).

The results of the present study show that the modal pattern of orientation of the superior lumbar articular facets changes from inwards at L1 to an oblique lie at L5. The C-shaped curvature occurs most frequently, but it becomes less marked at L5. The resistance to forward displacement thus becomes better as we go down the lumbar region, for the more backward orientation of the lower lumbar superior facets increases their ability to resist anterior shear forces and thus forward displacement of the vertebra above.

The more frequent occurrence of curved superior articular facets in the modern human series probably indicates the possibility and also effective control, of rotation. The more lateral orientation of the superior articular facets lower down in the lumbar region seems to permit more rotation

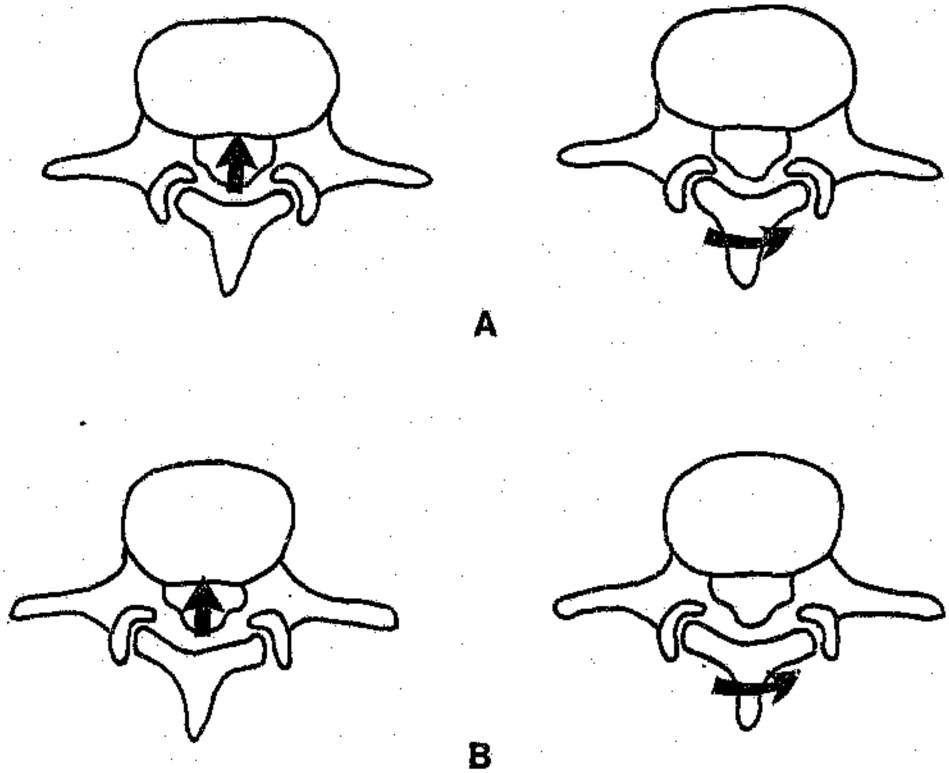


Fig. 7.3 The Mechanics of Curved Lumbar Artiular Facets; C-shaped (A) and J-shaped (B).

= Rotation

= Forward Displacement

than the more inwardly orientated superior articular facets of the superior lumbar region. This agrees with the findings of Gonon and Dimnet (1982), cited by Kénési and Lesur (1985).

The former workers find that the articular facets of the lower lumbar vertebrae seem mainly to undergo movements of rotation, with an instantaneous centre of rotation at the periphery of the intervertebral disc.

In the pongid series the facets are in general less curved than in the modern human series. Greater resistance to rotation is thus to be expected. The superior articular facets of the pongids face more medially from the first to the last lumbar vertebra. It seems thus as if the resistance to forward displacement through anterior shear forces decreases from above downwards in the pongid lumbar region. In the *Gorilla* columns, in which the superior articular facets of L4 are flat and face inwards, little resistance to anterior displacement is to be expected. The slightly C-shaped and J-shaped last lumbar superior articular facets of the *Pongo* columns would probably provide more resistance to anterior displacement and the more marked C-shaped facets of the *Pan* columns the most resistance. The seemingly lesser need for resistance against anterior displacement of the last lumbar vertebrae in the pongid columns may be explained by the absence of a lumbar lordosis and the fact that the lumbar vertebrae are embraced closely by the long ilia. In pongids the strong iliolumbar ligaments comprise an upper horizontal ligament between the third lumbar transverse process and the ilium, and a lower fan-shaped ligament from the fourth lumbar transverse process to the ilium. The fibres of these two components are continuous and the lower part is continuous with the anterior sacro-iliac ligament. The last two pongid lumbar vertebrae are thus firmly attached to the ilia which would seem to lessen the tendency to forward displacement.

The curvature and orientation of the *A. africanus* superior articular facets closely resemble those of the modern human columns. These features may indicate an increased ability to resist anterior shear forces and the forward displacement of the lower lumbar vertebrae, which characteristics accompany the lordotic curvature in modern man. Their presence in the early hominid thus suggests that a lumbar lordosis was present in *A. africanus*. This is the first time vertebral features other than the vertebral body height is thought to point at a lumbar lordosis in *A. africanus*. (The probable presence of a lumbar lordosis in *A. africanus* is again discussed in Chapter 8). The more outward orientation of the superior articular facets in the <u>lower</u> lumbar vertebrae of *A. africanus* may permit more rotation than the more inwardly orientated articular facets in the upper lumbar region.

C. The Configuration of the Lumbar Articular Facets

Fawcett (1932) points out that the configuration of the articular facets when viewed from behind can be used to serially recognise the individual modern human lumbar vertebrae. Seen from behind, the four articular facets form the angles of a four-sided figure. In L1 and L2 the figure is a trapezium with the base narrower than the top, while in L3 it makes a rectangle with long vertical sides. The figure in L4 is practically a square, while in L5 there is a rectangle elongated laterally (Fig. 3.2).

Are those configurations of the articular facets exclusively a modern human characteristic? Do variations in this pattern occur in modern *H. sapiens* and, if so, how frequently and at which levels? What is the pattern presented by articular facets in pongid and australopithecine vertebrae? In an attempt to answer these questions, the configuration of the articular facets in these other hominoids has been compared with those described by Fawcett (1932) in modern human lumbar regions. Since Sts 14 presents six lumbar vertebrae, special attention has here been paid to modern human columns with six lumbar vertebrae.

1. Results

1.1 Modern Human Series

In the seven Zulu male columns with four lumbar vertebrae each, variations in the articular facet configuration of the last three vertebrae are found in two columns only (Table 7.6). In these two columns the facet configuration pattern is the same as Fawcett's modal pattern for the first four vertebrae of a column with five lumbar vertebrae. Variation occurs in four columns at L1, with a rectangle being formed by the facets in three of these cases and a trapezium with the top narrower than base in the fourth case. In the remaining vertebral column the facet configuration pattern is the same as Fawcett's modal pattern for the last four vertebrae of a column with five lumbar vertebrae.

The eight Zulu male columns with six lumbar vertebrae each present six different patterns (Table 7.6). The last three vertebrae are again the least subject to variation. Only two columns present a square configuration at the third last vertebra whereas the remaining columns show Fawcett's modal pattern. At the L1 level only one column shows a variation in the form of a rectangle. At L2 three columns each present a trapezium, while five show a rectangle and at L3 two columns have a trapezium and six columns a rectangle.

TABLE 7.6

The Configuration of the Articular Facets of the Zulu Male Lumbar Vertebrae

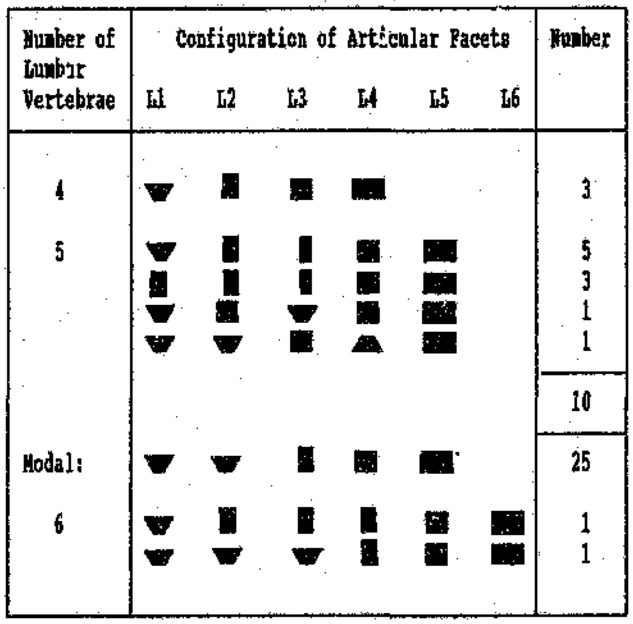
Number of Lumbar Vertebrae	L1	L2	L3	L4	L5	L6	Number
4	▼	■	■	■			1
	▼	▼	■	■			2
	■	■	■	■			3
	▲	■	■	■			1
							7
5	▼	■	■	■	■		6
	■	■	■	■	■		4
	■	■	■	■	■		2
	▼	■	■	■	■		1
	▼	■	■	▲	■		1
	■	▼	■	▲	■		1
	■	■	■	■	■		1
	▼	■	■	■	▼		1
							17
Modal:	▼	▼	■	■	■	■	49
6	▼	▼	▼	■	■	■	1
	▼	▼	■	■	■	■	1
	▼	■	■	■	■	■	3
	▼	■	■	■	■	■	1
	▼	■	▼	■	■	■	1
	■	▼	■	■	■	■	1
							8

The male Zulu columns with 23 PSV and those with 25 PSV which have five lumbar vertebrae show no departures from Fawcett's mode in the configuration of the articular facets. In the 66 columns with five lumbar vertebrae each, eight variants in the modal configuration of the articular facets are found in 17 columns (25,8%). These variations are listed in Table 7.6. In the variant which occurs the most frequently (in six columns) L2 presents also a rectangle, while the second commonest variation (four spines) shows rectangles in the first three lumbar vertebrae. The articular facet configurations of the last two lumbar vertebrae are the most stable, a larger width between the inferior articular facets than between the superior articular facets being seen in a few columns. In one column L5 presents a trapezium with the base narrower than the top.

The three female Zulu columns with four lumbar vertebrae each present a single pattern of facet configuration (Table 7.7). This pattern corresponds with that of the last four lumbar vertebrae in a column with five lumbar vertebrae which present the modal pattern. In the 35 columns with five lumbar vertebrae each, four variants occur in ten columns (28,6%). As in the male columns, the variant which occurs the most frequently (in five columns) is a rectangle at L2, while the second commonest variation (in three columns) shows rectangles in the first three lumbar vertebrae. The two columns with six lumbar vertebrae each show an additional rectangle or trapezium among the first three lumbar vertebrae. In the female columns, the articular facet configurations of the last two lumbar vertebrae are, as in the male columns, the most stable.

TABLE 7.7

The Configuration of the Articular Facets of the Zulu Female Lumbar Vertebrae



1.2 African and Asian Great Ape Series

In the African and Asian great ape series all three *Gorilla* columns present a different articular facet configuration at each lumbar level (Table 7.8). The two *Pan* columns differ at L1 where both show a trapezium, but the base is narrower in the one and broader in the other than the top. The two *Pongo* columns differ at L3: one presents a trapezium with a narrower base than top, while the other shows a rectangle with long vertical sides. Each of the seven ape columns thus presents a different pattern of articular facet configuration. In four of the columns L1 shows a trapezium which is narrower at the base than at the top, while three columns present a trapezium with the base broader than the top at the same level. At L2 three rectangles with long vertical sides, three trapezia with a narrower base and a trapezium with a broader base than top, are recorded. At L3 four columns show a trapezium with a narrower base than top and three columns show a rectangle with long vertical sides. In six columns the last lumbar vertebra (L4) shows a trapezium, with the inferior articular facets nearer to each other than the superior ones, while the seventh column, a juvenile male *Gorilla* column, shows a trapezium which is broader at the base than at the top.

TABLE 7.8

The Configuration of the Articular Facets of African and Asian Great Ape Lumbar Vertebrae

Ape	Configuration of Articular Facets L1	L2	L3	L4	L5
Gorilla:					
Za 1311	▲	▮	▮	▲	
Za 1312	▼	▲	▼	▼	
Za 95	▲	▼	▮	▼	
Pan:					
Za 1071	▼	▼	▼	▼	
Za 94	▲	▼	▼	▼	
Pongo:					
Za 93	▼	▮	▮	▼	
Za 1334	▼	▮	▼	▼	

1.3 Australopithecine Series

The articular facet configuration of L1 of Sts 14 shows a trapezium with a slightly narrower base than top. L2 presents the same kind of trapezium, while L3 shows a rectangle with its long sides vertical. At L4 there occurs a trapezium with the base slightly narrower than the top. L5 presents a square. The laminae and inferior articular facets of L6 are reconstructed with the superior articular facets of the sacral piece as guideline. According to this reconstruction, the articular facets form a rectangle with its long sides horizontal, when viewed from behind. In the AL 288-1 (*A. afarensis*, female) lumbar vertebra, classified by Johanson *et al.* (1982) as L3, the articular facets form a square when viewed from behind.

In Stw 431 only the left superior and inferior articular facets of the last lumbar vertebra (L5) are preserved. These facets are in line supero-inferiorly. The left superior articular facet of L4 is missing but the remaining facets form a rectangle, with its long sides vertical, when viewed from behind. The same configuration is found in L3, while L2 presents only inferior articular facets. Stw 8b presents superior and inferior articular facets on the right only. The facets of this vertebra seem to have formed also a rectangle with its long sides vertical.

2 Discussion

The most conspicuous difference seen in a comparison of the modern human and the pongid results is the difference in the configuration of the last lumbar articular facets. Though no modal pattern could be established from the few anthropoid ape columns studied, the last lumbar vertebra presents a trapezium with narrower base than top in six of the seven ape columns. This figure contrasts sharply with the rectangle with its long sides horizontal found in 119 of the 120 modern human columns. Whereas the inferior articular facets of a modern human last lumbar vertebra are placed as widely apart as the superior articular facets, or even slightly further apart, those of the anthropoid apes tend to be placed nearer to each other than are the superior articular facets.

The pattern presented by Sts 14 differs from the patterns presented by each of the six modern human vertebral columns with six lumbar vertebrae (Table 7.6). The configurations of the last two Sts 14 lumbar vertebrae correspond with that of the last two lumbar vertebra in all six modern human columns with six lumbar vertebrae.

Pal and Routal (1986, 1987) find that the articular facets of the last lumbar vertebra carry about 23% of the vertical load. The articular facets are placed far apart to withstand this force. From the results of this part of the study it is evident that the mode of weight transmission to the pelvis very probably differs between our modern human population and the anthropoid apes. The australopithecine and modern human last lumbar vertebrae, however, present the same articular facet configuration. This suggests that the posterior articular facets of the *A. africanus* last lumbar vertebra carried a major proportion of the vertical load, as in modern man, whereas those of the pongid columns seem to transmit less weight than the preceding vertebrae. In others words, on the evidence from our small pongid and australopithecine samples it seems that the mode of total transmission to the pelvis in *A. africanus* was unlike that in apes and like that in modern man. (Weight transmission to the pelvis is discussed again in Chapter 9.)

D. Summary and Conclusions

Foramina through the Base of Lumbar Transverse Processes

1. A total of 31 costotransverse foramina are recorded in the modern human (Zulu) series of 120 vertebral columns. Among 40 female columns four individuals with eleven affected vertebrae are found. Nine of these vertebrae present bilateral costotransverse foramina. Seven male individuals out of 80 with nine affected vertebrae are noted. Two of these vertebrae show bilateral costotransverse foramina while six present the foramen on the right side. The incidence of these foramina, which are probably instances of incomplete fusion of the costal and

transverse elements, is the highest at L1 in modern human columns. L1 of Sts 14 shows a costotransverse foramen on the left side.

2. The rib-like structure fused with the right pedicle of L1 in a *Pan* vertebral column is probably the result of no fusion between the costal and transverse elements.

3. Seven retrotransverse foramina are noted in six individuals of the modern human series. Four of the 40 female individuals present two vertebrae with bilateral retrotransverse foramina, two vertebrae with foramina on the left and one with a foramen on the right side. In 80 male columns only two retrotransverse foramina in two vertebrae of different individuals are noted. These foramina are probably formed through the ossification of the mamillo-accessory ligaments and they transmit the medial branch of the dorsal ramus of the spinal nerve, emerging through the intervertebral space immediately above.

The Curvature and Orientation of the Lumbar Superior Articular Facets

1. The results of the present study show that the curvature of the superior articular facets of modern human lumbar vertebrae range from flat or planar to markedly concave. The modal pattern of orientation of these facets seems to be inwards at L1, sloping downwards. At L5 the facets face as much posterior as medial.

2. The curvature of the pongid superior articular facets is less than that in modern human vertebrae. The *Gorilla* columns show flat superior articular facets, while the *Pan* columns present the most curved facets. In comparison with the modern human series, the general pattern

of superior articular facet orientation is reversed in the pongid series. The facets face progressively more medially from the first to the last lumbar vertebra.

3. The concavity of the *A. africanus* lumbar superior articular facets is fairly shallow. The orientation of the superior articular facets corresponds with that of the modern human vertebral columns.

4. From the biomechanics of the superior articular facets, it is evident that the extent of rotation is governed by the <u>curvature</u> of the facets. The <u>orientation</u> on the other hand plays an important rôle in the resistance to anterior shear forces. The more backwardly orientated articular facets of L5 in the modern human columns are thus more effective in the resistance to the [illegible] displacement of the lower lumbar vertebrae [illegible] oblique position of these vertebrae in the [illegible] lordosis. The presence of the same tendencies of these features in the *A. africanus* superior articular facets as in modern man, suggests that these vertebrae suffered the same stresses as do modern human vertebrae, in a lumbar lordosis. The correspondence in modern human and *A. africanus* superior lumbar articular facet curvature and orientation, in contrast with those of the pongid columns, thus suggests the presence of a lumbar lordosis in *A. africanus*.

The Configuration of the Lumbar Articular Facets.

1. Variants of the modal pattern of articular facet configuration when viewed from behind, as described by Fawcett (1932), are found in 25,8% of the male and 25,6% of the female Zulu columns. The last two lumbar vertebrae present the most stable condition.

2. In the pongid series each column presents a different pattern. A trapezium with its base narrower than its upper margin is, however, found in the last lumbar vertebra in six of the seven pongid columns examined.

3. The last two lumbar vertebrae of the *A. africanus* partial columns present the same configuration figures as the modal modern human configuration in these vertebrae.

4. A comparison of the three series shows that the modern human and australopithecine last lumbar vertebrae present a rectangle with its long sides horizontal. The pongid columns at this level present a trapezium with its base narrower than its top. In modern man the facets are probably placed further apart to carry a larger part of the vertical load. The same seems to be true for the *A. africanus* columns, while the reverse seems to obtain in the pongid columns.

CHAPTER 8

THE ABSOLUTE AND RELATIVE HEIGHTS OF THORACIC AND LUMBAR VERTEBRAL BODIES IN VARIOUS HOMINOIDS

When one looks at an articulated modern human vertebral column two features are conspicuous. These features are the presence of curvatures in the vertebral column and the increasing size of the vertebrae craniocaudally. The occurrence of these feature' in extant and ancient hominoids, as well as their functional applications, are examined and discussed in the next two chapters.

Contents of Chapter

Introduction

The vertical heights of the thoracolumbar vertebral bodies are expressed by means of two measurements and an index derived from them. The measurements are the anterior vertical height (M1) and the posterior vertical height (M2) of the vertebral bodies, measured in the midsagittal plane with a spreading caliper. The index derived from these measurements is the vertical vertebral index ($\frac{M2}{M1} \times 100$).

A. The Anterior Vertical Height (M1)

1. Modern Human Series

1.1 Present Study

The mean anterior vertical heights of Zulu male vertebral bodies increase from the first thoracic vertebra to the last lumbar vertebra (Fig. 8.1), save that a slight decrease in anterior vertical height appears from the third to the fifth thoracic vertebrae, while the third and fourth lumbar vertebrae present the same mean values.

The means of the anterior vertical heights of Zulu female thoracic and lumbar vertebral bodies (Table 8.1) increase from T1 to L3 (Fig. 8.1). From L3 to L5 a negligible decrease of 0,6mm occurs in the mean values.

TABLE 8.1

The Anterior Vertical Heights of Zulu Thoracic and Lumbar Vertebral Bodies (mm)

Vertebra	Males		Females	
	Mean ± SE	Observed Range	Mean ± SE	Observed Range
T1	14,8 ± 0,23	13 - 18	13,9 ± 0,16	12 - 16
T2	16,2 ± 0,21	15 - 20	14,9 ± 0,22	10 - 17
T3	16,2 ± 0,24	13 - 19	15,3 ± 0,16	14 - 17
T4	16,1 ± 0,27	14 - 21	15,3 ± 0,17	13 - 17
T5	16,0 ± 0,33	9 - 20	15,4 t 0,19	14 - 17
T6	16,6 ± 0,22	15 - 20	15,7 ± 0,20	14 - 18
T7	17,3 ± 0,18	16 - 19	16,2 ± 0,21	14 - 18
T8	17,8 ± 0,27	13 - 21	16,7 ± 0,17	15 - 19
T9	18,8 ± 0,29	15 - 29	17,7 ± 0,20	16 - 20
T10	20,1 ± 0,44	12 - 24	18,8 ± 0,19	17 - 20
T11	21,3 ± 0,21	19 - 24	19,3 ± 0,20	17 - 21
T12	22,0 ± 0,34	15 - 25	20,6 ± 0,20	18 - 23
L1	23,5 ± 0,49	12 - 27	22,7 ± 0,19	21 - 24
L2	23,9 ± 0,28	21 - 27	24,0 t 0,20	22 - 26
L3	24,5 ± 0,34	21 - 28	24,5 ± 0,24	22 - 26
L4	24,5 t 0,39	19 - 28	24,0 ± 0,24	22 - 27
L5	24,9 t 0,37	21 - 29	23,9 ± 0,32	20 - 27

Sex differences: The mean anterior vertical heights of all thoracic and lumbar vertebral bodies, apart from those of L2 and L3, are greater in Zulu male than in Zulu female vertebral columns (Fig. 8.1). The Student's t-Test shows (Table 8.2) that the differences between the mean anterior vertical heights of male and female vertebral bodies are highly significant (P<0,001) at all thoracic levels, except for T4 and T5. The difference between mean anterior vertical heights of male and female fourth thoracic vertebrae is probably significant, while no significant sexual difference is found between those of the fifth thoracic vertebrae. In the lumbar region, the differences between mean anterior vertical heights of the sexes are almost certainly significant only at the level of L5.

TABLE 8.2

t-Values of Sex Differences in the Anterior Vertical Heights of Zulu Thoracic and Lumbar Vertebral Bodies

Vertebra	Difference of means Male - Female	t-value	P<
T1	0,93	3,367	0,001
T2	1,37	4,484	0,001
T3	0,97	3,356	0,001
T4	0,77	2,382	0,02+
T5	0,60	1,569	0,10
T6	1,07	3,550	0,008
T7	1,07	3,853	0,003
T8	1,10	3,399	0,001
T9	1,13	3,197	0,002
T10	1,40	2,909	0,005
T11	2,00	6,923	0,0001
T12	1,40	3,525	0,001
L1	0,77	1,467	0,1
L2	-0,10	0,294	0,7
L3	0,07	0,160	0,8
L4	0,53	1,161	0,25
L5	1,20	2,458	0,01

Underlined = Almost certainly and highly significant
\+ = Probably significant

1.2 Comparative Series

Aeby (1878) gives values for the means of anterior vertical heights for 20 European spinal columns (males-plus- females). The results of his study are not used here. Hasebe (1913) gives the mean values for 20 Japanese male and 10 Japanese female vertebral columns and Lanier (1939) reports no significant difference between any two corresponding vertebrae from his American White (n = 96) and American Negro (n = 88) series. Allbrook (1956) cites the mean lumbar vertebral body height in 51 male and 21 female East African vertebral columns. Fig. 8.2 presents graphically the data from these studies on male vertebral columns and from the present study. The mean anterior vertical heights are the lowest in the S.A. Negro males (present study). Hasebe (1913) observed that the L4 was frequently of lower anterior vertical height than L3,

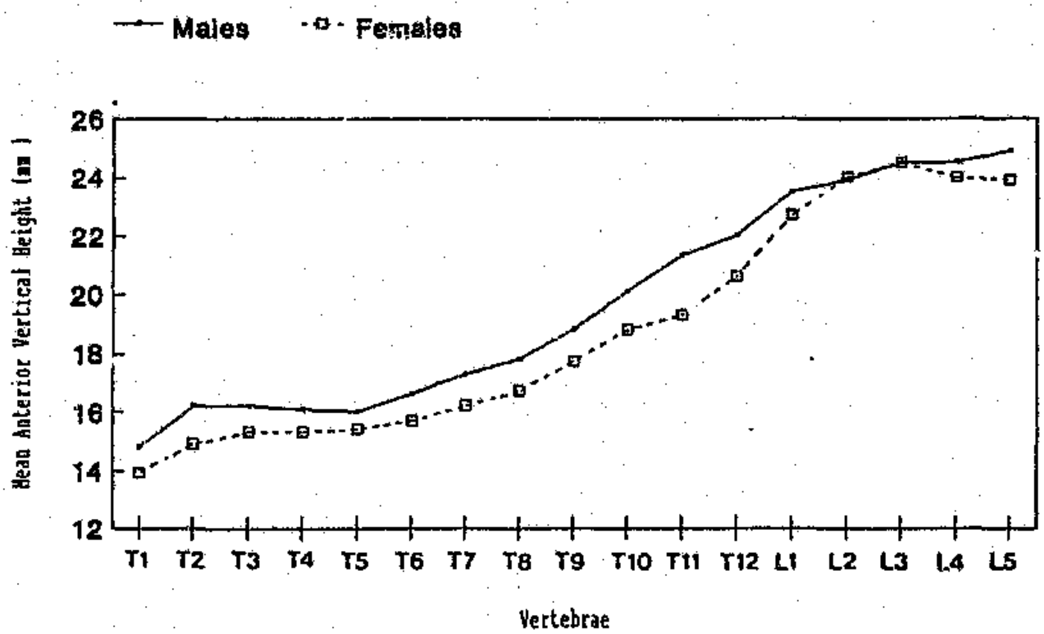


Fig. 8.1 The Mean Anterior Vertical Heights of Zulu Thoracic and Lumbar Vertebral Bodies.

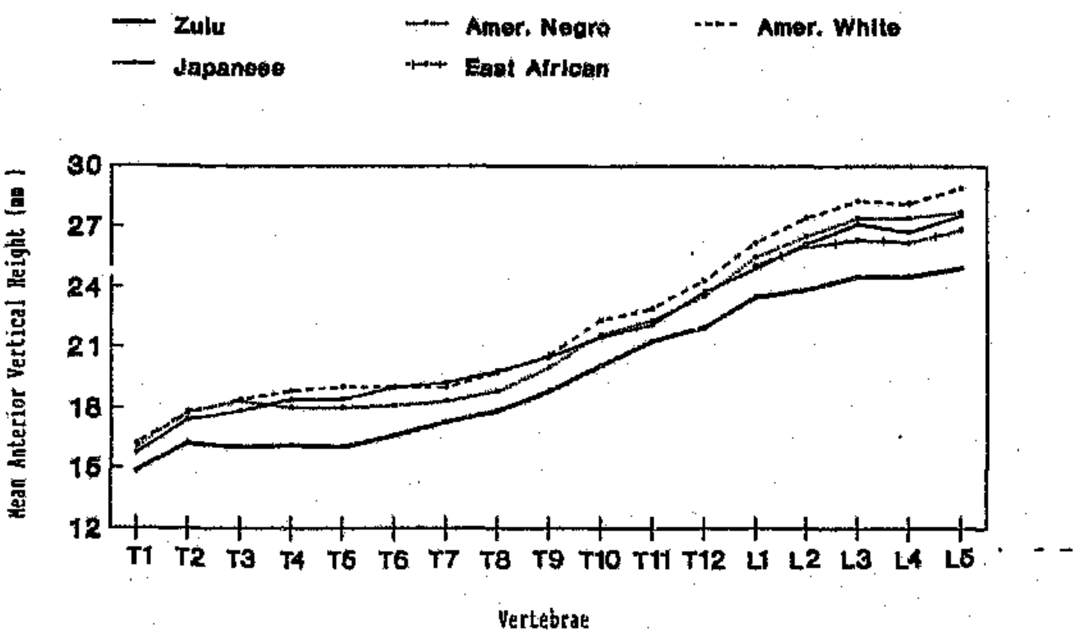


Fig. 8.2 The Mean Anterior Vertical Heights of Modern Human Male Thoracic and Lumbar Vertebral Bodies.

sometimes equal, but rarely was it higher. This observation is supported by the results of Lanier (1939) and of the present study. In the S.A. and American Negroes a slight decrease occurs from T3 to T5, which however is not paralleled in the Caucasoid and Mongoloid columns (Fig. 8.2).

The mean anterior vertical heights of female thoracic and lumbar vertebral bodies are presented in Fig. 8.3. The vertebral bodies of S.A. Negro females are lower than those of Japanese females and, in the lumbar vertebrae, of East African females. In contrast with the male vertebral columns, the last lumbar vertebrae of the female S.A. Negro and Japanese vertebral columns are slightly lower than L4; but in Allbrook's (1956) small series of East African females, the heights decrease from L3 to L4 followed by a slight increase at L5.

2. African and Asian Great Ape Series

2.1 Present Study

Only one *Pan* male vertebral column (Za 1071) was available for metrical analysis. The anterior vertical heights of this specimen's thoracic and lumbar vertebral bodies are listed in Table 8.3 and presented graphically in Fig. 8.4. With some exceptions, there is an increase in the mean anterior vertical heights from the first thoracic to the last lumbar vertebra. A sharp increase occurs from T9 to L2. The anterior vertical heights of L2 and L3 are the same, followed by an increase in the last lumbar vertebra which, in this case is L4.

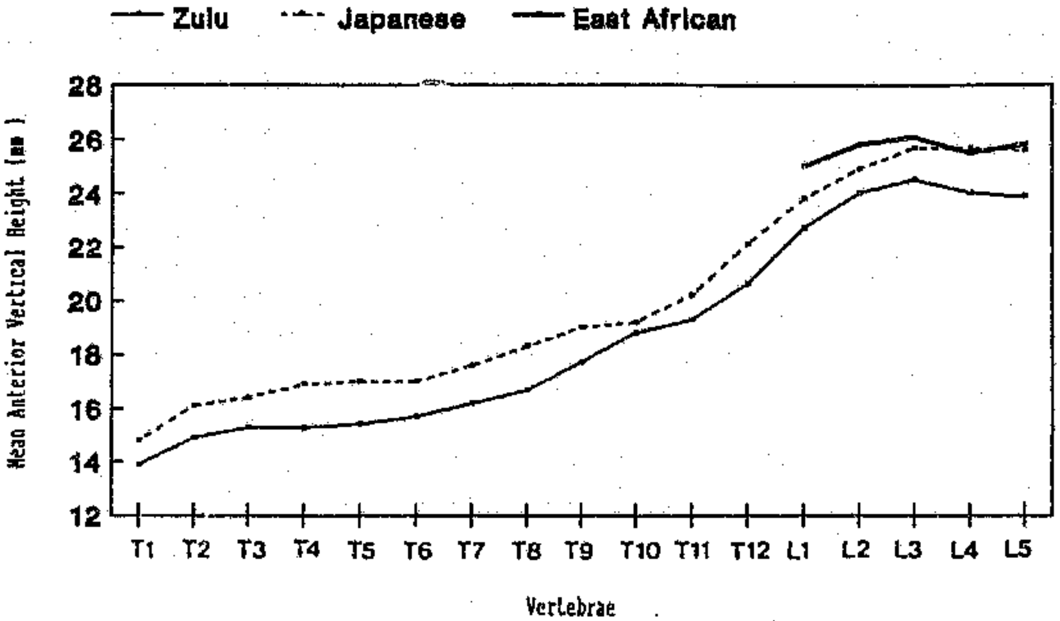


Fig. 8.3 The Mean Anterior Vertical Heights of Modern Human Female Thoracic and Lumbar Vertebral Bodies.

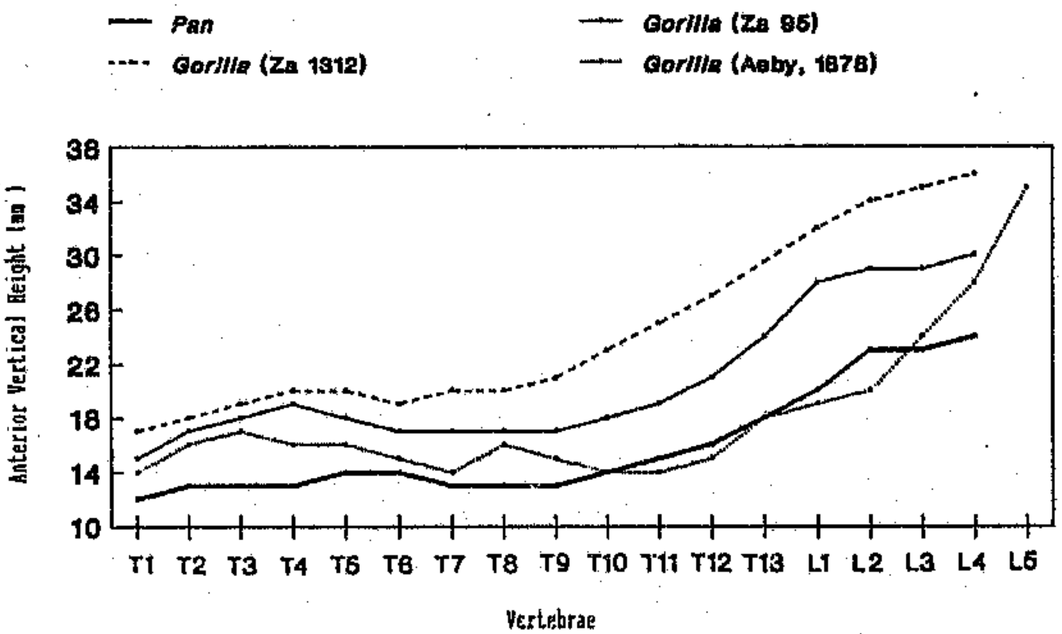


Fig. 8.4 The Anterior Vertical Heights in Individual Sets of *Gorilla* and *Pan* Thoracic and Lumbar Vertebral Bodies.

TABLE 8.3

The Anterior Vertical Heights of *Gorilla* and *Pan* Male Thoracic and Lumbar Vertebral Bodies (mm)

Vertebra	*Pan*	*Gorilla*		
	Za 1071	Za 95	Za 1312	Aeby (1878)
T1	12	15	17	14
T2	13	17	18	16
T3	13	18	19	17
T4	13	19	20	16
T5	14	18	20	16
T6	14	17	19	15
T7	13	17	20	14
T8	13	17	20	16
T9	13	17	21	15
T10	14	18	23	14
T11	15	19	25	14
T12	16	21	27	15
T13	18	24	-	18
L1	20	28	32	19
L2	23	29	34	22
L3	23	29	35	24
L4	24	30	36	28
L5				35

The mean anterior vertical heights of the thoracic and lumbar vertebral bodies in two *Gorilla gorilla* vertebral columns are recorded in Table 8.3. The mean anterior vertical heights of the vertebral bodies increase from T1 to T4, from where they decrease to T6 and increase again from T8 or T9 to L2. The anterior vertical heights decrease from L2 to L3 in Za 1312 but remain equal in Za 95. In both *Gorilla* specimens, an increase occurs again at L4 (Fig. 8.4).

The only disarticulated *Pongo* vertebral column available for study had suffered damage to the epiphyseal rings. As a result these measurements are not suitable for comparison.

2.2 Comparative Series

The only study which reports on the anterior vertical vertebral body heights known to the author is that of Aeby (1878) who reports results in a single male *Gorilla* vertebral column. The specimen he reports on possessed twenty-five presacral vertebrae. These data are listed in Table 8.3 and presented graphically in Fig. 8.4.

3 Australopithecine Series

The anterior vertical heights of *A. africanus* and *A. robustus* vertebral bodies recorded by the author are listed in Table 8.4. In addition, the results of Cook *et al.* (1983) on *A. afarensis* vertebrae are included.

Sts 14 vertebral bodies, which belong to a female partial skeleton (Robinson, 1972), present smaller anterior vertical heights than the corresponding verteb al bodies of the other *A. africanus* vertebrae (Fig. 8.5). This difference in the heights of the *A. africanus* vertebrae is further evidence of the high variability and presumed sexual dimorphism among the vertebral columns of this taxon as pointed out by Tobias (1980). On this basis Stw 8/41 and Stw 431 most probably belonged to males. The anterior vertical height of Sts 73, an isolated lower thoracic or upper lumbar vertebral body, is at 19mm intermediate between Sts 14 and Stw 8/41.

The anterior vertical height of SK 3981a, an *A. robustus* last thoracic vertebrae, is like Sts 73 midway between Sts 14 and Stw 8/41. The anterior vertical height of SK 3981b, a last lumbar vertebra, is however close to the corresponding values of the *A. africanus* male vertebrae.

TABLE 8.4

The Anterior Vertical Heights of Australopithecine Thoracic and Lumbar Vertebral Bodies (mm)

	A. africanus				*A. robustus*			*A. afarensis*			
	Sts 14	Stw 431	Stw 8/41*	Sts 73	SK 3981a	SK 3981b	AL-288	AL-333 81	AL-333 51	AL-333 X-12	AL-333 73
Thoracic:											
T2								11ε			
9th last	12										
8th last	12										
7th last	12						12				
6th last	13						12				
5th last	13						13		17		
4th last	13	?									
3rd last	13	16					13			13	
2nd last	-	17					14				
last	17	-	21*	19#	19						
Lumbar:											
L1	-	22	23*	19#							
L2	19	23	24				19				25
L3	20	22	23								
L4	19	23	21								
L5	19	22	-								
L6	19	-				21†					

* Stw 41 = last two thoracic or last thoracic and first lumbar vertebrae
\# Sts 73 = last thoracic or first lumbar vertebra
† SK 3981b = last lumbar vertebra, not known if it is L5 or L6
ε AL 333-81 = T2 based on reference to modern human samples (Cook *et al.*, 1983)

The anterior vertical heights of the AL 288 and corresponding vertebral bodies from the AL 333 locality also reveal dimorphism, the matching values for AL 288 and AL 333-X12 being smaller and for AL 333-51 much larger. Johanson and White (1979) used such dimorphism in both mandible and postcranial features to identify AL 288 as a female partial skeleton. Comparison of corresponding vertebrae of Sts 14, an *A. africanus* female, and AL 288, an *A. afarensis* female, reveal almost identical values in the anterior vertical heights of corresponding vertebral bodies.

4. Intergroup Comparisons

The biggest difference between matching values for apes and modern man, is in the upper thoracic region. In modern man, the mean anterior vertical heights increase from T1 to T2 or T3. From this level the values stay almost equal to T5 (Fig. 8.1). In the *Gorilla* columns a sharp increase occurs from T1 to T4 followed by a decrease to T6.

In the lower thoracic and upper lumbar regions the mean values in modern man increase from T6 to L3. In Sts 14 and the ape columns a plateau, spanning different segments in each column, occurs in the mid-thoracic region, before an increase occurs down to L2 in the apes or L3 in Sts 14.

At the last lumbar vertebra the mean anterior vertical height is increased in the ape columns, lower in Stw 8/41 and Stw 431, equal to that of the previous vertebra in Sts 14, increased slightly in Zulu males and decreased slightly in Zulu females.

In the thoracic region, Sts 14 is remarkably ape-like. On the other hand, in the lumbar region, the australopithecine partial columns, correspond with the spinal columns of Zulu females in respect of the sequence of anterior vertical heights.

B. The Posterior Vertical Height (M2)

1. Modern Human Series

1.1 Present Study

The mean posterior vertical heights (Table 8.5) of Zulu male vertebral bodies increase from T1 to L1 (Fig. 8.6). The first two lumbar vertebrae present the same mean posterior

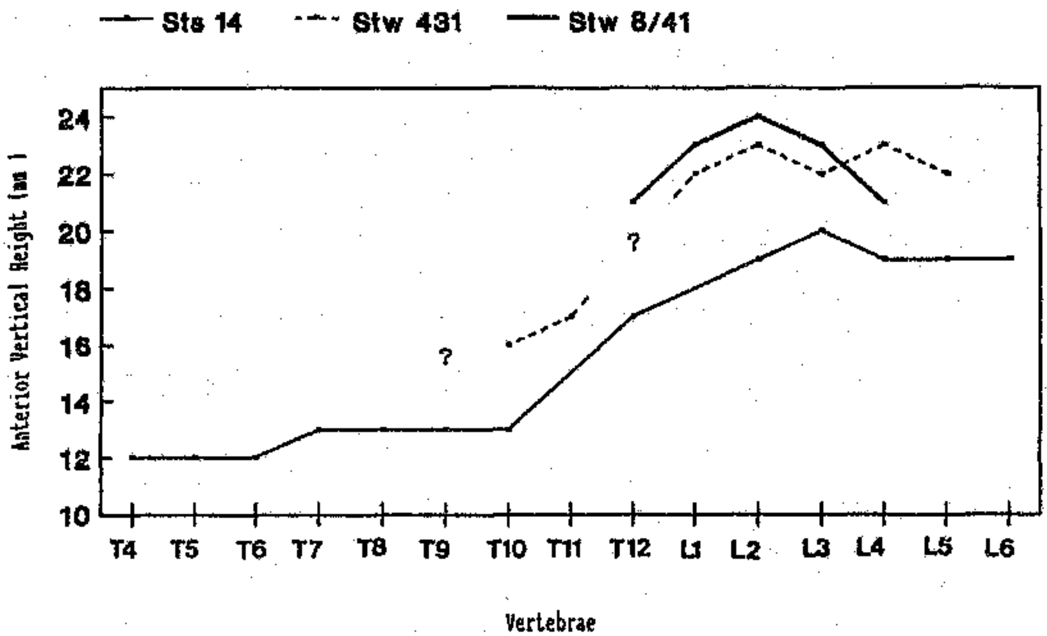


Fig. 8.5 The Anterior Vertical Heights in Individual Sets of *A. africanus* Thoracic and Lumbar Vertebral Bodies.

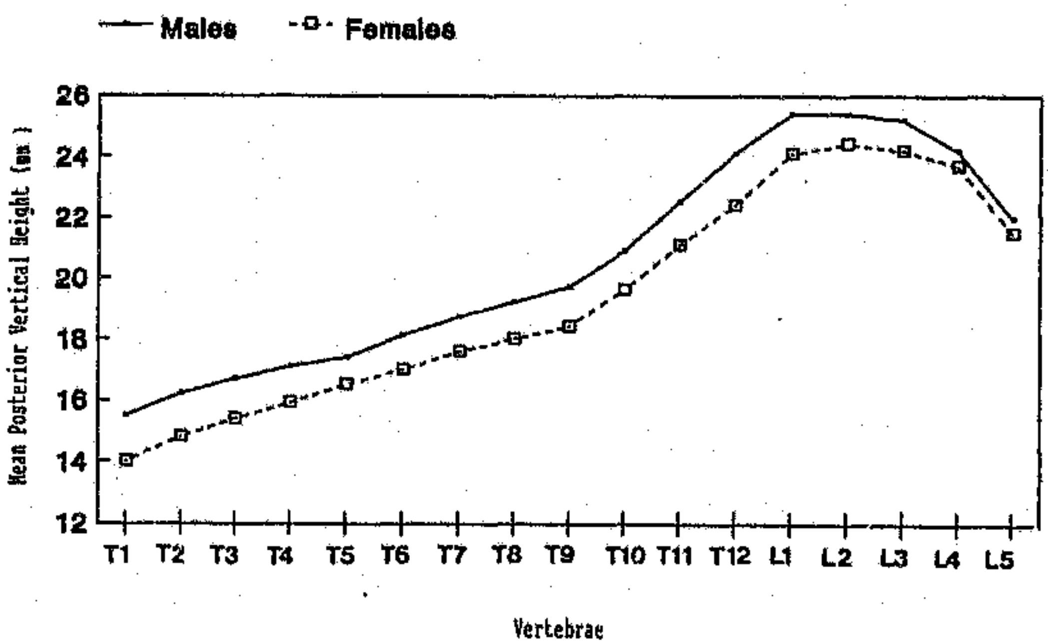


Fig. 8.6 The Mean Posterior Vertical Heights of Zulu Thoracic and Lumbar Vertebral Bodies.

vertical heights, followed by a decrease from L2 to L5. The first two lumbar vertebrae thus show the highest mean posterior vertical heights.

TABLE 8.5

The Mean Posterior Vertical Heights of the Thoracic and Lumbar Vertebral Bodies in the Zulu Series (mm)

Vertebra	Males		Females	
	Mean ± SE	Observed Range	Mean ± SE	Observed Range
T1	15,5 ± 1,07	14 - 18	14,0 ± 0,15	12 - 16
T2	16,2 ± 0,20	14 - 18	14,8 ± 0,19	12 - 16
T3	16,7 ± 0,25	14 - 20	15,4 ± 0,14	14 - 17
T4	17,1 ± 0,24	14 - 20	15,9 ± 0,15	15 - 17
T5	17,4 ± 0,26	15 - 21	16,5 ± 0,16	15 - 18
T6	18,1 ± 0,26	16 - 22	17,0 ± 0,13	15 - 18
T7	18,7 ± 0,21	17 - 22	17,6 ± 0,14	16 - 19
T8	19,2 ± 0,21	17 - 21	18,0 ± 0,15	16 - 19
T9	19,7 ± 0,24	18 - 22	18,4 ± 0,22	14 - 20
T10	20,9 ± 0,25	19 - 23	19,6 ± 0,18	18 - 22
T11	22,5 ± 0,30	20 - 25	21,1 ± 0,19	19 - 23
T12	24,1 ± 0,34	21 - 28	22,4 ± 0,23	21 - 25
L1	25,4 ± 0,30	22 - 29	24,1 ± 0,23	22 - 28
L2	25,4 ± 0,24	23 - 28	24,4 ± 0,22	22 - 27
L3	25,2 t 0,28	23 - 28	24,2 ± 0,25	22 - 28
L4	24,2 t 0,35	20 - 28	23,7 ± 0,25	21 - 27
L5	22,0 ± 0,33	19 - 25	21,5 ± 0,35	17 - 26

In the females, on the other hand, the mean values of the posterior vertical heights of the thoracic and lumbar vertebral bodies (Table 8.5) increase from L1 to L2 (Fig. 8.6). A decrease in the mean posterior vertical heights follows from L2 to L5. The second lumbar vertebra of Zulu female vertebral columns thus presents the highest mean posterior vertical height. These results are at variance with those for mean anterior vertical heights (cf. Figs. 8.1 and 8.6).

Sex differences: Zulu male thoracic and lumbar vertebral bodies show higher mean posterior vertical heights than Zulu female vertebral bodies. The Student's t-Test (Table 8.6) shows highly significant differences between the sexes in the means of the posterior vertical heights of all the thoracic and the first two lumbar vertebrae. At the level of L3, the difference in the mean posterior vertical heights between the sexes is almost certainly significant ($P<0,01$), while no significant differences occur between the sexes at the last two lumbar levels. The mean posterior vertical heights of the thoracic and lumbar vertebral bodies are thus significantly greater in males than in females, except in the last two lumbar vertebrae.

TABLE 8.6

t-Values for Sex Differences in Posterior Vertical Height of the Zulu Thoracic and Lumbar Vertebral Bodies

Vertebra	Difference of means Male - Female	t-Value	P<
T1	1,50	6,110	0,0001
T2	1,37	5,001	0,0001
T3	1,30	4,590	0,0001
T4	1,17	4,156	0,0001
T5	0,87	2,882	0,005
T6	1,09	3,751	0,005
T7	1,13	4,480	0,0001
T8	1,20	4,616	0,0001
T9	1,33	4,117	0,0001
T10	1,29	4,163	0,0001
T11	1,43	4,[illegible]80	0,0001
T12	1,70	4,180	0,0001
L1	1,33	3,531	0,0008
L2	0,93	2,865	0,005
L3	0,93	2,457	0,01
L4	0,57	1,330	0,1889
L5	0,50	1,037	0,3042

Underlined = highly significant and significant differences

1.2 Comparative Series

Hasebe (1913) reported the posterior vertical heights of Japanese vertebral bodies. He measured the vertebral bodies of 20 male and 10 female vertebral columns. Lanier (1939) has recorded the posterior vertical vertebral body heights in

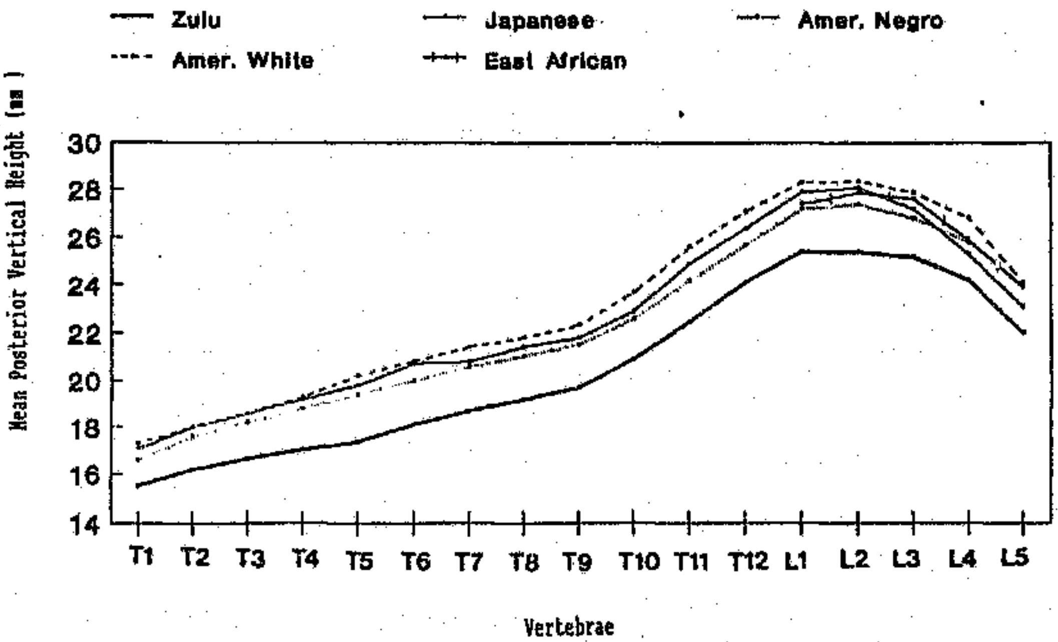


Fig. 8.7 The Mean Posterior Vertical Heights of Modern Human Male Thoracic and Lumbar Vertebral Bodies.

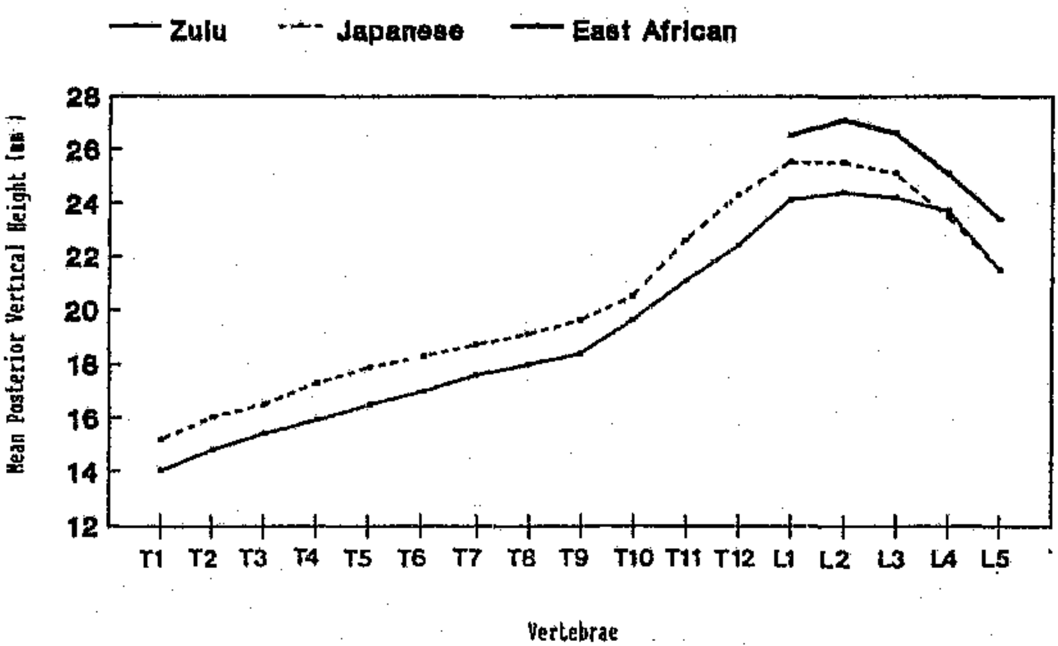


Fig. 8.8 The Mean Posterior Vertical Heights of Modern Human Female Thoracic and Lumbar Vertebral Bodies.

88 American Negro male and 96 American White male vertebral columns. He has compared his results with those of Hasebe (1913). These studies report on the presacral vertebrae with the exception of the first two cervical vertebrae. Allbrook (1956) has recorded the posterior vertical heights of East African lumbar vertebrae (51 male and 21 female columns). Fig. 8.7 (males) and Fig. 8.8 (females) present the mean posterior vertical heights of thoracic and lumbar vertebral bodies in spinal columns of some of these populations.

The results of the present study are in accordance with those of the studies mentioned earlier. In both male and female groups, the mean posterior vertical heights of Zulu thoracic and lumbar vertebral bodies are the lowest of the modern human groups. American White males (Lanier, 1939) present the highest posterior vertical heights of five groups of male vertebral columns, while East African Negro females (Allbrook, 1956) present the highest posterior vertical heights of three groups of female vertebral columns.

Berry *et al.* (1987) report the mean posterior vertical heights of Caucasoid male-plus-female vertebral columns. Since they do not report the sexes separately, their results are not included in this part of the present study.

2. African and Asian Great Ape Series

2.1 Present Study

The posterior vertical heights of the thoracic and lumbar vertebral bodies in the single *Pan troglodytes* male specimen studied (Za 1071) are listed in Table 8.7 and presented graphically in Fig. 8.9. The thoracic vertebral bodies show a gradual increase in the posterior vertical height from T1 to T10. From this level the posterior vertical heights increase more sharply to the second last lumbar vertebra followed by a small decrease to the last lumbar vertebra.

TABLE 8.7

The Posterior Vertical Heights of Individual *Pan* and *Gorilla* Thoracic and Lumbar Vertebral Bodies (mm)

Vertebra	*Pan*	*Gorilla*		
	Za 1071	Za 95	Za 1312	Aeby (1878)
T1	14	17	19	16
T2	14	18	19	19
T3	15	18	20	19
T4	15	18	20	18
T5	15	19	20	18
T6	15	19	20	18
T7	16	19	20	17
T8	16	19	20	16
T9	16	19	20	15
T10	16	19	23	17
T11	17	21	26	18
T12	19	23	29	20
T13	21	26		24
L1	23	29	33	27
L2	24	30	35	29
L3	26	-	36	29
L4	25	-	36	29
L5				-

The posterior vertical heights of the vertebral bodies in two *Gorilla gorilla* male vertebral columns are recorded (Table 8.7, Fig. 8.9). The posterior aspects of the last two lumbar vertebral bodies of Za 95 were damaged during the processes of articulation and disarticulation and it is not possible to measure these vertebrae accurately.

Both *Gorilla* vertebral columns, though spanning different numbers of segments at different levels, present a plateau in most of the thoracic region (between T2 and T9 or T10) and in this respect differ strikingly from those of modern human subjects (c.f. Figs. 8.8 and 8.9). The mean posterior vertical heights of the *Gorilla* vertebral bodies increase sharply from T9 or T10 to the second last lumbar vertebra (Fig. 8.9). The last two lumbar vertebrae of Za 1312 present the same posterior vertical heights.

The disarticulated *Pongo* vertebral column available for study suffered damage to its epiphyseal rings due to the clay used for articulation. The posterior vertical height could thus not be measured.

2.2 Comparative Series

The study of Aeby (1878) reported on the posterior vertical heights of vertebral bodies in one *Gorilla* male vertebral column. This specimen possessed 25 presacral vertebrae. The data from Aeby (1878) are also included in Fig 8.9.

3. Australopithecine Series

The posterior vertical heights of *A. africanus* and *A. robustus* vertebral bodies, recorded by the author, are listed in Table 8.8. In addition, the results of Cook *et al.* (1983) on *A. afarensis* vertebrae are included.

Sts 14 vertebral bodies have smaller posterior vertical heights than the corresponding vertebral bodies of the other *A. africanus* specimens (Fig. 8.10). The size difference in this dimension of the *A. africanus* vertebrae is further evidence of the dimorphic features of the vertebrae which have led Tobias (1980) to identify Stw 8/41 as a probable male, in contrast with Sts 14 which is female (Robinson, 1972). The similar sizes of Stw 8/41 and Stw 431 suggest that these vertebrae belonged to male individuals.

The posterior vertical heights of the *A. robustus* vertebral bodies fall within the sample range of *A. africanus* vertebral bodies. Corresponding vertebrae of Sts 14, an *A. africanus* female, and AL 288, an *A. afarensis* female (Johanson and White, 1979), show few differences in the posterior vertical heights of the vertebral bodies.

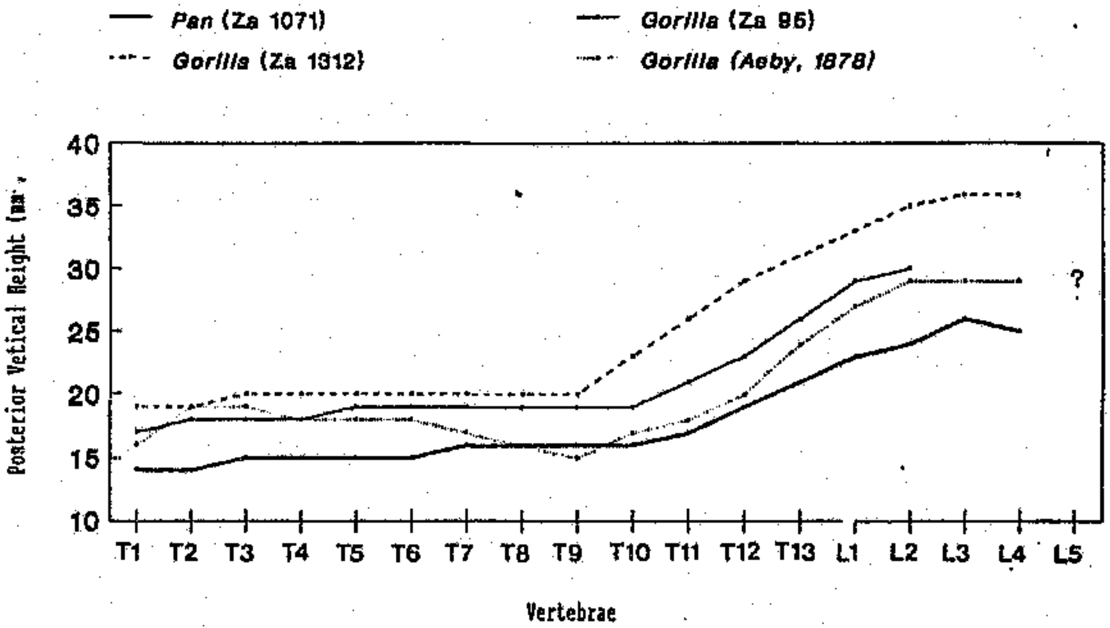


Fig. 8.9 The Posterior Vertical Heights in Individual Sets of *Gorilla* and *Pan* Thoracic and Lumbar Vertebral Bodies.

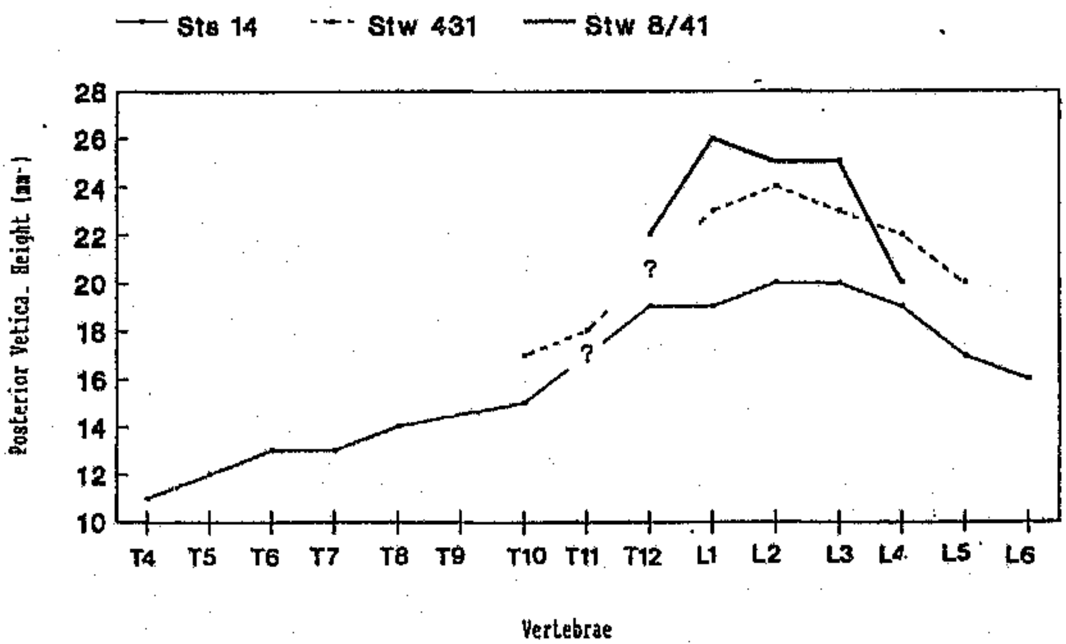


Fig. 8.10 The Posterior Vertical Heights in Individual Sets of *A. africanus* Thoracic and Lumbar Vertebral Bodies.

TABLE 8.8

The Posterior Vertical Heights of Australopithecine Thoracic and Lumbar Vertebral Bodies (mm)

Vertebra	*A. africanus*				*A. robustus*		*A. afarensis*				
	Sts 14	Stw 431	Stw 8/41	Sts 73	SK 3981a	SK 3981b	AL-288	AL-333			
								81	51	X-12	73
Thoracic:											
T2								12€			
9th last	12										
8th last	13								19		
7th last	13						13				
6th last	14						14				
5th last	14						14				
4th last	15										
3rd last	15	17					15				
2nd last		18					17				
last	19	-	22*	20#	19		-				
Lumbar:											
L1	19	23	26*	20#			-				
L2	20	24	25				22				
L3	20	23	25								24
L4	19	22	20								
L5	17	20	-								
L6	16	-				19°					

* Stw 41 = Last two thoracic or last thoracic and first lumbar vertebrae
\# Sts 73 = Last thoracic or first lumbar vertebrae
° SK 3981b = Last lumbar vertebra, not known if it is a fifth or a sixth lumbar vertebra
€ AL 333 - 81 = The second thoracic vertebra based on reference to modern human samples (Cook *et al.*, 1983)

4. Intergroup Comparisons

The sequence of mean posterior vertical heights of the great ape vertebrae is remarkably different from the modern human pattern in the thoracic and lower lumbar regions. The mean values increase from T1 to L1 or L2 in the modern human columns. In the ape columns plateaux occur between T1 and T9 or T10, spanning different numbers of segments in each column. The increase in posterior vertical height in the Sts 14 thoracic vertebrae corresponds with the pattern in the modern human columns.

In the lower lumbar region, both modern man and the australopithecine vertebrae present a decided decrease in posterior vertical height. In the ape columns the values increase down to L3 reaching a plateau or showing a slight drop in the last lumbar vertebrae.

C. The Vertical Vertebral Index ($\frac{H_2}{H_1} \times 100$)

The special vertical vertebral index,

$$\frac{\text{the posterior vertical height}}{\text{the anterior vertical height}} \times 100,$$

is designed to express the amount of postero-anterior wedging of individual vertebral bodies, as an indication of the bony adaptation of the individual vertebrae to the curvatures of the spinal column.

The general vertical vertebral index,

$$\frac{\Sigma \text{ the posterior vertical heights of the region}}{\Sigma \text{ the anterior vertical heights of the region}} \times 100,$$

indicates the amount of bony adaptation of the combined vertebrae in a region to the curvature of that region. For the purposes of comparison of general index values, Turner (1886, cited by Lanier, 1939) proposed three categories:

x - 97,9	=	Kurtorachic (anteriorly convex)
98 - 101,9	=	Orthorachic (straight)
102 - x	=	Koilorachic (anteriorly concave)

1. Modern Human Series

1.1 Present Study

The means of the vertical indices of individual Zulu male and female thoracic and lumbar vertebrae (special vertical index) are listed in Table 8.9.

In the Zulu male columns, the index values of T1 and of those between T3 and L3, all of which are greater than 100, indicate a larger posterior than anterior vertical height i.e. these vertebrae taper anteriorly. At T2 and L4 the anterior and posterior vertical heights are virtually equal, while L5 is appreciably posteriorly wedge-shaped.

The general index value of the thoracic region is 105,88%. According to Turner's categories this index value which is greater than 102% indicates good bony adaptation to the anterior concavity of the thoracic region. The general index value of the lumbar region is 100,77% : this value connotes an orthorachic curve. This indicates only moderate bony adaptation of the lumbar part of the spinal column to its anteriorly concave curve. In this instance we must assume that the intervertebral discs make a substantial contribution to the lumbar curve of Zulu male columns, or that there is a poorly developed lumbar curve.

In the Zulu female columns, the special index values of the individual vertebrae indicate that the anterior and posterior vertical heights are virtually equal in the first three thoracic vertebrae and in L3 and L4 . Between T3 and L2 the vertebral bodies are anteriorly wedge shaped, while L5 is posteriorly wedge shaped.

The general index values for the regions in Zulu female columns are 105,47% and 99,10% for the thoracic and lumbar regions respectively. According to Turner's categories, the general thoracic index value falls into the kurtorachic category and indicates good bony adaptation to the anteriorly concave thoracic curve. In the lumbar region the general index value falls into the orthorachic or straight category and indicates good bony adaptation to the anteriorly convex lumbar curve.

TABLE 8.9

The Mean Values of the Special Vertical Vertebral Index of Thoracic and Lumbar Vertebral Bodies in Zulu Males and Females (%)

Vertebra	Males				Females			
	Mean	SD	± SE	Observed Range	Mean	SD	± SE	Observed Range
T1	104,52	5,67	1,05	93,33 - 115,38	100,64	5,13	0,95	87,50 - 107,69
T2	99,99	6,40	1,19	87,50 - 113,33	100,64	13,49	2,51	82,35 - 160,00
T3	102,89	9,78	1,82	88,24 - 130,77	100,61	5,33	0,99	87,50 - 107,14
T4	106,54	6,90	1,28	94,44 - 120,00	104,15	5,85	1,09	93,75 - 115,38
T5	109,92	14,20	2,64	94,44 - 177,78	107,66	6,74	1,25	94,12 - 121,43
T6	108,08	6,12	1,14	94,12 - 120,00	108,69	7,27	1,35	93,75 - 121,43
T7	108,82	5,17	0,96	100,00 - 118,75	108,85	7,49	1,39	94,44 - 128,57
T8	109,58	7,90	1,47	100,00 - 138,46	108,02	6,33	1,18	94,12 - 120,00
T9	104,77	6,65	1,23	94,74 - 126,67	103,83	7,86	1,46	77,78 - 118,75
T10	104,94	14,62	2,72	90,48 - 158,33	104,50	6,85	1,27	90,00 - 123,53
T11	101,93	8,74	1,62	87,50 - 114,29	109,37	6,41	1,19	100,00 - 129,41
T12	109,90	7,51	1,39	100,00 - 140,00	108,92	6,74	1,25	100,00 - 131,58
L1	110,14	18,34	3,41	88,00 - 200,00	106,27	5,47	1,01	95,83 - 121,74
L2	106,43	7,07	1,31	92,00 - 118,18	101,86	3,92	0,73	95,65 - 109,09
L3	102,91	6,99	1,30	92,31 - 117,39	99,17	5,44	1,01	88,46 - 112,00
L4	99,08	6,90	1,28	89,29 - 116,67	98,81	6,54	1,21	87,50 - 113,64
L5	87,92	6,81	1,26	74,07 - 100,00	90,43	10,59	1,97	73,91 - 125,00

Sexual differences: The means of the special vertical vertebral indices show highly significant ($p<0,005$) differences between the sexes at the levels of T1, T11 and L2, (Table 8.10). The mean index values of T1 and L2 are significantly higher in males than in females. This indicates that the male vertebrae are significantly more anteriorly wedged at these levels than the corresponding female vertebrae. The mean index value of T11 is, on the other hand, highly significantly greater in the females than in the males. These vertebrae are thus highly significantly more anteriorly wedged in females than in males. At L3 the difference between the index values of the sexes is probably significant (Table 8.10), the male index values being higher. The mean general index values show no significant differences between the sexes in either the thoracic or the lumbar regions.

TABLE 8.10

t-Values for Sex Differences in the Vertical Vertebral Index of Zulu Thoracic and Lumbar Vertebral Bodies

Vertebra	Difference in index Male - Female	t-values
T1	3,88	2,78
T2	-0,65	-0,24
T3	2,28	1,12
T4	2,39	1,45
T5	2,26	0,79
T6	-0,61	-0,35
T7	-0,03	-0,02
T8	1,56	0,84
T9	0,94	0,50
T10	0,44	0,15
T11	-7,44	-3,76
T12	0,98	0,53
L1	3,87	1,11
L2	4,57	3,10
L3	3,74	2,31
L4	0,27	0,16
L5	-2,51	-1,09
Thoracic	0,41	0,49
Lumbar	1,67	1,57

1.2. Comparative Series

Hasebe (1913) lists the mean index values for individual lumbar vertebrae in various populations, data for which were drawn from the literature. Only his results on 20 Japanese males and 10 Japanese females are us.1 in the present study, for in the remaining data, either the sample size is less than 10 or the sexes are considered together or both. Trotter (1929) and Lanier (1939) report on the mean index values of individual lumbar vertebrae of American White and American Negro vertebral columns. These comparative data are listed in Table 8.11.

TABLE 8.11

The Mean Special Vertical Vertebral Index Values of Lumbar Vertebrae in Various Population Groups (%)

Author	Population	n	Lumbar Vertebrae				
			L1	L2	L3	L4	L5
Males:							
Present Study	Zulu	30	110,1	106,4	102,9	99,1	87,9
Trotter (1929)	Amer. Negro	52	106,6	104,2	99,6	95,5	85,6
Lanier (1939)	Amer. Negro	88	106,7	103,2	97,8	94,2	86,6
Trotter (1929)	Amer. White	52	107,6	103,9	99,2	94,1	84,1
Lanier (1939)	Amer. White	96	108,1	103,3	99,0	95,2	83,6
Hasebe (1913)	Japanese	20	112,0	107,7	100,4	94,8	84,0
Females:							
Present Study	Zulu	30	106,3	101,9	99,2	98,8	90,4
Trotter (1929)	Amer. Negro	23	103,0	99,1	95,8	91,8	85,7
Trotter (1929)	Amer. White	12	104,4	102,8	100,9	98,1	87,8
Hasebe (1913)	Japanese	10	107,1	102,4	97,7	91,4	84,0

L1 and L2 are anteriorly wedged in the male columns of all four population groups (Table 8.11). The Zulu males present anteriorly wedged vertebrae at L3, while Lanier's (1939) American Negro series show posteriorly wedged vertebrae at this level. Trotter's American Negro sample has approximately equal anterior and posterior vertical heights. At L4, the Zulu male columns present vertebrae with approximately equal anterior and posterior vertical heights, while the comparative samples present posteriorly wedged vertebrae. L5 is markedly posteriorly wedged in all four population groups.

In the female columns anteriorly wedged vertebrae occur at L1 in all four population groups (Table 8.11). At L2, the Zulu and American Negro series show vertebrae with approximately equal anterior and posterior vertical heights, while the Japanese and American White series show somewhat anteriorly wedged vertebrae. L3 and L4 show no wedging in the Zulu and American White female columns, while the Japanese and American Negro columns present posteriorly wedged vertebrae. L5 is approximately posteriorly wedged in all four population groups.

The study of Trotter (1929) is the only one known to the author which reports on the vertical vertebral indices of all three presacral regions. On the other hand, various authors report on the index of the lumbar regions alone. Hasebe (1913) lists the results of various authors, but for reasons mentioned earlier only the data of his own study are here used for comparison. Martin (1928) and Lanier (1939) also list some of the indices included in Hasebe's (1913) study. Lanier (1939) calculates the lumbar vertical index in 88 American Negro males and 96 American White males. He compares his results with those of Trotter (1929) on American Negro and White males and calculates an average cf their results. The mean general vertical vertebral index values of the thoracic and lumbar regions in various populations are listed in Table 8.12.

TABLE 8.12

The Mean General Vertical Vertebral Indices of the Thoracic and Lumbar Regions in Various Populations (%)

Author	Population	n		Vertical Vertebral Index	
		M	F	Males	Females
Thoracic:					
Present Study	Zulu	30	30	105,9	105,5
Trotter (1929)	Amer. Negro	52	23	105,9	104,3
Trotter (1929)	Amer. White	52	12	106,2	102,9
Lumbar:					
Present Study	Zulu	30	30	100,8	99,1
Trotter (1929)	Amer. Negro	52	23	97,9	95,0
Lanier (1939)	Amer. Negro	88	-	97,5	-
Trotter (1929)	Amer. White	52	12	97,5	98,7
Lanier (1939)	Amer. White	96	-	97,6	-
Hasebe (1913)	Japanese	20	10	99,8	96,4

All three populations, Zulu, American Negro and American Whites, show good bony adaptation to the anterior concavity of the thoracic region. In the lumbar region, Zulu and Japanese males fall within Turner's (1886) orthorachic category and show less bony adaptation to the anteriorly convex lumbar region than the American Negro and American White males. The Zulu and American White females also fall within the orthorachic category while the Japanese and American Negro females fall within the koilorachic category which connotes good bony adaptation to the anteriorly convex lumbar curvature.

2. African and Asian Great Ape Series

2.1 Present Study

The special vertical vertebral index values of one *Pan* and two *Gorilla* vertebral columns are listed in Table 8.13. The index values of Za 1071, a *Pan* male, and Za 1312, a *Gorilla* male, between T1 and L3 show a larger posterior than anterior vertical height, the only exception being T9 of Za 1312 which is posteriorly wedged. This indicates anteriorly wedge shaped vertebrae and thus bony adaptation to a continuous thoracolumbar anterior concavity. The last lumbar vertebrae of these columns present equal anterior and posterior vertical heights. The posterior vertical heights of the last two lumbar vertebrae of Za 95 are unknown. All of the remaining vertebrae of this column are anteriorly wedge-shaped.

The values of the general vertical index are 115,5% and 108,9% for the *Pan* thoracic and lumbar regions respectively. In the *Gorilla* columns, these values are 102,8% and 107,6% for the thoracic regions of Za 1312 and Za 95 respectively, while the value for the lumbar region of Za 1312 is 102,2%. Good bony adaptation to a continuous anterior concavity in both the thoracic and lumbar regions of the *Pan* and the *Gorilla* columns is thus evident.

TABLE 8.13

The Special Vertical Vertebral Indices of *Pan* and *Gorilla* Thoracic and Lumbar Vertebral Bodies (%)

Vertebra	*Pan*	*Gorilla*		
	Za 1071	Za 95	Za 1312	Aeby (1878)
T1	116,7	113,3	111,8	114,3
T2	107,7	105,9	105,6	118,8
T3	115,4	100,0	105,3	111,8
T4	115,4	94,7	100,0	112,5
T5	115,4	105,6	100,0	112,5
T6	107,1	111,8	105,3	120,0
T7	123,1	111,8	100,0	121,4
T8	114,3	111,8	100,0	100,0
T9	123,1	111,8	95,2	100,0
T10	114,3	105,6	100,0	121,4
T11	113,3	110,5	104,0	128,6
T12	118,8	109,5	107,4	133,3
T13	116,7	108,3	-	133,3
L1	115,0	103,6	103,1	142,1
L2	104,3	103,4	102,9	131,8
L3	118,2	-	102,9	120,8
L4	100,0	-	100,0	103,6
L5				-

The vertical vertebral indices of *Pongo* thoracic and lumbar vertebral bodies have not been calculated, for it was not possible to record the anterior and the posterior vertical heights of the vertebral bodies in the specimen available, due to the loss of the epiphyseal rings.

2.2 Comparative Series

The special vertical vertebral index values of one *Gorilla* male vertebral column calculated from Aeby's (1878) data are listed in Table 8.13. The index values show anteriorly wedged vertebra from T1 to L4. (The posterior vertical height of L5 of this specimen with five lumbar vertebrae is unknown.) This corroborates the results under 2.1 which indicate bony adaptation to a contiuous thoracolumbar anterior concavity. The general vertical index value is 117,5% for the thoracic region, while the value for the lumbar region is unfortunately unknown.

3. Australopithecine Series

In Sts 14 the anterior and the posterior vertical heights of the eighth and ninth last thoracic and the third and fourth lumbar vertebrae are the same, which yields index values of 100% (Table 8.14). The vertebrae are anteriorly wedged between the seventh last thoracic vertebra and L2, save that the index values are unknown for L1 and the second last thoracic vertebra. L3 and L4 have individual values of 100%, while L5 and L6 are posteriorly wedged, which indicates moderate to good bony adaptation to a lordotic lumbar curve. The general index value for the lumbar region of Sts 14, between L2 and L6 (the anterior vertical height of L1 being unknown), is 95,8%. This value falls within Turner's (1886) kurtorachic category. The lumbar region of Sts 14 thus expresses good bony adaptation to an anteriorly convex lumbar region.

The second and third last thoracic and the first three lumbar vertebrae of Stw 431 are anteriorly wedge shaped. The last two lumbar vertebrae are posteriorly wedge shaped. For the lumbar region as a whole the index value is 100% which place it in the orthorachic category. The bony adaptation to a lumbar curve appears to be less marked in Stw 431 than in Sts 14 and the contribution made by the intervertebral discs should have been larger in this male individual if the individually wedge shaped lower lumbar vertebrae are borne in mind, or a poorly developed lumbar curve occurred. This corresponds with the results in modern human males.

TABLE 8.14

The Special Vertical Vertebral Indices of Australopithecine Thoracic and Lumbar Vertebral Bodies (%)

Vertebra	*A. africanus*				*A. robustus*		*A. afarensis*			
	Sts 14	Stw 431	Stw 8/41	Sts 73	SK 3981a	SK 3981b	AL 288	AL 333		
								81	X-12	73
Thoracic:								109,1		
9th last	91,7									
8th last	100,0									
7th last	108,3						108,3			
6th last	100,0						116,7			
5th last	107,7						107,7			
4th last							-			
3rd last	115,4	106,3					115,4		115,4	
2nd last	-	105,9			100,0		121,4			
last	111,8	-	104,8	105,3			-			
Lumbar:										
L1	-	104,5	113,0	105,3			-			
L2	105,3	104,3	104,2				115,8			
L3	100,0	104,5	108,7							96,0
L4	100,0	95,7	95,2							
L5	89,5	90,9				90,5				
L6	84,2	-								

The vertical vertebral index value of the second last lumbar vertebra in Stw 8/41, which is either L4 or L5, is 95,2%. The index value of this vertebra indicates a posteriorly wedged body.

In Sts 14 and AL 288, the special vertical vertebral index values of corresponding thoracic vertebral bodies are the same in three instances. The values of this index for AL 333-73 (96,0%), an *A. afarensis* lumbar vertebra, and for SK 3981b (90,5%), an *A. robustus* lumbar vertebra, show posteriorly wedged vertebrae which indicates good bony adaptation to a possibly anteriorly convex lumbar curve in these australopithecines. Thus in all australopithecine spinal columns for which the relevant vertebrae are available, the lower two or perhaps even three lumbar vertebrae differ from those of the apes and resemble those of modern man in showing posteriorly-wedged vertebral bodies, that is bony adaptation to a presumed lumbar lordotic curve.

4. Intergroup Comparisons

The special vertical index of Zulu male and Zulu female vertebrae indicates anteriorly wedged thoracic vertebrae, save that T2 in the male columns is posteriorly wedged. The thoracic vertebrae of Za 1071, a *Pan* male vertebral column, are anteriorly wedged. In the *Gorilla* male columns, Za 95 shows an exception at T4 which is posteriorly wedged and Za 1312 shows a posteriorly wedged vertebra at T9 and vertebrae with equal anterior and posterior vertical heights at T4, T5, T7, T8 and T10. The general vertical index values of the thoracic regions (Table 8.15) indicate good bony adaptation to the anteriorly concave thoracic regions in both modern man and, despite the exceptional vertebrae, the African great apes.

The special vertical index values for modern human lumbar vertebrae indicate anteriorly wedged vertebrae at L1 (Table 8.11). The vertebrae are either anteriorly wedged or straight at L2. L3 is anteriorly wedged, straight or posteriorly wedged. At L4 the vertebrae are either straight or posteriorly wedge-shaped. L5 is posteriorly wedged in all population groups. The lumbar vertebrae of Za 1071 (*Pan* male) and Za 1312 (*Gorilla* male) are anteriorly wedge-shaped between L1 and L3 while L4 is straight. The last two lumbar vertebrae of Sts 14 (L5 and L6) and of Stw 431 (L4 and L5) and the second last (L4 or L5) of Stw 8/41 are posteriorly wedge-shaped. The last lumbar vertebra of *A. robustus*, SK 3981b, is also posteriorly wedged shape. Unfortunately no *A. afarensis* last lumbar vertebra is recovered yet.

TABLE 8.15

General Vertical Index Values of Modern Human, Anthropoid Ape and *A. africanus* Thoracic and Lumbar Vertebrae (%)

Series	General Vertical Index Thoracic		Lumbar	
	Males	Females	Males	Female
1. Modern human				
Zulu (present study)	105,9	105,5	100,8	99,1
Amer. Negro (Trotter, 1929)	105,7	104,3	97,9	95,0
Amer. Negro (Lanier, 1939)	-	-	97,7	-
Amer. Whites (Trotter, 1929)	106,2	102,9	97,5	98,7
Amer. Whites (Lanier, 1939)	-	-	97,5	-
Japanese (Hasebe, 1913)	-	-	99,8	96,4
2. Anthropoid apes				
Za 1071 (*Pan*)	115,5	-	108,9	-
Za 1312 (*Gorilla*)	102,8	-	102,2	-
Za 95 (*Gorilla*)	107,6	-	-	-
3. *A. africanus*				
Sts 14	-	-	-	95,8*
Stw 431	-	-	100,0	-

* Between L2 and L6.

The general vertical index values of the lumbar regions (Table 8.15) show orthorachic lumbar regions in Zulu males and females, American Negro males, American White females and Japanese males. In these groups the contribution to the lumbar curvature made by the intervertebral discs must be great. The remaining modern human groups (Table 8.10) show kurtorachic lumbar regions which indicate good bony adaptation to an anteriorly convex lumbar curve. On the other hand Za 95 and Za 1312, a *Pan* and a *Gorilla* male vertebral column, show koilorachic lumbar regions which indicate good bony adaptation to an anteriorly concave lumbar curve. Sts 14 shows, between L2 and L6, a kurtorachic and Stw 431 an orthorachic lumbar region. Good bony adaptation to an anteriorly convex lumbar region is thus found in Sts 14, while the bony adaptation to an anteriorly convex lumbar region is poorly developed in Stw 431. The results for *A. africanus* correspond thus with the findings for the modern human series. The relevant *A. afarensis* and *A. robustus* vertebrae are not available to calculate the general vertical index value of the lumbar region.

D. Discussion

One of the distinctive features of the modern human vertebral column is the presence of a marked normal lordosis - an anteriorly convex curve in the lumbar region, This curvature has been measured in various ways and expressed by various indices during the past century. Most recently Abitbol (1987a) measured the lumbosacral angle on radiographs in a comparative series of modern human and non-human vertebral columns.

The degree to which the anterior vertical height of a vertebral body exceeds its posterior vertical height shows the degree of posterior wedging of the vertebral body and thus the degree of bony adaptation of the vertebral bodies to a lordosis in the region as a whole. Lanier (1939) has calculated the difference between the anterior and the posterior vertical heights of each lumbar vertebra in American White and Negro males, while Allbrook (1956) has calculated the difference between the posterior and the anterior vertical heights of each lumbar vertebral body in East African vertebral columns. The ,special vertical index, used in the present study, expresses the relation between the posterior and the anterior vertical heights of a vertebra as a percentage. The general vertical index espresses the same relationship, but for the region as a whole. This index was devised by Turner (1886 cited by Lanier 1939). For purposes of comparison Turner (1886) grouped the individual values of the general index into three categories mentioned, above. The results obtained by some of the many authors who used this index are included in the modern human comparative study in this chapter.

In the present study, the general vertical index values of the thoracic regions indicate good bony adaptation to the anterior concave thoracic regions in both modern man and the African great apes. The general index values of the lumbar regions show good bony adaptation to an anteriorly convex lumbar curve in modern human female columns of various population groups and in Sts 14 (between L2 and L6), an *A. africanus* female partial column. The index values of the modern human male columns show kurtorachic to orthoracic lumbar regions which indicate moderate to good bony adaptation to an anteriorly convex curvature. Stw 431, an *A africanus* male, also shows an orthorachic region. On the other hand, the lumb: regions of a *Gorilla* and a *Pan* vertebral column show good bony adaptation to an <u>anteriorly concave</u> curvature.

The results of the present study on the general vertical vertebral index of modern man and the African great apes agree with those of Abitbol (1987a) on the lumbosacral angle, though the degree of lumbar curvature measured in the present study suggested smaller lumbar angles. The difference lies in the fact that the vertical vertebral index expresses the degree of wedging of a vertebral body or the curvature of a region as a whole, as presented by the vertebral body dimensions alone. It does not take the intervertebral discs, which may increase the lumbar curve, into account as the measurement of the lumbosacral angle on a radiograph does. The advantage of the vertical vertebral index is that it enables one to compare fossil vertebral bodies, of which the intervertebral disc thickness and shape are unknown, with the vertebral bodies of extant hominoids.

A last *A. robustus* lumbar vertebral body (SK 3981b) and a third *A. afarensis* vertebral body (AL 333-73) are both posteriorly wedged which indicates that they probably took part in the formation of an anteriorly convex lumbar curve.

The bony adaptation to a fully developed lordosis in the *A. africanus* partial vertebral columns, and the indications thereof in individual *A. robustus* and *A. afarensis* lumbar vertebral bodies, suggest that the trunk was carried fully erect and that the legs were probably extended in the australopithecines.

This conclusion on the australopithecine lumbar lordosis is in accordance with those of Robinson (1972) on the vertebrae of *A. africanus* and *A. robustus*. From his comparative study on the pelvis Robinson (1972) concluded that the nature of the similarities between the pelves of these fossil species and modern man suggests strongly that they were both capable of erect, bipedal locomotion. The differences in the pelves led him to suggest further that *A. africanus* was adapted to move efficiently and speedily while *A. robustus* showed a more power-orientated locomotor system, possibly for climbing trees in addition to bipedal locomotion on the ground. On the other hand, Lovejoy *et al.* (1973), from australopithecine pelves, could find no evidence for locomotor differences between the two forms.

The conclusion of the present study on the australopithecine lumbar lordosis differs from that of Abitbol (1987a) for *A. afarensis*. He cites a personal communication by Stern, who calculates the lumbosacral angle in AL 288, as thirty degrees. Abitbol (1987a) concludes that this relatively small angle confirms the primitive nature of the pelvic girdle of *A. afarensis* and suggests a manner of bipedalism that differed from that of modern humans, but he does not speak of the posture of *A. afarensis*. Unfortunately no AL 288 lumbar vertical vertebral indices are available, but the AL 288 thoracic vertebral index values are mostly identical to those of

Sts 14. The vertical vertebral index of AL 333-73, an *A. afarensis* male third lumbar vertebra, is posteriorly wedged (96,0%), which indicates that it might have taken part in the formation of an anteriorly convex lumbar curve.

The results of some of the studies on the adaptations of the australopithecine ilium and pelvis are in keeping with the findings of the present study on the lumbar vertebrae (first group), while some support the findings of Abitbol's (1987a) study (second group), and a third group are not in accord with the results of either study. The authors in the first group concluded from the pelvic adaptations that *Australopithecus* was capable of efficient, erect, bipedal locomotion which corresponded with the locomotion of modern man (e.g. Broom & Robinson 1947; Dart 1958; Leutenegger 1972; Robinson 1972; Lovejoy *et al.* 1973; McHenry 1975; Steudel 1978). Mednick (1955) and Zihlman and Hunter (1973) believe that the australopithecines walked erect and bipedally but that these early hominids lacked certain modifications for efficient bipedal locomotion. *Australopithecus* might have represented an intermediate stage. In the second group, which supports Abitbol's (1987a) study, Stern and Susman (1983) conclude from the *A. afarensis* pelvis:

> "The most compelling reasons for suggesting a bent-hip, bent-knee bipedality for the Hadar hominid are provided by the orientation of the iliac blade and the diminutive size of the anterior horn of the acetabular surface." (op.cit., p 312)

The third group, Oxnard (1975) and Ashton (1981), conclude that the australopithecines are unique, in that *Australopithecus* and modern man differ in dimensions relating to locomotor function just as much as each differs from the apes. Ashton (1981) stresses that *Australopithecus* is not intermediate between man and apes.

E. Summary and Conclusions

1. The results of the present study show that the patterns of increase and decrease in the mean anterior and in the mean posterior vertical heights of male and female Zulu vertebral bodies are in accord with those of various authors on various human population groups. Intergroup comparisons of the anterior vertical heights of corresponding modern human, anthropoid ape and *A. africanus* vertebral bodies show that Sts 14 is remarkably ape-like in the thoracic region. Comparisons of the posterior vertical heights show that Sts 14 is typically human in the thoracic region. In the lumbar region the anterior and the posterior vertical heights of both Sts 14 and Stw 431 show correspondence with the Zulu female lumbar region.

2. The general vertical vertebral index values of the thoracic region indicate good bony adaptation to the anteriorly concave thoracic regions in both modern human and African great ape columns.

3. The general vertical vertebral index values of female lumbar regions indicate good bony adaptation to an anteriorly convex lumbar curve in modern man and *A. africanus* (Sts 14). The modern human male lumbar regions of various populations show moderate to good bony adaptation to a lordosis. Moderate bony adaptation to an anteriorly convex lumbar region is expressed also by Stw 431, an *A. africanus* male partial column. In contrast the *Gorilla* and the *Pan* columns present good bony adaptation to an anteriorly <u>concave</u> lumbar region.

4. The special vertical vertebral index values of a last *A. robustus* lumbar vertebra, SK 3981b, and a third *A. afarensis* lumbar vertebra, AL 333-73, indicate posteriorly wedged vertebrae, as in *A. africanus*.

5. The bony adaptation to a developed lumbar lordosis in the *A. africanus* partial vertebral columns and the posteriorly wedged individual lumbar vertebrae of *A. robustus* and *A. afarensis*, which indicate that they might have taken part in the formation of an anteriorly convex lumbar region, lead the author to conclude that the australopithecines probably carried the trunk erect. Because of the close association between extended legs and the formation of the lumbar lordosis, it is further concluded that the australopithecines used extended legs. Thus our results suggest a mode of bipedalism in these early hominids that corresponds with that of modern humans.

6. The conclusion of the present study agrees with that of Robinson (1972) for *A. africanus*, but differs from that of Abitbol (1987a) for *A. afarensis*. The various studies on the adaptations of the *Australopithecus* ilium and pelvis are equivocal. Some agree with the conclusions of the present study, some support Abitbol's (1987a) conclusions, while others do not support the results of either of the studies.

CHAPTER 9

THE ABSOLUTE AND RELATIVE DIMENSIONS OF THE INFERIOR VERTEBRAL BODY AREA AND THE POSTERIOR ARCH DIMENSIONS OF THORACIC AND LUMBAR VERTEBRAE IN VARIOUS HOMINOIDS

Contents of Chapter

E. The Transverse Process Size
   1. Modern Human Series
   2. African and Asian Great Ape Series
   3. Australopithecine Series
   4. Intergroup Comparisons

F. The Body-Pedicle Angle
   1. Modern Human Series
   2. African and Asian Great Ape Series
   3. Australopithecine Series
   4. Intergroup Comparisons

G. Discussion

H. Summary and Conclusions

Introduction

In upright man the size of the vertebral bodies increases from the axis to the lumbosacral joint. This is expected since the compressive force increases from the head to the pelvis as each vertebra bears the weight of all of the body above it. For many years, as indicated in textbooks of anatomy and published investigations (Davis, 1961; Rosch and Burke, 1964; Taylor and Twomey, 1984, and Gracovetsky and Farfan, 1986), it has been believed that the vertebral bodies and the intervertebral discs sustain all the vertebral compressive force.

Following Davis's (1961) study, new concepts on spinal stability and weight-bearing in modern human vertebral columns have been introduced. He shows that the pedicles and transverse processes of the fifth lumbar vertebra are involved in the transmission of forces to the pelvis. Denis (1983) and Louis (1985) propose that the articular facets are involved in weight-bearing, while Pal and Routal (1986, 1987) develop an hypothesis according to which weight is transmitted also through the neural arch. The purpose of the investigations reported here is to determine whether the dimensions of African and Asian great ape and australopithecine vertebrae reflect the same mode of weight-bearing as in modern humans.

Comparative data on modern human vertebral bodies are from the studies of Pal and Routal (1986, 1987). No comparative data on African or Asian great apes or on australopithecine vertebrae are known to the author. In comparative graphs the last thoracic vertebrae of *Australopithecus africanus* partial vertebral columns are presented as T12 purely for the sake of convenience.

A. The Inferior Vertebral Body Area

1. Modern Human Series

1.1 Zulu Series

Table 9.1 lists the mean inferior surface area of male and female Zulu vertebral bodies. The mean inferior areas of male thoracic and lumbar vertebral bodies increase to 3,4 fold from T1 to L4 (Fig. 9.1). From L4 to L5 the mean area decreases by 1,4cm². The mean inferior areas of the Zulu female thoracic and lumbar vertebral bodies increase to 3,3 fold from T1 to L4. The decline of the female means between L4 and L5 is 0,8cm².

TABLE 9.1

The Mean Inferior Area of Zulu Thoracic and Lumbar Vertebral Bodies (cm^2)

Vertebra	Males Mean ± SD	Females Mean ± SD
T1	4,2 ± 0,37	3,7 ± 0,49
T2	4,3 ± 0,44	3,8 ± 0,41
T3	4,6 ± 0,51	4,1 ± 0,50
T4	5,1 ± 0,60	4,3 ± 0,40
T5	5,4 ± 0,50	4,6 ± 0,48
T6	5,9 ± 0,57	5,1 ± 0,67
T7	6,8 ± 0,75	5,6 ± 0,62
T8	7,4 ± 0,93	6,0 ± 0,69
T9	7,9 ± 0,99	6,7 ± 0,78
T10	8,7 ± 1,11	7,3 ± 0,80
T11	9,8 ± 1,16	8,2 ± 0,99
T12	10,3 ± 1,18	8,7 ± 0,92
L1	11,8 ± 1,50	9,8 ± 0,86
L2	12,5 ± 1,56	10,4 ± 1,02
L3	13,7 ± 1,45	11,5 ± 1,41
L4	14,3 ± 1,58	12,3 ± 1,37
L5	12,9 ± 1,87	11,5 ± 1,28

n = 30

Sex differences: The mean inferior area of all thoracic and lumbar vertebral bodies are greater in Zulu male than in Zulu female vertebral columns (Fig. 9.1). The Student's t-Test shows that these differences are highly significant ($P<0,0005$ and $P<0,005$) (Table 9.2).

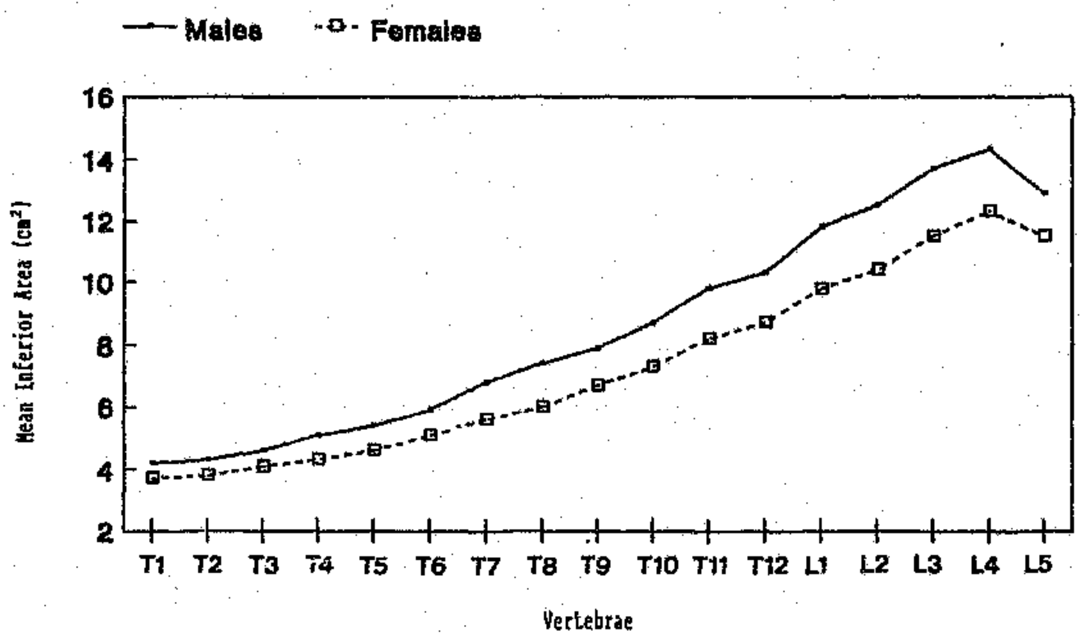


Fig. 9.1 The Mean inferior Areas of Zulu Thoracic and Lumbar Vertebral Bodies

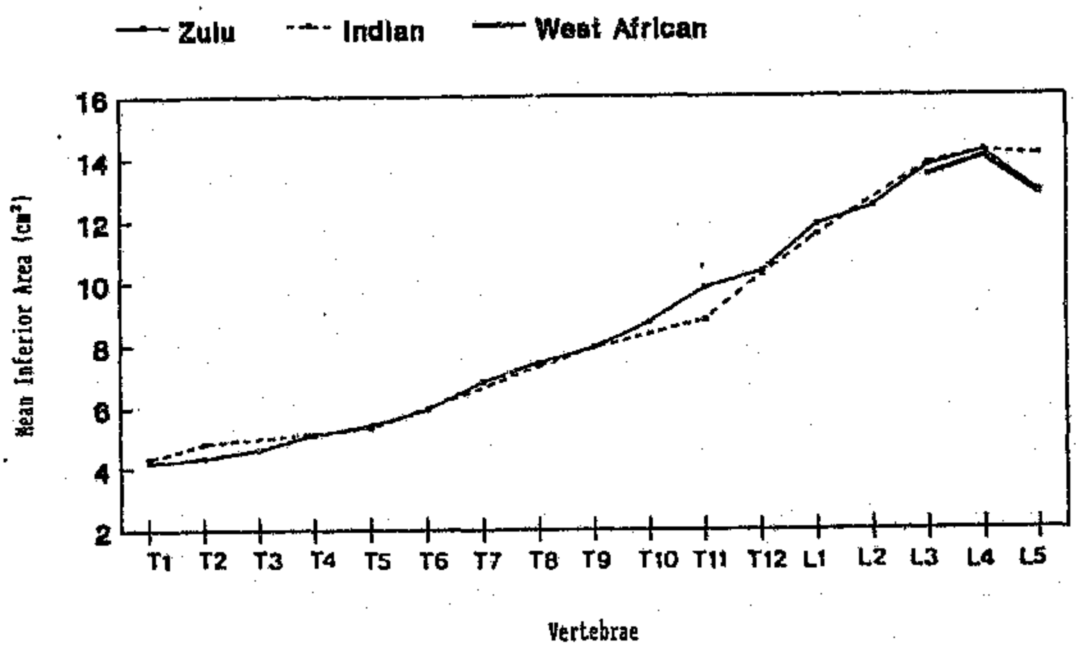


Fig. 9.2 The Mean Inferior Areas of Modern Human Male Thoraic and Lumbar Vertebral Bodies

TABLE 9.2

t-Values of Sex Differences in the Inferior Areas of Zulu Thoracic and Lumbar Vertebral Bodies

Vertebra	t-Value	P<
T1	4,460	0,0005
T2	4,554	0,0005
T3	3,834	0,0005
T4	6,076	0,0005
T5	6,322	0,0005
T6	4,981	0,0005
T7	6,754	0,0005
T8	6,622	0,0005
T9	5,215	0,0005
T10	5,604	0,0005
T11	5,747	0,0005
T12	5,657	0,0005
L1	6,336	0,0005
L2	6,171	0,0005
L3	5,958	0,0005
L4	5,238	0,0005
L5	3,383	0,005

1.2 Comparative Human Series

Davis (1961) gives values for the mean inferior vertebral body areas of L3, L4 and L5 in 35 male and 24 female West African columns. Pal and Routal (1986, 1987) report the mean values of certain thoracic and lumbar vertebral bodies of 44 adult male columns in the collection of the Government Medical College, Surat. Though the population group of these skeletons is not mentioned it is taken that they are Indian. Table 9.3 lists and Fig. 9.2 presents graphically the data from these studies and from the present study on male vertebral columns.

TABLE 9.3

The Inferior Vertebral Body Areas of Thoracic and Lumbar Vertebral Bodies in Various Modern Human Male Vertebral Columns.
Mean Value ± SD (cm^2)

Vertebrae	Present Study Zulu males (n = 30)	Pal & Routal (1986, 1987) Indian males (n = 44)	Davis (1961) West African males (n = 35)
T1	4,2 ± 0,37	4,3 ± 0,53	
T2	4,3 ± 0,44	4,8 ± 0,70	
T3	4,6 ± 0,51		
T4	5,1 ± 0,60		
T5	5,4 ± 0,50	5,3 ± 0,45	
T6	5,9 ± 0,57		
T7	6,8 ± 0,75		
T8	7,4 ± 0,93	7,3 ± 1,98	
T9	7,9 ± 0,99	7,9 ± 2,16	
T10	8,7 ± 1,11		
T11	9,8 ± 1,16	8,6 ± 1,10	
T12	10,3 ± 1,18	10,2 ± 1,53	
L1	11,8 ± 1,54	11,5 ± 2,16	
L2	12,4 ± 1,49		
L3	13,7 ± 1,45	13,8 ± 2,22	13,4 ± 1,1
L4	14,2 ± 1,57	14,2 ± 1,26	14,0 ± 1,2
L5	12,9 ± 1,87	14,1 ± 2,77	12,8 ± 1,3

The results of the present study agree with those of Davis's (1961) study. No significant differences is found between the Zulu and the West African values of corresponding vertebrae. In both the Zulu series and Pal and Routal's (1986, 1987) Indian series, the mean inferior vertebral body areas increase from T1 to L4. The decrease in the values from L4 to L5 in the latter series is not nearly as large as in either the Zulu or the West African vertebral columns. The difference between the mean inferior areas of L5 in Indian (14,1cm²) and in Zulu (12,9cm²) males is highly significant ($t = 3,390$; $P<0,005$). The mean inferior surface area of T2 is highly significantly smaller ($t = 2,859$; $P<0,005$) and that of T11 highly significantly greater ($t = 3,963$; $P<0,0005$) in Zulu than in Indian male vertebral columns. For all other vertebrae that may be compared, the Zulu and Indian mean values are very similar or identical.

The mean inferior surface areas of female thoracic and lumbar vertebral bodies are presented in Fig. 9.3. The values of the last three lumbar vertebrae show the same tendency in Zulu as in West African females. No significant difference is found between the values of corresponding ver‹ ‹brae.

1.3 Total and Average Percentage Increase

We have seen that the mean values of the inferior areas of the vertebral bodies increase from T1 to L4 in both male and female vertebral columns. The total percentage increase between T1 and L4, between T1 and T12, and between L1 and L4 are calculated <u>for each</u> vertebral column by the following formula:

$$\text{Total percentage increase} = \frac{\text{Inferior area most caudal vertebra} - \text{Inferior area most cranial vertebra}}{\text{Inferior area most cranial vertebra}} \times \frac{100}{1}$$

The mean total percentage increase is then calculated for each population and gende: subset.

The average percentage increase in inferior surface area between consecutive vertebral bodies in the thoracic and lumbar regions is also calculated for each column by the following formula devised by the author.

$$\text{Average percentage increase} = \frac{\text{Total percentage increase}}{\text{Number of vertebra involved}}$$

For each population and gender subset, the mean of all the average percentage increases is recorded. The mean inferior area of L5 is smaller than that of L4 in both sexes. The percentage decrease between these vertebrae is calculated for each individual and the mean percentage decrease for each series is recorded.

$$\text{Percentage decrease between L4 and L5} = \frac{\text{Inferior area L4} - \text{Inferior area L5}}{\text{Inferior area L5}} \times \frac{100}{1}$$

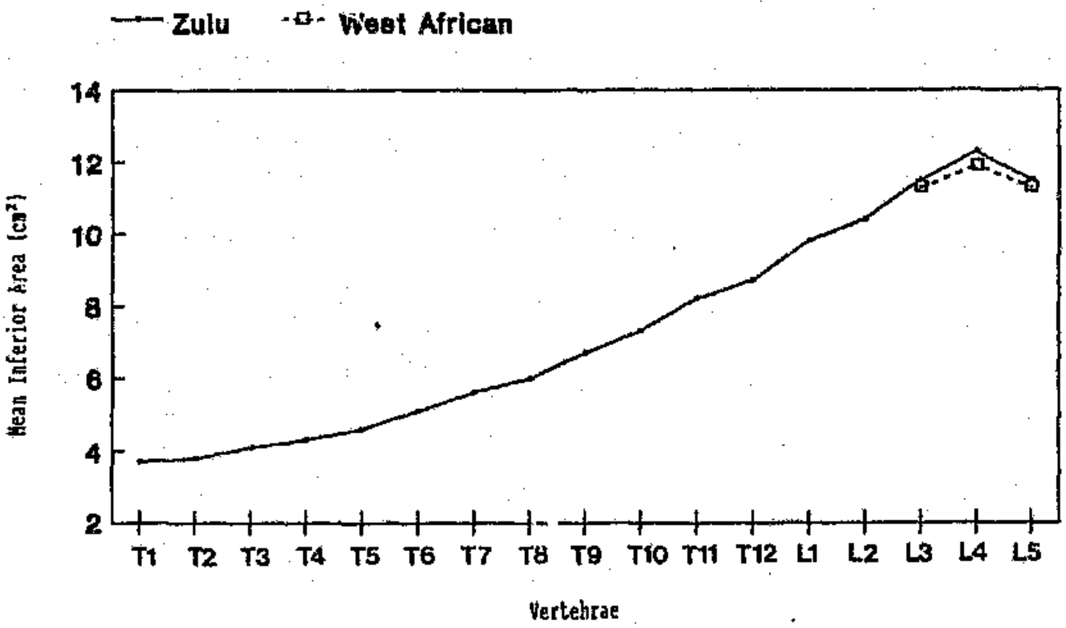


Fig. 9.3 The Mean Inferior Areas of Modern Human Female Thoracic and Lumbar Vertebral Bodies

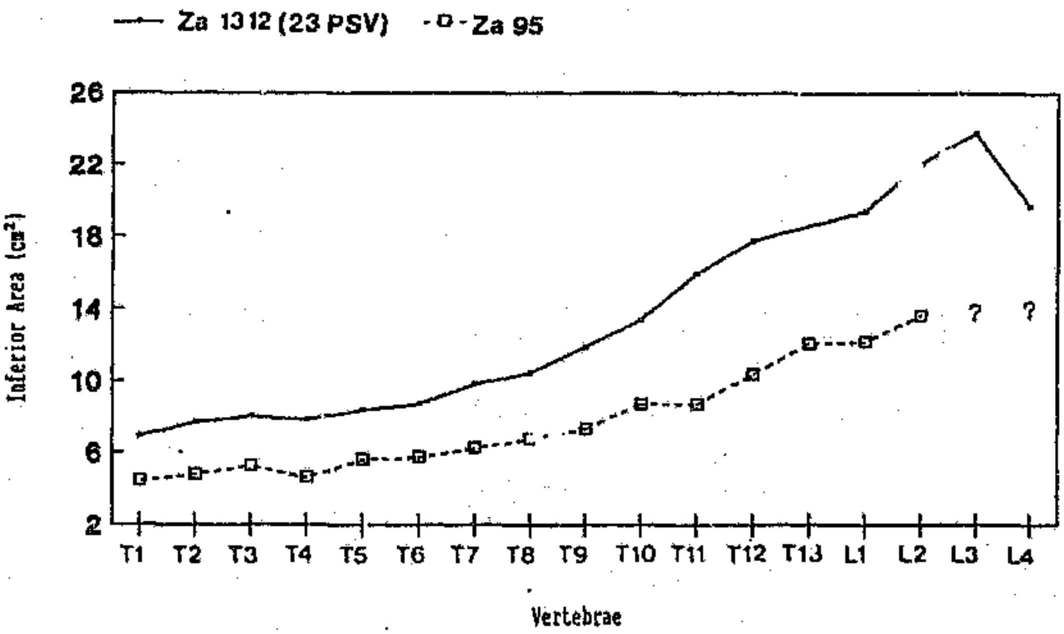


Fig. 9.4 The Inferior Areas in Two Sets of *Gorilla* Male Thoracic and Lumbar Vertebral Bodies

The results of these calculations in the Zulu series are listed in Table 9.4.

TABLE 9.4

The Mean Total and Mean Average Percentage Inferior Vertebral Body Area Increase in Zulu Spinal Columns

	Males Mean ± SD	Females Mean ± SD
T1 to L4		
Total percentage increase	242,63 ± 31,73	238,50 ± 36,43
Average percentage increase	15,18 ± 1,99	14,91 ± 2,28
T1 to T12		
Total percentage increase	146,57 ± 23,25	139,27 ± 39,15
Average percentage increase	12,22 ± 1,94	11,61 ± 2,68
L1 to L4		
Total percentage increase	21,44 ± 8,57	26,26 ± 12,03
Average percentage increase	5,36 ± 2,15	6,57 ± 3,01
L4 to L5		
Percentage decrease	11,53 ± 10,09	[illegible],25 ± 9,46

The results show a higher mean total percentage ircrease in inferior vertebral body area in the tho:acolumbar and thoracic regions of Zulu males than female.,. The average increase between consecutive vertebrae of these regions shows the same tendency. On the other hand female lumbar vertebral bodies (L1 to L4) rresent a higher mean total percentage and mean average per   cage increase in inferior area than male lumbar vertebra´   od'es. The decrease in inferior area between L4 and L5 is higher in males than in females. This difference, like the differences in the mean average percentage increase between consecutive vertebrae of the regions, proves not significant. The formula given in Chapter 3 to test the significance of difference between percentages is used.

2. African and Asian Great Ape Series

2.1 Present Study

The inferior surface area of the African and Asian great ape thoracic and lumbar vertebral bodies are listed in Table 9.5 and represented graphically in Figs. 9.4, 9.5 and 9.6.

In the *Gorilla* columns an increase in the inferior area of the vertebral bodies occurs from T1 to L3 (with the exception of T4) and then decrease to L4. The last two lumbar vertebrae of Za 95, a *Gorilla* male vertebral column with 24 PSV, are damaged at the posterior surface from previous mounting of the skeleton. The *Pongo* female and both *Pan* male vertebral columns show an increase in the inferior vertebral body area from T1 to L3 with a decrease to L4.

TABLE 9.5

The Inferior Vertebral Body Areas of Individual African and Asian Great Apes (cm^2)

Vertebra	Za 1312 *Gorilla* Male	Za 95 *Gorilla* Male	Za 1071 *Pan* Male	Za 94 *Pan* Male	Za 93 *Pongo* Female
T1	6,88	4,40	3,04	1,92	3,00
T2	7,68	4,80	3,36	2,20	3,48
T3	8,00	5,24	3,60	2,40	3,52
T4	7,84	4,60	3,72	2,60	3,80
T5	8,32	5,60	4,36	2,80	4,12
T6	8,72	5,72	4,36	2,96	4,52
T7	9,80	6,24	4,80	3,08	4,76
T8	10,44	6,76	4,92	3,24	5,16
T9	11,88	7,32	5,68	3,52	5,48
T10	13,36	8,72	5,84	4,24	5,80
T11	15,88	8,72	6,40	4,72	6,28
T12	17,76	10,32	7,36	5,20	7,08
T13		12,04	8,08	5,56	
L1	19,36	12,16	8,80	6,12	7,32
L2	22,04	13,60	10,36	6,40	8,76
L3	23,80	*	11,00	6,72	9,04
L4	19,64	*	10,20	5,60	7,56

* Damaged

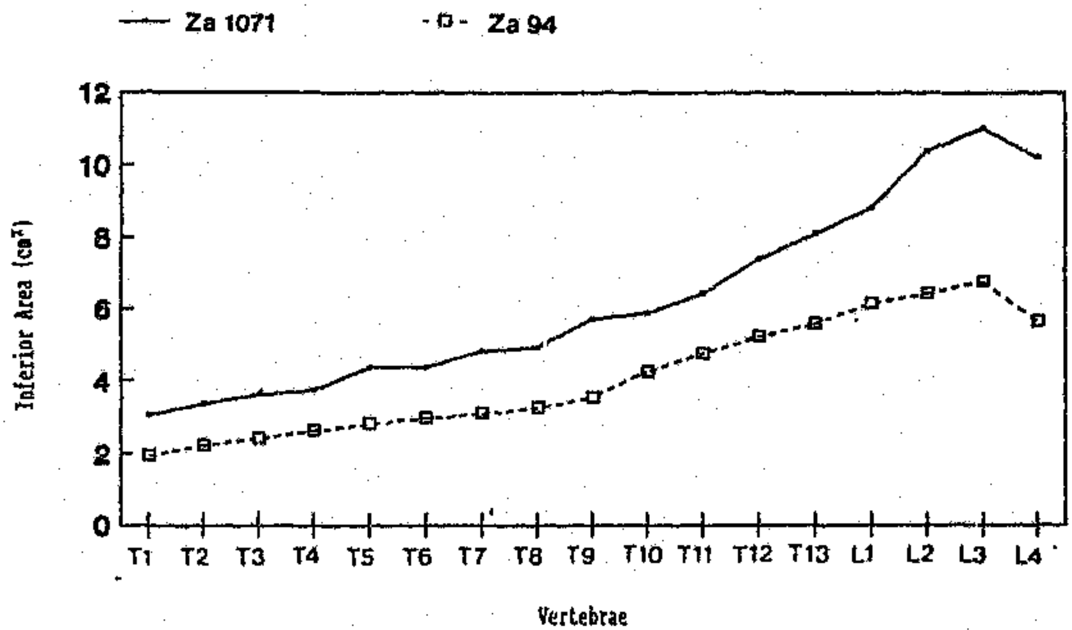


Fig. 9.5 The Inferior Areas in Two Sets of *Pan* Male Thoracic and Lumbar Vertebral Bodies

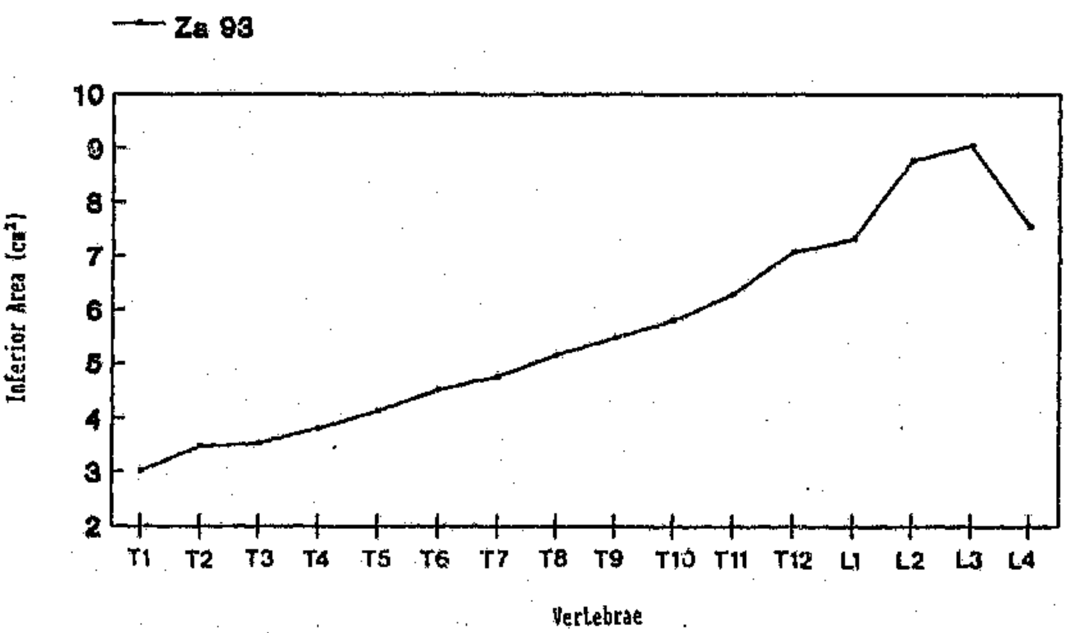


Fig. 9.6 The Inferior Areas in a Single Set of *Pongo* Female Thoracic and Lumbar Vertebral Bodies

2.2 Total and Average Percentage Increase

Table 9.6 lists the values for total and average percentage increase in the inferior area of African and Asian great ape vertebral bodies. Prominent is the low total percentage increase in the inferior area of the lumbar region (L1 to L3) of Za 94, a *Pan* column. This low percentage increase is reflected also in the low average percentage increase between consecutive lumbar vertebrae of this specimen. On the other hand Za 1071 - the other *Pan* vertebral column - shows a very small decline in inferior vertebral body area between the last two lumbar vertebrae. Further analysis of these relationships in pongids will have to await larger samples becoming available to the author.

<u>TABLE 9.6</u>

<u>The Total and Average Percentage Inferior Vertebral Body Area Increase in Individual African and Asian Great Ape Columns</u>

Percentage increase	*Za 95 *Gorilla* Male	Za 1312 *Gorilla* Male	Za 1071 *Pan* Male	Za 94 *Pan* Male	Za 93 *Pongo* Female
<u>T1 -L3</u>					
Total		245,93	261,84	250,00	201,33
Average		16,40	16,40	15,63	13,22
<u>T1 - T12/T13</u>					
Total	173,64	158,14	165,79	189,58	136,00
Average	13,36	13,18	12,75	14,58	11,33
<u>L1 - L3</u>					
Total		22,93	25,00	9,80	23,50
Average		7,64	8,33	3,27	7,83
Percentage decrease					
<u>L3 - L4</u>		21,18	7,84	20,00	19,58

* The last two lumbar vertebrae are damaged.

3. Australopithecine Series

3.1 Present Study

In Sts 14, an *A. africanus* female partial vertebral column, the outstanding feature is the decrease in inferior surface area of the last three (L4 to L6) lumbar vertebral bodies (Table 9.7, Fig. 9,7). Unfortunately less than half of the last two lumbar vertebral bodies (L4 and L5) of the male *A. africanus* partial column are preserved. In both partial columns an increase occurs from the last thoracic to L3.

TABLE 9.7

The Inferior Surface Area in Individual Sets of *A. africanus* and *A. robustus* Thoracic and Lumbar Vertebrae (cm^2)

	A. africanus		*A. robustus*	
	Sts 14	Stw 431	SK 3981a	SK 3981b
Thoracic:				
9th last	-			
8th last	-			
7th last	2,44			
6th last	2,32			
5th last	2,72			
4th last	2,88	5,08		
3rd last	-	-		
2nd last	-	-		
last	3,36	6,80*	7,68*	
Lumbar:				
L1	3,92	6,88		
L2	3,80	7,04		
L3	4,80	7,48		
L4	4,64	-		
L5	3,68	-		10,40*
L6	3,28			

* Only half of the vertebral body is preserved.
SK 3981b = last lumbar vertebra, not known if it is a fifth or a sixth lumbar vertebra.

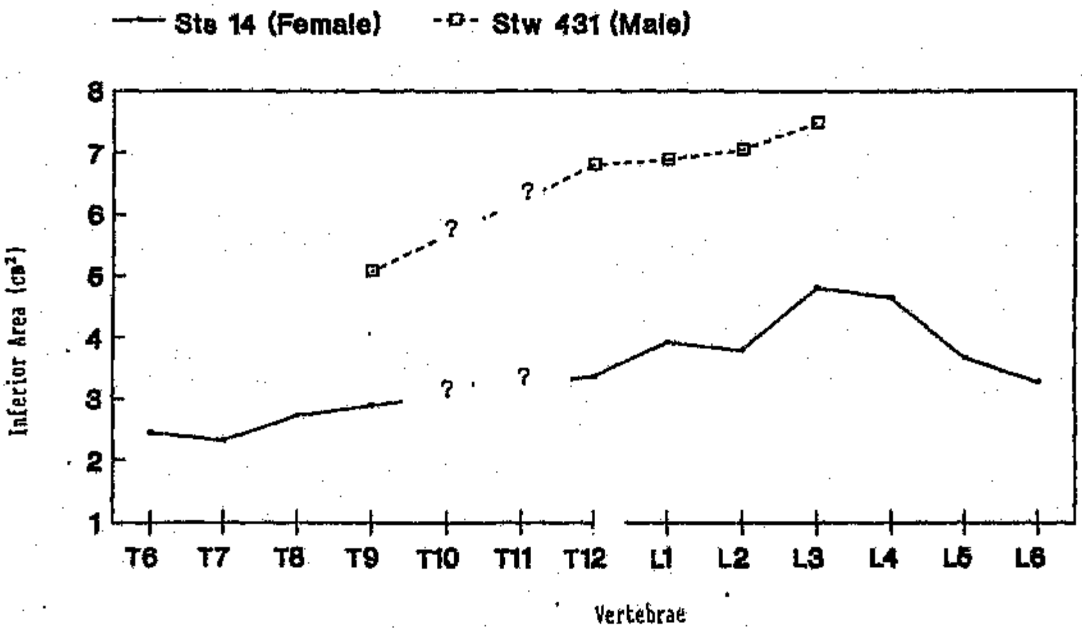


Fig. 9.7 The Inferior Areas in Two Sets of *A. africanus* Thoracic and Lumbar Vertebral Bodies

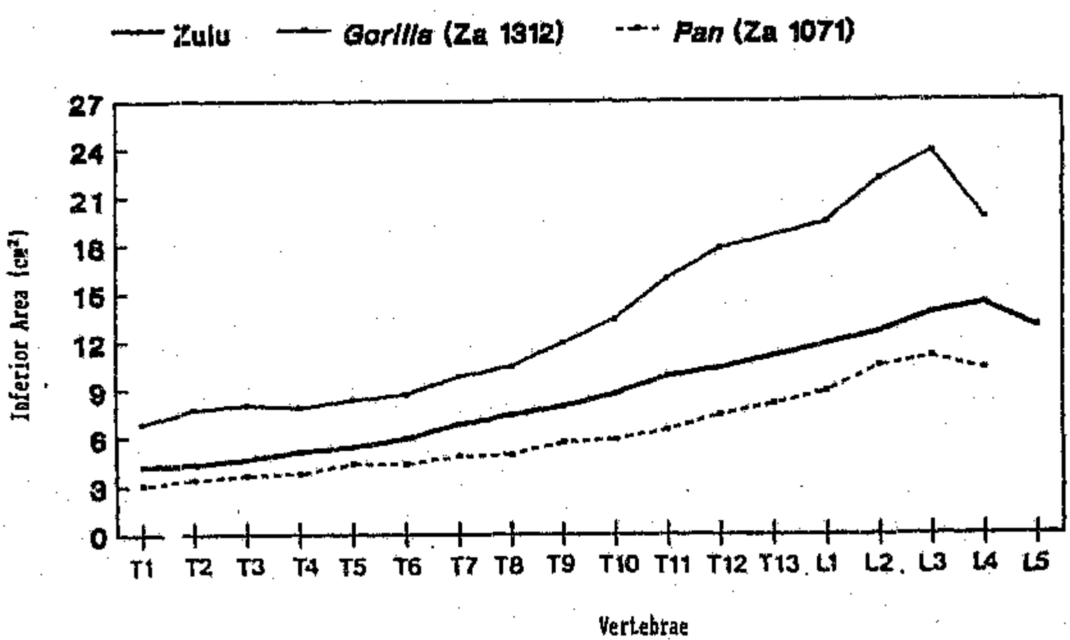


Fig. 9.8 The Inferior Areas of Modern Human (n=30), *Gorilla* (n=1) and *Pan* (n=1) Male Thoracic and Lumbar Vertebral Bodies

The inferior vertebral body surface areas of SK 3981a and b, respectively a last thoracic and a last lumbar vertebra of *A. robustus*, are larger than those of the *A. africanus* homologues. The inferior area of L6 in Sts 14 is 0,08 cm² (2,4%) smaller than that of its last thoracic vertebra, while SK 3981b, a last lumbar, is 2,72 cm² (7,38%) larger than SK 3981a, a last thoracic vertebra. It seems thus as if the *A. robustus* individual was more robust than the *A. africanus* individual, and that more weight is therefore carried by the lower lumbar vertebrae of this *A. robustus* column.

3.2 Total and Average Percentage Increase

In Sts 14, the total percentage increase of the inferior area between L1 and L3 is 22,45%. The average percentage increase between consecutive vertebrae is 7,48% per vertebra. From L3 a decrease of 46,34% occurs to L6. This presents an average percentage decrease of 11,59% between consecutive vertebrae. The total percentage increase between L1 and L3 of the partial column Stw 431 is only 8,72%, which presents an average percentage increase of 2,91% between consecutive vertebrae. It must be remembered that the inferior area values of L4 and L5 of this partial vertebral column are unknown.

4. Intergroup Comparisons

The inferior body area of the Zulu and the African great ape male vertebral bodies increase gradually from T1 to the second last lumbar vertebra and decrease then to the last lumbar vertebra. Figs. 9.8 and 9.9 present this comparison graphically. In Figure 9.8 Za 1071 is used since it is the largest of the two *Pan* vertebral columns and Za 1312 is preferred since it is complete, though it possesses only 23 presacral vertebrae.

The Zulu and *Pongo* female vertebral columns also show a gradual increase in inferior body area downward to the second last lumbar vertebra. The inferior body area of the last

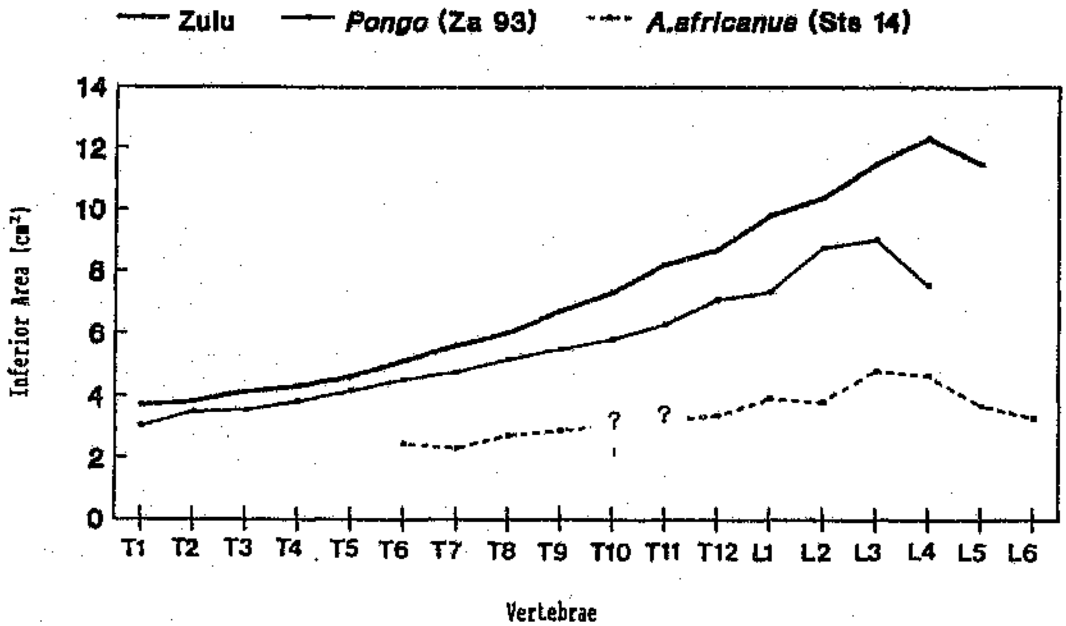


Fig. 9.9 The Inferior Areas of Modern Human (n=30), *Pongo* (n=1) and *A. africanus* (n=1) Female Thoracic and Lumbar Vertebral Bodies

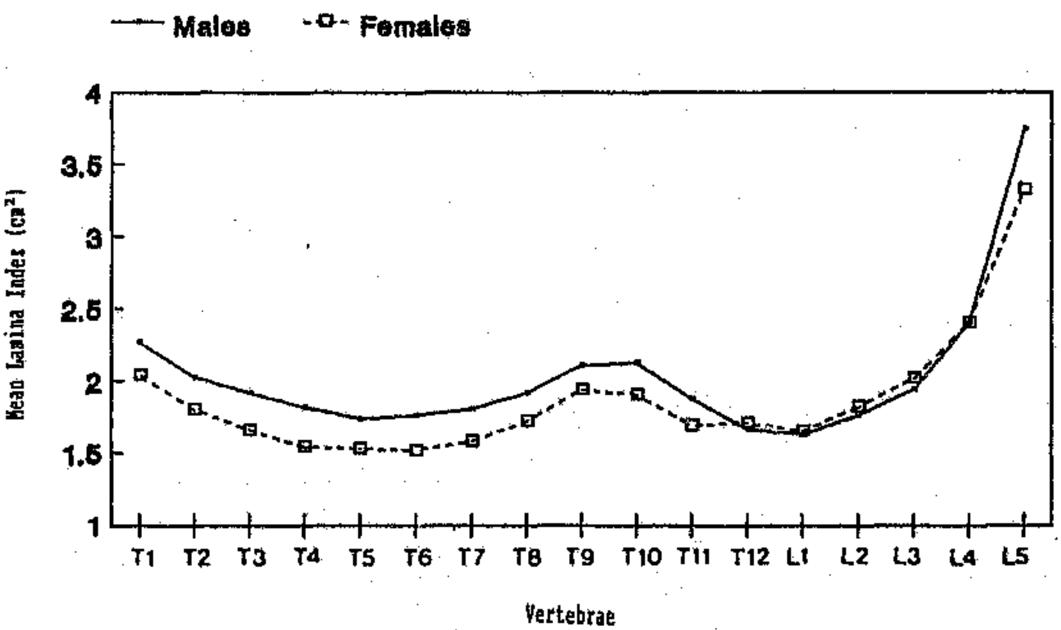


Fig. 9.10 The Mean Lamina Index Values of Zulu Thoracic and Lumbar Vertebrae

lumbar vertebra is smaller than that of the preceding vertebra in both groups. Sts 14 presents a gradual increase in inferior body area in the preserved vertebrae to L3. This increase is followed by a decrease in the last three lumbar vertebrae.

Conspicuous results among the total and average percentage increases in inferior vertebral body area are first, the low total percentage increase in the lumbar region (L1 to L3) of Za 94, a *Pan* male vertebral column (Table 9.6). This also results in a low average percentage increase between consecutive vertebrae. Secondly, Za 1071 (a *Pan* male vertebral column) presents a low percentage decrease (7,84%) to the last lumbar vertebra in comparison with the rest of the great ape sample in which the percentage decrease range between 19,53% and 21,18%. This low percentage decrease falls within the modern human range. The decrease between L4 and L5 is 11,83% in the Zulu males and 7,25% in the Zulu females. The results in Sts 14 differ from the other two series in that L3 is the largest vertebra, following which a decrease occurs <u>in the last three lumbar vertebrae</u>. This prolonged region of decrease seems to be a unique feature of *A. africanus* (Sts 14). Unfortunately the inferior body area values of the last two lumbar vertebrae of Stw 431 are unknown.

B. The Lamina Size

1. Modern Human Series

1.1 Zulu Series

1.1.1 Lamina Index (tlam x twl)

The lamina index is an indication of the cross-sectional area of the laminae. The distribution of these values in the Zulu series shows a biphasic curve in both sexes (Table 9.8, Fig.

9.10). The lamina area decreases from T1 to T5 in Zulu male columns. From T5 an increase occurs to T10 followed by the second decrease to L1. In th: lumbar region the lamina area increases markedly from L1 to L5. In the female spinal columns the first decline in lamina area occurs from T1 to T6. From T6 an increase occurs to T9 followed by a decrease to T11, a slight increase at T12, a decrease to L1 followed by a marked increase to L5.

TABLE 9.8

The Mean Lamina Index Values of Zulu Thoracic and Lumbar Vertebrae (cm^2)

Vertebra	Zulu Males			Zulu Females		
	Mean	±SD	Observed Range	Mean	±SD	Observed Range
T1	2,27	0,46	1,70 - 3,96	2,04	0,34	1,40 - 2,76
T2	2,03	0,36	1,49 - 2,96	1,80	0,31	1,24 - 2,70
T3	1,92	0,34	1,40 - 2,62	1,66	0,26	1,30 - 2,17
T4	1,82	0,31	1,35 - 2,64	1,54	0,30	1,08 - 2,24
T5	1,74	0,33	1,20 - 2,48	1,53	0,25	0,91 - 2,08
T6	1,76	0,35	1,20 - 2,72	1,52	0,23	1,20 - 1,98
T7	1,81	0,36	1,30 - 2,64	1,58	0,25	1,08 - 2,17
T8	1,92	0,37	1,45 - 3,04	1,72	0,23	1,35 - 2,24
T9	2,11	0,38	1,49 - 2,96	1,94	0,28	1,44 - 2,52
T10	2,13	0,36	1,60 - 2,85	1,91	0,34	1,10 - 2,64
T11	1,88	0,35	1,02 - 2,78	1,69	0,32	1,16 - 2,48
T12	1,67	0,27	1,26 - 2,13	1,71	0,32	1,25 - 2,52
L1	1,63	0,23	1,15 - 2,08	1,65	0,28	0,99 - 2,25
L2	1,76	0,26	1,27 - 2,38	1,82	0,31	1,15 - 2,56
L3	1,94	0,40	1,25 - 2,85	2,02	0,41	1,32 - 3,20
L4	2,40	0,49	1,33 - 3,66	2,46	0,43	1,71 - 3,78
L5	3,74	0,66	2,40 - 50,6	3,32	0,60	2,38 - 5,61

Sex differences: Student's t-Test shows that between T2 and T7, the Zulu male laminae are highly significantly greater ($P<0,0005$) than those of the corresponding female vertebrae. From T8 to T11 the males show probably significant ($P<0,05$; T9 and T11) and almost certainly significant ($P<0,01$; T8 and T10) greater laminae than the females. Between T12 and L4 the difference in lamina area between the sexes is not significant, while the difference between the sexes is probably significant ($P<0,05$) at T1 and almost certainly significant

(P<0,01) at L5. The mean lamina areas are thus greater in males than in females between T1 and T11. From T12 to L4, the area is more or less equal in the sexes but the males present greater laminae at L5.

1.1.2 Lamina Index/Inferior Body Area Ratio

The lamina area expressed as a percentage of the inferior body area (Table 9.9, Fig 9.11) shows a decline to the level of T7 in both male and female columns. Between T7 and T9 this ratio is almost equal, followed by a gradual decrease to L1. The ratios of the first three lumbar vertebrae are equal in the males and virtually equal in the females. This is followed by a sudden increase in lamina area in relation to inferior body area at L4 and L5 in both sexes.

This means that, as the inferior body area increases from T1 to L4, the lamina size values decrease from T1 to T7, are almost equal in the next three vertebrae and decrease again to the level of L1. In the first three lumbar vertebrae, the increase in inferior body area and the increase in lamina size are virtually equal. The increase in lamina size is larger than the increase in body area at L4, while the decrease in inferior body area at L5 is accompanied by a sharp increase in lamina size.

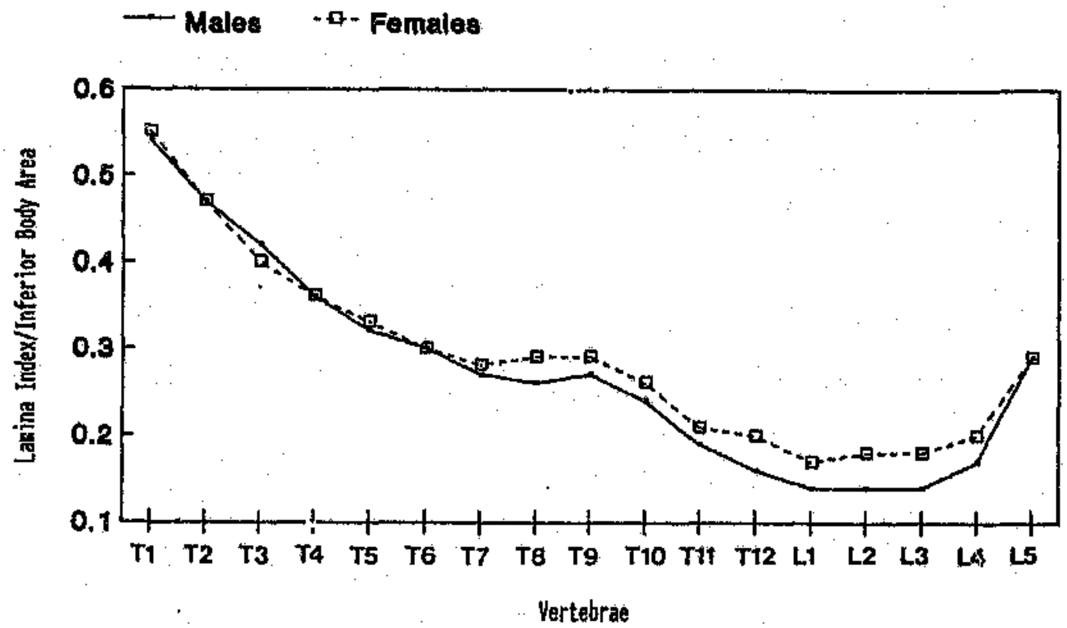


Fig. 9.11 The Lamina Index/Inferior Body Area Ratio Values of Zulu Thoracic and Lumbar Vertebrae

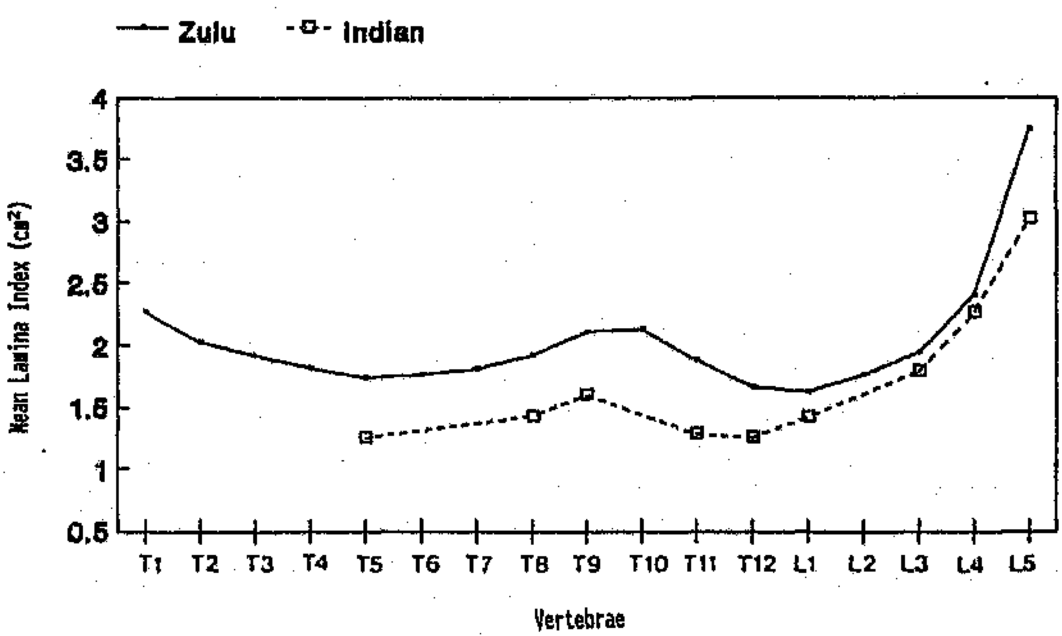


Fig. 9.12 The Mean Lamina Index Values of Modern Human Male Thoracic and Lumbar Vertebrae

TABLE 9.9

The Lamina Index/Inferior Body Area Ratio Values of Zulu Thoracic and Lumbar Vertebrae

Vertebra	Males	Females
T1	0,54	0,55
T2	0,47	0,47
T3	0,42	0,40
T4	0,36	0,36
T5	0,32	0,33
T6	0,30	0,30
T7	0,27	0,28
T8	0,26	0,29
T9	0,27	0,29
T10	0,24	0,26
T11	0,19	0,21
T12	0,16	0,20
L1	0,14	0,17
L2	0,14	0,18
L3	0,14	0,18
L4	0,17	0,20
L5	0,29	0,29

1.2 Comparative Series

The lamina index values show that the mean values of lamina area of Zulu male vertebrae are larger than those of Indian male vertebrae (Pal and Routal, 1987). The Zulu-Indian difference in lamina size is highly significant (P<0,0005) at all levels compared, except for L3 and L4. At the L3 level this difference is probably significant (P<0,05), while no difference in the lamina area of L4 occurs between the groups. Listed in Table 9.10 and presented graphically in Fig. 9.12, the values make it evident that the same biphasic pattern occurs in both groups.

TABLE 9.10

The Lamina Index Values of Zulu and Indian Male Thoracic and Lumbar Vertebrae (cm²)

Vertebra	Zulu Present Study n = 30	Indian Pal & Routal (1987) n = 44
T1	2,27 ± 0,46	
T2	2,03 ± 0,36	
T3	1,92 ± 0,34	
T4	1,82 ± 0,31	
T5	1,74 ± 0,33	1,25 ± 0,36
T6	1,76 ± 0,35	
T7	1,81 ± 0,36	
T8	1,92 ± 0,37	1,43 ± 0,24
T9	2,11 ± 0,38	1,60 ± 0,37
T10	2,13 ± 0,36	
T11	1,88 ± 0,35	1,28 ± 0,36
T12	1,67 ± 0,27	1,25 ± 0,27
L1	1,63 ± 0,23	1,42 ± 0,19
L2	1,76 ± 0,26	
L3	1,94 ± 0,40	1,79 ± 0,30
L4	2,46 ± 0,49	2,26 ± 0,53
L5	3,74 ± 0,66	3,01 ± 0,89

The decrease of the lamina area in relation to the inferior body area, followed by a sudden increase at L4 and L5, in Zulu male vertebrae corresponds with the results of Pal and Routal (1987) on Indian male vertebrae. These ratios are compared in Table 9.11 and Fig. 9.13. The increase in the lamina index/inferior body area ratio at L4 and L5 indicates that the increase in lamina size at L4 is proportionately larger than the increase in inferior body area. The decrease in inferior body area at L5 is accompanied by a sharp increase in lamina size.

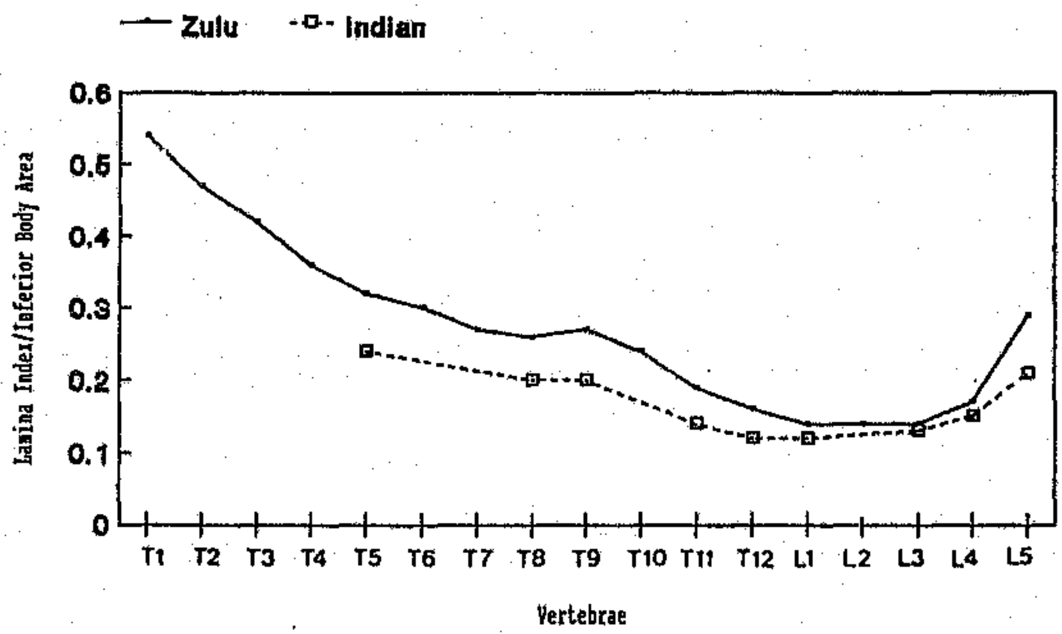


Fig. 9.13 The Lamina Index/Inferior Body Area Ratio Values of Modern Human Male Thoracic and Lumbar Vertebrae

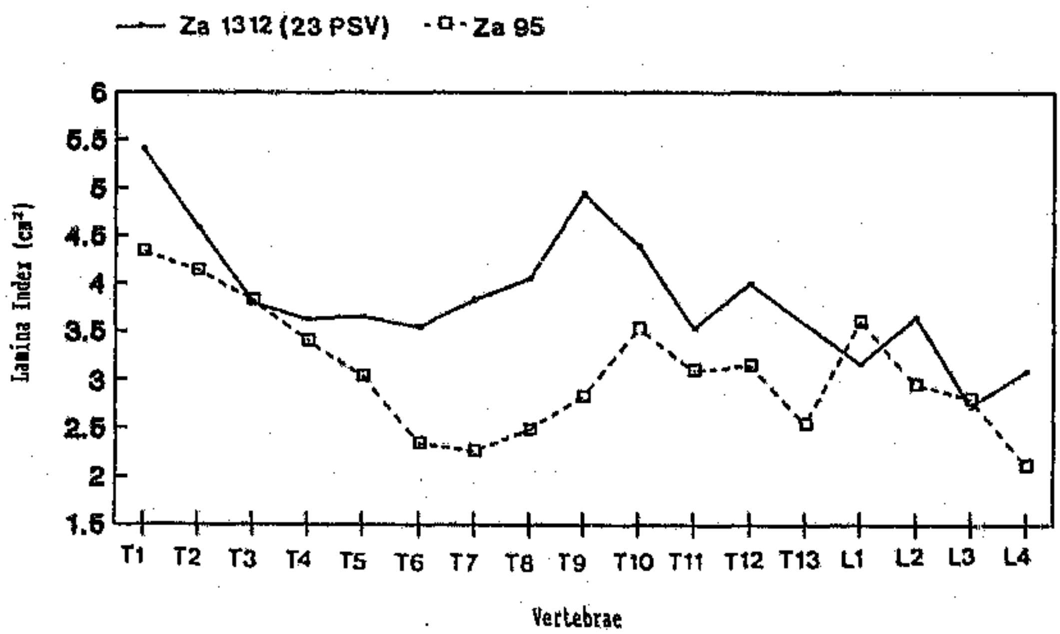


Fig. 9.14 The Lamina Index Values in Two Sets of *Gorilla* Male Thoracic and Lumbar Vertebrae

TABLE 9.11

The Lamina Index/Body Area Ratio Values of Zulu and Indian Male Thoracic and Lumbar Vertebrae

Vertebra	Males	
	Zulu Present Study n = 30	Indian Pal & Routal (1987) n = 44
T1	0,54	
T2	0,47	
T3	0,42	
T4	0,36	
T5	0,32	0,24
T6	0,30	
T7	0,27	
T8	0,26	0,20
T9	0,27	0,20
T10	0,24	
T11	0,19	0,14
T12	0,16	0,12
L1	0,14	0,12
L2	0,14	
L3	0,14	0,13
L4	0,17	0,15
L5	0,29	0,21

2. African and Asian Great Ape Series

2.1 Present Study

2.1.1 Lamina Index (tlam x twl)

The cross-sectional area of the laminae, as indicated by the lamina index, decreases from T1 to T6 or T7 in the *Gorilla* male columns (Table 9.12, Fig. 9.14). This decrease is followed by an increase to T9 or T10. In Za 1312 the lamina area decreases from T9 to T11 and increases again to T12, the last thoracic vertebra. In Za 95 the lamina area decreases from T10 to T13 and increases to L1. The area decreases from L1 to L4 in Za 95. On the other hand, Za 1312 presents an increase in lamina area from L1 to L2, a decrease to L3 and an increase to L4. The lamina area values of the thoracic and lumbar vertebrae are variable and inconsistent in the two *Gorilla* vertebral columns.

TABLE 9.12

Lamina Index Values in Individual Sets of African and Asian Great Ape Thoracic and Lumbar Vertebrae (cm^2)

Vertebra	*Gorilla*		*Pan*		*Pongo*
	Za 1312 Male	Za 95 Male	Za 1071 Male	Za 94 Male	Za 93 Female
T1	5,40	4,33	1,88	1,47	1,20
T2	4,59	4,14	1,60	1,28	0,91
T3	3,80	3,82	1,63	1,22	0,75
T4	3,62	3,40	1,67	1,13	0,79
T5	3,65	3,04	1,73	1,24	0,68
T6	3,54	2,34	1,94	1,39	0,65
T7	3,82	2,26	2,08	1,58	0,96
T8	4,05	2,49	2,19	1,67	1,00
T9	4,94	2,83	2,27	1,63	1,16
T10	4,39	3,53	2,01	1,46	1,26
T11	3,53	3,10	2,02	1,38	1,51
T12	3,99	3,15	1,76	1,27	1,10
T13		2,55	2,08	1,27	
L1	3,17	3,60	1,66	1,36	0,98
L2	3,65	2,96	1,39	1,12	0,91
L3	2,73	2,81	1,20	0,87	0,88
L4	3,09	2,11	1,23	0,53	0,75

The two *Pan* male vertebral columns also show a decline in lamina area in the upper thoracic region followed by an incline to T8 or T9. From this level the area declines again to T12. In Za 1071 a sudden increase in area occurs at T13 while the lamina area of T12 and T13 are equal in Za 94 followed by an increase at L1. In the lumbar region the lamina area decreases from L1 to L4 in Za 95 and to L3 in Za 1071. A slight increase in lamina area occurs at L4 in the latter (Table 9.12, Fig. 9.15).

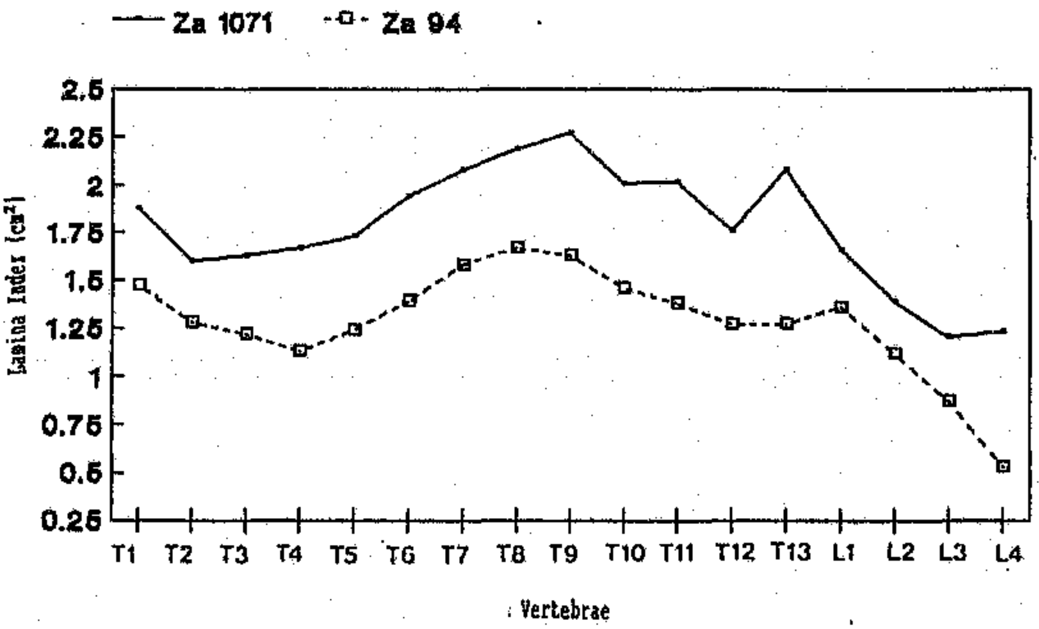


Fig. 9.15 The Lamina Index Values in Two Sets of *Pan* Male Thoracic and Lumbar Vertebrae

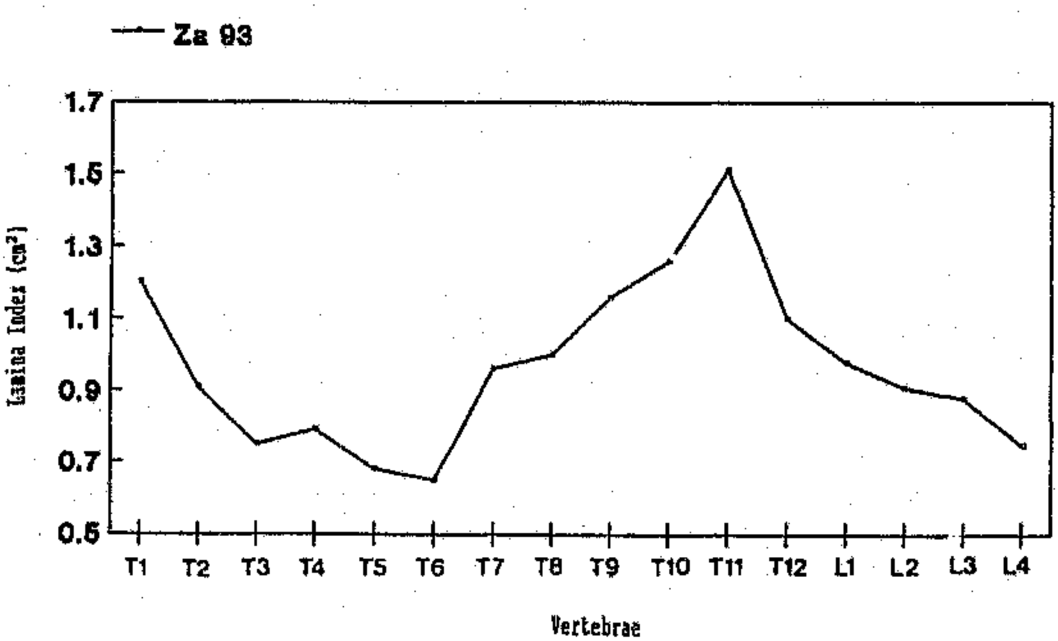


Fig. 9.16 The Lamina Index Values in a Single Set of *Pongo* Female Thoracic and Lumbar Vertebrae

The single available *Pongo* female spinal column shows the same pattern of decline in lamina area from T1 to T6 followed by an incline to T11. From this level the area declines to L4 (Table 9.12, Fig. 9.16).

2.1.2 Lamina Index/Inferior Body Area

In relation to the inferior body area, the lamina area decreases from T1 to T7 in the two *Gorilla* male columns (Table 9.13, Fig. 9.17). This decrease is followed by a slight increase to T9 in Za 1312 and to T10 in Za 95. In Za 1312 the lamina area decreases from T9 to L3 followed by a slight increase at L4. In Za 95 the area decreases from T10 to T13, increases to L1 and decreases to L2. Unfortunately the inferior surface areas of L3 and L4 are damaged which prevents the calculation of the index.

TABLE 9.13

The Lamina Index/Inferior Body Area Ratio Values in Individual Sets of African and Asian Great Ape Thoracic and Lumbar Vertebrae

Vertebra	*Gorilla* Za 1312 Male	*Gorilla* Za 95 Male	*Pan* Za 1071 Male	*Pan* F 94 Male	*Pongo* Za 93 Female
T1	0,78	0,98	0,62	0,76	0,40
T2	0,60	0,86	0,48	0,58	0,26
T3	0,48	0,73	0,45	0,51	0,21
T4	0,46	0,74	0,45	0,44	0,21
T5	0,44	0,54	0,40	0,44	0,16
T6	0,41	0,41	0,44	0,47	0,14
T7	0,39	0,36	0,43	0,51	0,20
T8	0,39	0,37	0,45	0,52	0,19
T9	0,42	0,39	0,40	0,46	0,21
T10	0,33	0,41	0,34	0,34	0,22
T11	0,22	0,36	0,32	0,29	0,24
T12	0,22	0,31	0,24	0,24	0,16
T13		0,21	0,26	0,23	
L1	0,16	0,30	0,19	0,22	0,13
L2	0,17	0,22	0,13	0,18	0,10
L3	0,11	*	0,11	0,13	0,10
L4	0,16	*	0,12	0,09	0,10

* Inferior area damaged

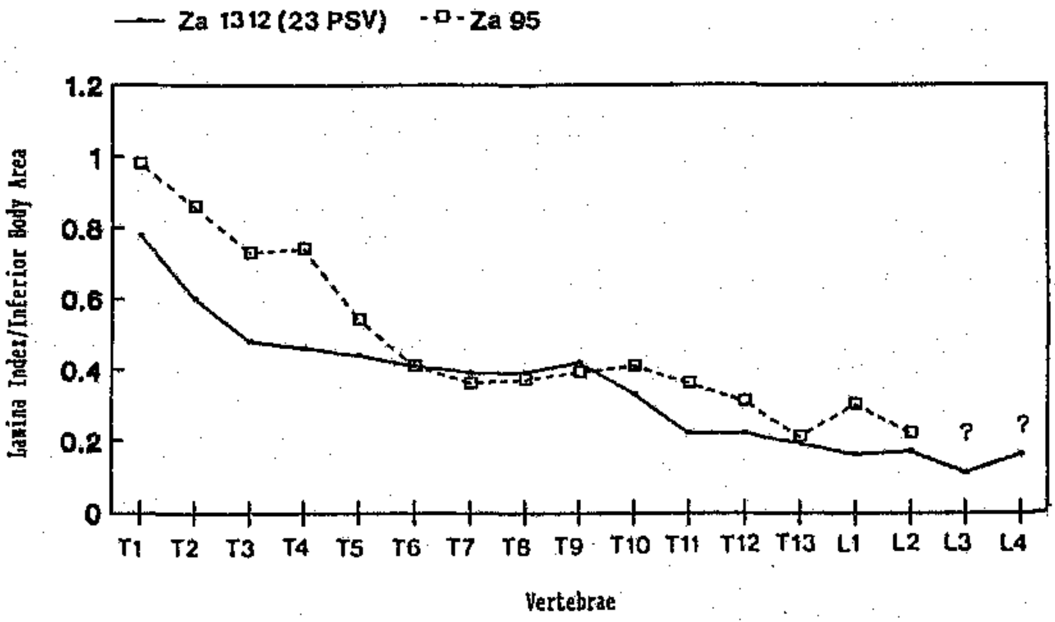


Fig. 9.17 The Lamina Index/Inferior Body Area Ratio Values in Two Sets of *Gorilla* Thoracic and Lumbar Vertebrae

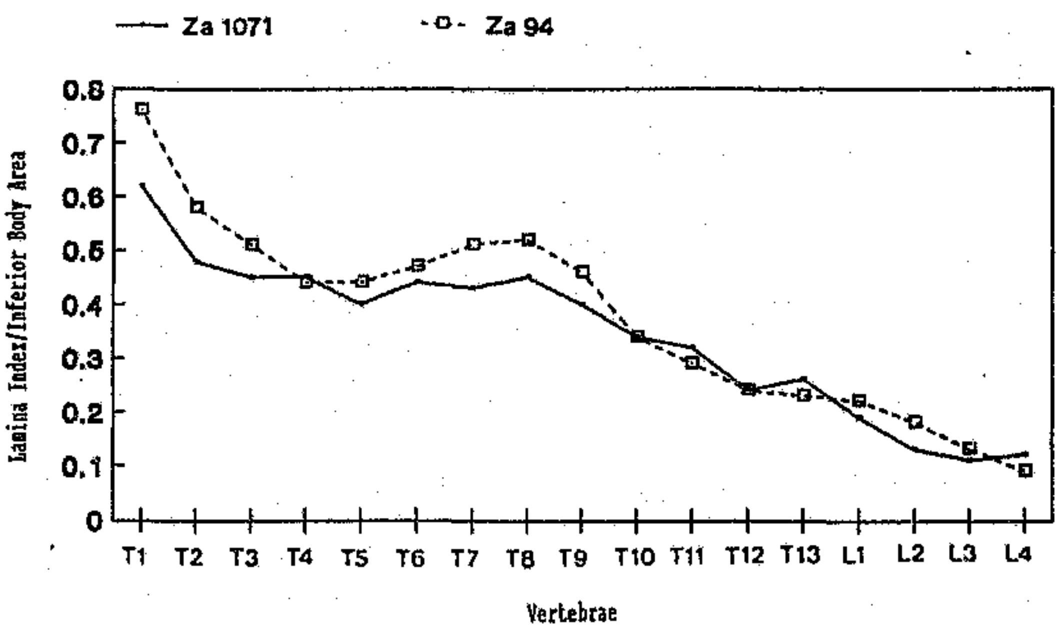


Fig. 9.18 The Lamina Index/Inferior Body Area Ratio Values in Two Sets of *Pan* Thoracic and Lumbar Vertebrae

In the *Pan* male columns the lamina area decreases in relation to the inferior body area from T1 to T5 followed by a slight increase to T8. From T8 the ratio decreases to L4 in Za 95 and to L3 in Za 1071. In Za 1071 L4 shows a slightly greater ratio than L3 (Table 9.13, Fig. 9.18).

In the *Pongo* female column the initial decrease in lamina size in relation to the inferior body area occurs to T6 followed by a gradual increase to T11. From T11 this ratio decreases to L2, L3 and L4 in which it is equal (Table 9.13, Fig. 9,19).

3. Australopithecine Series

3.1 Present Study

3.1.1 Lamina Index (tlam x twl)

The cross-sectional area of the laminae, as indicated by the lamina index, increases from the eighth last to the fourth last thoracic vertebra in Sts 14 (Table 9.14, Fig. 9.20). From the second last, the area decreases to the last thoracic vertebra, L1 and L2 which are equal. The lamina area increases from L2 to L3, decreases slightly at L4 and increases to L5. The lamina area of L6 is unknown.

In the Stw 431 partial column, the areas of preserved laminae show a sharp decrease from the second last thoracic vertebra to L1, followed by an increase to L2. The cross-sectional area of SK 3981a, an *A. robustus* last thoracic vertebra, is 86,9 mm^2.

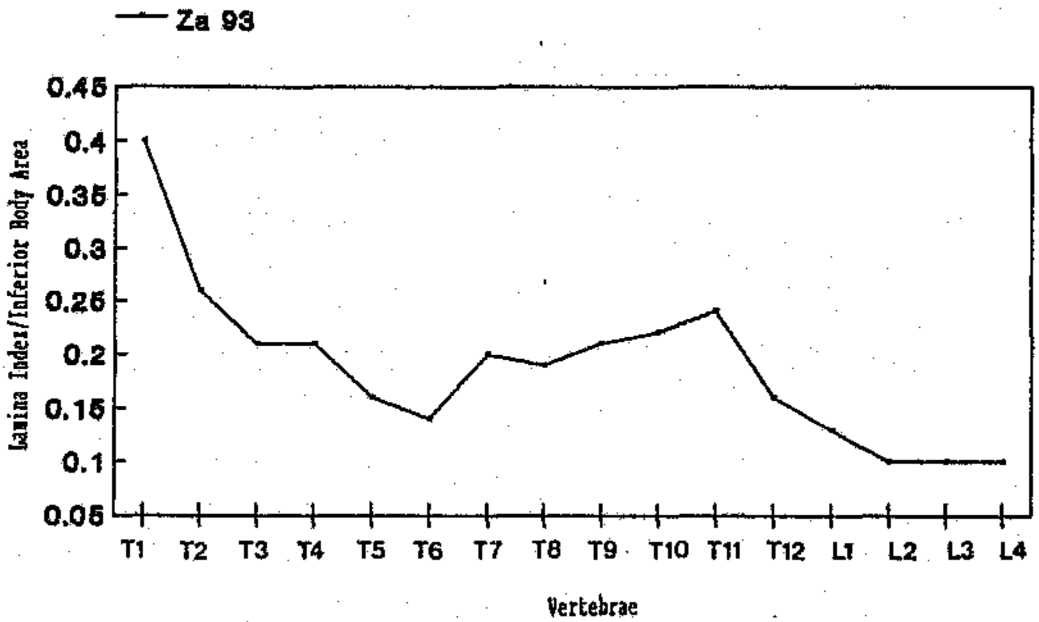


Fig. 9.19 The Lamina Index/Inferior Body Area Ratio Values in a Single Set of *Pongo* Female Thoracic and Lumbar Vertebrae

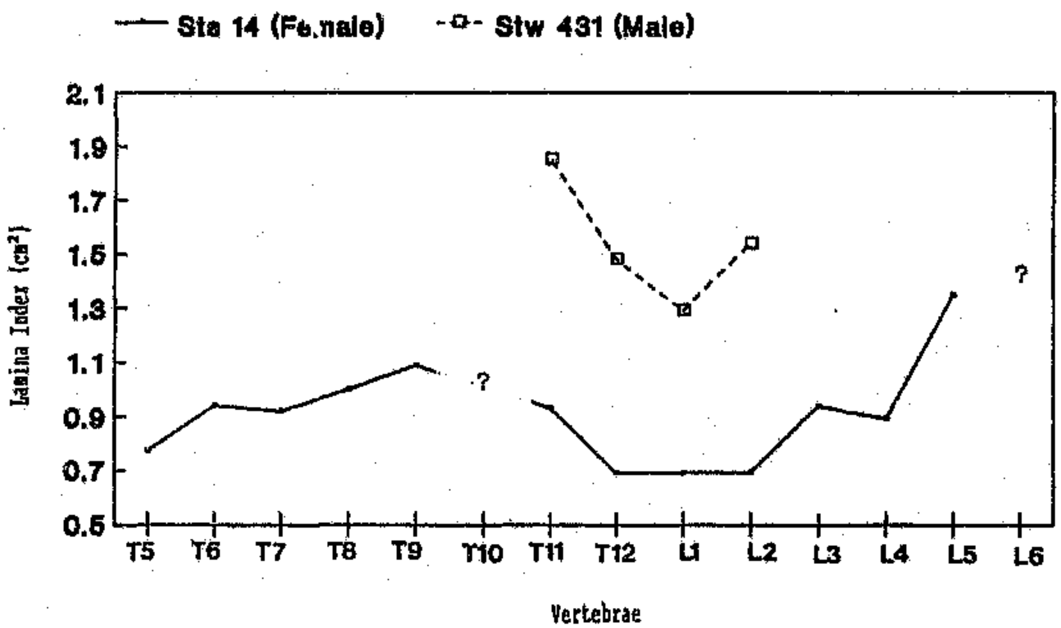


Fig. 9.20 The Lamina Index Values in Two Sets of *A. africanus* Thoracic and Lumbar Vertebrae

TABLE 9.14

The Lamina Index Values in Individual Sets of *A. africanus* Thoracic and Lumbar Vertebrae (cm^2)

Vertebra	Sts 14 Female	Stw 431 Male
Thoracic:		
9th last		
8th last	0,77	
7th last	0,94	
6th last	0,92	
5th last	1,00	
4th last	1,09	
3rd last	-	
2nd last	0,93	1,85
Last	0,69	1,48
Lumbar:		
L1	0,69	1,29
L2	0,69	1,54
L3	0,94	
L4	0,89	
L5	1,35	
L6	-	

3.1.2 Lamina Index/Inferior Body Area Ratio

Though the ratio for the third and second last thoracic vertebrae of Sts 14 are unknown, it seems as if the lamina size decreases from the seventh last thoracic vertebra to L4 in relation to the inferior body area. This decrease is followed by an increase at L5 (Table 9.15, Fig. 9.21). The ratio in the female (Sts 14) and male (Stw 431) partial vertebral columns are equal at the L1 level. The lamina index/inferior body area ratios of the last thoracic and upper five lumbar vertebrae of Sts 14 present a pattern very near to that of the modern human vertebral columns.

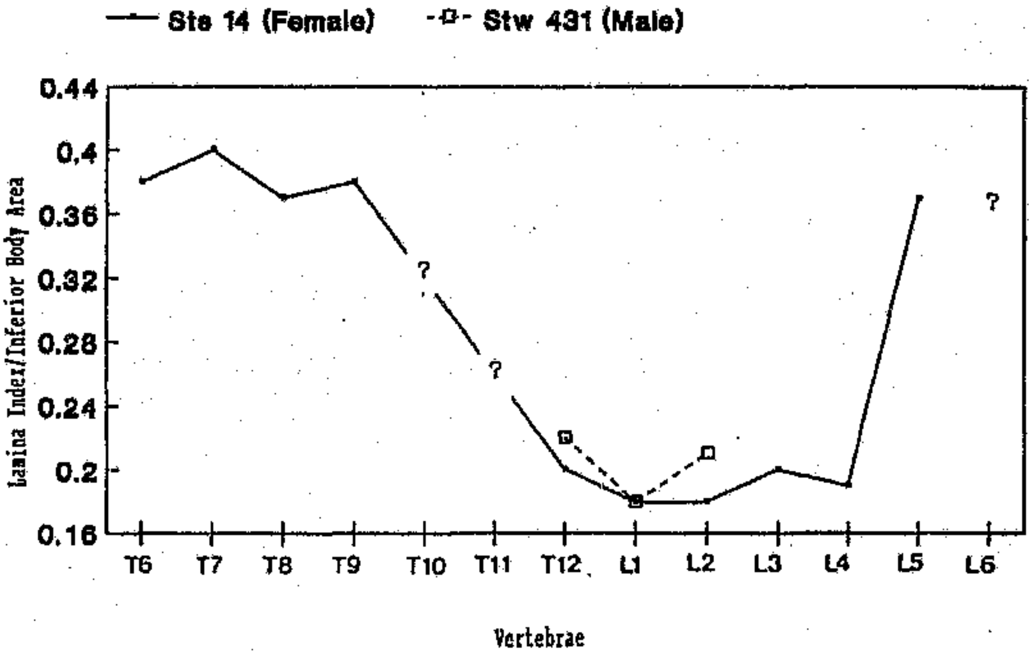


Fig. 9.21 The Lamina Index/Inferior Body Area Ratio Values in Two Sets of *A. africanus* Thoracic and Lumbar Vertebrae

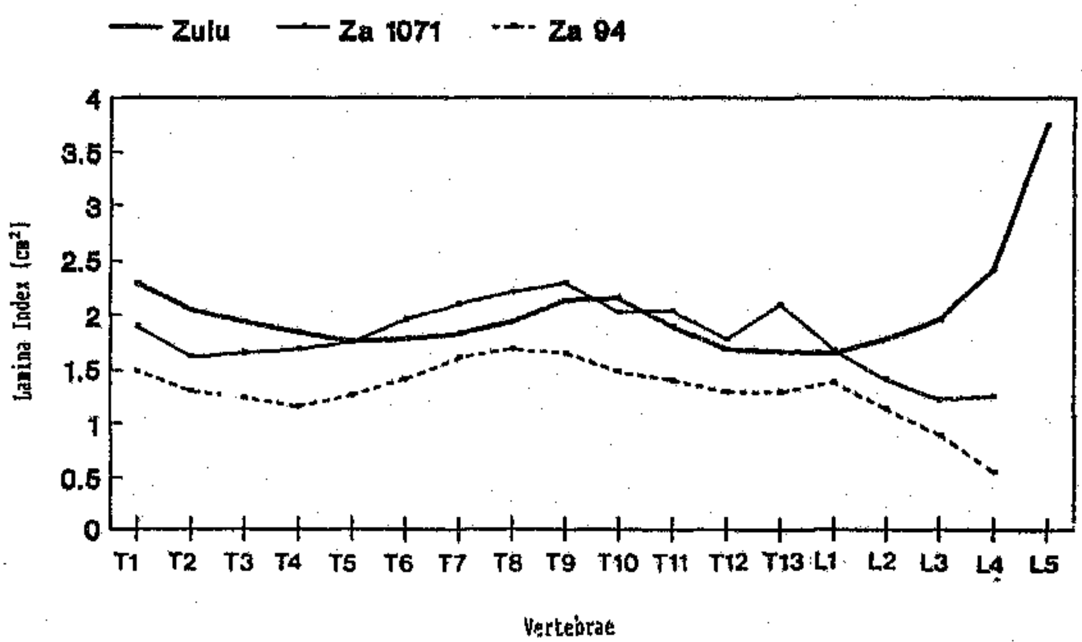


Fig. 9.22 The Lamina Index Values of Modern Human (n=30) and Two Sets of *Pan* Male Thoracic and Lumbar Vertebrae

TABLE 9.15

The Lamina Index/Inferior Body Area Ratio Values in Individual Sets *A. africanus* Thoracic and Lumbar Vertebrae

Vertebrae	Sts 14 Female	Stw Male
Thoracic		
9th	-	
8th	-	
7th	0,38	
6th	0,40	
5th	0,37	
4th	0,38	
3rd	-	
2nd	-	-
last	0,20	0,22
Lumbar:		
L1	0,18	0,16
L2	0,18	0,21
L3	0,20	
L4	0,19	
L5	0,37	
L6	-	

4 Intergroup Comparisons

4.1 Lamina Index (tlam x twl)

The general pattern of the lamina index in the African and Asian great ape series is a decrease in size in the upper thoracic vertebrae to ± T4 to T6 followed by an increase to the lower part of this region (± T8 to T11). From this level the lamina area decreases gradually to the last lumbar vertebra (Figs. 9.14, 9.15 and 9.16). It must be emphasized that this pattern is based upon a most inadequate sample of five spinal columns from three genera and species.

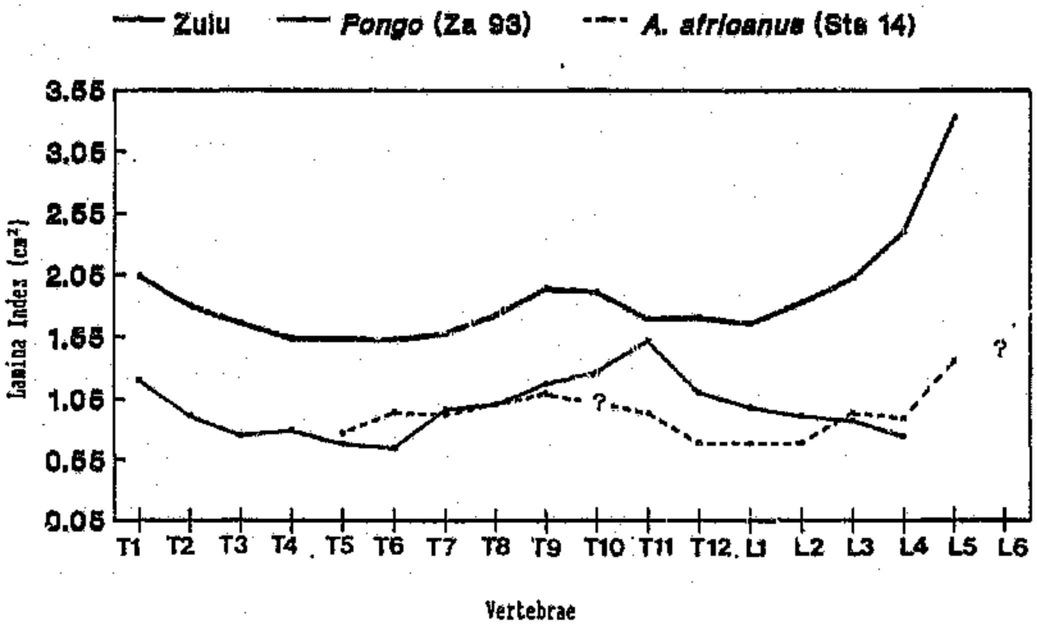


Fig. 9.23 The Lamina Index Values of Modern Human (n=30), *Pongo* (n=1) and *A. africanus* (n=1) Female Thoracic and Lumbar Vertebrae

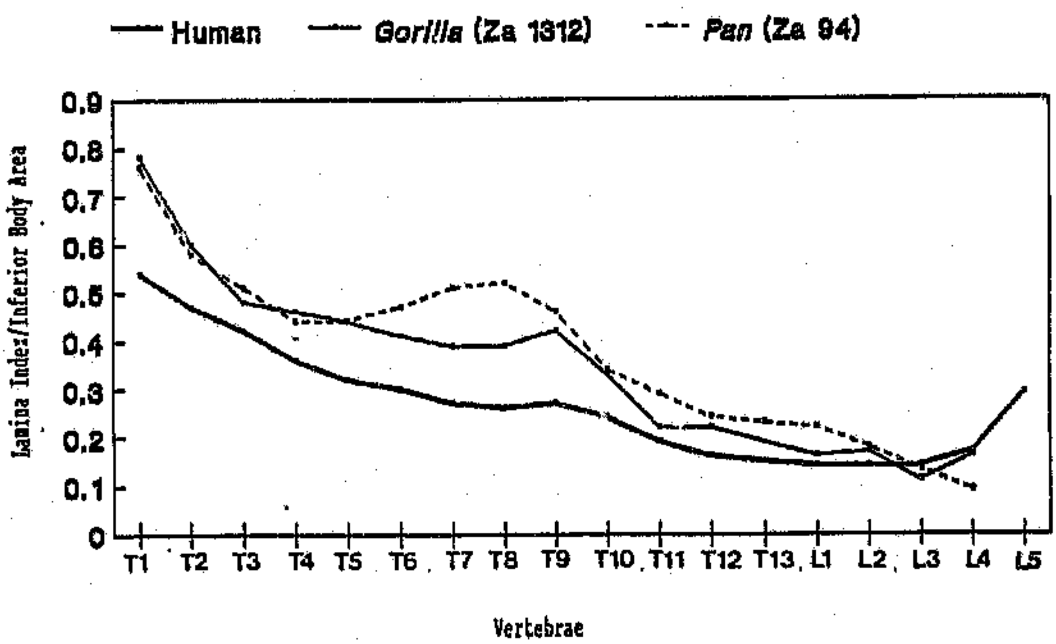


Fig. 9.24 The Lamina Index/Inferior Body Area Ratio Values of Modern Human (n=30), *Gorilla* (n=1) and *Pan* (n=1) Male Thoracic and Lumbar Vertebrae

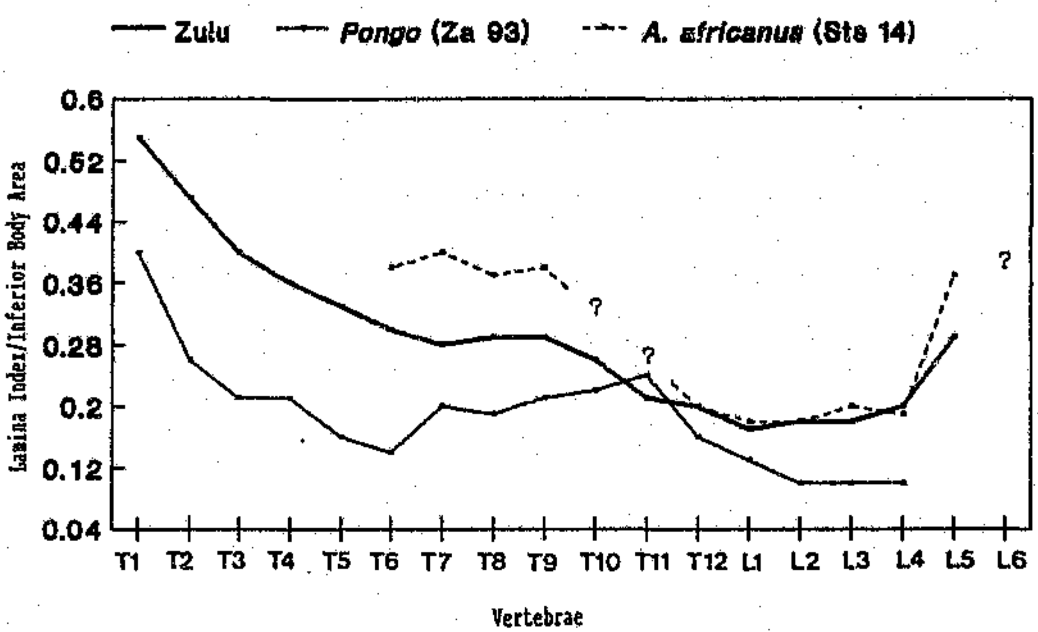


Fig. 9.25 The Lamina Index/Inferior Body Area Ratio Values of Modern Human (n=30), *Pongo* (n=1) and *A. africanus* (n=1) Female Thoracic and Lumbar Vertebrae

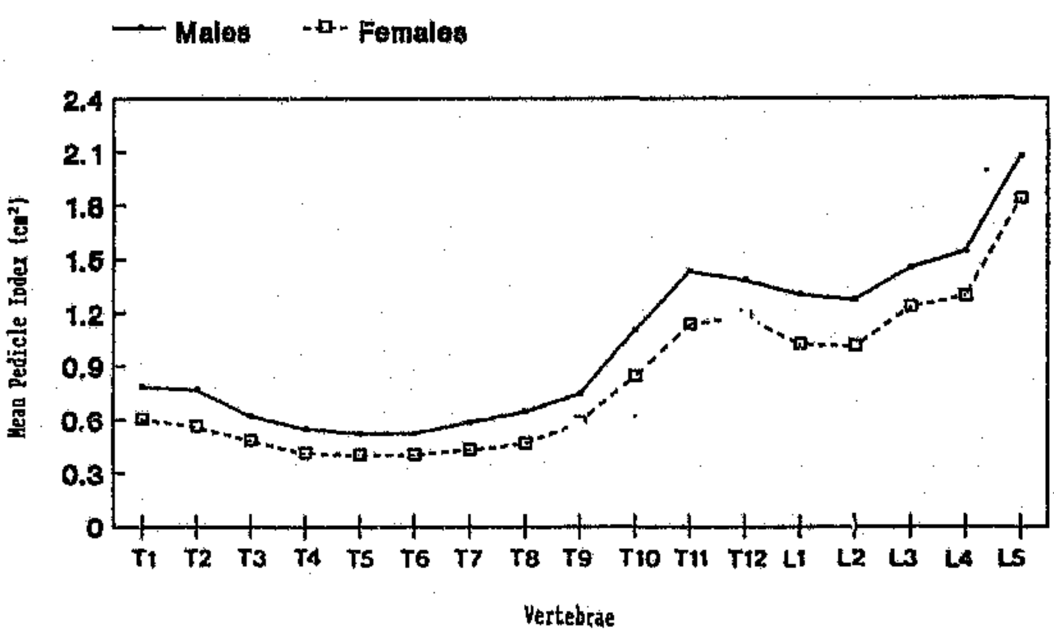


Fig. 9.26 The Mean Pedicle Index Values of Zulu Thoracic and Lumbar Vertebrae

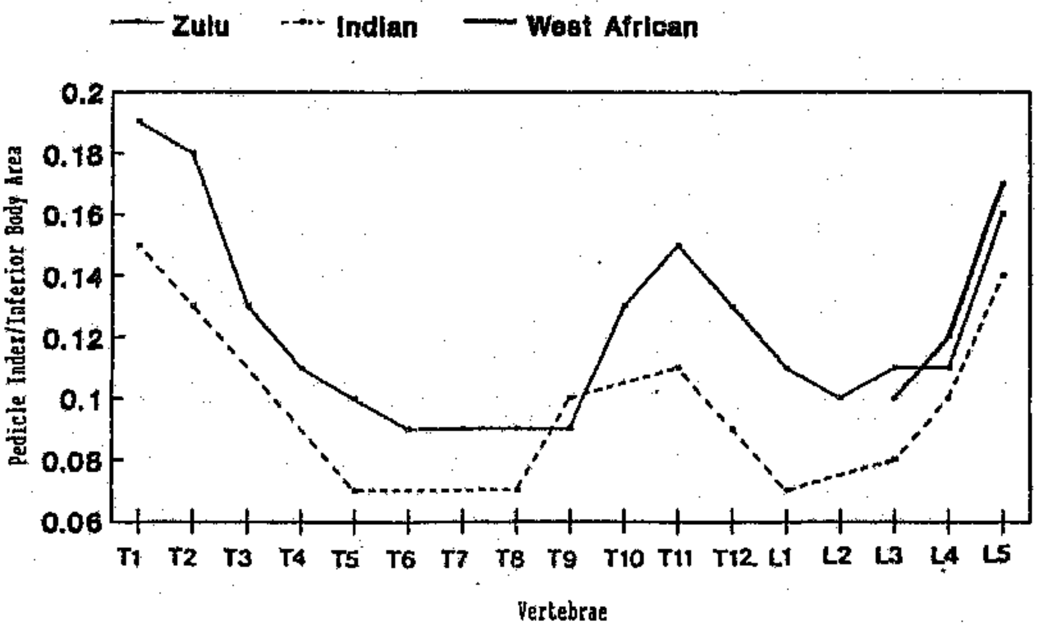


Fig. 9.29 The Mean Pedicle Index/Inferior Body Area Ratio Values of Modern Human Male Thoracic and Lumbar Vertebrae

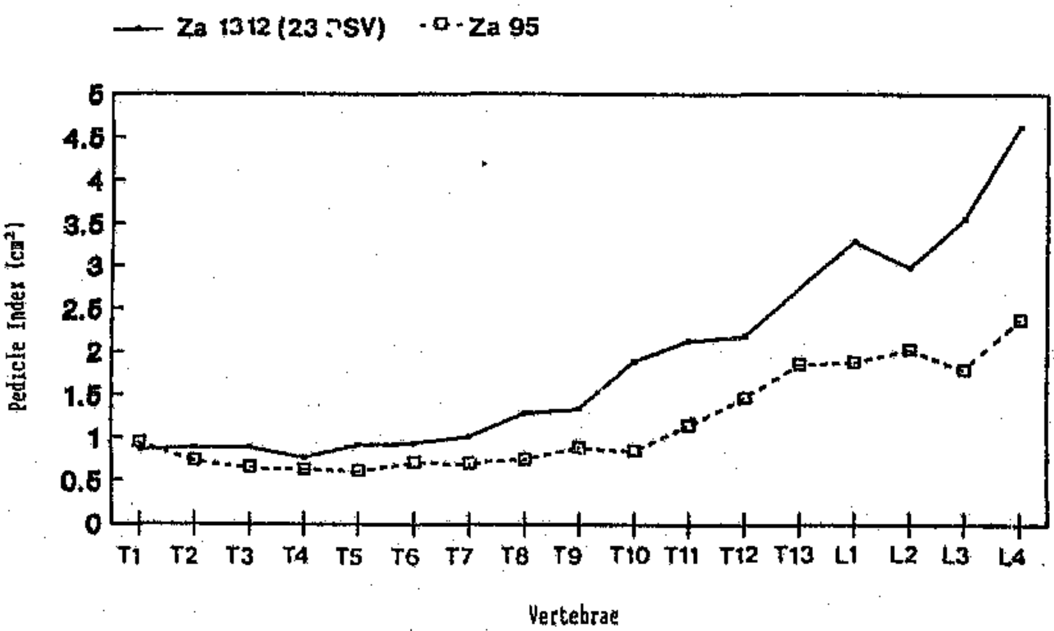


Fig. 9.30 The Pedicle Index Values in Two Sets of *Gorilla* Male Thoracic and Lumbar Vertebrae