

approximately midshaft are: c9.5 mm (supero-inferior), c12.3 mm (anteroposterior). The total length of the fragment is 97.9 mm. The sigmoid curvature of the specimen is moderately pronounced and scores a curvature value of 3 - 4 on the authors scale (see Figure).

7.3.1.2.3

A.L. 333-94

(left clavicular fragment (Figure 62))

(Lovejoy et al., 1982b)

This is a left lateral clavicle fragment that is 51.2 mm in length and includes part of the inferior surface, trapezoid line and origin of deltoid. The remainder of the specimen has either been lost or is too damaged to exhibit any identifiable surface morphology. The estimated anteroposterior diameter at the conoid tubercle is 13.4 mm. The estimated superoinferior diameter at the conoid tubercle is 8.6 mm.

approximately midshaft are: c9.5 mm

(supero-inferior), c12.3 mm (anteroposterior).

The total length of the fragment is 97.9 mm. The sigmoid curvature of the specimen is moderately pronounced and scores a curvature value of 3 - 4 on the authors scale (see Figure).

7.3.1.2.3

A.L. 333-94

(left clavicular fragment (Plate 62))

(Lovejoy et al., 1982b)

This is a left lateral clavicle fragment that is 51.2 mm in length and includes part of the inferior surface, trapezoid line and origin of deltoid. The remainder of the specimen has either been lost or is too damaged to exhibit any identifiable surface morphology. The estimated anteroposterior diameter at the conoid tubercle is 13.4 mm. The estimated superoinferior diameter at the conoid tubercle is 8.6 mm.

7.3.1.3

The Humeri

7.3.1.3.1

A.L. 288-1r

A.L. 288-1m

(left proximal humerus; right humerus (Figures 63
& 64))

(Taleb et al., 1975; Johanson et al., 1982)

A.L. 288-1m (Figure 64) is a right humeral fragment comprised of two separate pieces. The proximal end is badly damaged and the articular surface of the head only preserves the central portion. Most of the lesser tubercle and a portion of the greater tubercle are present. The superior part of the intertubercular groove appears undistorted. Johanson et al. (1982) report that most of the meaningful morphological detail has been lost in the head region. Reconstructed length of this specimen has been reported as 236.8 mm.

The A.L. 288-1r humerus (Figure 63) is better preserved in its proximal part. It is

comprised of approximately the superior one-third of the humerus. The articular surface of the head is almost completely preserved but has been damaged by compression distally and has been displaced posteromedially. This compression has not apparently altered the mediolateral diameter of the head and this is recorded as 31.1 mm. Anteroposterior diameter of the head must be estimated due to the compression damage and this is recorded as c26.8 by the author from a cast. The resulting humeral head index is 86.2%.

The anatomical neck of A.L. 288-1r is damaged by internal expansion. The intertubercular sulcus has been badly damaged and measurements are not possible. The lesser and greater tubercles of the head are both damaged and their surface morphology obscured. However, it does not appear that they would have projected over the articular surface of the head of the humerus.

7.3.1.3.2

A.L. 333-87

(left proximal humeral shaft (Figure 65))

(Lovejoy et al., 1982b)

A badly weathered proximal shaft of a left humerus that is missing the articular head. The specimen is extremely robust with what appears to be a deep intertubercular groove. A small portion of the greater tubercle is preserved and this exhibits a depressed area for the attachment of the infraspinatus muscle. Only a small lateral part of the lesser tubercle is preserved. The total length of the specimen is 149.3 mm.

7.3.1.3.3

A.L. 333-107

(right proximal humerus (Figure 67))

(Lovejoy et al., 1982b)

This specimen is the proximal one-third of a robust right humerus. It has a relatively well preserved head but the shaft is in poor condition due to exfoliation of the surface and generalised fracturing of the bone. It has a deep and wide intertubercular groove (minimum intertubercular width = c7.8 mm). There is a large ridge for the attachment of the teres major muscle. The

greater tubercle lies approximately 1.0 mm below the most superior point of the humeral head. There is a large circular depression on the posterior surface of this tubercle for the insertion of the infraspinatus muscle. The attachment area for the teres minor muscle is seen as a small boss just inferior and posterior to this depression.

The total length of the specimen is 128.2 mm. Mediolateral head diameter is 39.5 mm. Anteroposterior head diameter is c34.0mm. Mediolateral shaft width at the distal point of breakage is c30.0mm. Anteroposterior width at the same point is c29.5 mm.

7.3.1.3.4

A.L. 333-109

(right humeral shaft (Figure 66))

(Lovejoy et al., 1982b)

This specimen is the right shaft of an extremely robust humerus. The specimen is broken proximally just below the anatomical neck,

and distally just past mid-shaft. The total length of the specimen is c138.0 mm. Only the distal part of the intertubercular groove is preserved. The groove runs distally from the superior point of breakage for approximately 60.0 mm. Although the groove is wide (c8.5 mm), it is apparently not very deep. There is a strong ridge on the medial side of the groove that is presumably for the attachment of the teres major muscle.

The deltoid tuberosity is massive and pronounced, lying some 99.0 mm from the proximal point of breakage. The delto-pectoral junction is seen as a rugosity just posterior and inferior to the deltoid tuberosity. Just below this point, the shaft makes what appears to be a medial (retro)flexion of approximately 10°. The cortex of the specimen is extremely thick distally. The specimen is bowed medially over its whole length, possessing a distinct flattening of the medial surface from just below the surgical neck.

7.4 .

Specimens Referred to *Homo habilis*

7.4.1

Description

7.4.1.1

The Clavicle

7.4.1.1.1

OH 48

(left clavicle (Figure 70))

This specimen is a left clavicle from FLK NNI at Olduvai Gorge. It lacks both the medial and lateral ends. The clavicular fragment is c130.0 mm in length. The midshaft anteroposterior diameter is 14.8 mm and the supero-inferior diameter is 10.7 mm. Measurements at the most medial point of breakage are: 22.2 mm (anteroposterior), 22.4 mm (supero-inferior), c3.0 mm (average cortical bone thickness, range 2.4-3.5 mm). Measurements at the lateral point of breakage are: c16.8 mm (anteroposterior), and 10.2 mm (supero-inferior), c2.1 mm (average cortical bone thickness, range 2.0 - 2.4 mm).

The specimen presents pronounced sigmoid curvature and it thus scores a 5 on this author's scale. Oxnard (1969) has reported the angle of torsion of the OM - 48 clavicle at 52° - 60° .

7.5

Specimen Referred to Robust Australopithecines

7.5.1

Descriptions

7.5.1.1

The Humeri

7.5.1.1.1

OMO 119 - 2718

(left proximal humerus (Figure 71))

(Senut, 1978)

This specimen is the head and proximal shaft of a left humerus. The head of the specimen is well preserved with parts of both the greater and lesser tubercles preserved. The specimen has been damaged along the superior part of the articular surface, where cancellous bone has been

revealed. There is also some damage along the anterior and posterior rim of the articular surface that has given the head a somewhat ovoid appearance. The lateral part of the greater tubercle has been mostly removed, but this damage has not obscured the size of the tubercle, nor the superior areas of muscle insertions. The specimen has been broken across the shaft just below the surgical neck. A narrow fossilization crack runs from the greater tubercle inferiorly to the most distal point of breakage. Numerous other fossilization cracks are found on the shaft, but none appears to have distorted the specimen to any noticeable degree. There is approximately 115.0 mm of shaft preserved below the head. Total length of the damaged specimen is c147.0 mm.

On inspection, the head appears irregular in shape, but this impression is due mostly to the damage along the inferoposterior rim of the articular surface. The mediolateral head diameter is c40.7 mm, the anteroposterior head diameter c38.0 mm. Both the greater and lesser tubercles are pronounced, and the top of the

greater tubercle lies c4.0 mm below the top of the humeral head. On the greater tubercle, the areas of insertions for the infraspinatus and teres minor muscles are rugose. There is a considerable anterior projection of the tubercle at the level of insertion of the teres muscle. The lesser tubercle is broad. The insertion area of subscapularis into the tubercle is seen as a series of pits and fissures along the length of the tubercle. The intertubercular groove is wide at its most superior point (c8.0 mm). The attachment area of pectoralis major forms an overlapping ridge along the posterior edge of the groove as it blends superiorly with the crest of the greater tubercle. The insertion area of teres major forms a bulbous ridge along the crest of the lesser tubercle that runs some 52.0 mm inferiorly from the lesser tubercle. In the floor of the intertubercular groove a roughened area indicates the insertion area of the latissimus dorsi muscle.

On the anterior face of the shaft, c52.0 mm below the greater tubercle, is an extremely robust

area of origin for the lateral head of the triceps brachii. This area of origin continues for c60.0 inferiorly to the inferior break of the shaft. The shaft is relatively straight, exhibiting little curvature in any direction. Due to the general rugosity of the muscle attachments of the specimen, the humerus must have belonged to an extremely robust individual.

7.5.1.1.2

KNM-ER 739

(right humerus (Figure 69))

(Leakey et al., 1972)

This specimen is most of the shaft and trochlea of a large right humerus missing the head and a small part of the proximal shaft. The specimen has been assigned to the genus *Australopithecus* by several authors (R.E.F. Leakey, 1972; Leakey et al. 1971; McHenry, 1973; Day and R.E.F. Leakey, 1974; Day, 1976). The account that follows is taken almost wholly from the original description by Leakey et al. (1971).

The specimen is c310.0 mm in length. The shaft is gently curved along its entire length. It has been described as triangular in cross-section in its proximal two thirds, becoming ovoid in its distal third. The intertubercular sulcus crests are well developed. The minimum width of the intertubercular sulcus is c10.0 mm. The insertion area of the latissimus dorsi muscle is represented by a slight roughening of the floor of the sulcus. The insertion area of the pectoralis major muscle is prominent, and is visible as a strongly developed crest that may be regarded as a "distal continuation of the crest of the greater tuberosity". The pectoralis crest distally meets the deltoid impression some 167.0 mm proximal to the most distal part of the trochlea.

7.6

The Functional Morphology of the *Australopithecus africanus* Shoulder Girdle

7.6.1

The Scapula

The total morphological pattern exhibited by the *A. africanus* scapular fragments is different from that observed in any modern hominoid species. However, all the specimens exhibit individual features that are either pongid or humanlike whilst they also retain primitive anthropoid features in certain characters.

Below, the discussion of the *A. africanus* scapulae is divided into two parts: firstly, the glenoid area, head and spine and secondly, the body of the scapula.

7.6.1.1

The Glenoid Area, Head and Spine of the Scapula

The Stw 162 and Sts 7 scapular fragments are the only two *A. africanus* specimens that possess comparable glenoid, head and spine regions. These specimens are most similar in size to the scapulae of humans, chimpanzees and female orang-utans and are smaller than the scapulae of male orang-utan, and gorillas. Both specimens are considerably larger than those of the hylobatids.

One of the most striking features of the Sts 7 scapula, to which considerable functional morphological importance has been attached, is that the glenoid cavity of Sts 7 is longer and more narrow than one might expect in the scapulae of modern African apes and humans (Robinson, 1972; Senut, 1978; Vrba, 1979). The glenoid index of Sts 7 (c60.0%) indicates a glenoid cavity breadth to length relationship which is most like that observed in modern orang-utan (Figure 54 and Table 6). The predicted value of c60.0% places the glenoid index value of Sts 7 at

least one standard deviation below the mean index value recorded for all hominoids save for orang-utans and male hylobatids. Thus, regarding the observed glenoid index values, the species with the most comparable glenoid cavity shape to Sts 7 is the orang-utan but Sts 7's glenoid index fits within the sample ranges of all the hominoid species examined by the author.

The perceived very low glenoid index value observed in Sts 7 has led several workers to associate this specimen's glenoid morphology with possible adaptations for arboreal climbing or even brachiation behaviour (Robinson, 1972; Vrba, 1979). However, it is important to highlight several features in this specimen that indicate that the latter of these two suggestions is unlikely. Secondly, it is important to highlight that Sts 7 is not in fact as low in its glenoid index value, in relation to modern hominoids, as has been thought.

As discussed in detail in Chapter 6, modern hominoid species exhibit an extremely wide range

of observed variation in glenoid index values (Table 6 and Figure 33). The glenoid index value calculated for Sts 7 falls just within the lowest sample range observed for this index in all extant hominoid species save for siamangs and female gorillas (although admittedly only just below the lowest index value observed in the latter). However, the calculated mean index values for the data collected by this author are in almost every case skewed and may not be considered to be representative of the central tendencies of the data. The calculated weighted means for the data move the central tendencies of the human and gorilla data further from the Sts 7 index value. Nevertheless, the weighted means (Table 6) do not significantly alter the central tendencies of the data for any of the modern hominoid species. Therefore, one must conclude that the Sts 7 glenoid cavity is in fact extremely narrow compared to the mean values for modern hominoids. However, if Stw 162 also represents a member of *A. africanus*, it is likely that the narrow glenoid cavity of Sts 7 does not represent the *Australopithecus africanus* norm but rather

represents a specimen at the low extreme of observed variation for this species. The glenoid index value of Stw 162 (c70%) is most similar to those of modern humans, with the observed index value for this specimen lying very close to the mean index values calculated for *Homo sapiens* and *Symphalangus syndactylus* (respectively 73.5% and 73.9%) (Table 6). It is therefore likely that, with a sample range of 60.0% - 770.0% (n=2), the variation in glenoid cavity length to breadth ratios in *A. africanus* is high and that the narrow glenoid cavity of Sts 7 simply represents morphology that would be in the lower part of the range of observed variation in this species. Therefore, from the differences in the glenoid length to breadth relationships between these two specimens, one may infer that the sample range observed in the glenoid index values for *A. africanus* is not unlike that observed in all the modern, large-bodied hominoid species, but is not as great as that of the highly specialised gibbons.

Morphological features visible on the better preserved glenoid cavity of Stw 162 indicate further similarities in this specimen's architecture with that of humans. The costal margin notching of the glenoid cavity of Stw 162 is rarely observed in the scapulae of non-human hominoids, but is frequently present in robust human scapulae (Figure 32). The presence of a pronounced notch on the costal margin of the human glenoid cavity has been explained by Fahlstrom (1981) as indicating a robust and enlarged humeral lesser tubercle. This is presumably because an enlarged subscapularis attaches to a greater area of lesser tubercle surface. In addition, the increased notching of the costal glenoid cavity margin may indicate a general enlargement of the mass of the subscapularis muscle and its investing bursa, since the soft tissues of this muscle and its bursa pass near and press upon the costal edge of the glenoid rim. The resulting muscular stresses may be impressed on the bone during growth, thus creating a notch at or near their point of passage (Fahlstrom, 1981). Since the lesser tubercles of all the

humeri from Sterkfontein are very robust but do not rise above the articular surfaces of the humeral heads, the glenoid margin notching in Stw 162 may indicate expansion of the subscapularis muscle to the degree found in modern humans.

The articular surfaces of the glenoid cavities of both Sts 7 and Stw 162 are considerably flatter than those of modern humans, being most similar to those of extant apes. Churchill and Trinkaus (1991, p.152) have found that Neandertal scapulae also "have significantly flatter articular surfaces than that found in modern humans". To these authors, this feature indicates a greater freedom of movement at the glenohumeral joint in this archaic form of *Homo sapiens* than is found in modern humans. However, it may also indicate some loss of structural stability at the joint. The glenoid cavity depth index in the Sts 7 scapula (76.7%) falls just within one standard deviation of the mean observed in Churchill and Trinkaus's sample of Neandertal scapulae ($8.4\% \pm 1.9$, $n = 16$) but outside one standard deviation

from the mean of the modern human sample ($12.0\% \pm 1.6$, $n = 99$). In contrast, the glenoid depth index calculated for Stw 162 (73.9%) falls outside the lower limits of variation for modern humans and Neandertals, being most similar to the observed means in orang-utan.

If one were to consider the shallow glenoid cavity alone, one might surmise that the glenohumeral joint of Stw 162 possessed a higher degree of freedom of movement, but inherently less structural stability than is provided by the deeper glenoid cavity articular surfaces of modern humans. Thus, the glenohumeral joint would be more prone to dislocation. However, combined with the flatter articular surface of Stw 162, there is a wide and robust area of attachment for the glenoid labrum that is more pronounced than the labral attachment observed in most modern apes and humans. It is probable that this enlargement of the glenoid labrum attachment area may be directly associated with an enlargement of the whole labrum (Ferrari, 1990).

As the glenoid labrum is an important stabiliser in the rotator cuff, its enlargement would most likely act as a defence against external dislocating forces (Howell and Galis, 1989a,b). Therefore, whereas there is an increased likelihood of the Stw 162 shoulder suffering dislocation of the glenohumeral joint due to the glenoid cavity's shallow depth, the enlarged glenoid labrum would most probably compensate for the reduced structural stability of the joint surface by providing additional soft tissue support. To this author, this highly mobile, but structurally stable joint surface seems to indicate adaptations towards stresses that might be encountered during activities which require weight support as well as a high degree of freedom of movement at the glenohumeral joint. Since there are no modern hominoid species known to this author that combine flattened articular surfaces with enlarged glenoid labra, it is difficult to associate this feature with any single behaviour, although this author is tempted to associate such a combination of features generally with

adaptations to the stresses encountered during tree-climbing activities."

In her 1979 examination of the Sts 7 scapula, Vrba noted the presence of a "pronounced costolateral tubercular expansion" in the superior part of the glenoid cavity of Sts 7, which she named the "paraglenoid tubercle" (Vrba, 1979, p. 118) and this author confirms the presence of this feature. Since the superior part of the glenoid cavity of Stw 162 is damaged, the author is unable to discern whether this specimen also possessed a paraglenoid tubercle. The A.I. 288-1L specimen does not possess such a feature. However, in individual great ape scapulae it is not uncommon to find a tubercle which is similar in shape and form to the tubercle observed in Sts 7. Whilst Vrba does not attempt to explain the presence of this tubercle in Sts 7, one possible explanation presents itself to this author. It is suggested that enlargement of the long head of the biceps muscle, which has its tendinous origin at the supraglenoid tubercle, accompanied by an enlarged superior glenohumeral ligament, may be responsible

for the presence of this paraglenoid tubercle. In ape scapulae where these tubercles are observed, their presence is typically accompanied by an enlargement of the attachment area of the glenoid labrum (on the glenoid cavity articular surface) as well as a relative enlargement of the supraglenoid tubercle. In addition, in these specimens there is typically a widening and deepening of the bicipital groove. In combination, these features may indicate that the presence of a paraglenoid tubercle provides evidence for thickening of the superior glenohumeral ligament as well as enlargement of the long head of biceps.

Since the superior glenohumeral ligament, when acting with the anterior capsule of the shoulder helps to restrain external rotation and stabilise the glenohumeral joint as a whole (Ferrari, 1990), an enlarged superior glenohumeral ligament, if it were present in the Sts 7 shoulder, should have acted as an added stabiliser for the rotator cuff. However, it should be noted that in monkeys, an enlarged supraglenoid tubercle

has been shown to limit the degree to which the humerus can move upward in the glenoid cavity, since the tubercle wedges into the intertubercular groove on the humerus (Ciochon and Corruccini, 1976). Regardless of whether the paraglenoid tubercle observed in Sts 7 is in fact an attachment for an enlarged glenohumeral ligament, this tubercle must have placed some restrictions in movement on the humeral head within the glenoid cavity. In particular, contact with the humeral head would have occurred when the arm was raised above the head and moved posteriorly, a functional restriction which is most probably unacceptable in the scapula of a brachiator. This alone implies that the superior glenoid morphology of Sts 7 was not adapted to this specialised form of locomotion.

Of the two Sterkfontein scapulae, the infraglenoid tubercle of Sts 7 may be considered the more ape-like in morphology. It is elongate and transversely thin and is thus most similar in appearance to the infraglenoid tubercles observed in the scapulae of gorillas, chimpanzees and

female orang-utans and least like those observed in modern humans. There is a small protuberance just dorsolateral to the infraglenoid tubercle of Sts 7 which Vrba (1979, p.119) thought was a "postmortem deformation". However, as the long head of the triceps brachii muscle often continues its area of attachment dorsally in extant hominoids (see Chapter 5), it is possible that this protuberance in Sts 7 is simply an extension of the area of origin of the triceps muscle. In contrast to the morphology of the infraglenoid tubercle in Sts 7, the infraglenoid tubercle of Stw 162 is most similar in shape and form to those of modern humans, being bulbous and large relative to glenoid cavity size (Plate 1a). These differences may be associated with the more robust features of Stw 162 and could be accounted for if Stw 162 represented a male scapula and Sts 7 was from a small male or female. In addition, one may observe that infraglenoid tubercle morphology is highly variable amongst hominoids and similar tubercle morphology may be found in numerous individual ape scapulae. Therefore the differences in infraglenoid tubercle morphology

between the two Sterkfontein scapulae may not be specifically diagnostic and probably simply reflect individual variation within a species.

While there are overall similarities in the structure of the glenoid area between *A. africanus* and modern hominoids, the sample of *A. africanus* shares at least one important feature with the more pronograde cercopithecids. The difference concerns the relative length of the scapular neck. The two scapulae of *A. africanus* possess a *collum scapulae* which is more similar in length and morphology to those of the cercopithecids than it is to those of modern hominoids. This feature is best demonstrated when one plots the glenoid cavity length and breadth against that of the spinoglenoid notch depth. When compared, the spinoglenoid notch depth values for both Sts 7 and Stw 162 fall below the expected values observed in hominoid scapulae possessing similar glenoid dimensions (Figures 34, 35 and 36). In fact, the spinoglenoid notch depth values of both fossil specimens fall at the lowest extreme, or outside, the observed range of variation for this

measurement in medium and large sized extant hominoids. Thus, both the fossil scapulae attributed to *A. africanus* possess shortened scapular necks at the spinoglenoid notch relative to those of modern hominoid species.

The relationships of glenoid dimensions to scapular neck length expressed in Figures 34 and 35 indicate that the *A. africanus* scapular specimens possess anatomical relationships which lie between those of modern apes and quadrupedal monkeys. In fact, for this relationship Sts 7 plots outside the total observed plot of this relationship in any extant group examined by this author. Quantitatively, the outlying plotted position in Sts 7 is due to this specimen's relatively narrow glenoid cavity. The narrow glenoid cavity serves to compound the effects of an absolutely shallow spinoglenoid notch. In the same anatomical region, Stw 162 shares with Sts 7 a similar morphological relationship. However, the plotted values for Stw 162 fall just within the observed plot for modern humans, but outside the plotted variation of all other

extant hominoids (Figure 34). The plotted values for both fossil specimens lie between the lines of regression, and within the observed variation in values, of hominoid and cercopithecoid scapulae.

The apparently shortened scapular neck in *A. africanus* is, in its metrical relationships, at least as similar to those of quadrupedal monkeys as it is to apes (Figure 35). This may indicate functional adaptations in the scapular head region of *A. africanus* shared with quadrupedal forms, or possibly, a retained feature from an ancestral, pronograde form. However, one may not exclude the possibility that this feature is an autoapomorphy of *A. africanus*. This author acknowledges that it may be found that other extant primate species not examined in the present study may possess such skeletal relationships in their scapulae. However, there are no extant species known to this author that possess such features in combination with the other hominoid characters observed in the *A. africanus* scapulae.

A possibly important morphological difference between Sts 7 and Stw 162 is that the

architecture of the scapular head area of the Stw 162 scapula is more robust than the same region in Sts 7. Whereas the whole of the Sts 7 scapula is relatively gracile in architecture, Stw 162 is more robust. Given the differences in glenoid size between these two scapulae, the differences between them are in keeping with Sts 7 being either a small male or a female and Stw 162 male. However, Sts 7 was recovered in association with a "large... heavily worn mandible" of what was perceived to be an "old... adult male" australopithecine (Broom and Schepers, 1947). It has been assumed that the postcranial bones belong to the same individual as the mandible and the former were also considered to be male (Robinson, 1972).

On the other hand, as we have seen, the scapula of Sts 7 is far more gracile and female-like than Stw 162. This seeming contradiction raises several questions: has the mandible, in fact, been misidentified as male? Does the mandible belong to the same individual as the other bones? Is more than one species

represented by the sample? Is the Sts 7 a slender male in contrast with the more robust male Stw 162? The latter suggestion is supported by the relatively smaller absolute dimensions of the Sts 7 specimen when contrasted with those of Stw 162 but more so by the recent recovery of very large cranial specimens from Sterkfontein (Tobias, 1989; Tobias, in press). Thus, the Sts 7 scapula may in fact be that of a smaller male *A. africanus*, or that of a very large female.

The suggestion of a "second species" in the Member 4 sample has also been raised by Clarke (1985) but confirmation of this awaits more detailed analysis (Clarke, in preparation) and the recovery of associated cranial and postcranial elements.

The partially intact coracoid of Sts 7 is the only coracoid process to have been recovered from an australopithecine. Vrba (1979, p. 122), after preparation of the specimen, discovered that, contrary to the previous opinion that the coracoid process was complete (Broom and Robinson, 1950;

Campbell, 1966; Robinson, 1972; Roberts, 1974; Ciochon and Corruccini, 1976), in fact "the tip as well as bone dorsolateral to the tip, are missing". Many functional interpretations of the Sts 7 scapula have been based on the assumption that the coracoid was complete, and its shape "unique amongst all primates" (Ciochon and Corruccini, 1976). However, most functional interpretations based on coracoid shape that were made before Vrba's cleaning of this specimen are incorrect due to her revelation of substantial damage to this area.

Vrba (1979, p.122), examining the cleaned Sts 7 specimen, concludes that the coracoid of this specimen

"could well have extended significantly (perhaps by 10.0 (mm) in an inferolateral direction from the broken surface) ... and might have approached that seen in Pongo, but was less pronounced than those seen in other modern hominoids".

D

C

This author concurs with Vrba that indeed the coracoid of Sts 7 is broken and would have extended inferolaterally. Unfortunately, the present writer is unable to reproduce Vrba's results and predict the distance the coracoid might have projected over the glenoid cavity. However, based solely on qualitative observations, one may hold that the surviving coracoid fragment of Sts 7 is larger than one would expect in a hominoid scapula of comparable size. As Ciochon and Corruccini (1979, p. 80) note, the coracoid fragment "is triangular in shape with the apex at its most medial extent and a broadened base at its most lateral extent". Whereas this morphology is not typical of the coracoid in orang-utans, it is fairly similar to the same region in modern humans, chimpanzees and gorillas.

This author finds no basis for the claim that the "small slivers of *in-situ* bone" that "curve from the superior surface onto the lateral edge", are indicative of "little laterally extending bone" as Vrba (1979, p. 122) suggests. The most

which this author may ascertain from these small slivers of bone is that there was indeed some lateral extension of the coracoid prior to damage and this indicates that the lateral extension of the coracoid would have been greater than that which is presently observed in the fossil specimen. Unfortunately, this information alone is functionally and taxonomically of little value.

Vrba (1979) also concludes that the pronounced tubercle, which is located at the highest part of the coracoid fragment of *Sts 7*, is homologous with the point of attachment of the conoid ligament, an interpretation with which the author agrees... then suggests that the conoid attachment in *Sts 7* differs from those of the extant pongids in "lacking a pronounced dorsal projection" (Vrba, 1979, p. 122). It is likely that in *Sts 7* the coracoclavicular ligament, of which the conoid ligament is a part, was more similar to those of modern humans than to those of modern pongids. This humanlike orientation may be related to upright posture in *A. africanus* since both components of the coracoclavicular

ligament bind the clavicle to the scapula and thus indicate, to some degree, the position of the clavicle in relation to that of the thorax. The more dorsally projecting tubercles that are observed in the scapulae of pongids are consonant with the different position of the clavicle on the thorax in animals that practise terrestrial quadrupedalism. In addition, the conoid ligament is considered to be part of the major support structures of the superior part of the glenohumeral joint in humans. In part, it is for this reason that Vrba (1979) has suggested that the enlargement of the conoid ligament may be due to a general enlargement of the upper limbs of *A. africanus*. Thus Vrba associates the observed similarities in orientation of this tubercle between *A. africanus* and modern humans with the similarities in forces which the shoulders of the two forms encounter as terrestrial bipeds.

In contrast to the above finding, Vrba (1979) assesses that the two components of coracoid curvature in the Sts 7 scapula are more comparable to the condition found in extant pongids and

differ decidedly from the condition found in modern humans. Indeed, the angle between the long axis of the glenoid cavity and neck of the coracoid process appears to be considerably greater than in the modern human scapulae examined in the present study. In addition, the coracoid curvature in Sts 7 appears to exceed the degree of angulation of the coracoid process in most individual African ape scapulae and is most similar to that observed in orang-utans.

Because of the extreme scoring on the dorsal aspect of the base of the spine, it is difficult to confirm Vrba's claim that the base of the spine medial to the spinoglenoid notch is "somewhat more thickened . . . than is usual in modern man" (Vrba, 1979, p. 120). She goes further and explains that this thickened appearance is due to the "less sharply angular demarcation between spine and upper scapular surface". Since there has been a loss of an indeterminate amount of surface bone on both the superior and lateral aspects of the base of the spine, it seems to be more likely that the apparent thickening of this region is simply a



result of loss of bone surface on the superior and lateral aspects of the base of the spine. In addition, much damage has occurred on the superior and inferior surfaces of the base of the spine, and along with the loss of bone laterally, this indicates that the apparent basal thickening in the specimen is most likely a preservation phenomenon (what P.V. Tobias calls a taphotypic feature), and not a morphological feature. In contrast to that of the Sts 7 specimen, the base of the spine of Stw 162 is extremely robust and well defined. The angle between the neck of the scapula and the base of the spine is wide. At the point of dorsal breakage the spine has not started its lateral curve over the glenoid cavity. The general appearance of the base of the spine of Stw 162 is most like that in modern humans.

From Broom's (1950) plate and illustration of the Sts 7 scapula (Broom *et al.*, 1950, Plate 2 and Figure 9), it appears that the acromion fragment was nearly complete. Unfortunately, some time after the recovery of the specimen by Broom in 1947, but prior to 1965 when the rest of the Sts 7

scapula was again carefully examined, the acromion has been lost (Robinson, 1972). Robinson, Vrba (1979) and the present author have searched extensively through the fossil collections of the Transvaal Museum for the missing fragment to no avail. Fortunately, a photograph of the Sts 7 specimen, still encased in matrix, but clearly showing the intact acromion, appears in the 1950 monograph (Broom et al., 1950). From this plate Vrba (1979) surmises that the acromion of Sts 7 projects "well over the glenoid cavity as it does in other Hominoidea". Further, she notes that the acromion appears to pass over the glenoid rim at approximately the midpoint of the glenoid cavity. This morphology would be expected in the scapulae of all modern hominoids and arboreal monkeys, but it is unlike the position of the acromion in more terrestrial primates.

Broom's plate of Sts 7 indicates that as the acromion passed laterally over the rim of the glenoid cavity, it flared out into a fanlike shape. This fan shape appears to represent part of the base of the "head" of the acromion. The

base fragment is largest cranially, which makes the whole acromion fragment appear to be orientated superiorly. If one assumes that the lateral projection of the acromion fragment visible in Broom's (1950) plate represents the original lateral edge of the Sts 7 acromion process, then the acromion does not project as far laterally as is found in modern humans, gorillas and chimpanzees, but is more similar to the condition found in orang-utans. However, there apparently is damage to the superior edge of the acromion which indicates that there was probably some additional cranial continuation of the acromial head, a feature shared by all extant hominoids.

The axillospinal angle cannot be estimated in the new Sterkfontein scapula. However, much discussion has been published on the probable axillospinal angle of the Sts 7 specimen (Coon, 1962; Campbell, 1966; Oxnard, 1968a; Robinson, 1972; Vrba, 1979). In particular, Vrba (1979, p. 120) notes that

"in spite of the damage which Sts 7 has suffered, the small remaining spinal fragment provides tantalizing hints that placement and orientation of the spine in this specimen (Sts 7) may have differed significantly from the condition in Homo sapiens".

Unfortunately, two important qualifiers limit the importance of the estimated axillospinal angle value in Sts 7. First, the observed ranges of values for this angle in extant hominoid species overlap considerably (Coon, 1962; Ashton et al., 1965), and in most cases include the total range of values between 7° and 30° that have been estimated for this angle in Sts 7 (Coon, 1962; Oxnard, 1968; Vrba, 1979). Secondly, due to the high variability in the position of the medial continuation of the spine of the scapula and the caudal continuation of the axillary margin of the scapula in extant hominoids, estimations of this angle in a specimen as fragmentary as Sts 7 are beset with a high margin of error.

Nevertheless, only one of the scientists who has examined the Sts 7 scapula has predicted a value for the axillospinal angle outside the extant hominoid range of variation: Robinson (1972), who estimates a value of 7 degrees on the specimen. After repeated attempts at estimating the possible range of values for this angle, this author finds it difficult to accept such a low value for the axillospinal angle in this specimen.

Bearing in mind the qualifiers mentioned in the previous paragraph, it seems reasonable to infer that the axillospinal angle would not have fallen below approximately 15° and not above 30° , figures that fall well within modern hominoid variation.

This author's "best guess" for the angle would approximate that of Vrba (1979), namely $c27^{\circ}$.

7.6.1.2

The Axillary Margin and Body of the Scapula

Only two specimens, Sts 7 and Stw 431 have sufficient axillary margin parts preserved to warrant comparison. Of these two, the Stw 431

scapula fragment is most important because it possess the only complete australopithecine axillary margin and inferior angle in the entire Plio-Pleistocene fossil hominid record. Although its relative size is difficult to compare without a preserved glenoid cavity, the specimen compares most closely in size and robustness to the scapular axillary margins of adult female chimpanzees and orang-utans observed by the author.

Compared to human scapular axillary margins, that of Stw 431 is absolutely very long. If one accepts the most superior point of damage as representing a point just below the glenoid cavity (i.e. the superior point where the greatest length of the axillary margin is measured), then the absolute length of the axillary margin (143.0 mm) lies in the upper 20% of the observed variation in adult male modern humans (Table 20).

In addition, the axillary margin length of the specimen falls within one standard deviation of the mean axillary margin lengths observed in female chimpanzees and female orang-utans.

The expanded areas of attachment for the origin of the triceps muscle in both Sts 7 and Stw 431 are apelike in morphology, since in humans the origin of the long head of triceps is usually confined to the infraglenoid tubercle. Thus, the *A. africanus* shoulder was most probably capable of powerful adduction of the humerus and powerful extension at the elbow, abilities required by climbing primates. In addition, the expanded origin of this muscle is indicative of increased support of the whole shoulder joint from below.

Since no glenoid cavity is preserved in Stw 431, the axilloglenoid angle cannot be determined. However, the Sts 7 scapula preserves sufficient axillary margin below the glenoid cavity for estimates of this angle to be made. As Vrba (1979) pointed out, the exact position of the axillary arm of the axilloglenoid angle of Sts 7 cannot be positively known. Nevertheless, numerous attempts have been made to estimate the axilloglenoid angle of the specimen by projecting

a line through the missing inferior angle and producing a "best guess" axis (Campbell, 1966; Oxnard, 1968a; Robinson, 1972; Vrba, 1979). The most recent estimate of 120° has been made by Vrba (1979) after preparation of the axillary margin.

This author's estimate of the Sts 7 axilloglenoid angle agrees closely with her best guess of 120° . Compared to the values observed in modern humans these values are very low and place Sts 7's axilloglenoid value close to the lower limit of the observed values of modern humans but within the ranges observed for extant great apes (Figure 68 and Table 12). If the $c120^\circ$ estimate is correct, the glenoid cavity of Sts 7 is oriented more cranially than has been observed in modern humans. However, it must be cautioned that the range of observed values for the axilloglenoid angle in modern humans is extensive. If the Sts 7 scapula's original axilloglenoid angle was estimated at only 1° greater, then its value would fall into the lower limit of observed range of variation in modern human scapulae. The

low axilloglenoid angle in Sts 7 indicates a more apelike, cranially orientated glenoid cavity.

This feature has been associated with apes which habitually use their arms in a raised position during climbing activities (Oxnard, 1963).

Therefore, one may surmise that at least in this feature, the Sts 7 scapula is most similar to the scapular morphologies observed in modern great apes.

Amongst all early hominids, only Stw 431 preserves the distal one third of the axillary margin and the inferior angle. The slight costal curvature, which increases as one moves distally along the axillary margin of the Stw 431 scapula, indicates it lay on a gently curving thorax and was probably positioned most similarly on the thorax to the scapulae of hominoids.

The exact inferior angle value for Stw 431 cannot be measured since the medial margin has been lost. However, the angle does not appear to be as narrow as is observed in chimpanzees, orang-utans and gorillas, nor as broad as that

observed in quadrupedal monkeys, being most similar to the inferior angles of modern humans. The ranges of values which represent this author's "best guesses" for reconstruction of the inferior angle of Stw 431 are illustrated on the specimen in Figure 57. While this author acknowledges that these are only estimates, the maximum and minimum values do illustrate the apparently very wide, human-like inferior angle possessed by this specimen (Figure 56). The wide inferior angles observed in human scapulae are most probably associated with the enlargement of the subscapularis muscle. In addition, the enlarged area would provide a larger area for the attachment of serratus anterior, a muscle whose enlargement is associated with maintaining the position of the scapula on an erect thorax.

Despite the relative gracility of the Stw 431 specimen, all the observable muscle attachment areas are very rugose. Judging by the position and size of the various muscle attachments that are visible on the specimen, the Stw 431 scapula shares some similarities with apes but a majority

of its muscular attachments appear most similar in position, shape and form to those of humans.

However, one exception is that the attachment area of the teres major muscle near the inferior angle is more similar in appearance and positioning to those of apes. In shape and form it is most comparable to the attachment areas of this muscle observed in male chimpanzees and male gorillas and is least similar to those observed in orang-utans and hylobatids. The attachment area for this muscle is certainly positioned more cranially than one would expect in the scapula of a modern human. In addition, the expansion of the axillary margin at the area of attachment of the teres major muscle, to the degree observed in the Stw 431 scapula, is rarely observed in the scapulae of humans yet is commonly observed in those of apes.

It has been established that in chimpanzees, teres major is actively involved in assisting the lowering of the forelimb during the first half of the swing phase during pendular arm-swinging, as well as providing propulsive power during the

second half of pendular arm-swinging (Jungers and Stern, 1984; Larson and Stern, 1986; see also Chapter 5, this study). Therefore, the similarity of this muscle's position and size in Stw 431 to those of chimpanzees may indicate some form of habitual arm-swinging or suspensory behaviour that was practised by the Stw 431 individual.

The subscapularis muscle was large and strongly affixed to the scapula in Stw 431, as is evidenced by the rugose muscular lines of attachment visible on the costal surface of the inferior angle. As subscapularis reaches its largest size in humans, and more commonly leaves large, muscular lines of attachment in this group than any other, the muscle's position and size at the scapular attachment was probably most similar to the condition observed in modern humans. The likely reason for the probable enlargement of the subscapularis muscle in *A. africanus* has already been discussed.

In Stw 431, the attachment area of serratus magnus in the inferomost part of the anterior surface of the inferior angle does not appear to be confined to the apex of the inferior angle and is thus positioned more similarly to those observed in humans than to those in apes. This suggests that this muscle was acting in Stw 431 as it does in humans, most notably to assist in the support the scapula on an erect thorax (See Chapter 5).

7.6.1.3

Synopsis

Despite Day's (1978) assertion that the Sts 7 scapula is "anatomically inadequate and too poorly preserved for meaningful interpretation of the mode of locomotion for which it is adapted", there are certainly important morphological features which are preserved and observable in the specimen which indicate that the Sts 7 individual was probably using its upper limbs in ways very different from modern hominoids. Furthermore, with the addition of the new *A. africanus* scapular

specimens from Member 4, greater light is shed on the morphology of this species' scapula and for the first time, intraspecies morphological interpretations may be made. The data presented in this section indicate that there are numerous structural convergences in the *A. africanus* scapular anatomy with the extant Hominoidea; there are also significant divergences from the total morphological pattern exhibited by modern hominoids.

The combination of morphological features associated with orthograde posture with features suggestive of arboreal behaviour imply to this author that the *A. africanus* scapular morphology is not incompatible with that which might be observed in a non-specialized climber, although one which practiced behaviour that involved arm-swinging or suspension. It is improbable that the combined morphologies of the specimens indicate adaptations towards any form of habitual pronograde or quadrupedal locomotion, or of specialised brachiation.

The morphologies of the scapular specimens indicate that the *A. africanus* shoulder shares more similar characters with modern humans and orang-utans than it does with African pongids or gibbons. The morphologies of the *A. africanus* glenoid cavities as well as the interpretations of the soft tissue associated with the glenohumeral joint's mobility and stability, are most similar to, but not identical with, those of humans. In combination with the features associated with a high degree of mobility, the scapula of *A. africanus* also possesses powerful adductors and abductors of the arm, which are most apelike in morphology. In contrast to these apparently apelike characters of the soft tissues, several musculoskeletal features which are, in humans, associated with support of the scapula on an erect thorax, are present in the *A. africanus* scapula.

In particular, the apparent enlargement of the subscapularis muscle in both Stw 162 and Stw 431 implies in these specimens that this muscle was adapted to exerting and resisting forces on an upright thorax in ways very similar to that of modern humans.

However, the *A. africanus* scapula cannot be considered simply a combination of orang-utan, generalised ape and human morphologies as it is additionally unique in its combined morphology by possessing features in the scapular neck region which one might consider convergent with adaptations observed only in pronograde primates. One is tempted to associate the relatively shortened scapular neck exhibited by both Stw 162 and Sts 7 with the primarily uni-directional stresses met with during pronograde quadrupedalism, where stresses are passed through the scapular neck. Thus, one might infer that the presence of this feature in the scapulae of *A. africanus* indicates that the head of the scapula is either adapted to receiving stresses in similar ways to those of primates that practise pronograde forms of locomotion or, more plausibly, has retained characters from an ancestor that practised some form of pronograde or palmigrade locomotor behaviour. Since the remainder of the scapular morphology, as well as that of almost every other postcranial area, suggest that the

species *A. africanus* possesses both an erect thorax and was a capable biped (Broom and Schepers, 1946; Robinson, 1963, 1972; Napier, 1963; Walker, 1973; Wood, 1976; Lovejoy, 1978; Corruccini and McHenry, 1978; Day, 1978; McHenry, 1986; Jungers, 1991; Reed et al., 1993), then it seems likely that this species was not practising any form of pronograde locomotion as has been suggested by Sarmiento (pers. comm.). It is most probable that the apparently pronograde characters possessed by the *A. africanus* scapulae are plesiomorphies.

This author would concur with Senut's (1978) and Vrba's (1979) suggestions that the morphology of the Sts 7 scapula is consistent with a more apelike morphology for the whole upper limb of *A. africanus*. The examination of the new scapular material from Sterkfontein suggests a similar conclusion to this author. In addition, not only does the size of the conoid tubercle suggest that the upper limb was heavier and perhaps longer than in similarly sized humans, as has been suggested by Vrba (1979), but the sheer large sizes of

all of the scapular material attributed to *A. africanus* suggest upper limb proportions that are very different from those of modern humans.

In conclusion, the available scapular morphological evidence suggests that *A. africanus* was not using nor carrying its upper limbs in the same ways as modern hominoid species. The scapula of *A. africanus* does not appear to be specialised for the locomotor behaviour of gorillas or chimpanzees, nor for specialised brachiation, as has been suggested by Oxnard (1968a, 1969) and Campbell (1967). As has also been previously suggested (Senut, 1978; Vrba, 1978), the *A. africanus* scapula appears adapted towards the potential for climbing and suspensory behaviour, but this must be a behaviour that is not incompatible with maintaining a bipedal posture. The morphology of the glenoid area of the *A. africanus* scapula allows for a high degree of freedom of movement, yet it appears to maintain a high degree of structural stability through the soft tissues of the rotator cuff.

The Clavicle

The Stw 431 clavicular fragment appears to possess a relatively low degree of sigmoid curvature, being more similar to the same region observed in chimpanzees and orang-utans than it is to similarly sized human clavicles. The cross section profile at mid-shaft is anteroposteriorly flattened but relatively broad supero-inferiorly and may be considered more apelike than humanlike.

The deltoid muscle seems to have been enlarged in the individual and attached more similarly to those observed in chimpanzees and some pronograde monkeys. However, without more complete specimens the functional implications of this positioning are at present unclear. The strongly projecting tubercle of what appears to be the area of attachment of the coracoclavicular ligament, indicates a strong contact between the clavicle and scapula. This feature is more frequently observed in the clavicles of apes, where dislocating forces are at their highest during suspensory behaviour and thus may be

associated with an emphasis on climbing.

However, it is cautioned that a pronounced conoid tubercle is not unknown in humans and in these instances has not been reported to be associated with any unusual behaviour (see Chapter 4).

In summary, whilst fragmentary, the Stw 431 clavicle is more apelike in its total morphological pattern. In fact, it bears little resemblance to any human clavicle and may be considered to exhibit definite adaptations towards tree-climbing behaviour.

7.6.3

The Humerus

All three of the humeral specimens referred to *A. africanus* are very similar in size, being metrically most comparable to the proximal humeri of adult male humans, male chimpanzees and female orang-utans. The specimens are also relatively robust. However, it is impossible to apply a classical robusticity index to these specimens since in only the Sts 7 humerus is there some

shaft preserved and this is very fragmented. However, as with the scapular material associated with this species, it may be surmised that the humeral specimens are surprisingly large given current weight and stature reconstructions for *A. africanus* (see Hartwig-Scherer, 1993 for a recent review of this subject).

Both Stw 517 and Sts 7 possess very rounded articular surfaces that are most comparable to those of humans, orang-utans and gibbons (Table 15 and Figure 58). Alone, this feature indicates that *A. africanus* possessed a high degree of freedom of movement at the glenohumeral joint. However, as is true for a flattened glenoid cavity articular surface, a more rounded, bulbous humeral head offers less neck area for the attachment of the capsule of the shoulder joint. Thus in a humerus possessing a rounded head, stability and security in the joint are traded, to some degree, for a high degree of freedom of movement at the glenohumeral joint.

Although only two specimens, Sts 7 and Stw 328, possess even a portion of the superior part of the greater tubercle, neither specimen appears to have either a greater or lesser tubercle that extends higher than the articular surface of the humerus. In this respect they are very unlike the humeral heads of modern quadrupeds and most similar to those of the extant Hominoidea. In addition, in each of the specimens, both the greater and lesser tubercles are very robust relative to overall size, a condition observed most frequently in hominoids. Among hominoids, this is due primarily to the increased attachment needs of the enlarged short scapular muscles in shoulder joints which are required to withstand multi-directional dislocating force. The relative size of the attachments at the humeral tubercles of these so called short scapular muscles has been associated with the stabilisation of the glenohumeral joint (Ashton and Oxnard, 1963; Robinson, 1972). Therefore, one may infer that the soft tissues that surrounded the head of the humerus in *A. africanus* acted as powerful stabilisers for the whole joint. It is

unfortunate that it is not possible to infer any greater functional detail from this region due to the damage to this area found in all the available specimens.

To judge by the width of the intertubercular groove of Stw 328, the biceps brachii muscle and associated tendinous sheath were robust and similar in size to those of extant hominoids.

Both Stw 517 and Sts 7 possess intertubercular grooves which are broad and deep being similar in relative size to those of African hominoids but not to orang-utans and siamangs. One may thus infer that, as in most modern great apes, *A. africanus* possessed an enlarged biceps brachii muscle. The enlargement of this muscle in apes has been associated with an increased ability to flex and to supinate the forearm powerfully whilst preventing dislocation of the humeral head from the glenoid cavity by acting as a powerful stabiliser of the joint (Basmajian and De Luca, 1985; Larson and Stern, 1985). However, the muscle was not developed in the *A. africanus* scapula to the degree observed in orang-utans.

This indicates to this author that the *A. africanus* shoulder was most probably not adapted to withstanding the powerful dislocating forces encountered during brachiation.

7.6.3.1

Synopsis

The proximal humeral specimens referred to *A. africanus* do not exhibit an exclusive suite of morphological features that would classify them as being adapted for any single, recognizable form of locomotion, as practised by modern hominoids. In addition, it may be ascertained that *A. africanus* possesses proximal humeral heads that differ little in their morphologies from those of extant hominoids in the permitted range of shoulder movements and are most similar to the rounded, very mobile joints possessed by orang-utans, gibbons and humans.

All the short muscle attachments at the head of the *A. africanus* humerus are robust implying a great deal of structural stability in the

glenohumeral joint. This emphasis on stability in the *A. africanus* glenohumeral joint is a characteristic of the joints of non-human hominoids and is almost certainly related to the requirements of resisting dislocation forces during climbing behaviour.

The author's ability to make further functional conclusions is extremely limited by the fragmentary nature of the humeral specimens. This author finds little that the morphology of the new Sterkfontein humeral specimens add to Robinson's (1972) functional morphological assessment of the *A. africanus* humerus based solely on the Sts 7 humeral fragment. In short, Robinson concludes that the morphology of the *A. africanus* humerus allows free ranging shoulder movement, but this is combined with well-developed stabilising muscles and thus may indicate adaptations to arboreal behaviour.

Interpretation of the Total Functional Morphology of the

A. africanus Shoulder Girdle

With the addition of the new Sterkfontein shoulder girdle elements attributable to *A. africanus*, we are closer than ever before to developing a modal species model of this anatomical region. Based solely on the morphology of Sts 7, it is understandable that many early researchers have concluded that *A. africanus* was performing some form of specialised locomotor behaviour such as brachiation, that might be equated to a modern ape analogue (Campbell, 1967; Oxnard, 1968; Roberts, 1972; Vrba, 1979). However, with the inclusion of the new fossil material from Sterkfontein, as well as the present re-analysis of the Sts 7 material, a clearer picture of the functional morphology of the *A. africanus* shoulder girdle is revealed. From these new data it may be ascertained that the *A. africanus* ~~shoulder~~ does not appear to be

specialised towards any recognised form of upper limb dependent locomotion, nor towards frontal body manipulative behaviour as performed by modern humans. The *A. africanus* shoulder girdles' apparent capabilities are incompatible neither with some form of non-specialised climbing behaviour, nor with the flexibility of movement that characterises orthograde, erect posture, although, in the latter instance, not identical to that practised by modern humans.

As has been suggested by Vrba (1979), one is tempted to conclude that the bones of the shoulder girdle of *A. africanus* were positioned on the thorax more similarly to those of extant apes rather than to those of modern humans, since the skeletal elements possess such apelike features as a low axilloglenoid angle, a long axillary margin, a laterally positioned conoid ligament and a clavicle that exhibits a low degree of sigmoid curvature. However, without a complete clavicle and acromion process from *A. africanus* it is difficult to assess whether the shortened scapular neck would have affected the

position of the glenoid cavity on the thorax. It is plausible that the whole shoulder girdle was oriented quite laterally on the thorax as in modern humans and quadrupeds, in order to facilitate free-ranging movement at the shoulder, but the final answer to this question will have to await the discovery of further, more complete specimens.

The physically large size of the *A. africanus* shoulder girdle fossils, combined with the observation that these elements share many similar muscle attachments with extant apes, indicate to this author that *A. africanus* was most likely practising some form of arboreal, upper limb dependent locomotion that is not the same as any upper limb dependent behaviour practised by modern non-human hominoids. In addition, the new material supports the suggestions of Senut (1978) and Vrba (1979) that in size alone, the upper limbs of *A. africanus* were more robust and probably longer than those of comparably sized modern humans.

Combined with the apparently arboreally oriented upper limb dependent mode of locomotion that this author suggests for *A. africanus*, it appears that *A. africanus* was also a fully capable biped, albeit practising bipedalism which was different from that currently practised by modern humans. The relatively scarce pelvic and lower limb material from Sterkfontein and Makapansgat seems to imply that *A. africanus* was a capable, facultative biped (Broom et al., 1950; Robinson, 1963, 1972; Napier, 1963; Le Gros Clark, 1971; W. 1978; Lovejoy, 1978; Day, 1978; Jungers, 1982; McHenry, 1986; Reed et al., 1993). Thus one may infer that *A. africanus* was a functionally capable biped, which additionally practised capable arboreal behaviour involving extensive use of the upper limbs to bear weight and provide active force during climbing. In other words, it was a generalized arboreal/terrestrial biped probably as capable of climbing in trees as of bipedal activities on the ground.

Generalized climbing behaviour as part of a locomotor repertoire for *A. africanus* has already

been suggested by Senut (1978) and Vrba (1979). Whilst slow climbing or vertical climbing behaviour, as suggested by Sarmiento (1985) and Hunt (1990) for australopithecines, are plausible modes of locomotion for *A. africanus*, without modern analogues an interpretation of the exact form of arboreal locomotion practised by *A. africanus* remains speculative. The question of whether the above-described shoulder girdle morphology precludes use of the forelimb in precise, manipulative activities, such as are required for stone tool manufacture seems to have been addressed by Ricklan and Tobias (in press), who find that the *A. africanus* hand appears well suited to manipulative behaviour of precision levels equal to the requirements of a stone tool culture and to a greater degree than is possessed by modern apes.

Finally, given the currently suggested stature reconstruction for *A. africanus*, the observations made in the present study indicate that *A. africanus* possessed very large shoulder girdle

complexes for their proposed heights and weights (see Hartwig-Scherer, 1993, for a review). The *A. africanus* shoulder girdles are more similar in size to those of large male humans, male chimpanzees and female orang-utans than they are intermediate in size between chimpanzees and humans, as has been suggested by other postcranial elements (Broom et al., 1950; McHenry, 1988; Jungers, 1988; Reed et al., 1993). This may indicate different upper-body to lower body size relationships than have been previously proposed (McHenry, 1988; Jungers, 1988). As has been suggested by Hartwig-Scherer (1993), weight reconstructions for *A. africanus* that have been based solely on human stature models are almost certainly inaccurate. Models that use ape upper-to lower-body size relationships may be more applicable, but must be used with some restraint since there are no living, bipedal, non-human hominoids to include in the model.

There are few observable size differences between the *A. africanus* shoulder girdle specimens that might suggest a degree of sexual dimorphism

that is any greater than that observed in modern humans. However, several authors have recently noted in other postcranial bones, as well as in the crania, that the sexual dimorphism present in this species may have been more equivalent to, or greater than, that observed in modern chimpanzees (Hartwig-Scherer, 1993; Reed *et al.*, 1993 etc.).

One may thus conclude that there are no features observable in shoulder girdle specimens that originate from Sterkfontein Member 4 that point to a greater degree of morphological diversity than one would expect in a single modern hominoid species.

7.7

The Functional Morphology of the *A. afarensis* Shoulder Girdle

7.7.1

The Scapula

In size, the A.L. 288-1L scapula is only slightly larger in all metrical dimensions than the scapulae of gibbons and smaller than even the smallest female human specimens observed in the present study. Whilst admittedly fragmentary, it possesses several intriguing anatomical features that indicate convergence with both ape and human morphology. However, one may infer that the A. L. 288-1L scapular morphology is unique when contrasted with that of the modern Hominoidea.

The glenoid cavity may be described as generalised in its morphology. The values of 67.5% and 70.8% calculated for the glenoid index (Senut, 1978; Johanson et al., 1982) fall within one standard deviation of the means of the values calculated for the entire extant hominoid

series save for the orang-utans (Table 6 and Figure 54). However, the estimated values are within the range of variation of the values observed for the latter species. The calculated glenoid index value for A.L. 288-11 is therefore of little taxonomic or functional value since it falls at a point of extreme overlap of the observed values for the hominoid series. Nevertheless, one may infer that the glenoid cavity shape possessed by A.L. 288-11 was not restrictive and would have offered a high degree of freedom of movement at the glenohumeral joint.

All the attachment areas for the stabilising muscles of the rotator cuff that are discernible on the specimen are robust. The supraglenoid tubercle is strongly developed, most probably indicating that the long head of biceps was well developed at its area of attachment. The attachment area for the glenoid labrum is pronounced wherever visible. As the size of the glenoid labrum attachment area may be directly related to a general enlargement of the whole

labrum (Ferrari, 1990) and since the glenoid labrum is also considered to be an important stabiliser in the rotator cuff (Howell and Galinet, 1988; Chadwick et al., 1990; Ferrari, 1990), its enlargement in A.L. 288-11 is most likely a defence against dislocating force in relation to a large humeral head. Thus the glenoid cavity articular surface area of A.L. 288-11 presents a morphology that may be described as generalised when compared to those of extant hominoids, but which allows a high degree of freedom of movement whilst maintaining structural stability at the glenohumeral joint.

The glenoid cavity of A.L. 288-11 is orientated more cranially in relation to the line of the axillary margin than is typically observed in modern humans. However, as was noted for the Sts 7 specimen, it must be strongly cautioned that the range of observed values for this axilloglenoid angle in modern humans is high. Stern and Susman's (1983) and Susman et al.'s (1985) estimates for the axilloglenoid angle of A.L. 288-11, as well as this author's upper

estimates for it, are within the lower end of the calculated range of values for this index in modern human scapulae (Figure 68). Only Senut's (1978) "best guess" of around 115 degrees for this angle is outside the range of variation observed in modern humans. Nevertheless, all the estimates for the axilloglenoid angle values of A.L. 288-11 are closest to the mean observed in orang-utans and within the range of variation observed in the scapulae of both chimpanzees and gorillas.

A low axilloglenoid angle has been associated with ape-like behaviour in which the forelimbs are habitually used in a raised position during climbing activities (Oxnard, 1963). It is tempting to infer from this feature of A.L. 288-11 that *A. afarensis* exhibited climbing behaviour.

The neck of the scapula of A.L. 288-11 may be considered short relative to its glenoid cavity dimensions when compared to that observed in modern humans and apes (Figure 55). Whilst admittedly not within the 95% confidence limits of the data for any extant hominoid, the relative

neck length is still within the bounds of the slope representing the outer limits of the total range of variation observed in the scapulae of modern hominoids.

Because of the small size of the *A. afarensis* scapula, it is difficult to assess the relative robustness of the specimen. However, the overall architecture of the specimen may be described as more gracile than one might expect in even a very small human scapula, and is only slightly more robust than those of similarly sized gibbons. As overall gracility of architecture is considered by this author to be a character possessed by the more arboreal modern groups (Chapter 6), one is tempted to infer that this is also true for the *A. afarensis* scapula. However, one must be extremely cautious in his interpretations based on the apparent gracility of the A.L. 288-11 scapula. Given the potential difficulties inherent in assessing allometric changes in such a small specimen when the only comparable-sized extant hominoid practises a highly specialised form of upper limb dependent

arboreal locomotion, one must approach behavioural elucidations with some caution.

7.7.1.1

Synopsis

The available scapular morphology of *A. afarensis*, based on the single A.L. 288-11 specimen, may be described as unique amongst modern hominoids, if solely because the specimen combines extraordinarily small size with functionally unspecialised morphology. Overall, its morphology is more apelike than humanlike. It is small when compared to the scapulae of most modern hominoids, the only exceptions being those of gibbons and siamangs. The low axilloglenoid value indicates that the A.L. 288-11 scapula was most likely positioned on the thorax more similarly to those of extant apes. The presence of a glenoid cavity whose surrounding soft tissues provide stabilising strength, yet allow a high degree of mobility, implies an adaptation towards stress resistance similar to those observed in the

scapulae of modern hominoids that include tree-climbing in their locomotor repertoire.

7.7.2

The Clavicle

The variation in size in the *Australopithecus afarensis* clavicular series is extreme and emphasises the apparent high degree of sexual dimorphism in this species (Hartwig-Scherer, 1993). A.L. 288-1 is the smallest specimen in the series being most similar in size to the clavicles of siamangs and those of the smallest female humans. The largest clavicles are the two specimens from the so-called "first family", A.L. 333-94 and A.L. 333-6/9. These specimens are relatively gracile in build but most similar in size to those of chimpanzees and female orang-utans.

Due to the universally poor preservation and the lack of articular ends, there is little of functional morphological value which may be ascertained from the anatomy of these specimens.

However, in general, the morphological architecture of all the specimens may be described as being more apelike than humanlike. All the specimens possess the flattened inferior surface and concave superior surface that is more commonly observed in the clavicles of modern non-human hominoids. The observable muscle attachment areas do not differ significantly enough from those observed in any of the large bodied hominoids to make meaningful functional interpretations. It may be stated that the sigmoid curvature exhibited by A.L. 333-6/9 is at the low end of normal variation for human clavicles and is most similar to those of chimpanzees, gorillas and some orang-utans.

7.7.2.1

Synopsis

The clavicles of *A. afarensis* appear somewhat more apelike than humanlike in possessing a relatively low degree of sigmoid curvature and supero-inferiorly flattened bodies. However, due to the fragmentary nature of the sample, it is

difficult to make any meaningful functional statements about the specimens.

7.4.4.3

The Humerus

Despite there being more proximal humeral fragments preserved in the *A. afarensis* series than in any other early hominid series, the severe exfoliation of the bone surfaces, as well as the fragmentary nature of the humeral articular surfaces, make this material of limited value for taxonomic comparisons and functional interpretations. Nevertheless, several interesting functional interpretations may be made from the two specimens that have relatively intact heads, A.L. 288-1r and A.L. 333-107.

The humeral head index is low in both the A.L. 299-1r and A.L. 333-107 specimens, being outside the range of the index values of all the great apes and siamangs and only just within the range of values observed in humans and gibbons (Figure 58 and Table 15). The index values

observed in the two Hadar humeri are remarkably similar despite the appreciable size differences between A.L. 288-1R and A.L. 333-107. This may indicate that the long narrow humeral articular surface is typical of *A. afarensis*. Functionally, one may infer that this feature is indicative of adaptations to an erect thorax, since both extant species (human and gibbons) which exhibit humeral head index values as low as those found in *A. afarensis* share the relatively unique primate locomotor behaviour of not using any form of quadrupedalism in their locomotor repertoire (Fleagle, 1988).

The short muscle attachments at the head of the *A. afarensis* humeri are robust and this implies structural stability in the glenohumeral joint. This emphasis on stability in the glenohumeral joint is more a feature of non-human hominoids that are forelimb-dependent climbers and is most likely related to the requirements of resisting dislocation forces during these activities.

The intertubercular sulcus width index (intertubercular sulcus width / humeral head breadth x 100) indicates that the A.L. 333-107 humerus is most similar, in humeral head breadth to intertubercular sulcus width relationship, to those of modern humans (Figure 69). However, the estimated value of 22.9 for this index in the Hadar specimen falls within one standard deviation of the means for the observed index values in all extant hominoids (Table 16).

As recently demonstrated by Hartwig-Scherer (1993), the size differences between the humeral elements from the A.L. 333 site and those of "Lucy" (A.L. 228-11) are extreme. Her multivariate analyses of the postcranial bones have indicated, that if all of these specimens represent a single species and if the may be considered as representative of the sexual dimorphism within that species, then the degree of sexual dimorphism exhibited may be greater than that found in any extant ape. The humeral specimen A.L. 333-107 provides her most reliable upper weight estimate of 90kg, whilst the "Lucy" humerus indicates a

body weight of around 27kg, the latter being approximately one-third of the former estimate (Hartwig-Scherer, 1993).

7.7.4

Interpretation of the Total Functional Morphological Pattern of the *A. afarensis* Shoulder Girdle

Functional and morphological analysis of the *Australopithecus afarensis* shoulder girdle is made difficult by the very fragmentary nature of the fossil shoulder girdle material as well as the absence of key skeletal parts. Because there is only a single *A. afarensis* scapular specimen, and the articular surfaces of almost every other Hadar fossil bone examined here are severely damaged, it is impossible to develop an accurate picture of the total morphological and functional pattern of the shoulder girdle for this species.

Nevertheless, based on this fragmentary sample, the total functional morphological pattern of the *A. afarensis* shoulder girdle may be described as generalised, being suited to almost any

non-specialised climbing behaviour. However, several features, including the moderately low axilloglenoid angle value estimated for the scapula, indicate that the functional anatomy of the *A. afarensis* shoulder girdle is not adapted to frontal body manipulative behaviour as is performed by modern humans. It is equally unlikely that *A. afarensis* practised any form of forelimb-dependent quadrupedal locomotion or specialised brachiation due to the high axilloglenoid level when compared to modern gibbons and the low axilloglenoid angle when compared to monkeys, as well as reduced breadth of the humeral head articular surface. The latter feature alone may indicate that *A. afarensis* possessed adaptations in its glenohumeral joint to the freedom of movement benefits and restrictions that are dictated by an erect thorax.

The evidently strengthened short muscles of the scapular head area which are observable in the specimens, combined with the overall robustness of the humeri of the larger *A. afarensis* morphotype, also indicate probable

utilisation of the forelimb in climbing behaviour.

This author suspects that the general skeletal enlargement indicates enlarged musculature of the upper limb. In addition, the moderately low axilloglenoid angle observed in the scapula and the reduced sigmoid curvature observed in the clavicle, indicate that the scapular glenoid cavity faced more superiorly than one would expect in the scapula of a modern human. This feature alone indicates adaptations for use of the forelimbs in a raised position as in the more arboreal apes.

Despite the above-mentioned indications that *A. afarensis* practised a capable, arboreal, upper-limb dependent mode of locomotion, it appears that this species was also a fully capable terrestrial biped, albeit one which practised a form of bipedalism different from that performed by modern humans (Day, 1978; Lovejoy, 1978; Tardieu, 1979, 1981, 1983; Johanson et al., 1982; Jungers, 1982; Jungers and Stern, 1983; Schmid, 1983, 1991; Stern and Susman, 1983; Senut and Tardieu, 1985; Susman et al., 1985 etc.).

Thus one may infer that *A. afarensis* was a functional terrestrial biped, that also practised some form of arboreal behaviour involving extensive use of the upper limbs for weight-bearing during suspension and for withstanding active dislocating forces during climbing. As was suggested for *A. africanus*, slow climbing behaviour, or large circumference vertical climbing behaviour, as suggested by Sarmiento (1985) and Hunt (1990) for early hominid locomotor behaviour, are both plausible hypotheses for a mode of locomotion for which the *A. afarensis* shoulder girdle is adapted. Regardless of the exact form of locomotion practised by *A. afarensis*, based on the observable shoulder girdle morphology, this author concurs with the previous results of other researchers which conclude that the postcranial locomotor morphology of *A. afarensis* exhibits a propensity for climbing and probably suspensory behaviour as well as bipedalism (Senut, 1978, 1980; Tardieu, 1979, 1981, 1983; Tuttle, 1981; Jungers, 1982; Schmid, 1983; Stern and Susman, 1983; Susman, 1983;

Jungers and Stern, 1983; Senut and Tardieu, 1985; Zisman et al., 1985).

The evidence provided by the present analysis neither confirms nor rejects the single species status of *A. afarensis*, but the large size difference in the sample may support a two species hypothesis. However, whereas the degree of sexual dimorphism in the *A. afarensis* series is large, the humeri of both the large and small morphotypes are relatively homogeneous in their functional anatomy, but these features may also be considered widespread throughout the hominoid family. The same is apparently true in other postcranial regions and in the craniodental remains referred to this species (Tardieu, 1981; Zihlman, 1985; Johanson et al., 1982b; Lovejoy et al., 1982; Senut and Tardieu, 1985; Aiello and Dean, 1990; Hartwig-Scherer, 1993), suggesting that the species possibly exhibits greater sexual dimorphism than is present in any extant ape species with the exception of gorillas (Tardieu, 1981; Zihlman, 1985; Senut and Tardieu, 1985; Hartwig-Scherer, 1993).

7.8

The Functional Morphology of the *Homo Habilis* Shoulder Girdle

7.8.1

The Clavicle

The Olduvai clavicular specimen was originally described as being morphologically indistinguishable from those of modern *Homo sapiens* (Leakey et. al., 1964). However, subsequent evaluations of the specimen have indicated that there may be some morphological similarities that are comparable with modern ape clavicular morphology (Napier, 1965; Oxnard, 1969).

In the positions of its muscular markings the specimen does not differ from those of modern man (Napier, 1965). However, Oxnard (1969) has noted that the angle of torsion of the OH - 48 clavicle (52° - 60°) differs markedly from the angle observed in modern man, being most similar to the

degree of torsion measured in extant pongids (Figure 48). This indicates that the relative degree of angulation of the clavicle at the shoulder was more similar to that of modern non-human hominoids in being oriented superiorly. However, as discussed in Chapter 6 (this volume) the measurement of clavicular torsion is extremely difficult in specimens that lack articular ends and Oxnard's (1969) results must be viewed in light of this information.

7.9

The Functional Morphology of the Robust Australopithecine Shoulder Girdle

7.9.1

The Humeri

Both the humeral specimens are large and robust, being equivalent in size and robustness to the proximal humeri of male orang-utans, male modern humans or even small female gorillas. In the Omo humerus, the preserved part of the

shaft is straight and is most similar in this respect to those of modern humans. In contrast, the Koobi-Fora humerus is massive but it also possesses a great deal of curvature along the length of the shaft. McHenry (1973) and Day (1978) have pointed out the uniqueness of the morphology of the KNM-ER 739 humerus, indicating that there are no apparent adaptations towards knuckle-walking in the morphology of the specimen. However, this author cannot agree with Day's interpretation that the specimen's "sheer size would appear to rule out brachiation as an habitual form of locomotion" since male orang-utans certainly possess humeri as long and large as this specimen. In addition, there are no morphological features observable on the specimen that would conclusively rule out arboreal locomotion. In fact, the great length of the specimen, the massive deltoid attachment area and the hypertrophic appearance of all muscular markings most likely imply some form of upper-limb dependent behavioural adaptations. It is worth mentioning that the only other early hominid fossil humeri which exhibit such massive

bending of the shaft and expansion of the deltoid are the larger specimens at Hadar. The taxonomic association of this specimen with the genus *Australopithecus* (R.E.F. Leakey, 1972; R.E.F. Leakey et al., 1972; McHenry, 1973; Day, 1978) is valid since, as Day (1978) indicated, it almost certainly exceeds the recognised variation for humeral morphology seen in members of the genus *Homo*. However, one must be cautious in one's taxonomic assignment given the scant fossil record of the humeri of early members of the genus *Homo*.

Functional interpretation of the articular head of the Omo 119-2718 humerus are difficult due to the damage to the anterior surface. However, the length to breadth relationship of the humeral articular surface is most similar to that observed in modern humans in being long relative to its breadth (Figure 58). In contrast, the pronounced lipping of the articular surface over the infra-articular area is most commonly observed in the humeri of chimpanzees and gorillas. The sizes of the lesser and greater tubercles indicate that the short scapular muscles were

robust and one may thus infer that the glenohumeral joint of this specimen was stable. Since the only craniodental remains recovered from the area in which this specimen was recovered are of the "robust" australopithecine, *A. aethiopicus* (Kimbel and White, 1988), it seems reasonable to associate this specimen taxonomically with this group.

7.10

**Functional Anatomical and Evolutionary
Relationships Among the Early Fossil Hominidae
Based on the Total Morphology of the
Shoulder Girdle Elements**

Direct comparison of the two largest samples (Sterkfontein and Hadar) of early hominid fossil shoulder girdle material is made difficult by relatively small samples and by the generally poor preservation. Nevertheless, several morphological areas are preserved in both the two large samples, as well as in the individual elements from other sites, allowing direct comparisons to be made.

Size Differences Amongst the *A. africanus* and *A. afarensis* Samples

Tables 18 and 19 contrast the measurements and indices of the fossil hominid scapular glenoid cavities of *A. africanus* and *A. afarensis*.

There are two distinct sizes of early hominid scapulae: large (Stw 162 and Sts 7) and small (A.L. 288-1L). While the two Sterkfontein specimens may be described as belonging to medium to large-sized hominoids, the A.L. 288 - 1L specimen is extremely small, being roughly the same size as a male hylobatid and approximately 25% smaller than the more gracile (and smallest) of the two *A. africanus* scapulae (Sts 7). If, as suspected, Sts 7 represents either a small male or a large female *A. africanus*, and if A.L. 288-1L were included within the *A. africanus* sample, then the intrasample size variation would be around 30%.

If one compares the measurements of the heads of the Sterkfontein humeri (Sts 7, Stw 328 and Stw

512) with those of the Hadar humeri A.L. 333-107 and A.L. 288-1 (Table 21), one finds that one is once again able to group the early hominid specimens into large- and small-sized hominids. The three Sterkfontein humeri are all very similar in size to the A.L. 333-107 humerus and thus may be grouped together as the large-sized specimens, while the Lucy humerus (alone) is in the small group. The gross difference in size between the two samples is approximately 25% to 30%.

Hartwig-Scherer (1993) has compared the differences in size of all of the individual postcranial elements from the *A. afarensis* series, and has calculated a sexual dimorphism index of around 3.3 (or an average difference in size of approximately 30% within the sample). Thus, based on the size of individual elements alone, the Sterkfontein *A. africanus* upper limb material might be grouped with the larger sized individuals (in particular the 333 material) of the *A. afarensis* series.

Whilst several authors have raised the possibility that the extreme size differences observed between the A.L. 288-1L skeleton and the A.L. 333 sample may be so great as to preclude the two being from the same species (e.g. Senut, 1980; Hartwig-Scherer, 1993), at least two studies (Tobias, 1980; Reed et al., 1993) have indicated that the degree of sexual dimorphism (or size variation) within the *A. africanus* sample may be as great as that observed in an *A. afarensis* sample that includes A.L. 288-1. In addition, several recently recovered cranial and postcranial specimens from Sterkfontein Member 4 further indicate that the sexual dimorphism within *A. africanus* may be extreme. The possibility must again be raised that there are two species represented within the A.L. 333 / A.L. 288 series, a larger more ancient (and primitive?) species represented by the A.L. 333 series and a more gracile (and derived?) species represented by the A.L. 288 skeleton. One must then also consider this possibility for the Sterkfontein assemblage. However, this author would caution the use of size comparisons within the *A. afarensis* or *A.*

africanus series, since, at least for the former, the samples are not chronologically sympatric.

The extreme size variation observed between A.L. 288-1 and the A.L. 333 might not be representative of the sexual dimorphism of a population of early hominids but it could represent the potential size variation within a single species. Certainly a 30% size difference may even be found between the bones of two individual *Homo sapiens*, a species considered to be only "moderately" sexually dimorphic.

7.10.2

Discrete Morphological Features

In the present study, it was shown that morphological "packages" of features could be used to discriminate between extant hominoid species, but singular features are nearly useless, since overlap in variation occurs in almost every case. Unfortunately, as mentioned previously, the bone surface preservation from Hadar is poor. More

importantly, however, there are few comparable individual shoulder girdle fragments preserved between the two larger variants (A.L. 333 and Sterkfontein), making specific comparisons difficult. Nevertheless, we must consider whether the total shoulder girdle morphology of the Sterkfontein, A.L. - 333 and the A.L. 288-1 elements are different enough to preclude them belonging to a single species.

Certainly there are notable differences between the morphology of the A.L. 288-1 elements and the Sterkfontein specimens, but it is unclear whether these are purely allometric differences or whether they are differences related to variation in function. The Lucy scapula does not possess the pronounced costal glenoid margin notching that is present in the Sterkfontein scapulae, although this may be a product of lighter musculature of the small A.L. 288-1 hominid. Furthermore, the apparent shortening of the "neck" of the scapula in Lucy is not as great as in the two Sterkfontein specimens, but this may also be related to the small size of A.L. 288-1. The axilloglenoid angle

estimated for both Sts 7 and A.L. 288-1L (120°), a feature not related to size, indicates that the scapula was positioned on the thorax in an apelike rather than humanlike fashion in both these forms.

The humeral specimens present very similar morphology. The attachment areas and areas of passage for the biceps muscle are relatively enlarged in each of the specimens over the modern human condition, and are most similar to the degree of enlargement one observes in extant apes. The humeral head articular surfaces are rounded, indicating that the modern hominoid pattern of an extremely mobile and freely moving glenohumeral joint was developed in the early hominids. With the exception of the Lucy humerus, the humeri of all the early hominids are uniformly large and robust, being relatively more robust than one would expect to find in chimpanzees and orang-utans, the only extant comparables being heavily muscled humans and gorillas. Nevertheless, it seems that the Hadar specimens

are slightly more robust in the shaft than the Sterkfontein specimens.

The clavicle from Sterkfontein and the Hadar clavicles are very apelike in appearance, being anteroposteriorly flattened and possessing apparently reduced degrees of sigmoid curvature.

The Stw 431 clavicle is the most distinctive specimen examined since it possesses an enlarged deltoid crest that no other clavicular specimen exhibits.

Individually, all of the early hominid shoulder girdle specimens exhibit robust attachment areas for the ligamentous and muscular structures, at least to the degree that these may be interpreted from their attachment areas on bone. In particular, the soft tissue areas that appear most enlarged are those related to stabilisation of the joints (glenoid labrum, biceps brachii) and abduction, adduction and extension (biceps, serratus magnus, teres major, deltoid), all of which are movements which one would expect to be emphasised in a climber.

The Comparative Functional Morphology of the *A. afarensis* and *A. africanus* Samples

Comparisons of the functional morphology of the shoulder girdles of *A. afarensis* and *A. africanus* suggest that both species were capable of performing some form of upper limb dependent arboreal tree-climbing and/or suspensory behaviour. However, the differences in the morphology of the *A. africanus* and *A. afarensis* shoulder girdles from those of the extant apes, suggest that the climbing behaviour may not have been identical to that practised by modern apes, a conclusion also reached by Oxnard (1968b). Moreover, although both *A. afarensis* and *A. africanus* are apparently partially arboreally adapted, slow climbing hominids, this should not be interpreted as meaning that Lucy, the A.L. 333 group and the Sterkfontein australopithecines were practising the same form of arboreal locomotor behaviour.

The shoulder girdles of both *A. afarensis* and *A. africanus* are as close to the functional morphological adaptations that are observed in the shoulder girdles of extant apes as they are to those of modern humans, but not identical to either group. In particular the shoulder girdles of *A. africanus* appear in some ways to be more primitive in morphology, since they exhibit at least one probable symplesiomorphy, namely the short scapular neck. This morphology indicates possible common ancestry with a hominoid practising arboreal (or terrestrial) quadrupedal locomotor behaviour.

Current cladistic analyses, based primarily on craniodental evidence, suggest that *A. africanus* evolved from *A. afarensis* (Skelton et al., 1986; McHenry, 1991). If true, one may predict that when more complete scapular material of *A. afarensis* is recovered, it will present similar, or more primitive, morphology to the *A. africanus* scapulae. If *A. afarensis* is found to possess the more derived, modern hominoid scapular morphology, the proposed phyletic position of *A. africanus* as

the ancestor of the genus *Homo* would have to be re-evaluated (Johanson and White, 1979). In addition, the proposed position of *A. afarensis* as the direct common ancestor of *A. africanus* would be brought into question.

The question of whether the Sterkfontein Member 4 shoulder girdle elements and the large Hadar series may be interpreted as a single functional morphotype, or two closely related functional morphotypes remains unanswered, although there are undeniably gross similarities in the behaviour inferred from the morphology.

7.10.4

Comparison of the Functional Morphology of the Early Hominid Shoulder Girdle Elements Not Associated with *A. africanus* or *A. afarensis*

From the very limited number of shoulder girdle elements attributed to the robust australopithecine lineage (Omo 119-2718 and KNM-ER 739), it appears that the functional

morphology of this region is more similar to that observed in the gracile lineage of australopithecines than it is to at least some chronologically sympatric members of the genus *Homo*. Certainly the two humeral specimens examined here are very large and robust, exhibiting enlarged musculature and robust areas of attachment for the ligamentous structures that may be associated with stability in the shoulder girdle. Recent analysis of the shoulder girdle morphology of the approximately 1.7 million year old juvenile Nariokotome *Homo erectus* (= *H. ergaster*, Wood, 1992), KNM-WT 15000, indicates that this individual possesses relatively modern, humanlike shoulder girdle morphology (Leakey and Walker, 1988; Walker and Leakey, 1993). In contrast, the very fragmentary postcranial material of the partial skeleton O.H. 62, which has been attributed to *Homo habilis* and dates to around 1.8 mya (Johanson et al., 1987), presents tantalising evidence that the intermembral index of this species of early *Homo* may have been more apelike than humanlike (Johanson et al., 1987; Hartwig-Scherer, 1993). The O.H. 7 clavicle,

which is also attributed to this species of early *Homo*, adds little information to this debate although it stands out from the early hominid sample in being rounded and humanlike and by possessing a high degree of sigmoid curvature.

7.10.5

The Functional Morphology of the Early Hominid Shoulder Girdle and Inferred Relationships with the Evolution of Early Hominid Behaviour

The results of this study suggest that the emergence of modern human dependence on terrestrial bipedalism appears to have occurred over a considerable time. The *A. afarensis* and *A. africanus* shoulder girdle morphology reveals a stage of behaviour in which locomotor adaptations of the upper limb appear to be adapted to tree-climbing, while the lower limb is adapted to terrestrial bipedalism. A similar suggestion was put forward by Rose (1991, Figure 2) on the basis of the presumed locomotor repertoire of the hypothetical "prothominid". This study thus also supports the suggestion that the movement of early

hominids out of closed forests and open woodlands and into open grassland had most likely not yet occurred for at least the gracile australopithecines (Rodman and McHenry, 1980).

At the earliest appearance of African *Homo erectus* in the fossil record, as indicated by the Nariokotome partial skeleton, the upper limbs in this species approach the adaptive morphological level of modern humans, indicating that this may have been the stage at which hominids moved from arboreal dependency to pure terrestrial bipedalism. Nevertheless, even at this comparatively late stage of hominid evolution, certain areas of the lower limb morphology of this early species of *Homo* appear to reveal some features related to arborealism retained from an australopithecine ancestor (Leahey and Walker, 1988; Walker and Leahey, 1993).

It is therefore the opinion of this author that the evolution of early hominid locomotor behaviour is relatively clear in the evolution of the functional morphology of the shoulder girdle.

The earliest forms of australopithecine may be characterised by adaptations in their upper limbs to arboreal, suspensory lifestyles, a form of locomotion that might best be described as a "facultative climber". These australopithecines were most probably at least facultative terrestrial bipeds but their upper limb morphology indicates that they were capable of highly adept climbing. Models such as Rose's (1991, Figure 2) that predict the arboreal behaviour of australopithecines consuming approximately 26% of the time allocated to locomotion are, based on the results of this study, most likely too conservative.

The early East African robust australopithecines (*A. aethiopicus* and *A. boisei*) and possibly the earliest forms of *Homo* (in particular *Homo habilis*) may retain arboreal capability. At the emergence of African *Homo erectus*, the requirements for upper limb morphological adaptations to arboreal behaviour have apparently been lost, and this presumably indicates the first true adaptation to a total

dependency on a terrestrial, bipedal lifestyle in the hominid fossil record.

7.11

Conclusions

The present study is limited in several ways. Small sample sizes have been used for the osteometrics and there is considerable overlap of observed ranges for most of the quantitative features. The fragmentary nature of the fossil hominid shoulder girdle material often precludes comparison of features with both the modern and fossil samples. Nevertheless, many points discussed have relevance for the functional morphology of the early hominid shoulder girdle as well as for a consideration of relationships amongst fossil hominid taxa. As a whole the results support the hypothesis of many previous researchers who have examined the fossil hominid shoulder girdle material; namely, that the shoulder girdle of the gracile australopithecines is adapted for some forms of arboreal behaviour. In the opinion of this author, there can be no

doubt that at least *A. africanus*, whilst apparently adapted to tree-climbing, is also a capable biped. In addition, the observed shoulder morphologies of *A. afarensis* and *A. africanus* have been shown to be unique amongst known hominoid morphologies.

As Stern and Susman (1985) have noted

"many people find it intuitively difficult to accept the existence of an animal that spent a significant amount of time in the trees without being as adept as an ape and that also lived on the ground without being as quick and agile on two legs as humans. We find it equally difficult to conceive of such a stage having been averted by the human lineage"

It is this author's contention that the preponderance of evidence, from this study as well as almost every study of the functional morphology of other postcranial elements of the *A. afarensis* and *A. africanus* fossils, indicates that both of these species are behaviourally and structurally intermediate between forms that are entirely arboreally adapted and forms that are adapted to terrestrial bipedalism.

The results of the present analysis indicate that comparison of the shoulder girdle morphology of the middle Miocene hominoids with that of early hominids may prove productive. One should be able to isolate the most probable candidates for common ancestry with the early australopithecines whilst eliminating forms which possess scapular morphology that is too derived to have given rise to the *A. africanus* scapula. Nevertheless, when making predictions as to the probable form of locomotion of the common ancestor of the apes and *A. africanus*, it seems reasonable to eliminate the specialised forms of locomotion practised by extant apes.

An important result of the present study is that there are indications that the shoulder girdle morphology of the early hominids changed between the period 2.5 - 2.0 mya, changes almost certainly related to changes in locomotor behaviour. It may or may not be a coincidence that the apparent transition between the apelike morphology of the shoulder girdle of *A. africanus*

and the basically modern human shoulder girdle morphology, as exhibited by African *Homo erectus*, occurs at about the same time as, or slightly later than the first evidence for stone tool manufacture (2.4-2.5 mya) (Kuman, in press). Thus one might surmise that the morphological changes which indicate movement from a primarily arboreal to a terrestrial lifestyle might also be linked in some ways to complex tool manufacture and usage. Further researches into the restrictions that an apelike shoulder girdle morphology would have on frontal body manipulative behaviour are indicated.

The results of this study strengthen previous arguments that the gracile australopithecine shoulder girdle is adapted for arboreal locomotor behaviour. In particular, they support the conclusions of Senut (1978, 1980) that the shoulder girdle morphology of the gracile australopithecines indicate that they were generalist climbers that most probably spent a considerable amount of time in trees. However, the present investigation suggests that there is

strong evidence that the locomotor repertoire of the australopithecines was fundamentally different from those forms of locomotor behaviour practised by any extant hominoid species and thus strengthens the conclusions of Oxnard (1968b). In particular, the new specimens from Sterkfontein indicate that *A. africanus* most likely practised frequent arboreal, upper limb dependent behaviour that was functionally unique (if only because of its coexistence with bipedalism) compared to those practised by modern hominoids. The same was apparently true for the slightly more ancient species *A. afarensis*, although the fossil shoulder girdle material attributed to this species is very incomplete. Finally, if the few perceived differences in morphology between the shoulder girdle elements of *A. africanus* and *A. afarensis* prove to be typical of these forms, then the shoulder girdle may be found to be useful as a taxonomic indicator.

The results of this study have implications for the phylogenetic relationships of early hominids. If *A. africanus* is the early hominid

species that gave rise to the genus *Homo*, then the transition from apelike to humanlike shoulder girdle morphology appears to have occurred at some time before 2.0 mya. The earliest African *H. erectus* appears to possess a fundamentally modern human shoulder girdle morphology. Therefore, chronologically and phylogenetically, the most probable candidate for a morphology transitional between the australopithecine shoulder girdle morphology and that of African *H. erectus* is either *H. habilis*, or the proposed species *H. rudolfensis* (Wood, 1992). It remains to be seen whether one or both of these species represent the transitional phenotype, or whether both retain the more primitive australopithecine shoulder girdle morphology. The recovery of more hominid partial skeletons which are taxonomically attributable, in well-dated sediments in the 2.0 - 2.5 mya period, may resolve this question.

Finally, the robust australopithecine species also appear to possess adaptations in their shoulder girdle morphologies to arboreal behaviour. Although the fossil evidence is

admittedly paltry, the two humeral fragments attributed to robust australopithecines appear to suggest that this group retained the primitive shoulder girdle morphology of the gracile australopithecine lineage. This may indicate fundamental locomotor differences between these latest australopithecines and the chronologically sympatric species assigned to the genus *Homo*. If this proves to be the case with the recovery of more complete shoulder girdle material, then this anatomical region may prove useful in assigning taxonomic status to specimens where more than one species is found to be sympatric.

Reference List

Abe, K. (1964) On the coracoclavicular joint and its incidence. *Acta Anat. Nippon* 39, 227-231.

Aiello, L.C. (1981) *On analysis of shape and strength in the long bones of higher primates*, University of London: Ph.D. Thesis.

Aiello, L. and Dean, C. (1990) *An introduction to human evolutionary anatomy*, London: Academic Press.

Ashton, E.H., Healy, M.J.R., Oxnard, C.E. and Spence, T.F. (1965) The combination of locomotor features of the primate shoulder girdle by canonical analysis. *J. Zool* 147, 406-429.

Ashton, E.H. and Oxnard, C.E. (1963) The musculature of the primate shoulder girdle. *Trans. Zool. Soc. Lond.* 142, 49-66.

Ashton, E.H. and Oxnard, C.E. (1964) Locomotor patterns in primates. *Proc. Zool. Soc. Lond.* 142, 49-66.

Avis, V. (1962) Brachiation : the crucial issue for man's ancestry. *Southw. J. Anthropol.* 18, 199-148.

Bainbridge, D. and Tarazaga, S.G. (1956) A study of the sex differences in the scapula. *J. Royal Anthropol. Inst.* 86, 109

Basmajian, J.V. and Bazant, F.J. (1959) Factors preventing downward dislocation of the adducted shoulder joint. *J. Bone Joint Surg.* 41A, 1182

Basmajian, J.V. and De Luca, C.J. (1985) *Muscles alive. Their functions revealed by electromyography*, 5th edn. Baltimore: Williams and Wilkins Co..

Basmajian, J.V. and Latif, A. (1957) Integrated actions and functions of the chief

flexors of the elbow: a detailed
electromyographical analysis. *J. Bone Joint Surg.*
39A, 1106-1118.

Bass, W.A. (1971) *Human Osteology: A
laboratory and field manual*, Columbia, Mo.:
Missouri Archaeological Society.

Bass, W.A. (1979) *Human Osteology: a
laboratory and field manual*, 2nd edn.
Columbia, Mo.: Missouri Archaeological Society.

Bass, W.M. (1987) *Human Osteology: A
laboratory and field manual*, 3rd edn.
Columbia, Mo.: Missouri Archaeological society.

Bauer, W., Ropes, M.W. and Waine, H. (1940)
Physiology of articular structures. *Physiol. Rev.*
20, 273-312.

Bearn, J.G. (1961) an electromyographical
study of the trapezius, deltoid, pectoralis major,
biceps and triceps muscles, during static loading
of the upper limb. *Anat. Rec.* 140. 103-108.

Berge, C. (1984) Multivariate analysis of the pelvis for hominids and other extant primates: implications for the locomotion and systematics of the different species of australopithecines. *J. Hum. Evol.* 13, 555-562.

Berge, C. (1991) Quelle est la signification fonctionnelle du pelvis très large de *Australopithecus afarensis* (AL 288-1)? In: Coppens, Y. and Senut, B., (Eds.) *Origine(s) de la bipédie chez les hominides*, pp. 113-120. Paris: (Cahiers de Paléanthropologie), Editions du CNRS.

Berger, L.R. (1993) A preliminary estimate of the age of the Gladysvale australopithecine site. *Palaeont. Afr.* 30, 51-55.

Boaz, N.T. (1980) A hominoid clavicle from the Mio-Pleistocene of Sahabi, Libya. *Am. J. Phys. Anthrop.* 53: 49-54.

Bonnefille, R., Vicens, A. Buchet, G. (1987) Palynology, stratigraphy and palaeo-environments

of a Pliocene hominid site. *Palaeogeogr.*,
Palaeoclimatol., *Palaeoecol.* 60, 249-281.

Brace, C.L. (1979) Biological parameters and
Pleistocene hominid lifeways. In: Bernstein, I.S.
and Smith, E.O., (Eds.) *Primate ecology and human
origins: ecological influences on social
organization*, pp. 263-289. New York: Garland STPM
Press.

Broca, W (1878) as quoted by Hrdlicka, A.
(1942) The adult scapula: additional observations
and measurements. *Am. J. Phys. Anthropol.* 29:
364-415.

Broom, R. (1950a) *Finding the missing link*,
London: Watts and Co..

Broom, R. (1950b) The genera and species of
the South African fossil ape-man. *Am. J. Phys.
Anthropol.* 8, 1-14.

Broom, R., Robinson, J.T. and Schepers, G.W.H.
(1950) Sterkfontein ape-man, *Plesianthropus*.
Transv. Mus. Mem. 4, 1-117.

Broom, R. and Schepers, G.W.H. (1946) The
South African ape-men - the Australopithecinae.
Transv. Mus. Mem. 2.

Brown, F.H. and Feibel, C.S. (1988) 'Robust'
hominids and Plio-Pleistocene paleogeography of
the Turkana Basin, Kenya and Ethiopia. In: Grine,
F.E., (Ed.) *Evolutionary history of the 'robust'
australopithecines*, pp. 325-341. New York: Aldine
de Gruyter.

Brown, F.H., Harris, J., Leakey, R. and
Walker, A. (1985) Early *Homo erectus* skeleton from
west Lake Turkana. *Nature* 316, 788-792.

Cain, P.R., Mutschler, T.A., Fu, F.H. and Lee,
S.K. (1987) Anterior stability of the glenohumeral
joint: a dynamic model. *Am. J. Sports Med.* 15,
144

Campbell, B.G. (1966) *Human evolution: an introduction to man's adaptations*, Chicago: Aldine Publishing Company.

Cave, A.J.E. (1961a) The nature and morphology of the costoclavicular ligament. *J. Anat.* 95, 170-179.

Cave, A.J.E. (1961b) The nature and morphology of the costoclavicular ligament. *Ann. Med. Nav. Trop.* 62, 458-460.

Chadwick, P., J.A. Ferry, Schiller, A.L., Zarins, B. (1990) Histological studies of the glenoid labrum from fetal life to old age. *J. Bone Joint Surg.* 72 1344-1348.

Charles-Dominique, L. (1974) *Ecology and behaviour of nocturnal primates*, London: Duckworth.

Chivers, D.J. (1980) *Malayan Forest Primates*, New York: Plenum.

Chivers, D.J. (1984) Gibbons. In: All the Worlds Primates. Torstar, New York. 119-123.

Churchill S.E. and Trinkaus, E., (1990) Neandertal scapular glenoid morphology. *Am. J. Phys. Anthropol.* 83:147-160.

Ciochon, R.L. and Corruccini, R.S. (1976) Shoulder joint of Sterkfontein *Australopithecus*. *S. Afr. J. Sci.* 72, 80-82.

Ciochon, R.L. and Corruccini, R.S. (1977) The coraco-acromial ligament and projection index in man and other anthropoid primates. *J. Anat.* 124, 627-632.

Clarke, M.D., Sidles, J.A. and Matsen, M.D. (1989) The relationship of the glenohumeral joint capsule to the rotator cuff. *Clin. Orthopaedics Rel. Res.* 29-34.

Clarke, R.J. (1985) Early Acheulean with *Homo habilis* at Sterkfontein. In: Tobias, P.V., (Ed.)

Hominid evolution: past present and future, pp.
287-298. New York: Alan R. Liss.

Clarke, R.J. (1988) A new *Australopithecus*
cranium from Sterkfontein and its bearing on the
ancestry of *Paranthropus*. In: Grine, F.E., (Ed.)
Evolution of the 'robust' australopithecines, pp.
285-292. New York: Aldine de Gruyter.

Cockshott, W.P. (1958) Anatomical anomalies
observed in radiographs of Nigerians. *West Afr.*
Med. J. 7, 179-184.

Cockshot, W.P. (1979) The coracoclavicular
joint. *Diag. Rad.* 131, 313-316.

Codman, E.A. (1934) *The shoulder*, Boston:
Thomas Todd.

Cooke, H.B.S. (1963) Pleistocene mammal faunas
of Africa, with particular reference to southern
Africa. In Howell, F.C. and Bourliere, F. (eds)
African ecology and human evolution, Aldine,
Chicago, 65-116.

Coon, C.S. (1962) *The origin of races*. A.L. Knopf, New York.

Coppens, Y. (1975) La grande aventure paléontologique est-africaine. *Courrier CNRS* 16, Paris: 1693-1696.

Coppens, Y. and Howell, F.C. (1976) Mammalian faunas of the Omo group : distributional and biostratigraphical aspects. In: Coppens, Y., Howell, F.C., Isaac, G.L.I. and Leakey, R.E.F., (Eds.) *Earliest man and environments in the Lake Rudolf Basin*, pp. 177-192. Chicago: Chicago University Press.

Corruccini, R.S. and Clochon, R.L. (1976) Morphometric affinities of the human shoulder. *Am. J. Phys. Anthropol.* 45, 19-38.

Cvesen, J. and Nielsen, S. (1985) Stability of the shoulder joint: Cadaver study of stabilizing structures. *Acta Orthop. Scand.* 56, 149

Dart, R.A. (1925) *Australopithecus africanus* :
the ape-man of South Africa. *Nature* 115, 195-197.

Dart, R.A. (1959) *Adventures with the missing
link*, New York: Harper.

Darwin, C. (1859) *The origin of species by
means of natural selection*. John Murray, London.

Day, M.H., Leakey, R.E.F., Walker, A.C. and
Wood, B.A. (1976) New hominids from East Turkana,
Kenya. *Am. J. Phys Anthropol.* 45, 369-436.

Day, M.H. (1978) Functional interpretations of
the morphology of postcranial remains of early
African hominids. In: Jolly, C.J., (Ed.) *Early
hominids of Africa*, pp. 311-345. New York: St.
Martin's Press.

Day, M.H. (1985) Hominid locomotion - from
Taung to Laetoli footprints. In: Tobias, P.V.,
(Ed.) *Hominid locomotion: past, present and
future*, pp. 115-127. New York: Alan R. Liss.

Day, M.H. (1986) *Guide to fossil man*, London: Cassels.

Day, M.H. and Leakey, R.E.F. (1974) New evidence for the genus *Homo* from East Rudolf Kenya. *Am. J. Phys. Anthropol.* 41, 367-380.

Day, M.H. (1991) Bipedalism and prehistoric footprints . In: Coppens and B. Senut eds. *Origine(s) de la bipedie chez les hominides*, Cah. Paleoanthrop. CNRS: Paris, 199-214.

de Sousa, O.M. Vitti, M. (1966) Estudio electromiografico de los musculos adductores largo y mayor. *Arch. Mex. Anat.* 7, 52-53.

del Valle, D. and Giordano, A. (1943) Síndrome doloroso cervico-braquial originada por articulacion coracoclavicular -operacion - curacion. *Revista Argentina-Norte Americana de Ciencias Medicas* 1, 687-694.

Delmas, A. (1972) L'homme devant
l'hominisation. *quaderni di Anatomia Practica*
XXVIII, 22-56.

Delson, E. (1984) Cercopithecoid biochronology
of the African Plio-Pleistocene: correlation among
eastern and southern hominid bearing localities.
Cour. Forsch. Inst. Senckenberg 69, 199-218.

Delson, E. (1988) Chronology of the South
African australopithecine site units. In: Grine, F.E.,
(Ed.) *Evolutionary history of the 'robust'*
australopithecines, pp. 317-324. New York: Aldine
de Gruyter.

DePalma, A.F., Cooke, A.J. and Prabhaker, M.
(1967) The role of subscapularis in recurrent
anterior dislocations of the shoulder. *Clin.*
Orthop. 54, 35

DePalma, A.F. (1983) *Surgery of the shoulder*,
Philadelphia: J.B. Lippincott.

Dobzhansky, T. (1937) *Genetics and the origin of species*, New York: Columbia University Press.

Dorsey, R. (1887) as quoted by Hrdlicka, A. (1942) The adult scapula: additional observations and measurements. *Am. J. Phys. Anthropol.* 29: 364-415.

Doyle, W.J. (1994) Functionally induced alteration of adult scapular morphology. *Acta. anat.* 99, 173-177.

Doyle, W.J., Siegal, M.I. and Kimes, K.R. (1980) Scapular correlates of muscle morphology in *Macaca mulatta*. *Acta. anat.* 106, 493-501.

Edgerton, R.B. (1968) *Like lions they fought*. Macmillan, Great Britain.

Eickhoff, R. (1988) Origin of bipedalism - when, why, how, and where. *S. Afr. J. Sci.* 84, 486-488.

Erikson, G.E. (1952) Locomotor types and body proportions in the New World monkeys. *Anat. Rec.* 112, 326

Erikson, G.E. (1963) Brachiation in New World monkeys and in anthropoid apes. *Symp. Zool. Soc. Lond.* 10, 135-164.

Evans, F.G. (1973) Mechanical properties of bone. Thomas, Springfield.

Fahlström, G. (1981) The Glenohumeral Joint in Man: an anatomic-experimental and archaeo-osteological study on joint function. *Ossa* 8, 1-

Feibel, C.S., Brown, F.H. and McDougall, I. (1989) Stratigraphic context of fossil hominids from the Omo Group deposits: Northern Turkana Basin, Kenya and Ethiopia. *Am. J. Phys. Anthropol.* 78, 595-622.

Fernando-Ballesteros, M.L., Buchtall, F., Rosenfalck, P. (1964) The pattern of muscular

activity during the arm swing of natural walking.

Acta Physiol Scand. 63, 296-310.

Ferrari, D.A. (1990) Capsular ligaments of the shoulder. *Am. J. Sports Med.* 18, 20-24.

Fischer, L., Vuillard, P. and Blanc, J.F.

(1971) L'articulation coracoclaviculaire. *Lyon Med.* 225, 1257-1260.

Fleagle, J.G. (1988) *Primate Adaptation and Evolution*, San Diego, California: Academic Press.

Fleagle, J.G., Stern, J.T., Jungers, W.L.,
Susman, R.L., Vangor, A.K. and Wells, J.P. (1981)
-Climbing : a biomechanical link with brachiation
and with bipedalism. *Symp. Zool. Soc. Lond.* 48,
359-375.

Flower, W.H. (1870) *Osteology of the mammalia*,
London:

Frankel, V.H. & Nordin, M. (1980) Basic biomechanics of the skeletal system. Lea & Febiger, Philadelphia.

Frassetto, F. (1903) Sulla genesi del foro coracoideo. *Bul. Mus. Zool. & Anat.* XVIII, 1-9.

Frost, H.M. (1973) *Bone modelling and skeletal modelling errors*. Charles C. Thomas, Springfield, Ill.

Galdikas, B.M.F. (1985) Subadult male orang-utan sociality and reproductive behaviour at Tanjung. *Am. J. Primatol.* 8: 87-99.

Gardner, E.D. (1950) Physiology of moveable joints. *Physiol. Rev.* 30, 127-176.

Gardner, E., Gray, D.J. and O'Rahilly, R. (1969) *Anatomy: a regional study of human structure*, 3rd edn. Philadelphia: Saunders Co..

Gerber, C., Terrier, F., Zehnder, R. and Garz, R. (1987) The subcoracoid space. An anatomic study. *Clin. Orthop. Rel. Res.* 215, 132-138.

Ghiglieri, M. P. (1984) *The chimpanzees of Kibale forest*. New York: Columbia University Press.

Gomberg, D.N. and Latimer, B. (1984) observations on the transverse tarsal joint of *A. afarensis* and some comments on the interpretation of behaviour from morphology. *Am. J. Phys. Anthropol.* 63, 164.

Goodall, J. (1965) Chimpanzees of the Gombe Stream Reserve. In: DeVore, (Ed.) *Primate Behavior*, pp. 425-473. New York: Rinehart and Winston.

Gowland, W.P. (1915) Preliminary note on diarthrodial articulation between clavicle and the coracoid. *J. Anat. Physiol.* 49, 187-189.

Gradoyevitch, W.P. (1939) Coracoclavicular joint. *J. Bone Joint Surg.* 21, 918-920.

Grausz, H.M., Leakey, R.E.F., Walker, A.C. and Ward, C.V. (1988) Associated cranial and postcranial bones of *Australopithecus boisei*. In: Grine, F.E., (Ed.) *Evolutionary history of the robust australopithecines*, pp. 127-132. New York: Aldine de Gruyter.

Graves, W.W. (1921) The types of scapulae: a comparative study of some correlated characters in human scapulae. *Am. J. Phys. Anthrop.* IV, 111-128.

Gregory, W. K. (1928) Were the ancestors of man brachiators?. *Proc. Am. Phil. Soc.* 67, 129-150.

Gruber, W. (1861) Die oberschulterhackenschleimbeutel (Bursae mucosae supracoracoideae). *Memoire de l'Academie Imperiale des Sciences, St. Petersburg* 3, 1-28 (cited by Hrdlicka, 1942).

Hall, M.C. (1965) *The locomotor system: Functional anatomy*, Springfield, Illinois: Thomas.

Harcourt, A.H. (1984) Gorillas. In: *All the Worlds Primates*. Torstar, New York, 137-143.

Harryman, D.T., Sidles, J.A., Clark, J.M., McQuade, K.J., Gibb, T.J. and Matsen, F.A. (1990) Translation of the humeral head on the glenoid with passive glenohumeral motion. *J. Bone Joint Surg.* 72A, 1334-1343.

Hartwig-Scherer, S. (1993) Body weight prediction in early fossil hominds: towards a taxon-"independent" approach. *Am. J. Phys. Anthropol.* 92, 17-36.

Hay, R.L. (1976) *Geology of Olduvai Gorge*, pp. 1-203. Berkeley: Univ. of California Press.

Heilm, J.L. (1979) *700 000 siècles d'histoire humaine*, Paris: Eyrolles.

Henke, W. (1863) *Handbuch der anatomie und mechanik der gelenke*. Wintersche Verlag, Leipzig und Heidelberg.

Hill, W.C.O (1953) *Primates: comparative anatomy and taxonomy*, The University Press, Edinburgh.

Hotton, F., Leguebe, A. and Louryan, S. (1984) L'acquisition de la marche bipède, témoin de la l'hominisation. *Medica Physica* 7, 121-126.

Howell, F.C. (1978) Hominidae. In: Maglio, V.J. and Cooke, H.B.S., (Eds.) *Evolution of African mammals*, pp. 154-248. Cambridge: Harvard University Press.

Howell, S.M., Imobersteg, A.M., Seger, D.H. and Marone, P.J. (1986) Clarification of the role of the supraspinatus muscle in shoulder function. *J. Bone Joint Surg.* 68A, 398

Howell, S.M., Galinet, B.J., Renzi, A.J. and Marone, P.J. (1988) Normal and abnormal mechanics of the Glenohumeral joint in the horizontal plane. *J. Bone Joint Surg.* 70A, 227-232.

Howell, S.M. and Galinet, B.J. (1989a) The glenoid-labral socket. *Clin. Orthop. Rel. Res.* 243, 122-125.

Howell, S.M. and Galinet, B.J. (1989b) The glenoid-labral socket: a constrained articular surface. *Clin. Orthop.* 243, 122-125.

Hrdlicka, A. (1907) *Anatomy. Handbook of the American Indian*. Bureau of American Ethnology, Bull. 30, Part 1. Washington D.C., Government Printing Office.

Hrdlicka, A. (1910) Contributions to the anthropology of the Central and Smith Sound Eskimo. *Anthrop. Papers Amer. Mus. Nat. Hist.*, N. Y.

Hrdlicka, A. (1931) Anthropology of the Sioux. *Am. J. Phys. Anthropol.* 16: 123-166.

Hrdlicka, A. (1932) The principal dimensions, absolute and relative, of the humerus in the white race. *Am. J. Phys. Anthropol.* 16: 431-450.

Hrdlicka, A. (1937) Human typogeny. *Proc. Am. Phil. Soc.* LXXVIII, 79-95.

Hrdlicka, A. (1942) The adult scapula: additional observations and measurements. *Am. J. Phys. Anthrop.* 29: 364-415.

Hughes, H. (1952) the factors determining the direction of the canal for nutrient artery in the long bones of mammals and birds. *Acta. Anat.* 15: 261-280.

Hunt, K. (1990) Implications for chimpanzee positional behavior for the reconstruction of early hominid locomotion and posture. *Am. J. Phys. Anthrop.* 81, 242

Hunt, K. (1993) The mosaic lifeways of our australopithecine ancestors: piecing in some fragments from the world of chimpanzees. *Anthro Quest.* 47, 3-6.

Inman, V.T., Saunders, J. and Abbot, L.C.
(1944) Observations on the function of the
shoulder joint. *J. Bone Joint Surg.* 26, 1-29.

Inskeep, R.R. (1978) The Bushman in prehistory.
In P.V. Tobias ed. *The bushman*. Human & Rosseau,
Cape Town.

Jaluvka, V. (1956) Articul^{us}
coracoclavicularis. *Ceskoslovenská Morfologie* 4,
99-107 (cited by Jaluvka, 1959).

Jaluvka, V. (1957) Über die schleimbeutel und
faserknopelige berührungsflächen in der Umgebung
des ligamentum coracoclaviculare. *Scripta Medica
Brunesis et Olomucensis* 30, 221-228 (cited by
Jaluvka, 1959).

Jaluvka, V. (1959) Rentengenologicka studie o
korakoklavikulárním kloubu. *Ceskoslovenska
Rentgenologie* 13, 176-180.

Jelbert, M. (1970) A pilot study of the incidence and distribution of certain skeletal and soft tissue abnormalities. *S. Afr. J. Med.* 16, 37-40.

Jenkins, F.A., Dombrowski, P.J. and Gordon, E.P. (1978) Analysis of the shoulder in brachiating spider monkeys. *Am. J. Phys. Anthrop.* 48, 65-76.

Jit, I. and Kaur, H. (1986) Rhomboid fossa in the clavicles of North Indians. *Am. J. Phys. Anthrop.* 70, 97-103.

Johanson, D.C., White, T.D. and Coppens, Y. (1978) A new species of the genus *Australopithecus* (Primate : Hominidae) from the Pliocene of Eastern Africa. *Kirtlandia* 28, 1-14.

Johanson, D.C., White, T.D. and Coppens, Y. (1980) New discoveries of Pliocene hominids and artifact in Hadar : Expedition to Ethiopia (fourth and fifth field season 1975-1977). *J. Hum. Evol.* 9, 583-585.

Johanson, D.C., Taieb, M. and Coppens, Y.
(1982) Pliocene hominids from the Hadar Formation,
Ethiopia (1973-1977) : stratigraphic, chronologic
and paleoenvironmental contexts, with notes on
hominid morphology and systematics. *Am. J. Phys.
Anthrop.* 57, 373-402.

Johanson, D.C., Masao, F.T., Eck, G., White,
T.D., Walter, R.C., Kimbel, W.H., Asfaw, B.,
Manega, P., Ndessokia, P. and Suwa, G. (1987) New
partial skeleton of *Homo habilis* from Olduvai
Gorge, Tanzania. *Nature* 327, 205-209.

Johanson, D.C. and White, T.D. (1979) A
systematic assessment of early African hominids.
Science 203, 321-330.

Johnson, L.L. (1987) The shoulder joint.
Clin. Orthop. 223, 113-125.

Jolly, A. (1966) *The evolution of Primate
behaviour*, New York: Macmillan.

Jolly, A. (1972) *The evolution of Primate behaviour*, New York: Macmillan.

Jolly, A. (1985) *The evolution of primate behaviour*. Macmillan Publishing, New York.

Jolly, C.J. (1970) The seed-eaters : a new model of hominid differentiation based on baboon analogy. *Man* 5, 1-26.

Jungers, W.L. (1982) Lucy's limbs: skeletal allometry and locomotion in *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 60, 279-317.

Jungers, W.L. (1988a) New estimates of body size in australopithecines. In: Grine, F.E., (Ed.) *Evolutionary history of the "robust" australopithecines*, pp. 115-126. New York: Aldine de Gruyter.

Jungers, W.L. (1988b) Lucy's length : stature reconstruction in *Australopithecus afarensis* (A.L. 288-1) with implications for other small-bodied hominids. *Am. J. Phys. Anthropol.* 76, 227-231.

Jungers, W.L. and Stern, J.T. (1983) Body proportions, skeletal allometry and locomotion in the Hadar hominids. A reply to wolpoff, J. *Hum. Evol.* 12: 673-684.

Kamon, E. (1966) Electromyography of static and dynamic postures of the body supported on the arms. *J. Appl. Physiol.* 21, 1611-1618.

Kajava, Y. (1924) Scapula scaphoidea. *Hels.* 12, 1-60.

Kapandji, I.A. (1982) *The physiology of joints*, Edinburgh: Churchill Livingstone.

Kaur, H. and Jit, I. (1991) Brief Communication: coracoclavicular joint in Northwest indians. *Am. J. Phys. Anthrop.* 85, 457-460.

Keats, T.E., Teeslink, R., Diamond, A.E. and Williams, J.H. (1966) Normal axial relationships of the major joints. *Radiology* 87, 904-907.

Keith, A. (1923) Man's posture: its evolution and disorders. *Brit. Med. J.* 1, 669-672.

Kimbel, W.H., White, T.D. and Johanson, D.C.
(1984) Cranial morphology of *Australopithecus afarensis*: A comparative study based on a composite reconstruction of the adult skull. *Am. J. Phys. Anthropol.* 64, 337-388.

Kimbel, W.H., White, T.D. & Johanson, D.C.
(1988) Implications of KNM-WT 17000 for the evolution of "robust" australopithecus. In: Grine, F.E., (Ed.) *The evolutionary history of the 'robust' australopithecines*, pp. 259-268. New York: Aldine De Gruyter.

Kimes, K.R., Siegel, M.I. and Doyle, W.J.
(1979) Functional modification of the scapula by compressive muscles in *Papio cynocephalus*. *Acta anat.* 104, 414-420.

Kimes, K.R., Siegel, M.I. and Doyle, W.J.
(1980) A comparison of the functional modification

of the scapula by compressive forces in *Macaca fascicularis* and *Papio cynocephalus*. *Acta. anat.*

Knussman, R. (1967) Humerus, ulna and radius der Simiae. *Bib. Primat.* Basel, S. Karger. 1-399.

Krahl, V.E. (1944) An apparatus for measuring the torsion angle in long bones. *Science* 99, 498

Kuman, K. (in press) The archaeology of Sterkfontein: Past and Present. *J. Hum. Evol.*

Lacroix, P. (1951) *The organisation of bones*, London: Churchill.

Lane, A.W. (1886) Some points on the physiology and pathology of the changes produced by pressure on the bony skeleton of the trunk and shoulder girdle. *Guy's Hosp. Rep.* 38, 321-434.

Lane, A.W., Poland, J. and Dunn, L.A. (1887) Abnormalities observed in the dissecting room of Guy's Hospital. *Guy's Hosp. Rep.* 29, 399-412.

Larson, S.G. (1988) Subscapularis function in gibbons and chimpanzees : implications for interpretation of humeral head torsion in hominoids. *Am. J. Phys. Anthropol.* 76, 449-462.

Larson, S.G. and Stern, J.T. (1986) The scapulohumeral muscles in the chimpanzee during reaching and 'arboreal' locomotion. *Am. J. Anat.* 176, 171-190.

Larson, S.G. and Stern, J.T. (1989) Role of supraspinatus in the quadrupedal locomotion of vervets (*Cercopithecus aethiops*) ; implications for interpretation of humeral morphology. *Am. J. Phys. Anthropol.* 79, 369-377.

Latimer, B. (1991) Locomotor adaptations in *Australopithecus afarensis* : the issue of arboreality. In: Anonymous, (Ed.) *Origin(s) de la Bipédie chez les hominides*, pp. 169-176. Paris: Colloque International de la Fondation Singer-Polignac.

Le Gros Clark, W.E. (1971) *The antecedents of man*, 3rd ed. University Press, Edinburgh.

Leakey, L.S.B. (1960) Recent discoveries at Olduvai Gorge. *Nature* 188, 1050-1052.

Leakey, L.S.B., Tobias, P.V. and Napier, J.R. (1964) A new species of the genus *Homo* from Olduvai Gorge. *Nature* 202, 7-9.

Leakey, R.E.F. (1972) Further evidence of Lower Pleistocene hominids from East Rudolf. *Nature* 231, 241-245.

Leakey, R.E.F. (1973) Further evidence of Lower Pleistocene hominids from East Rudolf, Northern Kenya. *Nature* 242, 170-173.

Leakey, R.E.F. (1976) New hominid fossil from the Koobi Fora Formation in Northern Kenya. *Nature* 261: 547-576

Leakey, R.E.F., Mungai, J.M. and Walker, A.
(1971) New australopithecines from East Rudolf,
Kenya. *Am. J. Phys. Anthropol.* 35, 175-186.

Leakey, R.E.F., Mungai, J.M. and Walker, A.C.
(1972) New australopithecines from East Rudolf,
Kenya (II) *Am. J. Phys. Anthropol.* 36, 235-251.

Leakey, R.E.F. and Walker, A. (1988) New
Australopithecus boisei specimens from East and
West Turkana, Kenya. *Am. J. Phys. Anthropol.* 76,
1-24.

Leakey, R.E.F., Walker, A., Ward, C.V. and
Grausz, H.M (1989) A partial skeleton of a gracile
hominid from the Upper Burgi Member of the Koobi
Fora Formation, East lake Turkana, Kenya. *Proc.*
2nd Int. Cong. of Hum. Pal. 170-172.

Lewis, J.J. (1959) The coraco-clavicular
joint. *J. Anat.* 93, 295-303.

Livon, M. (1879) *De l'omoplate et de ses indices de largeur dans les races humaines*, Paris (cited by Senut, 1978)

Lockhart, R.D., G.F. Hamilton, and F.W. Fyfe (1959) *Anatom of the Human Body*. Faber and Faber, London.

Longia, G.S., Agarwal, A.K. Thomas, R.J., Jain, P.N., and Saxena, S.K. (1982) Metrical study of rhomboid fossa of clavicles. *Anthrhopol. Anz.* 40: 111-115.

Lovejoy, C.O. (1974) The gait of *Australopithecus*. *Yrbk. Phys. Anthropol.* 17, 147-161.

Lovejoy, C.O. (1976) *The locomotor skeleton of basal pleistocene hominids*, UISPP IX congress Nice colloque IV, 145-176.

Lovejoy, C.O. (1978) A biomechanical review of the locomotor diversity of early hominids. In:

Jolly, C.J., (Ed.) *Early hominids of Africa*, pp. 403-429. New York: St. Martin's Press.

Lovejoy, C.O. (1981) The origin of man. *Science* 23, 341-350.

Lovejoy, C.O., Johanson, D.C. and Coppens, Y. (1982a) Elements of the axial skeleton recovered from the Hadar formation. *Am. J. Phys. Anthropol.* 57, 631-635.

Lovejoy, C.O., Johanson, D.C. and Coppens, Y. (1982b) Hominid upper limb bones recovered from the Hadar formation : 1974-1977 collections. *Am. J. Phys. Anthropol.* 57, 637-650.

Macalister (1867) as quoted by Hrdlicka, A. (1942) The adult scapula: additional observations and measurements. *Am. J. Phys. Anthropol.* 29: 364-415.

MacGregor, L. (1936) Rotation of the shoulder, a critical inquiry. *Brit. J. Surg.* 24, 425-438.

Mackinnon, J. (1974) The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). Anim. Behav. 22, 3-74.

Maglio, V.J. & Cooke, H.B.S. (1978) *Evolution of African Mammals*. Cambridge, Harvard Univ. Press.

Maki, S. and Gruen, T. (1976) Anthropometric studies of the gleno-humeral joint. Trans. Orthop. Res. Soc. 1, 173

Martin, C.P. (1922) A note on the movements of the shoulder joint. Brit. J. Surg. 20, No. 77, 61-66.

Martin, R. (1928) *Lehrbuch der Anthropologie*, 2nd edn. Jena: Gustav Fischer.

Martin, R. and Saller, K. (1957) *Lehrbuch der Anthropologie*, 3rd edn. Stuttgart: Gustav Fischer.

McHenry, H.M. (1973) Early hominid humerus from East Rudolf, Kenya. *Science* 180, 739-741.

McHenry, H.M. (1974) How large were the australopithecines?. *Am. J. Phys. Anthrop.* 40, 329-340.

McHenry, H.M. (1978) Fore- and hind-limb proportions in Plio-Pleistocene hominids. *Am. J. Phys. Anthrop.* 49, 15-22.

McHenry, H.M. (1986) The first bipeds : a comparison of the *A. afarensis* and *A. africanus* postcranium and implications for the evolution of bipedalism. *J. Hum. Evol.* 15, 177-191.

McHenry, H.M. (1988) New estimates of body weight in early hominids and their significance to encephalization and megadontia in "robust" australopithecines. In: Grine, F.E., (Ed.) *Evolutionary history of the "robust" australopithecines*, pp. 133-148. New York: Aldine de Gruyter.

McHenry, H.M. (1991) First steps? Analyses of the postcranium of early hominids. In: Coppens, Y. and Senut, . (Eds.) *Origine(s) de la bipédie chez les hominidés*, pp. 133-142. Paris: (Cahiers de Paléanthropologie), Editions du CNRS.

McHenry, H.M. and Skelton, R.R. (1985) Is *Australopithecus africanus* ancestral to Homo?. In: Tobias, P.V., (Ed.) *Hominid Evolution: Past, Present and Future*, pp. 221-226. New York: Alan R. Liss.

McHenry, H.M. (1992) Body size and proportions in early hominids. *Am. J. Phys. Anthropol.* 87: 407-431.

McKee, J.K. (1991) Palaeo-ecology of the Sterkfontein hominids: a review and synthesis. *Palaeont. Afr.* 28, 41-51.

McKee, J.K. (1993) The faunal age of the Taung hominid deposit. *J. Hum. Evol.* 25, 363-376.

McKee, J.K., Thackeray, J.F. and Berger, L.R.
(1994) Faunal assemblage seriation of Southern
African Pliocene and Pleistocene fossil deposits.
Am. J. Phys. Anthrop. (In Press)

Miller, R.A. (1932) Evolution of the pectoral
girdle and forelimb in the primates. *Am. J. Phys.
Anthrop.* 17, 1-56.

Mittermeier, R.A. and Fleagle, J.G. (1976) The
locomotor and postural repertoires of *Ateles*
geoffroyi and *Colobus guereza*, and a reevaluation
of the locomotor category semibrachiation. *Am. J.
Phys. Anthrop.* 45, 235-256.

Mivart, S.G. (1868) On the appendicular
skeleton of the primate. *Phil. Tr. Lond.* 157,
301-306. (cited by Hrdlicka, 1942).

Montagu, M.F. (1960) *An introduction to
physical anthropology*, 3rd edn. Springfield,
Illinois: Thomas.

✓
McKee, J.K., Thackeray, J.F. and Berger, L.R.
(1994) Faunal assemblage seriation of Southern
African Pliocene and Pleistocene fossil deposits.
Am. J. Phys. Anthrop. (In Press)

Miller, R.A. (1932) Evolution of the pectoral
girdle and forelimb in the primates. *Am. J. Phys.
Anthrop.* 17, 1-56.

Mittermeier, R.A. and Fleagle, J.G. (1976) The
locomotor and postural repertoires of *Ateles*
geoffroyi and *Colobus guereza*, and a reevaluation
of the locomotor category semibrachiation. *Am. J.
Phys. Anthrop.* 45, 235-256.

Mivart, S.G. (1868) On the appendicular
skeleton of the primates. *Phil. Tr. Lond.* 157,
301-306. (cited by Hrdlicka, 1942).

Montagu, M.F. (1960) *An introduction to
physical anthropology*, 3rd edn. Springfield,
Illinois: Thomas.

Montgomery, G.D. (1988) Rhythmical man : an alternative hypothesis to ape-human evolution. *Speculations in Science and Technology* 11, 153-159.

Moore, R.D. and Ranner, R.R. (1957) Coracoclavicular joint. *Am. J. Roentgenol* 78, 86-88.

Napier, J. (1963) Brachiation and Brachiators. In: Napier, J. and Barnicot, N.A., (Eds.) *The primates*, pp. 183-196. Symp. Zool. Soc. Lond..

Napier, J. (1970) *The roots of mankind*, London: G. Allen and Unwin Ltd..

Napier, J.R. (1963) The locomotor functions of hominids. In: S.L. Washburn, (Ed.) *Classification and human evolution*, pp. 178-189. Chicago: Aldine.

Napier, J.R. (1964) The evolution of bipedal walking in the hominids. *Arch. Biol. (Liège)* 75, 673-635.

Napier, J.R. (1967) Evolutionary aspects of primate locomotion. *Am. J. Phys. Anthropol.* 27, 333-342.

Napier, J.R. and Napier, P.H. (1985) *The natural history of the primates*, Cambridge, Mass.: MIT Press.

Nutter, P.D. (1941) Coracoclavicular articulations. *J. Bone Joint Surg.* 23, 177-179.

Ohnsorge, K. (1932) Die bedeutung der oberarmauswärtswröller für die hebung des armes in der frontalebene. *Zeitschrift für orthopedische chirurgie*, 58 (1), 382-389.

Oikawa, M. and Hatafuku, Y. (1970) Statistical observations of the coracoclavicular joint. *Rinsho Hosha* 15, 516-517.

Oliver, G. (1976) The stature of *Australopithecus*. *J. Hum. Evol.* 5, 529-534.

Olivier, G. (1951) Anthropologie de la
clavicule III La clavicule du Français. *Bull. Soc.
Anthrop.* 2, 121-157.

Olson, T.R. (1981) Basicranial morphology of
the extant hominoids and Pliocene hominids: the
new material from the Hadar Formation, Ethiopia
and its significance in early human evolution and
taxonomy. In: (C.B. Stringer ed) *Aspects of Human
Evolution*, pp. 99-128. London, Taylor and Francis.

Olson, T.R. (1985) Cranial morphology and
systematics of the Hadar formation hominids and
Australopithecus africanus. In: Delson, E., (Ed.)
Ancestor : the hard evidence, pp. 102-119. New
York: Alan Liss.

Oxnard, C.E. (1963) Locomotor adaptations in
the primate forelimb. *Am. J. Phys. Anthrop.* 26,
219-240.

Oxnard, C.E. (1967a) Aspects of the mechanical
efficiency of the scapula in some primates. *Anat.
Rec.* 157, 296

Oxnard, C.E. (1967b) The functional morphology of the primate shoulder as revealed by comparative anatomical, osteometric and discriminant function techniques. *Am. J. Phys. Anthropol.* 26, 219-240.

Oxnard, C.E. (1968a) A note on the Olduvai clavicular Fragment. *Am. J. Phys. Anthropol.* 29, 429-432.

Oxnard, C.E. (1968b) A note on the fragmentary Sterkfontein scapula. *Am. J. Phys. Anthropol.* 28, 213-218.

Oxnard, C.E. (1968c) The architecture of the shoulder in some mammals. *J. Morph.* 126, 249-290.

Oxnard, C.E. (1969) Evolution of the human shoulder : some possible pathways. *Am. J. Phys. Anthropol.* 30, 319-332.

Oxnard, C.E. (1972) Functional morphology of primates : some mathematical and physical methods. In: Tuttle, R.H., (Ed.) *Functional and*

evolutionary biology of primates, pp. 305-336.

Chicago: Aldine-Atherton.

Oxnard, C.E. (1973a) *Form and pattern in human evolution*, Chicago: University of Chicago Press.

Oxnard, C.E. (1973b) Functional inferences from morphometrics : problems posed by uniqueness and diversity among primates. *Syst. Zool.* 22, 409-424.

Oxnard, C.E. (1975) The place of australopithecines in human evolution : grounds for doubt?. *Nature* 258, 389-395.

Oxnard, C.E. (1976) *The morphological-behavioural interface in extant primates: some implications for systematics and evolution.*, New York: Viking Fund Publications in Anthropology, Wenner-Gren Foundation for Anthropological Research.

Oxnard, C.E. (1984) *The order of man*, New Haven: Yale University Press.

Oxnard, C.E., Crompton, R.H. and Lieberman, S.S. (1990) *Animal lifestyles and anatomies: the case of the prosimian primates*, St. Louis: University of Washington Press.

Oxnard, C.E., German, R., Francoise-K, J. and Lessertisseur, J. (1981) A morphometric study of limb proportions in leaping prosimians. *Am. J. Phys. Anthropol.* 54, 421-430.

Oxnard, C.E. and Neely, P.M. (1969) An analysis of certain dimensions of the primate shoulder by neighborhood limited classification. *J. Morph.*

Parker, S.T. (1987) A sexual selection model for hominid evolution. *Hum. Evol.* 2, 235-253

Parsons, F.G. (1898a) The muscles of mammals with special reference to human myology. *J. Anat. Physiol.*, Lond. 32, 428-450.

Parsons, F.G. (1898b) The joints of mammals compared with those of man. *J. Anat. Physiol.* 34, 41-68.

Parsons, F.G. (1916) as quoted by Hrdlicka, A. (1942) The adult scapula: additional observations and measurements. *Am. J. Phys. Anthropol.* 29: 364-415.

Partridge, T.C. (1982) The chronological positions of the fossil hominids of southern Africa. *Proc. Cong. Int. de Pal. Humaine* 2, 617-675.

Partridge, T.C. and Watt, I.B. (1991) the stratigraphy of the Sterkfontein hominid deposit and its relationship to underground cave system. *Palaeontologia Afr.* 28, 35-40

Peat, M. (1986) Functional anatomy of the shoulder complex. *Phys. Therapy* 99, 1855 - 1865

Pickford, M., Johanson, D.C., Lovejoy, C.O., White, T.D. and Aronson, J.L. (1983) A hominid

humeral fragment from the Pliocene of Kenya. *Am. J. Phys. Anthrop.* 60, 337-346.

Pilbeam, D. (1972) *The ascent of man*, New York: MacMillan.

Pillay, V.K. (1967) The coraco-clavicular joint. *Singapore Med. J.* 8, 207-213.

Poirier, P. (1890) La clavicule et ses articulations, bourses sèreuses des ligaments costoclaviculaire trapezoïde et conoïde. *J. Anat. Physiol* 26, 81-103 (quoted by Hrdlicka, 1942).

Poirier, P. (1911) *Traité d'anatomie humaine*, Paris: P.Charpy & Nicolas (cited by Hrdlicka, 1942).

Pondé, A. and Silveira, J. (1938) Estudos radiolôgicos da articulacao coracoclavicular. *J. Clin.* 22, 325-328.

Poppen, N.K. and Walker, P.S. (1976) Normal and abnormal motion of the shoulder. *J. Bone Joint Surg.* 58A, 195-201.

Preuschoft, H. (1966) Functional anatomy of the upper extremity. In: Bourne, (Ed.) *The chimpanzee*, pp. 34-120. Basel: Karger.

Preuschoft, H. (1971) Body posture and mode of locomotion in early Pleistocene hominids. *Folia primatol.* 14, 209-240.

Preuschoft, H. (1973) Functional anatomy of the upper extremity. In: Bourne, G.H., (Ed.) *The chimpanzee*, Vol. 6, 2nd edn. pp. 34-120. Basel: Karger.

Preuschoft, H. and Witte, H. (1991) Biomechanical reasons for the evolution of hominid body shape. In: Copeans, Y. & Senut, B. (Eds.) *Origine(s) de la bipède chez les hominides* 59-77.

Prost, J.H. (1980) Origin of bipedalism. *Am. J. Phys. Anthrop.* 52, 175-189.

Rak, Y. (1985) Australopithecine taxonomy and phylogeny in light of facial morphology. *Am. J. Phys. Anthrop.* 66, 281-287.

Rak, Y. (1991) Lucy's pelvic anatomy : its role in bipedal gait. *J. Hum. Evol.* 20, 283-290.

Ranke, J. (1905) Zur anthropologie des schulterblattes. *Corresp'Bl. d. Ges. Anthrop.* XXXV, 139-144.

Raven, H. (1950) *The anatomy of the gorilla*, New York: Columbia University Press.

Ray, L.J. (1959) Bilateral coraco-clavicular articulation in the Australian aboriginal. *J. Bone Joint Surg.* 41B, 180-184.

Reed, K.E., Kitching, J.W., Grine, F.E., Jungers, W.L. and Sokoloff, L. (1993) Proximal femur of *Australopithecus africanus* from member 4, Makapansgat, South Africa. *Am. J. Phys. Anthrop.* 92, 1-16.

Reeves, B. (1968) Experiments on the tensile strength of the anterior capsular structures of the shoulder region. *J. Bone Joint Surg.* 50B, 858

Reynolds, V. (1976) *The biology of human action*, San Francisco: Freeman.

Reynolds, T.R. (1985) Stresses in the limbs of quadrupedal primates. *Am. J. Phys. Anthropol.* 67: 351-362.

Roberts, D. (1974) Structure and function of the primate scapula. In: Jenkins, F.A., (Ed.) *Primate Locomotion*, pp. 171-200. New York: Academic Press.

Robinson, J.T. (1954) The genera and species of the australopithecinae. *Am. J. Phys. Anthropol.* 12, 181-200.

Robinson, J.T. (1972) *Early hominid posture and locomotion*, Chicago: University of Chicago Press.

Robinson, J.T. (1978) Evidence for locomotor difference between gracile and robust early hominids from South Africa. In: Jolly, C.J., (Ed.) *Early hominids of africa*, New York: St. Martin's Press.

Rodman, P.S. and McHenry, H.M. (1980) Bioenergetics and the origin of bipedalism. *Am. J. Phys. Anthropol.* 52, 103-106.

Romanes, G.J. (1964) *Cunningham's textbook of anatomy*, London: Oxford University Press.

Rose, M.D. (1984) Food acquisition and the evolution of positional behaviour: the case of bipedalism. In: Chivers, D.J., Wood, B.A. and Bilsborough, A., (Eds.) *Food acquisition and processing in primates*, pp. 509-524. New York: Plenum Press.

Rose, M.D. (1991) The process of bipedalization in hominids. In: Coppens, Y. and Senut, B., (Eds.) *Origine(s) de la Bipédie chez*

les hominidés, pp. 37-48. Paris: (Cahiers de Paléanthropologie), Editions du CNRS.

Saha, A.K. (1953) *Theory of the shoulder mechanism, descriptive and applied*. Charles C. Thomas, Springfield, Ill.

Saha, A.K. (1961) *Theory of shoulder mechanism: descriptive and applied*, Springfield Illinois: Charles C. Thomas.

Saha, A.K. (1971) Dynamic stability of the glenohumeral joint. *Acta Orthop. Scandinavica* 42, 491-505.

Saha, A.K. (1973) Mechanics of elevation of the glenohumeral joint. *Acta. Orthop. Scand.* 44, 668

Salter, N., Sammarco, J. and Sandberg, L.B. (1990) Methods of measurement of muscle and joint function. *J. Bone and Joint Surg.* 137, 474-491.

Sarmiento, E.E. (1985) *Functional differences in the skeleton of wild and captive orang-utans and their adaptive significance*, Ph.D. Dissertation: New York University.

Sarrafian, S.K. (1983) Gross and functional anatomy of the shoulder. *Clin. Orthop.* 173, 11-19.

Schaller, G.B. (1963) *The Mountain Gorilla: ecology and behaviour*, Chicago: University Chicago Press.

Schlyvitch, B. (1937) Über den articulus coracoclavicularis. *Anat. Anz.* 85, 89-93.

Schmid, P. (1983) Eine rekonstruktion des skelettes von A.L. 288-1 (Hadar) und deren konsequenzen. *Folia primatol.* 40, 238-306 (cited by Schmid, 1991).

Schmid, P. (1991) The trunk of the australopithecines. In: Coppens, Y. and Senut, B., (Eds.) *Origine(s) de la bipédie chez les*

hominidés, pp. 225-234. Paris: Cahiers de Paléoanthropologie.

Schultz, A.H. (1930) The skeleton of the trunk and limbs of higher primates. *Hum. Biol.* 19, 489-581.

Schultz, A.H. (1933) Observations on the growth, classification and evolutionary specializations of gibbons and siamangs. *Hum. Biol.* 5, 212-255.

Schultz, A.H. (1937) Proportions, variability, and asymmetries of the long bones of the limbs and the clavicles in man and apes. *Hum. Biol.* 9, 281-328.

Schultz, A.H. (1947) Variability in man and other primates. *Am. J. Phys. Anthropol.* 5, 1-13.

Schultz, A.H. (1969) The skeleton of the chimpanzee. In: Bourne, G.H., (Ed.) *The chimpanzee*, Baltimore: Univ. Park Press.

Schultz, A.H. (1973) The skeleton of the Hylobatidae and other observations on their morphology. *Karger* 2, 1-54.

Senut, B. (1978) *Contribution à l'étude de l'humerus et des articulations chez les hominides du Plio-Pleistocene*, Paris: Diplôme de Docteur 3e cycle.

Senut, B. (1981a) Humeral outlines in some hominoid primates and in Plio-Pleistocene hominids. *Am. J. Phys. Anthropol.* 56, 275-283.

Senut, B. (1981b) L'humerus et ses articulations chez les Hominides Plio-Pleistocene. *CNRS: Paris*, 53-60.

Senut, B. (1982) Réflexions sur la brachiation et l'origine des Hominidés à la lumière des Hominoïdes miocènes et des Hominidés plio-pléistocènes. *Géobios, mém. spéc.* 6, 335-344.

Senut, B. (1984) Des Australopithèques dans les arbres?. *La Recherche* 15, 864-865.

Senut, B. (1989) Climbing as a crucial preadaptation for human bipedalism. *Ossa* 14, 35-44.

Senut, B. (1991) Origines de la bipédie humaine, approche paléontologique. *Cahiers de Paléanthropologie*, CNRS. pp 245-257

Senut, B. and Tardieu, C. (1985) Functional aspects of Plio-Pleistocene hominid limb bones : implications for taxonomy and phylogeny. In: Delson, E., (Ed.) *Ancestors: the hard evidence*, pp. 193-201. New York: Alan R. Liss.

Shapiro, L.J. and Jungers, W.L. (1988) Back muscle function during bipedal walking in chimpanzee and gibbon : implications for the evolution of human locomotion. *Am. J. Phys. Anthropol.* 77, 201-212.

Shipman, P., Walker, A. and Birchell, D.
(1985) *The human skeleton*, Cambridge: Harvard
University Press.

Simpson, G.G. (1961) *Principles of animal
taxonomy*, New York: Columbia University Press.

Skelton, R.R., McHenry, H.M. and Drawhorn,
G.M. (1986) Phylogenetic analysis of early
hominids. *Curr. Anthropol.* 27, 21-43.

Slowik, F. (1945) *Vergleichend-morphologische
untersuchungen in der clavicula des menschen und
anderen Primaten*. Stampfenbach, Zurich.

Sonntag, C.F. (1923) On the anatomy,
physiology and pathology of the chimpanzee. *Proc.
Zool. Soc. Lond.* 1, 323-429.

Sonntag, C.F. (1924) *The morphology and
evolution of the apes and man*, London: J. Bale,
Sons and Danielsson.

Srivastava, U., Bahl, I., Kaul, M. Garg, K.
and Barry, K. (1977) Rhomboid fossa - an
anatomical study. *Indian J. Radiol.* 31: 209-210.

Steindler, A. (1955) *Kinesiology of the human
body under normal and pathological conditions.*
Springfield, IL, Charles C Thomas.

Stern, J.T. (1976) Before bipedality. *Yearb.
Phys. Anthrop.* 19, 59-68.

Stern, J.T. and Jungers, W.L. (1987) Absence
of a relationship between the capitular joint of
the first rib and locomotor use of the upper limb.
Am. J. Phys. Anthrop. 72, 257

Stern, J.T. and Susman, R.L. (1981)
Electromyography of the gluteal muscles in
Hylobates, *Pongo* and *Pan*: implications for the
evolution of hominid bipedality. *Am. J. Phys.
Anthrop.* 55, 279-317.

Stern, J.T. and Susman, R.L. (1983) The locomotor anatomy of *Australopithecus afarensis*. *Am. J. Phys. Anthrop.* 60, 279-317.

Stern, J.T., Wells, J.P., Vangor, A.K. and Fleagle, J.G. (1977) Electromyography of some muscles in the upper limb in *Ateles* and *Lagothrix*. *Yrbk. Phys. Anthrop.* 20, 498-507.

Stewart, TD (1954) Evaluation of evidence from the skeleton. In : Gradwohl REH (ed) Legal medicine. Mosby, St. Louis. pp. 407-450.

Stewart, T.D. (1962) Neanderthal scapulae with special attention to the Shanidar Neanderthals. *Anthropos* 57, 779-800.

Straus, W.L. (1962) Fossil evidence of the evolution of the erect, bipedal posture. *Clinical Orthoped.* 25, 9-19.

Struhsaker, J.T. (1978) Interrelations of red colobus monkeys and rain forest trees in the

Kibale Forest, Uganda, In: *ecology of the arboreal folivores*, G.G. Montgomery (ed.) pp. 397-492.

Susman, R.L. - The locomotor behaviour of *Pan paniscus* in the Lomako Forest. In R.L. Susman ed. *The pygmy chimpanzee: evolutionary biology and behaviour*, Plenum Press, New York, 369-393.

Susman, R.L. (1988a) Hand of *Paranthropus*. *Science* 240, 781-784.

Susman, R.L. (1988b) New postcranial remains from Swartkrans and their bearing on the functional morphology and behavior of *Paranthropus robustus*. In: Grine, F.E., (Ed.) *Evolutionary history of the 'robust' australopithecines*, pp. 149-172. New York: Aldine de Gruyter.

Susman, R.L. and Brain, C.K. (1988) New first metatarsal (SKX 5017) from Swartkrans and the gait of *Paranthropus robustus*. *Am. J. Phys. Anthropol.* 77, 7-15.

Susman, R.L., Stern, J.T. and Jungers, W.L.
(1985) Locomotor adaptations in the Hadar
hominids. In: Delson, E., (Ed.) *Ancestors: the
hard evidence*, pp. 184-192. New York: Alan R.
Liss.

Susman, R.L. and Stern, J.T. (1984)
Arboreality and bipedality in the Hadar hominids.
Folia primatol. 43, 113-156.

Susman, R.L. and Stern, J.T. (1991) Locomotor
behaviour of early hominids : epistemology and
fossil evidence. In: Coppens, Y. and Senut, B.,
(Eds.) *Origine(s) de la bipédie chez les
Hominidés*, pp. 121-132. Paris: Cah. Paléanthrop..

Sutton, J.B. (1885) On the nature of
ligaments. *J. Anat. & Physiol.* XIX, 38-39.

Suzuki, R. (1985) Human adult walking. In:
Kondo, S., (Ed.) *Primate Morphophysiology,
Locomotor analysis and Human Bipedalism*, pp. 3-24.
Tokyo: University of Tokyo Press.

Swindler, D.R. and Wood, C.D. (1973) *An atlas of Primate gross anatomy : Baboon, Chimpanzee and Man*, Seattle: Univ. Washington Press.

Szalay, F.S. and Delson, E. (1979) *Evolutionary history of the Primates*. New York, Academic Press.

Tardieu, C. (1979) *Analyse morpho-fonctionnelle de l'articulation du genou chez les primates. Application aux Hominidés fossiles*, Paris: Thèse de Paleontologie Humaine.

Tardieu, C. (1982) Caractères plésiomorphes et apomorphes de l'articulation du genou chez les primates hominoïdes. *Géobios* 6, 321-334.

Tardieu, C. (1983) Analyse morpho-fonctionnelle de l'articulation du genou chez les primates. Application aux hominidés fossiles. *Cah. Paléanthrop.* 1-108.

Tobias, P.V. (1978) *The Bushmen*. Human & Rousseau, Cape Town.

Tobias, P.V. (1980) *Australopithecus afarensis* and *Australopithecus africanus* : critique and an alternative hypothesis. *Palaeont. Afr.* 23, 1-17.

Tobias, P.V. (1985a) Single characters and the total morphological pattern redefined: the sorting effected by a selection of morphological features of the early hominids. In: *P. V. Tobias, E. (Ed.) Ancestors: the hard evidence*, pp. 94-101. New York: Alan R. Liss.

Tobias, P.V. (1985b) 19th Annual report of PARU, University of the Witwatersrand,

Tobias, P.V. (1986) 20th Annual report of PARU, University of the Witwatersrand,

Tobias, P.V. (1987) 21st Annual PARU report, University of the Witwatersrand,

Tobias, P.V. (1988a) 22nd Annual report of PARU, University of the Witwatersrand,

Tobias, E.V. (1988b) Numerous synapomorphic features in *Australopithecus robustus*, *Australopithecus boisei*, and *Homo habilis* : support for the Skelton-McHenry-Drawhorn hypothesis. In: Grine, F.E., (Ed.) *The evolutionary history of the 'robust' australopithecines*, pp. 293-308. New York: Aldine de Gruyter.

Tobias, P.V. (1989) 23rd Annual report of PARU, university of the Witwatersrand,

Tobias, P.V. (1990) 24th annual report of PARU, University of the Witwatersrand,

Tobias, P.V. (1991a) 25th annual report of PARU, University of the Witwatersrand,

Tobias, P.V. (1991b) Olduvai Gorge, the skulls endocasts and teeth of *Homo habilis*. Camb. Univ. Press. 4. pp 1-921.

Tobias, P.V., Arnold, M. and Allan, J.C.
(1988) *Man's anatomy, a study in dissection*, 4th
ed., Witwatersrand University Press, Johannesburg.

Turkel, S.J., Panio, M.W., Marshall, J.L. and
Girgis, F.G. (1981) Stabilizing mechanisms
preventing anterior dislocation of the
glenohumeral joint. *J. Bone Joint Surg.* 63A, 1208

Turner, S.W. (1886) The scapula. Report on
the human crania and other bones of the skeleton.
Challenger Reports XVI, 81-88.

Turnquist, J.E. (1983) Forelimb musculature
and ligaments in *Ateles*, the spider monkey. *Am.*
J. Phys. Anthrop. 62, 209-226.

Tuttle, R.H. (1969) Knuckle-walking and the
problem of human origins. *Science* 166, 953-961.

Tuttle, R. (1975) Parallelism, brachiation and
hominid phylogeny. In: Lockett, W.P. and Szalay,
F.S., (Eds.) *Phylogeny of the primates, a*

Multidisciplinary approach, pp. 447-480. New York:
Plenum Press.

Tuttle, R. (1981) Evolution of hominid
bipedalism and prehensile capabilities. *Phil.
Trans. Roy. Soc., Lond., Ser. B* 292, 89-94.

Tuttle, R.H. and Basmajian, J.V. (1974)
Electromyography of brachial muscles in *Pan
gorilla* and hominoid evolution. *Am. J. Phys.
Anthrop.* 41, 71-90.

Tuttle, R.H. and Basmajian, J.V. (1977)
Electromyography of pongid shoulder muscles and
hominoid evolution. I. Retractors of the humerus
and rotators of the scapula. *Yrbk. Phys. Anthropol.*
20, 491-497.

Tuttle, R.H. and Basmajian, J.V. (1978a)
Electromyography of pongid shoulder muscles. II.
Deltoid, rhomboid and 'rotator' cuff. *Am. J.
Phys. Anthropol.* 49, 47-56.

Tuttle, R.H. and Basmajian, J.V. (1978b)
Electromyography of pongid shoulder muscles. III.
Quadrupedal positional behavior. *Am. J. Phys.*
Anthrop. 49, 57-78.

Vallois, H.V. (1924) La formation de
l'omoplate humaine. *Bull. Mus. d'Hist. Nat. Paris*
65-70.

Vallois, H.V. (1926a) Les anomalies de
l'omoplate chez l'homme. *Bull Soc. Anthropologie*
7, 19-36.

Vallois, H.V. (1926b) Variations de
l'echancrure coracoidienne de l'omoplate. *Ann.*
Anat. Path. etc. III, 111-113.

Vallois, H.V. (1927) L'omoplate des Négrilles
et celle des Négritos. *Bull. Mus. Nat. d'Hist.*
Nat. V, 1-3.

Vallois, H.V. (1928) L'omoplate humaine, étude
anatomique et anthropologique. *Bull. et Mem. Soc.*
Anthrop. Paris VII, 129-168.



Vallois, H.V. (1932) as quoted by Hrdlicka, A.
(1942) The adult scapula: additional observations
and measurements. *Am. J. Phys. Anthrop.* 29:
364-415.

Vrba, E.S. (1976) The fossil bovidae of
Sterkfontein, Swartkrans and Kromdraai. *Transv.
Mus. Mem.* 21,

Vrba, E.S. (1979) A new study of the scapula
of *Australopithecus africanus* from Sterkfontein.
Am. J. Phys. Anthrop. 51, 117-130.

Vrba, E.S. (1982) Biostratigraphy and
chronology, based particularly on Bovidae, of
southern African hominid-associated assemblages:
Makapansgat, Sterkfontein, Taung, Kromdraai,
Swartkrans; also Elandsfontein (Saldanha), Broken
Hill (now Kabwe) and Cave of Hearths.. In:
deLumley, H. and deLumley, M.A., (Eds.) *Proc.
Congres international de paleontologie humaine*,
pp. 707-752. Nice: Union International des
Sciences Prehistoriques et Protohistoriques.

Walker, A. and Leahey, R.E.F. (1993) The Nariokotome *Homo erectus* skeleton. Springer, Ijmuiden.

Warburg, F. (1913) Uber scapula scaphoidea, *Med. klin. Jhg.* 9, 1851 (cited by Hrdlicka, 1942).

Warren, R.F., Kornblatt, I.B. and Marchand, R. (1984) Statistic factors affecting posterior shoulder instability. *Orthop. Trans.* 8, 1

Washburn, S.L. (1967) Behaviour and the origin of man. *Proc. Roy. Anthropol. Inst.* 21-27.

Washburn, S.L. (1968) Speculation on the problem of man's coming to the ground. In: Rothblatt, B., (Ed.) *Changing perspectives on man*, pp. 191-206. Chicago: Univ. Chicago Press.

Washburn, S.L. (1971) On the importance of the study of primate behavior for anthropologists. In: Wax, M.L., Diamond, S. and Gearing, F.C., (Eds.)

Anthropological perspectives on education, pp.

91-97. New York:

Webster, D. and Webster, M. (1974) *Comparative vertebrate morphology*. New York, Academic Press.

Wertheimer, L.G. (1948) Coracoclavicular joint. *J. Bone Joint Surg.* 30A, 570-578.

White, T.D., Johanson, D.C. and Kimbel, W.H. (1981) *Australopithecus africanus* : its phyletic position reconsidered. *S. Afr. J. Sci.* 77, 445-470.

White, T.D. and Suwa, G. (1987) Hominid footprints at Laetoli : facts and interpretations. *Am. J. Phys. Anthropol.* 72, 489-514.

Williams, P.L. and Warwick, R. (1980) *Gray's Anatomy*. 36th Ed. Edinburgh: Churchill Livingstone.

Williams, P.L., Warwick, R., Dyson, M. and Bannister, L. (1989) *Gray's Anatomy*. 37th ed. Edinburgh: Churchill Livingstone.

Wolffson, D.M. (1950) Scapula shape and muscle function with special reference to the vertebral border. *Am. J. Phys. Anthropol.* 8, 331-341.

Wolpoff, M. (1980) *Paleoanthropology*, New York: Knopf.

Wolpoff, M.H. (1983a) Lucy's lower limbs: long enough to be fully bipedal?. *Nature* 304, 59-61.

Wolpoff, M.H. (1983b) Lucy's little legs. *J. Hum. Evol.* 12, 443-453.

Wood, B.A. (1974) Olduvai Bed I post-cranial fossils: a reassessment. *J. Hum. Evol.* 3, 373-378.

Wood, B.A. (1978) An analysis of early hominid fossil postcranial material ; principles and

methods. In: Jolly, C.J., (Ed.) *Early hominids of Africa*, pp. 347-360. New York: St. Martin's Press.

Wood, B.A. (1991) *Koobi Fora Research Project Vol. 4 Hominid Cranial Remains*. Oxford: Clarendon Press.

Wood, B.A. (1992) Early hominid species and speciation. *J. Hum. Evol.* 22, 351-365.

Wood-Jones (1964) as quoted by Senut, B. (1991) Origines de la bipédie humaine. approche paleontologique. *Cahiers de Paleanthropologie*, CNRS. pp 245-257

Wrangham, R. (1980) Bipedal locomotion as a feeding adaptation in gelada baboons, and its implications for hominid ancestor. *J. Hum. Evol.* 9, 329-331.

Wright, S. (1977) *Evolution and the genetics of populations. Volume 3. Experimental results and evolutionary deductions*, Chicago: University of Chicago Press

Yamshon, L.J. & Bierman, W. (1948)
Kinesiologic electromyography. II The trapezius.
Arch. Phys. Med. 29, 647-651.

Zapfe, H. (1960) Di primatenfunde aus der
miozänen spaltenfüllung von Neudorf an der March
(Devinska Nova Ves), Tschechoslowakei. Schweiz.
Palaeontol. Abh. 78, p-293, pp 102-106,

Zihlman, A. (1985) *Australopithecus afarensis*
: two sexes or two species?. In: Tobias, P.V.,
(Ed.) *Hominid evolution : past, present and
future*, pp. 213-220. New York: Alan R. Liss.

Zihlman, A. and Tanner, N.M. (1978) Gathering
and the hominid adaptation. In: Tiger, L. and
Fowler, H., (Eds.) *Female hierarchies*, pp.
163-194. Chicago: Beresford Book Service.

**FUNCTIONAL MORPHOLOGY OF THE
HOMINOID SHOULDER, PAST AND
PRESENT**

Lee Rogers Berger

Volume II

Tables 1 - 21

Figures 1 - 71

&

Plates 1 - 5

List of Tables, Figures and Plates in Volume II

List of Tables

<u>Table</u>	<u>Page</u>
1 Summary of Extant Hominoid Shoulder Girdle Elements	1
2 Summary of Fossil Hominid Shoulder Girdle Elements by Locality	2
3 Observed Frequency of the Coraco- clavicular Joint in Modern Human Populations	3
4 Comparative Summary: The Muscles - Variation in the Origins of Selected Muscles	4
5 Comparative Summary: The Muscles - Variation in the Insertions of Selected Muscles	7
6 Variation in the Glenoid Index Amongst Hominoidea	9
7 Variation in the Coracoacromial Index (Coracoid Length / Acromion Length X 100) Amongst Hominoidea	10
8 Variation in the Scapular Index (Scapular Breadth / Scapular Length X 100) Amongst Hominoidea	11

9	Variation in the Scapular Index (Scapular Length / Scapular Breadth X 100) in Different Populations of Humans	12
10	Variation in the Fossorial Index (Area of Supraspinous Fossa / Area of Infraspinous Fossa X 100) Amongst Hominoidea	13
11	Variation in the Acromion Projection Index ((Acromion Projection - Spino- glenoid Notch Depth X 100) / Anatomical Length of the Scapula) Amongst Hominoidea	14
12	Variation in the Axilloglenoid Angle Amongst Hominoidea	15
13	Variation in the "Bar Glenoid Angle" Amongst Hominoidea	16
14	Humerus Greater Tubercle Height Relative to the Humeral Head	17
15	Variation in the Humeral Head Index (Humeral Head Breadth / Humeral Head Length X 100) Amongst Hominoidea	18
16	Variation in the Intertubercular Sulcus / Humeral Head Index Amongst	

	Extant Hominoidea (ISW / HNB X 100)	19
17	Variations in Humeral Torsions	
	Amongst the Hominoidea	20
18	Metrical Characters of the Glenoid	
	Cavities of the Scapulae of	
	Australopithecines	21
19	Metrical Characters of the Body of	
	the Scapulae of Australopithecines	22
20	Variation in the Length of the	
	Scapular Axillary Margin Amongst	
	Extant Hominoidea and Stw 431	23
21	Metrical Characters of the Humeral	
	Heads of Australopithecines	24

List of Figures

<u>Figure</u>		<u>Page</u>
1	Distribution of extant hominoid species examined in the present study	25
2	Map of South African early hominid fossil sites in the Krugersdorp District illustrating the position of Sterkfontein relative to other well known localities where early hominid fossils have been discovered	26
3	Map of East African fossil hominid localities where shoulder girdle elements examined in the present study have been found	27
4	Approximate chronologic relationships of Plio-Pleistocene African Hominids. Chronologic relationships established by radiometric and faunal evidence as discussed in the text.	28
5a	Dorsal view of a human scapula illustrating landmarks and distances, as defined in the text	29

5b	Lateral view of human scapula illustrating landmarks and distances, as defined in the text	30
5c	Superior view of a human scapula illustrating landmarks and distances, as defined in the text	31
6	Superior and dorsal view of a right human humerus illustrating landmarks and distances, as defined in the text	32
7	Inferior view of a left human clavicle illustrating landmarks and distances, as defined in the text	33
8	Dorsal view of a human scapula illustrating landmarks used in the calculation of angles. Landmarks are defined in the text	34
9	Two dimensional diagrammatic consideration of the areas of the infraspinous (a) and supraspinous (b) fossae traced during area calculation using the image analysis technique of scapular surface area reconstruction	35
10	Diagrammatic consideration of the two	

	dimensionality of the areas of the infrascapular and scapular fossae of a human scapula when traced using the image analysis technique of scapular surface area reconstruction	36
11	The position of the scapula and the clavicle on the thorax in a quadrupedal monkey and a bipedal human	37
12	A two dimensional reconstruction of the degrees of freedom of movement of the human shoulder girdle	38
13	The thorax, scapula and forelimb of an antelope showing the morphology of a typical terrestrial quadruped	39
14	The three degrees of freedom in the hominoid glenohumeral joint	40
15	Diagrammatic representation of the attachment areas of the glenoid labrum on a human scapular glenoid cavity	41
16	Rotation of the clavicle at the acromioclavicular and sternoclavicular joints in combination with the rotation and angulation of the scapula	

in the human	42
Key to Figures 17-28	43
17 The muscular attachments on the human scapula	44
18 The muscular attachments on the gorilla and chimpanzee scapulae	45
19 The muscular attachments on the orang-utan scapula	46
20 The muscular attachments on the hylobatid scapula	47
21 The muscular attachments on the human clavicle	48
22 The muscular attachments on the gorilla & chimpanzee clavicles	49
23 The muscular attachments on the orang-utan clavicle	50
24 The muscular attachments on the hylobatid clavicle	51
25 The muscular attachments on the human humerus	52
26 The muscular attachments on gorilla & chimpanzee humeri	53
27 The muscular attachments on the orang-utan humerus	54

28	The muscular attachments on the hylobatid humerus	55
29	A composite (right) hominoid scapula with characteristic morphological features illustrated and labelled	56
30	A composite (right) hominoid clavicle with morphological features illustrated and labelled	57
31	A composite (right) hominoid humerus with morphological features illustrated and labelled	58
32	Shapes of the (right) scapular glenoid cavity in various hominoids	59
33	Comparison of the glenoid index values for modern hominoid scapulae	60
34	Spinoglenoid notch depth vs. glenoid cavity maximum breadth	61
35	Spinoglenoid notch depth vs. glenoid cavity maximum length	62
36	Spinoglenoid notch depth vs. glenoid cavity maximum breadth	63
37	Illustrations of the differences in orientation of the coracoid process between chimpanzee and human scapulae	64

- 38 Comparison of the shape of the body of
a scapula among hominoid genera and
monkeys 65
- 39 Bivariate plot of the supraspinous
index and the infraspinous index in
hominoids and Old world monkeys 66
- 40 Area of infraspinous fossa vs. Area
of supraspinous fossa in extant
hominoids 67
- 41 Area of infraspinous fossa vs. Area
of supraspinous fossa in extant
hominoids illustrating regression lines of
individual species 68
- 42 Illustration of the angle of
insertion of the trapezius muscle
in the hominoid scapula as represented
by angle A 69
- 43 Calculated values for the angle of
insertion of the trapezius muscle in
humans, apes and quadrupedal monkeys 70
- 44 The orientation of components of the
force couple made up of the trapezius
and serratus magnus muscles (angle B)
in the scapulae of hominoids and

	monkeys	71
45	The angulation of the trapezius/ serratus magnus force couple in hominoids	72
46	Humeral torsion and the relationship of the intertubercular sulcus to the head of the humerus	73
47	Anterior views of human and chimpanzee right clavicles illustrating the marked cranial twisting of the lateral end of the chimpanzee clavicle	74
48	The angle of torsion in the clavicles of hominoids	75
49	Models of left hominoid clavicles illustrating the varying degrees of sigmoid curvature	76
50	Cross-sectional shapes of the bodies of clavicles in hominoids	77
51	Cross-sectional shapes of the sternal ends of clavicles in hominoids	78
52	Reconstruction of the Sts 7 scapula	79
54	Comparison of hominoid scapular glenoid shape	80
55	Spinoglenoid notch depth vs. glenoid	

	breadth in extant hominoids and monkeys	81
56	Comparison of australopithecine scapular shape (inferior angle)	82
57	Diagram illustrating this author's justification for his minimum and maximum estimates of the inferior angle	83
58	Comparison of australopithecines humeral shape (Humeral head index)	84
59	Illustration of AL 288-11	85
60	Illustration of AL 288-bz	86
61	Illustration of AL 333x-6/9	86
62	Illustration of AL 333-94	87
63	Illustration of AL 288-1r	88
64	Illustration of AL 288-1m	89
65	Illustration of AL 333-87	90
66	Illustration of AL 333-109	90
67	Illustration of AL 333-107	91
68	Comparison of australopithecine scapular shape (axilloglenoid angle)	92
69	Illustration of KNM-ER 739	93
70	Illustration of OH 48	94
71	Illustration of OMO 119-2718	95

List of Plates

<u>Plate</u>		<u>Page</u>
1	Stw 162 scapula	96
2	Stw 431 scapula	97
3	Stw 431 clavicle	98
4	Stw 328 humerus	99
5	Stw 511 humerus	100

Table 1. *Summary of Extant Hominoid Shoulder Girdle Elements*

Species	Gender	Number of Specimens	Source
<i>Homo sapiens</i>			
	male	29	UW
	female	27	UW
	male	18	SI
	female	22	SI
<i>Gorilla gorilla</i>			
	male	3	UW
	male	12	SI
	female	5	SI
<i>Pan troglodytes</i>			
	male	11	SI
	female	9	SI
<i>Pongo pygmaeus</i>			
	male	12	SI
	female	20	SI
<i>Hylobates species</i>			
	male	9	SI
	female	6	SI
<i>Symphalangus syndactylus</i>			
	male	1	SI
	female	3	SI
<i>Papio ursinus</i>			
	male	16	UW
	female	12	UW
<i>Cercopithecus aethiops</i>			
	male	20	UW
	female	16	UW

UW, Department of Anatomy and Human Biology, University of the Witwatersrand; SI Smithsonian Institution. Each specimen numbered refers to a complete set of shoulder girdle elements from a single individual.

Table 2. *Summary of Fossil Hominid Shoulder Girdle Elements by Locality*

Locality	Catalogue #	Description
Sterkfontein	Sts 7	R. proximal humerus; rt. scapular fragment.
	Stw 162	L. scapular fragment.
	Stw 328	R. proximal humeral fragment.
	Stw 431	R. clavicular fragment; rt. scapular axillary margin.
	Stw 517	L. proximal humeral fragment.
Olduvai Gorge	OH 48	L. clavicle.
Koobi Fora	KNM-ER 739	R. humeral shaft.
	KNM-ER 1473	R. proximal humeral fragment.
Omo	OMO 119-2718	L. proximal humerus.
Hadar	A.L. 288-1	R. scapular fragment; R. clavicular fragment; R. humerus; L. proximal humerus.
	A.L. 333-94	L. clavicular fragment.
	A.L. 333X-6/9	R. clavicular shaft.
	A.L. 333-87	L. proximal humeral shaft.
	A.L. 333-107	R. proximal humerus.
	A.L. 333-109	R. humeral shaft.

Table 3. *Observed Frequency of the Coracoclavicular Joint in Modern Human Populations*

Population or Region	Frequency Percentage	(n) (shoulders)	Method
Russian	2.63 ¹	38	Dissection
French	3.60 ²	56	Dissection
	33.00 ³	-	Dissection
	0.60 ²	453	Radiological
Japanese	7.60 ⁵	96	Dissection
	9.90 ⁴	91	Radiological
	0.12	3189	Radiological
Singapore	27.00 ⁶	300	Dissection
	2.60 ⁶	4644	Radiological
European	0.30 ⁷	358	Osteological
	1.40 ⁸	282	Osteological
	2.80 ⁹	180	Osteological
	5.10 ¹⁰	491	Osteological
	6.80 ²	117	Osteological
Argentina	0.04 ¹²	2300	Radiological
Hawaii	0.18 ¹³	7772	Radiological
Nigeria	0.60 ¹⁴	2000	Radiological
Brazil	0.80 ¹³	277	Radiological
U.S.A.	1.20 ¹⁶	1000	Radiological
Czech	1.38 ¹⁷	3470	Radiological
Malay	3.00 ¹	300	Radiological
Indian	4.30 ⁴	276	Radiological
Phil. est.	21.00 ⁴	480	Radiological

Frequency refers to the percentage of observed occurrences in the total number of shoulders examined. References: 1, Gruber (1861); 2, Fischer et al. (1971); 3, Poirier (1890); 4, Cockshott (1979); 5, Abe (1964); 6, Pillay (1967); 7, Cambridge and Tarazaga (1956); 8, Parsons (1916); 9, Vallois (1926); 10, Jaluvka (1956); 11, Oikawa and Hatafuku (1970); 12, Ponde and Silveira (1938); 13, Moore and Renner (1957); 14, Cockshott (1958); 15, Wertheimer (1948); 16, Nutter (1941); 17, Jaluvka (1959).

Table 4. Comparative Summary: the muscles - variation in the origins of selected muscles

Muscle	<i>H. sapiens</i>	<i>G. gorilla</i>	<i>P. troglodytes</i>	<i>P. pygmaeus</i>	<i>Hylobates</i> species
(1) Deltoid	Caudal surface scapular spine, lateral upper surface of acromion, ventrolateral 1/3 to 1/4 of the clavicle.	as in humans	as in humans	ventrolateral 1/2 of the clavicle.	as in humans
(2) Biceps (short head)	lateral part coracoid process.	as in humans.	as in humans	as in humans	superior part humeral head.
(3) Teres major	inferior angle of scapula, tendinous attachment at the superior lateral margin of the scapula.	reduced area of attachment at the inferior angle of the scapula, tendinous attachment more superiorly positioned on the lateral margin of the scapula.	as in gorillas.	as in gorillas.	as in gorillas.
(4) Teres minor	superior 2/3 to 1/2 of the axillary margin.	reduced area of attachment over that observed in humans.	as in gorillas	as in gorillas	as in gorillas
(5) Subscapularis	subscapular fossa of the scapula	reduced area of attachment over that observed in humans.	as in gorillas.	as in gorillas.	as in gorillas
(6) Trapezius	the ligamentum nuchae, spines of the 7th cervical and all the thoracic vertebrae, the ligamenta supraspinalia, the superior nuchal line and occipital protuberance.	as in humans.	lack a nuchal surface attachment at occipital.	as in humans.	slight occipital attachment.
(7) Atlanto-scapularis anterior	usually absent. V ventral transverse process of the atlas	attaches as in humans but always present.	as in gorillas.	as in gorillas. rV additional attachment at occiput.	as in gorillas.

Table 4. *continued*

Muscle	<i>H. sapiens</i>	<i>G. gorilla</i>	<i>P. troglodytes</i>	<i>P. pygmaeus</i>	<i>Hylobates</i> species
(8) Levator scapulae	transverse processes C1 to C4. V reduced to C2 and C3. V additional attachments to C5 and C6.	as in humans.	as in humans.	as in humans. V additional attachment to mastoid process.	as in humans.
(9) Rhomboids	ligamentum nuchae, spine of C7, spine of T1, posterior tubercles C3, C4 and associated ligamenta supraspinalia.	as in humans.	as in humans.	as in humans. V spines of T5 and T6 rV external occipital protuberance. rV superior nuchal line.	as in humans.
(10) Latissimus dorsi	spines and supraspinous ligaments of T5 to T12, the iliac crest, the fascia thoracolumbalis. V slips from lower 3 or 4 ribs. rV inferior angle of scapula.	as in humans.	as in humans.	as in humans.	no attachment at ilium.
(11) Coracobrachialis	apex coracoid process. V slips from the lesser tubercle of the humerus.	as in humans.	as in humans.	as in humans.	as in humans.
(12) Subclavius	cranial border of the 1st rib at the costochondral junction.	as in humans.	as in humans.	as in humans.	as in humans but attachment extends over ribs 1 through 3.
(13) Atlantoclavicularis	absent in humans.	spinous process of the atlas.	as in gorillas.	as in gorillas.	as in gorillas.
(14) Pectoralis minor	outer ventral surface of ribs 1 through 5.	outer ventral surface of ribs 1 through 3. V also ribs 4 and 5.	as in gorillas.	as in gorillas.	as in gorillas.

Table 4. *continued*

Muscle	<i>H. sapiens</i>	<i>G. gorilla</i>	<i>P. troglodytes</i>	<i>P. pygmaeus</i>	<i>Hylobates</i> species
(15) Pectoralis major	medial 1/2 of clavicle, sternoclavicular joint area, manubrium sterni, 2 to 7th costal cartilages, aponeurosis of the external oblique muscle.	as in humans but the clavicular attachment is absent. rV clavicular attachment.	as in humans.	as in humans.	as in humans.
(16) Triceps	infraglenoid tubercle, upper posterior and lateral humeral shaft, capsule of the shoulder joint, inferior 1/3 to 1/2 of the humerus shaft.	superolateral 1/2 axillary margin, attachment on upper shaft more distal, attachment on inferior part of humerus more distal.	as in gorillas.	as in gorillas.	as in gorillas.
(17) Sternocleidomastoid	superior surface of the clavicle near the sternal end, manubrium sterni	sternal attachment more localized than in humans. V encroaches on sternal articular surface.	as in gorillas.	as in gorillas.	as in gorillas.

V refers to a common variant; rV refers to a rare variant.

Table 5. *Comparative Summary: the muscles - variation in the insertions of selected muscles*

Muscle	<i>H. sapiens</i>	<i>G. gorilla</i>	<i>P. troglodytes</i>	<i>P. pygmaeus</i>	<i>Hylobates</i> species
(1) Trapezius	lateral end of the clavicle, superolateral acromion process, cranial border of the scapular spine and medial tubercle of spine.	as in humans but clavicular insertion is heavier.	as in gorillas.	as in gorillas.	as in gorillas.
(2) Atlantoscapularis anterior	rV cranial margin of acromion process, lateral margin of the scapular body.	cranial margin of acromion process, lateral margin of the scapular body. V lateral clavicular attachment.	as in gorillas.	as in gorillas.	as in gorillas.
(3) Latissimus dorsi	floor of the intertubercular sulcus. V floor & medial lip of the intertubercular sulcus	as in humans.	as in humans.	as in humans.	as in humans but never attaches on the medial lip of the intertubercular sulcus.
(4) Coraco-brachialis	mid-shaft of the humerus opposite the deltoid tuberosity.	as in humans.	as in humans.	as in humans.	medial crest of bicipital groove only.
(5) Subclavius	inferior surface of clavicle near mid-body. rV coracoid process.	clavicular attachment more lateral, additional fibres to hum. nentum costo-coracoideum.	as in gorillas.	as in gorillas.	as in gorillas.
(6) Atlanto-clavicularis	absent	lateral end of clavicle adjacent to trapezius.	as in gorillas but often indistinguishable from trapezius.	as in gorillas.	as in gorillas.

Table 5. *continued*

Muscle	<i>H. sapiens</i>	<i>G. gorilla</i>	<i>P. troglodytes</i>	<i>P. pygmaeus</i>	<i>Hylobates</i> species
(7) Omohyoid	superior border of the scapula near the scapular notch.	as in humans.	middle of the superior border of the scapula.	as in humans.	as in chimpanzees.
(8) Pectoralis minor	coracoid process. rV rim of glenoid cavity.	as in humans but with an additional attachment at the capsule of the shoulder joint.	as in gorillas.	as in gorillas.	as in gorillas.

V refers to a common variant; rV refers to a rare variant.

Table 6. Variation in the Glenoid Index Amongst Hominoidea

Taxon	Observed range	Mean of the Index Values	(n)	SD
<i>Homo sapiens</i>				
male ¹	58.2 - 83.4	69.2	(30)	6.5
female ¹	56.7 - 79.9	67.5	(32)	4.7
both sexes ¹	56.7 - 83.4	68.3	(62)	5.7
both sexes ²	66.6 - 85.7	76.7	(100)	
weighted mean		73.6	(162)	
<i>Gorilla gorilla</i>				
male ¹	59.2 - 77.4	66.1	(12)	4.3
female ¹	62.8 - 70.7	65.2	(5)	3.3
both sexes ¹	59.3 - 77.4	65.8	(17)	4.0
both sexes ²		76.9	(2)	
weighted mean		67.0	(19)	
<i>Pan troglodytes</i>				
male ¹	60.1 - 73.4	66.9	(7)	4.3
female ¹	57.7 - 68.7	65.5	(9)	3.7
both sexes ¹	57.7 - 73.4	66.1	(16)	3.9
weighted mean		66.1	(16)	
<i>Pongo pygmaeus</i>				
male ¹	54.0 - 72.5	61.4	(10)	5.9
female ¹	56.3 - 67.7	63.3	(19)	3.5
both sexes ¹	54.0 - 72.5	62.7	(29)	4.5
both sexes ²	56.5 - 73.3	64.5	(10)	
weighted mean		63.1	(39)	
<i>Hylobates species</i>				
male ¹	53.0 - 89.2	66.7	(3)	19.6
female ¹	89.7 - 99.3	92.3	(5)	4.0
both sexes ¹	53.0 - 99.3	82.7	(8)	17.1
both sexes ²		84.4	(2)	
weighted mean		83.0	(10)	
<i>Symphalangus syndactylus</i>				
male ¹	84.8		(1)	
female ¹	67.0 - 76.2	70.2	(3)	5.2
both sexes ¹	67.0 - 84.97	73.9	(4)	8.5
weighted mean		73.9	(4)	

¹This author; ²Vallois (1928 - 1946); ³Senut (1978); ⁴Churchill and Trinkaus (1990).

Table 7. Variation in the Coracoacromial Index (Coracoid length / Acromion length x 100) Amongst Hominoidea

Taxon	Mean of the Index Values	(n)	SD
<i>Homo sapiens</i>	55%	(26)	7.0
<i>Gorilla gorilla</i>	62%	(22)	8.0
<i>Pan troglodytes</i>	63%	(23)	9.0
<i>Pongo pygmaeus</i>	46%	(24)	8.0
<i>Hylobates species</i>	89%	(22)	9.0

The data presented in this table are derived from Clochon and Corruccini (1977)

Table 8. Variation in the Scapular Index (scapular breadth / scapular length x 100) Amongst Hominoidea

Taxon	Mean of the Index Values	SD	CV	Observed range	(n)
<i>Homo sapiens</i>					
male	62.55	5.83	9.33	49.90 - 73.09	46
female	65.14	5.48	8.41	54.25 - 73.56	37
both sexes	63.70	5.79	9.09	49.90 - 73.56	83
<i>Gorilla gori</i> ¹¹					
male	77.37	7.09	9.17	63.90 - 92.31	15
female	79.57	3.91	4.91	75.96 - 85.85	5
both sexes	77.92	6.35	8.18	63.90 - 92.31	20
<i>Pan troglodytes</i>					
male	76.92	10.32	13.42	62.18 - 101.89	11
female	74.35	6.45	8.68	65.06 - 87.89	9
both sexes	75.76	8.46	11.17	62.18 - 101.89	20
<i>Pongo pygmaeus</i>					
male	70.93	8.29	11.68	58.57 - 89.90	12
female	68.63	5.81	8.46	58.74 - 78.43	19
both sexes	69.52	7.15	9.83	58.57 - 89.90	31
<i>Hylobates species</i>					
male	123.65	22.54	18.22	95.12 - 161.08	9
female	128.85	19.60	15.21	95.94 - 145.40	6
both sexes	125.73	20.84	16.57	95.12 - 161.08	15
<i>Symphalangus syndactylus</i>					
male	124.40				1
female	102.92	9.70	9.42	91.98 - 110.49	3
both sexes	108.29	13.35	12.32	91.98 - 124.40	4

The data presented in this table are derived from calculations made by the author. The mean values for both sexes are the weighted average of means.

Table 9. Variation in the Scapular Index (Scapular Length / Scapular Breadth x 100) in Different Populations of Humans*

Population (n)	Male (M) Mean Index Values	Female (F) Mean Index Values
Afr. Black (58M,15F)	66.6	68.2
Am. Negro (126M,46F)	66.7	67.2
Egyptian (20M,15F)	68.2	70.0
Egyptian (11M,6F)	66.5	68.6
Eskimo (4M,4F)	61.9	62.0
Eskimo (239M,1. F)	62.4	65.6
European Whites (146M,102F)	63.7	66.8
Finnish (72M,14F)	62.4	63.9
French (78M,68F)	65.2	65.9
Fuegian (35M,28F)	61.8	64.3
Fuegian (47M,2F)	64.3	66.1
Fuegian (4M,6F)	64.8	65.7
Japanese (64)		64.9
Melanesian (20M,11F)	68.6	69.1
Mexican Ind. (9M,12F)	65.5	70.7
Mongoloid (20M,4F)	66.9	65.1
Negrillo (4M,6F)	77.1	73.8
North Amer. Indian (229M,179F)	65.9	70.7
North West Indian (10M,14F)	64.3	66.1
Oceanic Black (9M,9F)	66.5	67.9
Pecos Ind. (79M,24F)	68.3	73.5
Peruvian Ind. (55M,39F)	64.2	66.5
Portuguese (37M,20F)	64.4	66.5
Pre-Koniag (53M,59F)	60.9	62.2
Pueblo Indian (46M,36F)	67.3	73.0
Utah Indian (18M,10F)	67.4	70.6
Whites (1200M,457F)	65.0	66.3

*All data from tables compiled by Hrdlička (1942) from Livon (1879); Hrdlička (1910, 1931, 1937); Kajava (1924); Vallois (1924, 1926a,b, 1927, 1928) and Martin (1928).

Table 10. Variation in the Fossorial Index (Area of Supraspinous Fossa / Area of Infraspinous fossa $\times$ 100) Amongst Hominoidea

Taxon	Mean of the Index Values	Observed range (n)	SD	CV
<i>Homo sapiens</i>	43.7	30.5 - 59.3 (64)	5.9	13.6
<i>Gorilla gorilla</i>	66.2	54.9 - 80.3 (16)	8.5	12.8
<i>Pan troglodytes</i>	67.6	52.8 - 93.8 (16)	10.7	15.9
<i>Pongo pygmaeus</i>	38.2	25.8 - 51.4 (26)	6.0	15.8
<i>Hylobates species</i>	89.6	59.2 - 119.5 (13)	17.2	19.2

The data presented in this table are derived from measurements made by the author.

Table 11. Variation in the Acromion Projection Index
 ([Acromion Projection - Spinoglenoid Notch Depth $\times$ 100] / Anatomical Length of the Scapula)
 Amongst Hominoidea and Old World Monkeys

Taxon	Observed Range (n)	Mean of the Index Values	SD
<i>Homo sapiens</i>	15.8 - 46.4 (87)	34.2	4.8
<i>Gorilla gorilla</i>	20.0 - 38.8 (20)	32.0	4.8
<i>Pan troglodytes</i>	27.1 - 46.8 (20)	36.3	5.2
<i>Pongo pygmaeus</i>	23.6 - 47.3 (30)	34.5	5.5
<i>Hylobates species</i>	19.2 - 35.5 (15)	26.5	4.3
<i>Symphalangus syndactylus</i>	28.3 - 34.3 (3)	31.9	3.1
<i>Papio ursinus</i>	-1.3 - 12.4 (28)	4.6	3.2
<i>Cercopithecus aethiops</i>	0.4 - 13.9 (6)	5.2	

The data in this table are derived from calculations made by the author.

Table 12. Variation in the Axilloglenoid Angle Amongst Hominoidea and Old World Monkeys

Taxon	Mean	SD	CV	Observed range	(n)
<i>Homo sapiens</i>					
male	135.10	5.59	4.14	124.00 - 150.50	54
female	132.55	5.75	5.09	120.90 - 152.70	42
both sexes	133.98	5.22	4.64	120.90 - 152.70	96
<i>Gorilla gorilla</i>					
male	116.47	5.89	5.02	106.00 - 131.00	15
female	117.40	4.39	3.74	113.00 - 124.00	5
both sexes	116.70	5.87	5.02	106.00 - 131.00	20
<i>Pan troglodytes</i>					
male	116.17	7.08	6.09	104.00 - 128.00	11
female	116.33	6.84	5.88	107.00 - 126.00	9
both sexes	116.23	6.62	5.69	104.00 - 128.00	20
<i>Pongo pygmaeus</i>					
male	120.67	10.20	8.45	101.00 - 137.00	12
female	120.95	8.26	6.83	109.00 - 150.00	20
both sexes	120.84	8.88	7.35	101.00 - 150.00	32
<i>Hylobates species</i>					
male	106.00	7.05	6.65	94.00 - 114.00	9
female	106.67	7.29	6.83	97.00 - 117.00	6
both sexes	106.27	6.89	6.49	94.00 - 117.00	15
<i>Symphalangus syndactylus</i>					
male	96.00				1
female	101.00	3.61	3.57	98.00 - 105.00	3
both sexes	99.75	3.86	3.87	96.00 - 105.00	4
Monkeys (<i>Papio ursinus</i> & <i>Cercopithecus aethiops</i>)					
both sexes	139.60	4.45	3.83	124.00 - 158.00	64

The data presented in this table are derived from measurements made by the author. The means given for "both sexes" are weighted means.

Table 13. Variation in the "Bar Glenoid Angle" Amongst Hominoidea

Taxon	Mean	SD	n
<i>Homo sapiens</i>	145.0	4.3	50
<i>Gorilla gorilla</i>	131.6	2.1	9
<i>Pan troglodytes</i>	126.3	2.8	11
<i>Pan paniscus</i>	125.9	3.4	12
<i>Pongo pygmaeus</i>	127.4	3.4	5

The data in this table are derived from Cornucini and Clochon (1976). These authors report that by subtracting 10.6 degrees from the bar glenoid angles presented in this table, one may compare these data with those studies which use the axilloglenoid angle to express the orientation of the glenoid cavity in relation to the axis of the axillary margin.

Table 14. Humerus Greater Tubercle Height Relative to the Humeral Head

Taxon	Observed range	Mean	(n)	CV	SD
<i>Homo sapiens</i>					
both sexes	-0.3 - -3.5	-1.7	(95)	33.2	0.6
<i>Gorilla gorilla</i>					
both sexes	-0.7 - -3.4	-1.9	(19)	35.9	0.7
<i>Pan troglodytes</i>					
both sexes	1.2 - -2.1	-0.5	(20)	48.5	0.8
<i>Pongo pygmaeus</i>					
both sexes	-1.3 - -4.4	-2.7	(30)	29.6	0.8
<i>Hylobates</i> species					
both sexes	0.3 - -2.1	-1.2	(15)	47.6	
<i>Symphalangus syndactylus</i>					
both sexes	-1.1 - -1.6	-1.3	(4)	18.5	0.2

The data in this table are compiled by the author. Values recorded as negative indicate the distance by which the top of the greater tubercle is below the most superior part of the humeral head articular surface.

Table 15. Variation in the Humeral Head Index (Humeral Head Breadth / Humeral Head Length x 100)
Amongst Hominoidea

Taxon	Observed range	Mean of the Index Values	(n)	SD
<i>Homo sapiens</i>				
both sexes ¹	84.5 - 102.8	94.9	94	4.1
both sexes ²	86.8 - 104.9	96.2	30	
weighted mean		95.2	124	
<i>Gorilla gorilla</i>				
both sexes ¹	99.7 - 110.6	103.2	19	3.3
both sexes ²	78.6 - 116.5	105.8	25	
weighted means		104.7		
<i>Pan troglodytes</i>				
both sexes ¹	91.1 - 113.7	101.0	20	5.3
both sexes ²	96.8 - 118.9	104.3	28	
weighted mean		102.9		
<i>Pongo pygmaeus</i>				
both sexes ¹	90.7 - 109.1	98.3	29	4.6
both sexes ²	92.8 - 114.2	98.3	18	
weighted mean		98.3		
<i>Hylobates species</i>				
both sexes ¹	83.4 - 104.3	97.5	15	5.1
both sexes ²	92.5 - 108.7	99.4	15	
weighted mean		98.5		
<i>Symphalangus syndactylus</i>				
both sexes ¹	99.6 - 104.7	102.1	4	2.2

References: ¹ This author; ² Senut, 1978.

Table 16. Variation in the Intertubercular Sulcus / Humeral Head Index Amongst Extant Hominoidea & Old World Monkeys
(ISW / HHB X 100)

Taxon	Observed range	Mean of the Index Values	(n)	SD
<i>Homo sapiens</i>				
both sexes	9.7 - 39.9	22.8	(94)	5.5
<i>Gorilla gorilla</i>				
both sexes	10.3 - 30.5	18.4	(19)	6.1
<i>Pan troglodytes</i>				
both sexes	12.2 - 29.6	20.6	(20)	4.7
<i>Pongo pygmaeus</i>				
both sexes	18.0 - 46.1	26.3	(30)	6.2
<i>Hylobates</i> species				
both sexes	10.5 - 24.8	19.5	(15)	3.8
<i>Symphalangus syndactylus</i>				
both sexes	18.8 - 23.9	21.7	(4)	2.3
Monkeys (<i>Cercopithecus aethiops</i> & <i>Papio ursinus</i>)				
both sexes	26.6 - 44.7	34.0	(64)	5.3

The data presented in this table were calculated by the author.

Table 17. Variations in Humeral Torsion Amongst the Hominoidea

Taxon	Observed range	Mean	SD	(n)
<i>Homo sapiens</i>				
both sexes ¹	146.1 - 172.4	161.2	7.4	50
both sexes ²		162.8	9.2	98
both sexes ³		145.1	11.2	150
<i>Gorilla gorilla</i>				
both sexes ¹	136.7 - 147.5	143.1	3.3	4
both sexes ²		143.4	5.8	59
both sexes ³		137.3	9.4	29
both sexes ⁴		141.1		16
<i>Pan troglodytes</i>				
both sexes ²		141.1	5.8	65
both sexes ³		133.9	10.9	33
both sexes ⁴		128.1		12
<i>Pongo pygmaeus</i>				
both sexes ²		113.1	10.2	52
both sexes ³		119.5	12.7	14
both sexes ⁴		120.3		7
<i>Hylobates species</i>				
both sexes ²		113.5	10.9	80
both sexes ³		110.7	9.7	48
both sexes ⁴		112.0		10
<i>Symphalangus syndactylus</i>				
both sexes ³		113.8	12.7	8

The data in this table are derived from the work of ¹this author; ²Sarmiento (1985); ³Knussman (1967) and ⁴Broca (1898).

Table 18. *Metric characters of the glenoid cavities of the scapulae of australopithecines*

	Glenoid length (GL) mm	Glenoid breadth (GB) mm	Articular breadth (AB) mm	Glenoid depth (GD) mm	Glenoid index (GI) %
Sts 7	c38.0	22.0, 23.0 ^a	19.0, 19.5 ^a	1.5	58.0, 60.5 ^a
Stw 162	c37.0	25.8	17.1	1.0	69.7
A.E. 288-IL	25.7 ^b	18.1 ^c	-	-	67.5, 70.4

^aThe two values presented for the GB, AB and GI of Sts 7 are respectively based on the measurements of this author and of Vroba (1979).

^bThe GL measurement in this table is that published by Johanson et al. (1982). Senut (1978) has published a GL measurement for the same specimen of 26.3. The latter measurement is included in the GI values.

Table 19. *Metrical characters of the body of the scapulae of australopithecines*

	SGD millimetres	AML	IA	AGA
Sts 7	c12.0			120.0°
Stw 162	13.7			
Stw 431		c143.0 ^a	30° - 60°	
A.L. 288-IL	10.0 ^b			120.0°

SGD, spinoglenoid notch depth; AML, axillary margin length; IA, inferior angle; AGA, axilloglenoid angle.

^aThis measurement assumes that the axillary margin of Stw 431 is nearly complete at the superior point of damage.

^bThis measurement is determined from a cast of the specimen.

Table 20. Variation in the Length of the Scapular Axillary Margin Amongst Extant Hominoidea and Stw 431

Taxon	Observed range	Mean	(n)	SD
<i>Homo sapiens</i>				
male	108.0 - 150.6	131.9	(54)	9.3
female	101.8 - 136.8	119.7	(40)	7.9
both sexes	101.8 - 150.6	126.7	(94)	10.6
<i>Gorilla gorilla</i>				
male	203.0 - 253.5	231.1	(14)	15.5
female	172.5 - 187.7	182.8	(5)	5.95
both sexes	172.5 - 253.5	218.4	(19)	27.9
<i>Pan troglodytes</i>				
male	135.6 - 167.5	151.9	(11)	10.2
female	135.5 - 161.1	149.1	(9)	10.4
both sexes	135.5 - 167.5	152.5	(20)	10.3
<i>Pongo pygmaeus</i>				
male	137.1 - 183.3	167.1	(10)	15.1
female	112.6 - 157.0	139.3	(19)	11.0
both sexes	112.6 - 183.3	148.9	(29)	20.1
<i>Hylobates</i> species				
male	56.0 - 84.4	73.8	(9)	9.3
female	66.9 - 80.5	73.6	(6)	5.1
both sexes	56.0 - 84.4	73.7	(15)	7.7
<i>Symphalangus syndactylus</i>				
male	85.0	(85.0)	(1)	
female	86.8 - 94.5	90.8	(3)	3.9
both sexes	85.0 - 94.5	89.4	(4)	4.3
<i>Stw 431</i>	143.0*			

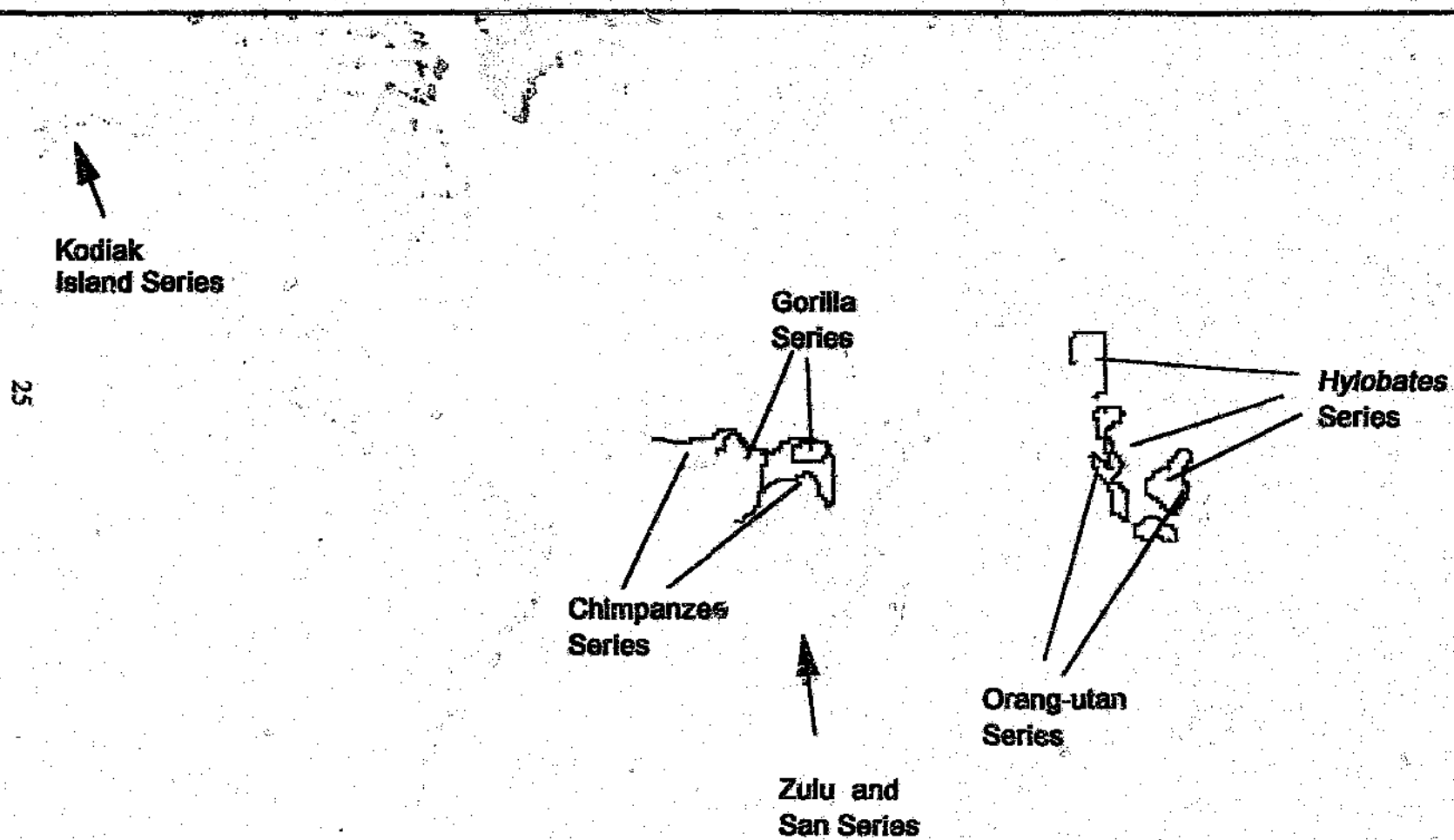
The data presented in this table were collected by the author. * As discussed in the text, the length of the axillary margin for Stw 431 presented in this table represents this author's "best guess".

Table 21. *Metrical characters of the humeral heads of australopithecines (millimetres)*

	mediolateral head diam. (MHD)	anteroposterior head diam. (AHD)	humeral head index (%) (HHI)	intertubercular sulcus width (ISW)	mid-shaft diam. (MSD)	humerus length (HL)
Sts 7 ¹	39.9	35.1	88.0	c5.0		
Stw 328 ¹	34.0			c5.0		
Stw 517 ¹	c36.3	34.0	93.7	c6.0		
A.L. 288-1r ²	31.1	c26.8	86.2			236.8
A.L. 333-107 ³	39.5	c34.6	86.1	c7.8	c30.0	
A.L. 333-109 ³				c8.5		
Omo 119-2718 ⁴	c40.7	c38.0	93.4	c8.0		
KNM-ER 739 ⁵				c10.0		

The data in this table were derived from measurements taken by ¹this author; ²Johanson et al., 1982; ³Lovejoy et al., 1982; ⁴Pickford, 1973; ⁵Leakey et. al., 1973.

Figure 1. Distribution of extant hominoid species examined in the present study.



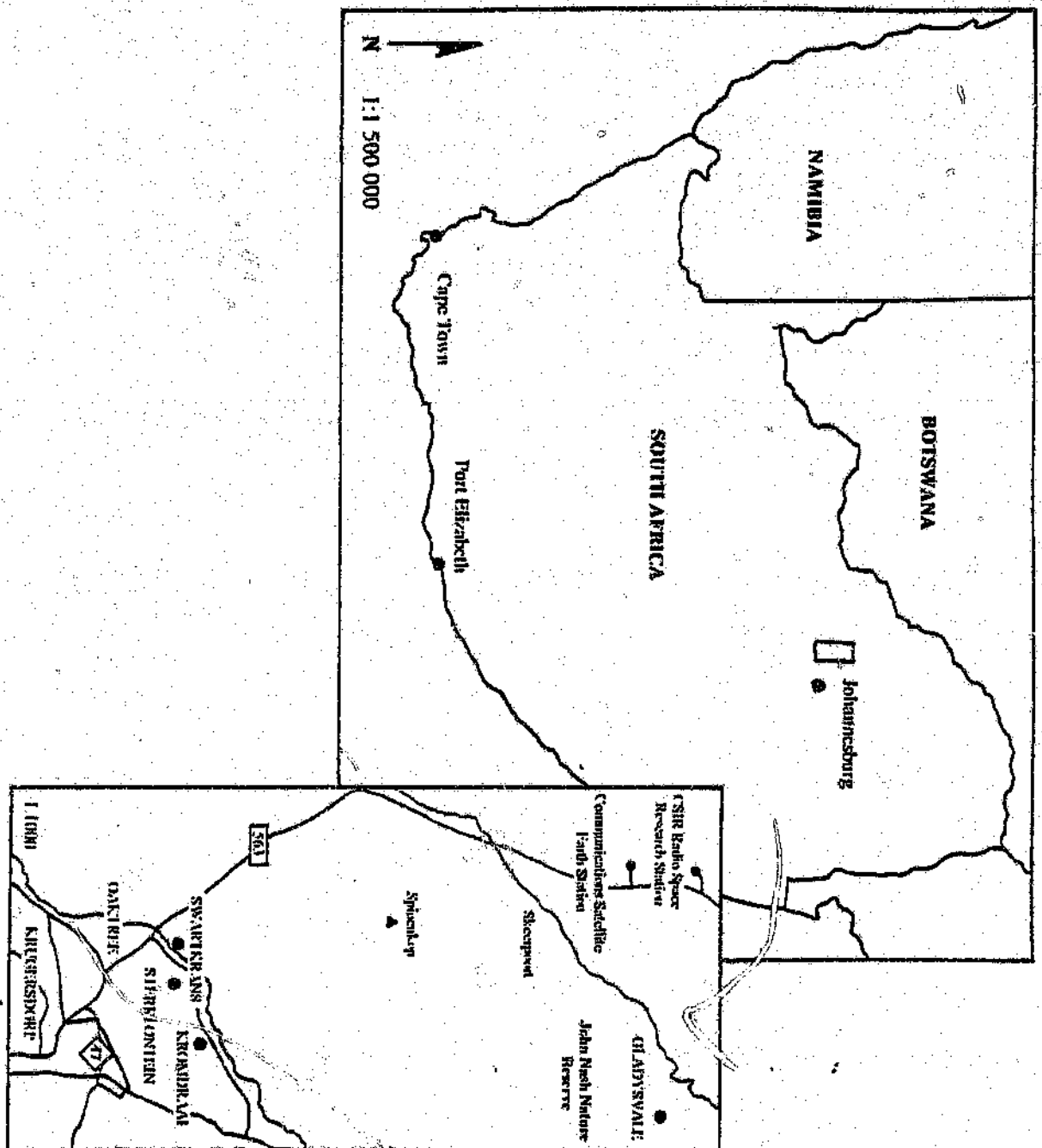


Figure 2. Map of South African early hominid fossil sites in the Krugersdorp District illustrating the position of Sterkfontein relative to other well known localities where early hominid fossils have been discovered.

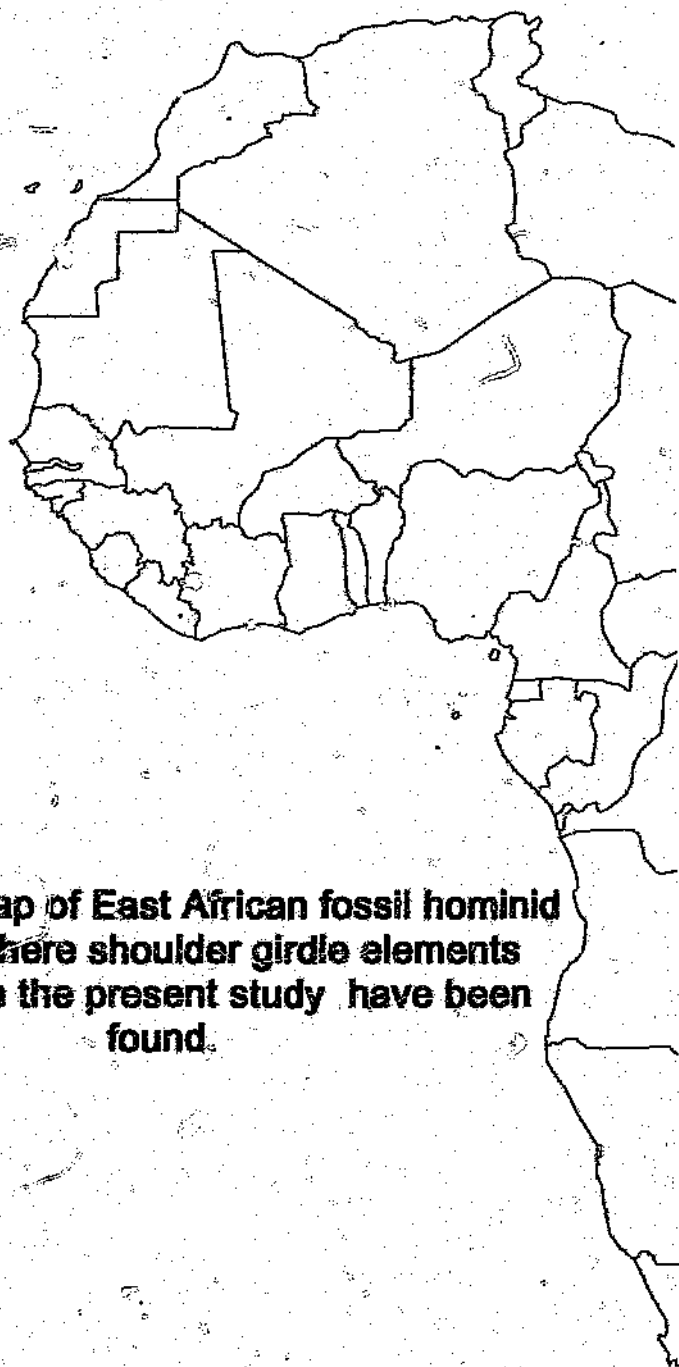


Figure 3. Map of East African fossil hominid localities where shoulder girdle elements examined in the present study have been found.

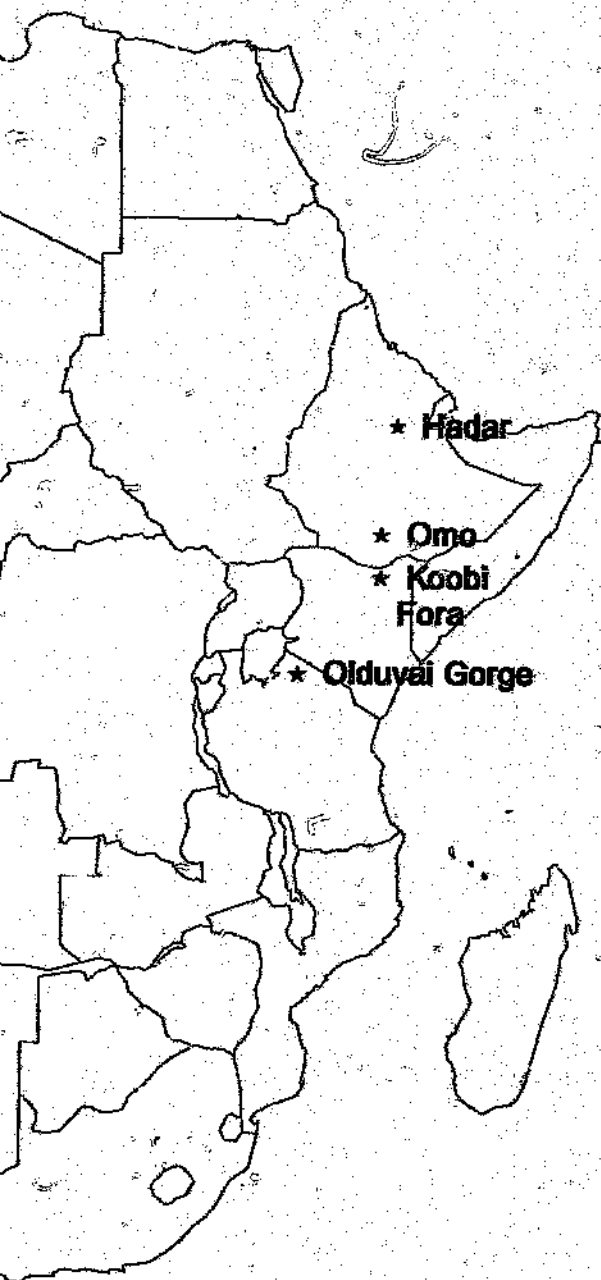
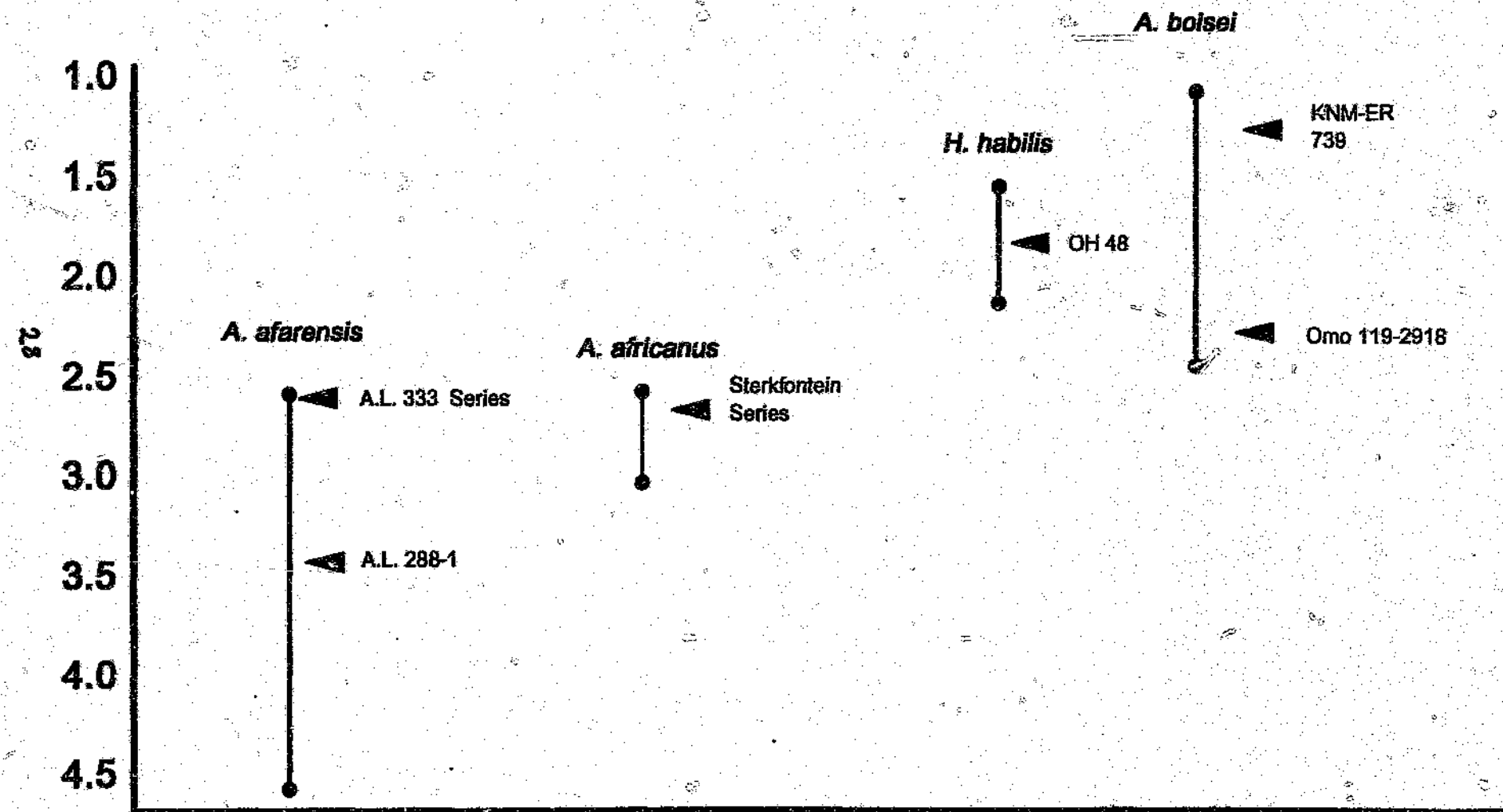


Figure 4. Approximate chronologic relationships of Plio-Pleistocene African Hominids. Chronologic relationships established by radiometric and faunal evidence as discussed in the text.

m.y.a.



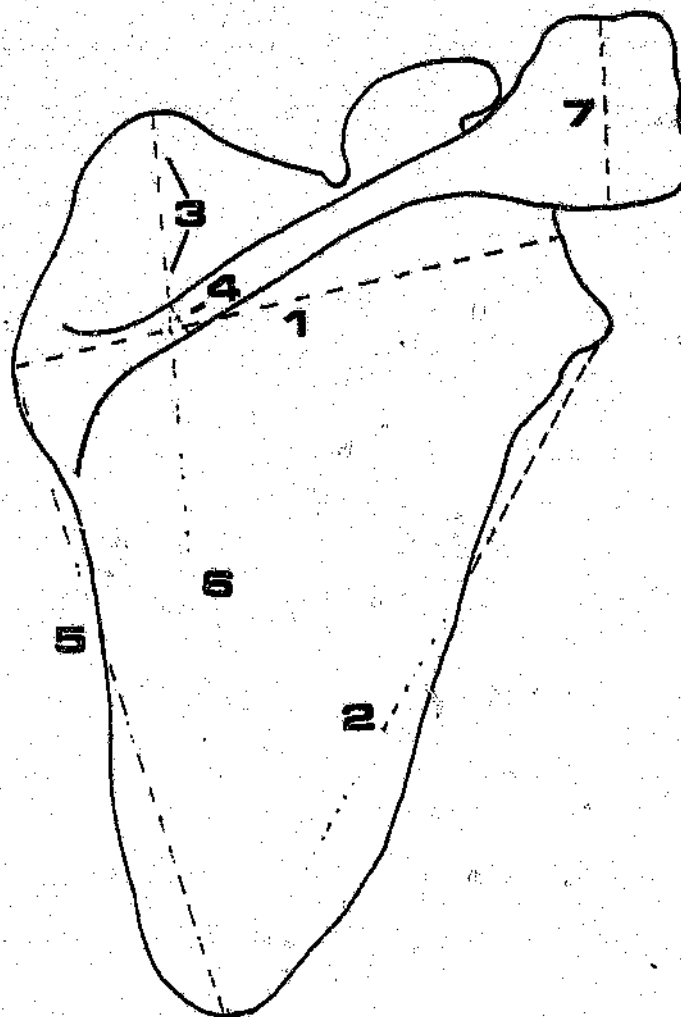


Figure 5a. Dorsal view of a human scapula illustrating landmarks and distances, as defined in the text.

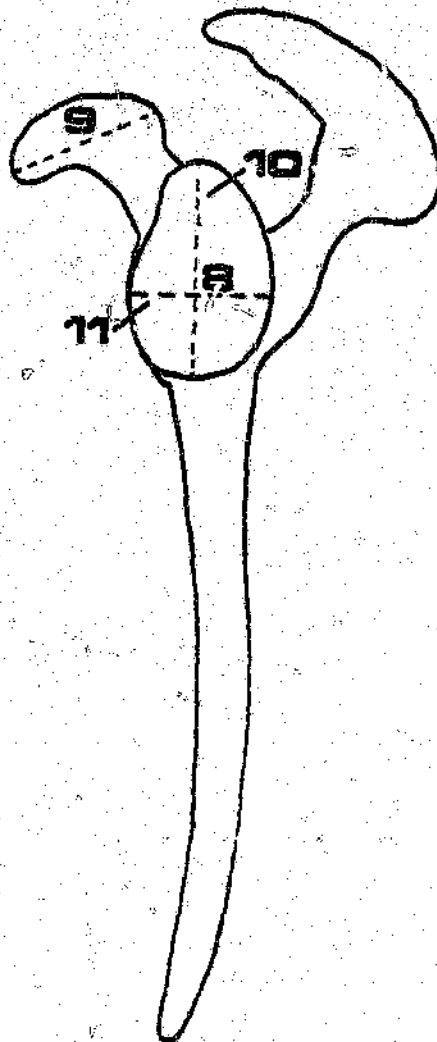


Figure 5b. Lateral view of a human scapula illustrating landmarks and distances, as defined in the text.

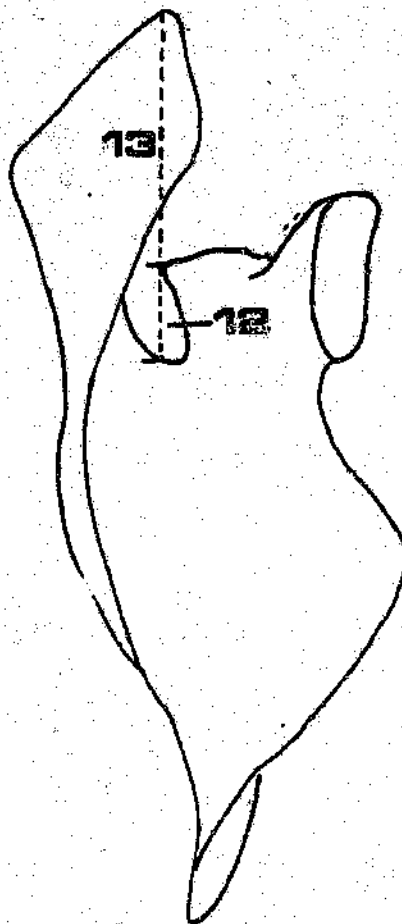


Figure 5c. Superior view of a human scapula illustrating landmarks and distances, as defined in the text.

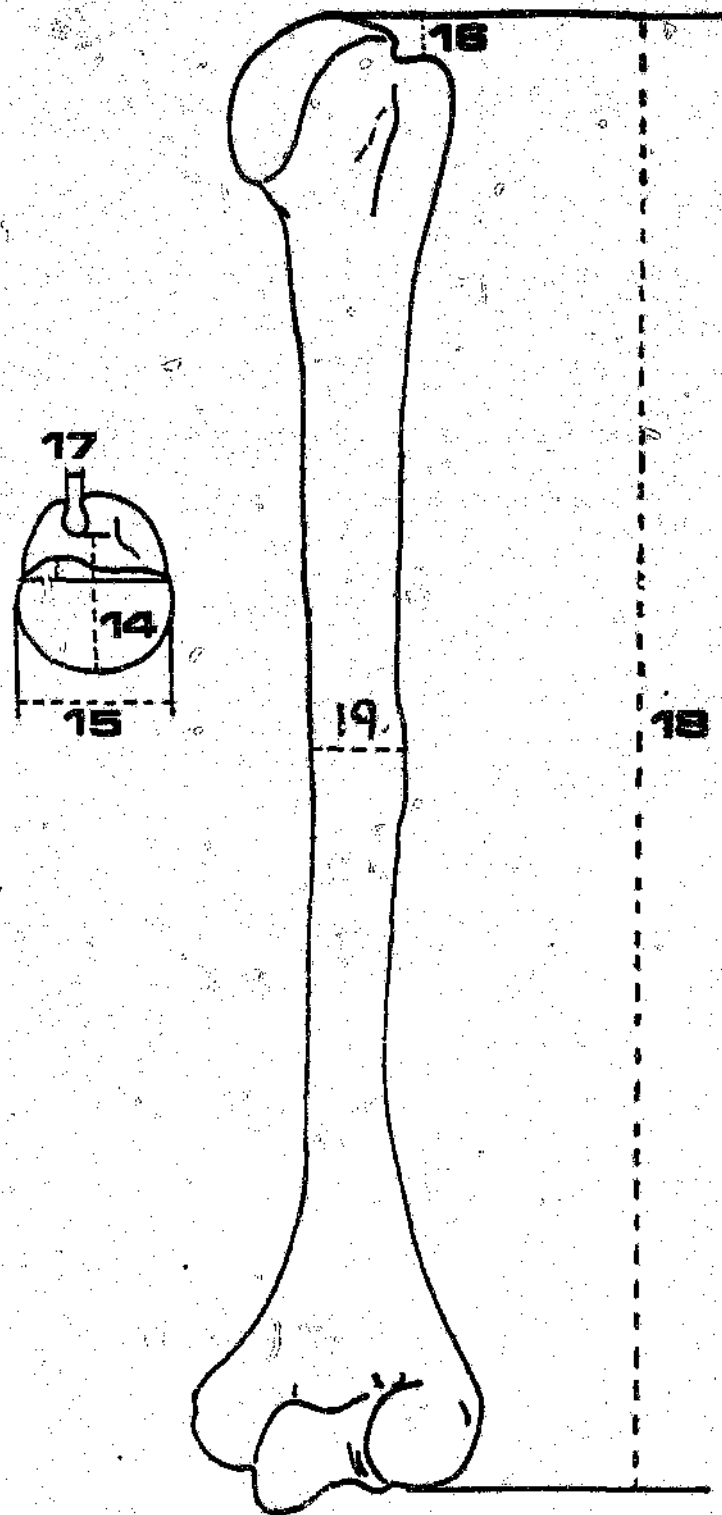


Figure 6. Superior and dorsal view of a right human humerus illustrating landmarks and distances, as defined in the text.

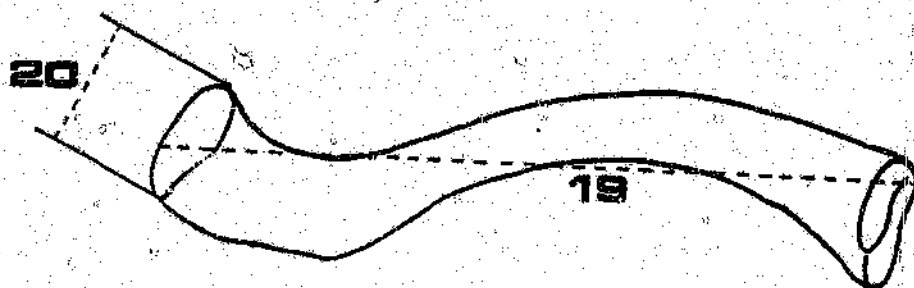


Figure 7. Inferior view of a left human clavicle illustrating landmarks and distances, as defined in the text.

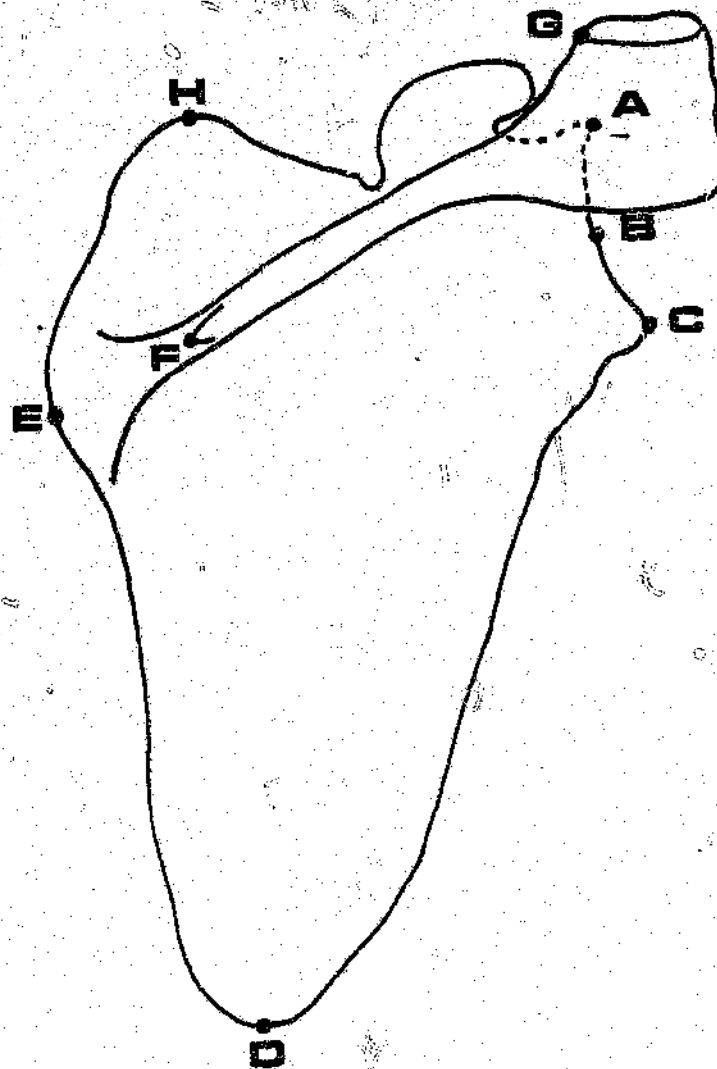


Figure 8. Dorsal view of a human scapula illustrating landmarks used in the calculation of angles. Landmarks are defined in the text.

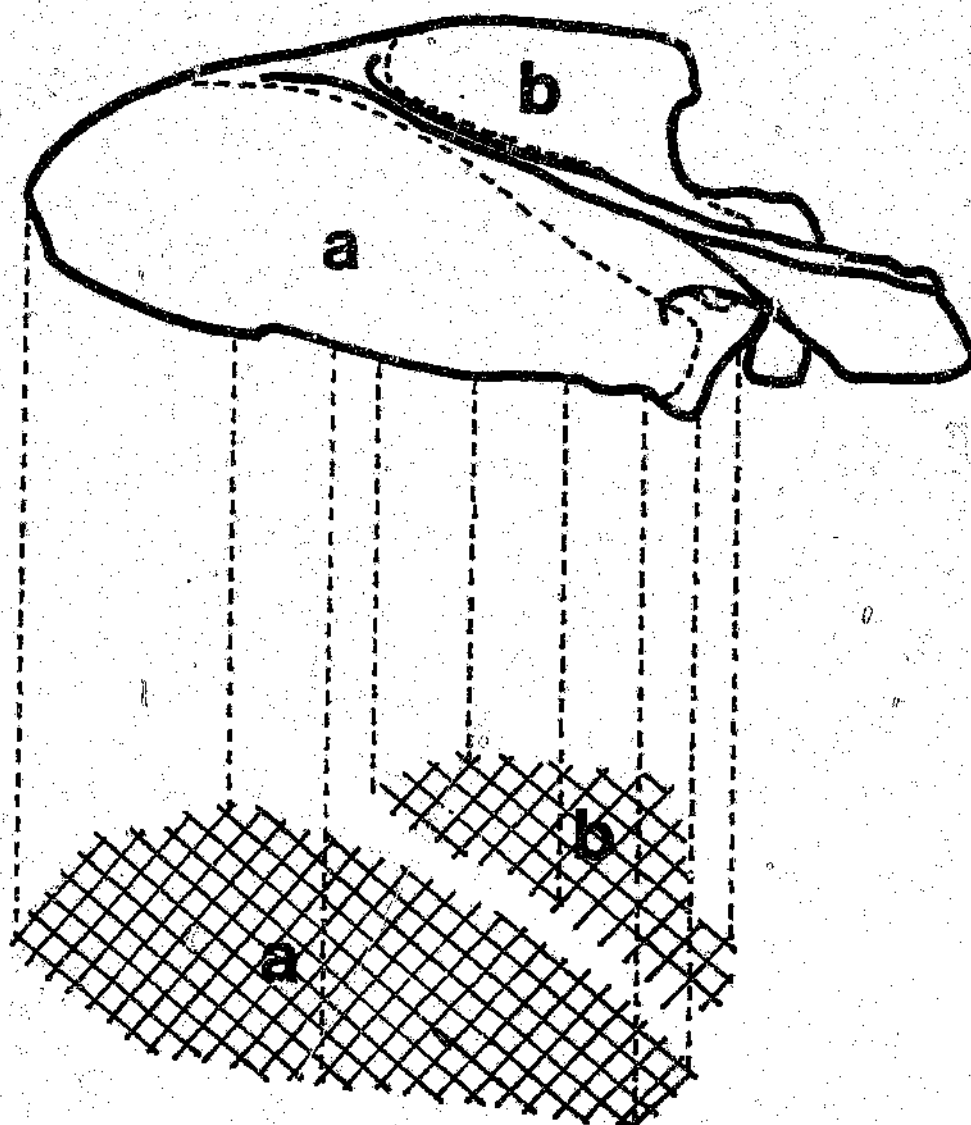


Figure 9. Two dimensional diagrammatic consideration of the areas of the infraspinous (a) and supraspinous (b) fossae traced during area calculation using the image analysis technique of scapular surface area reconstruction.

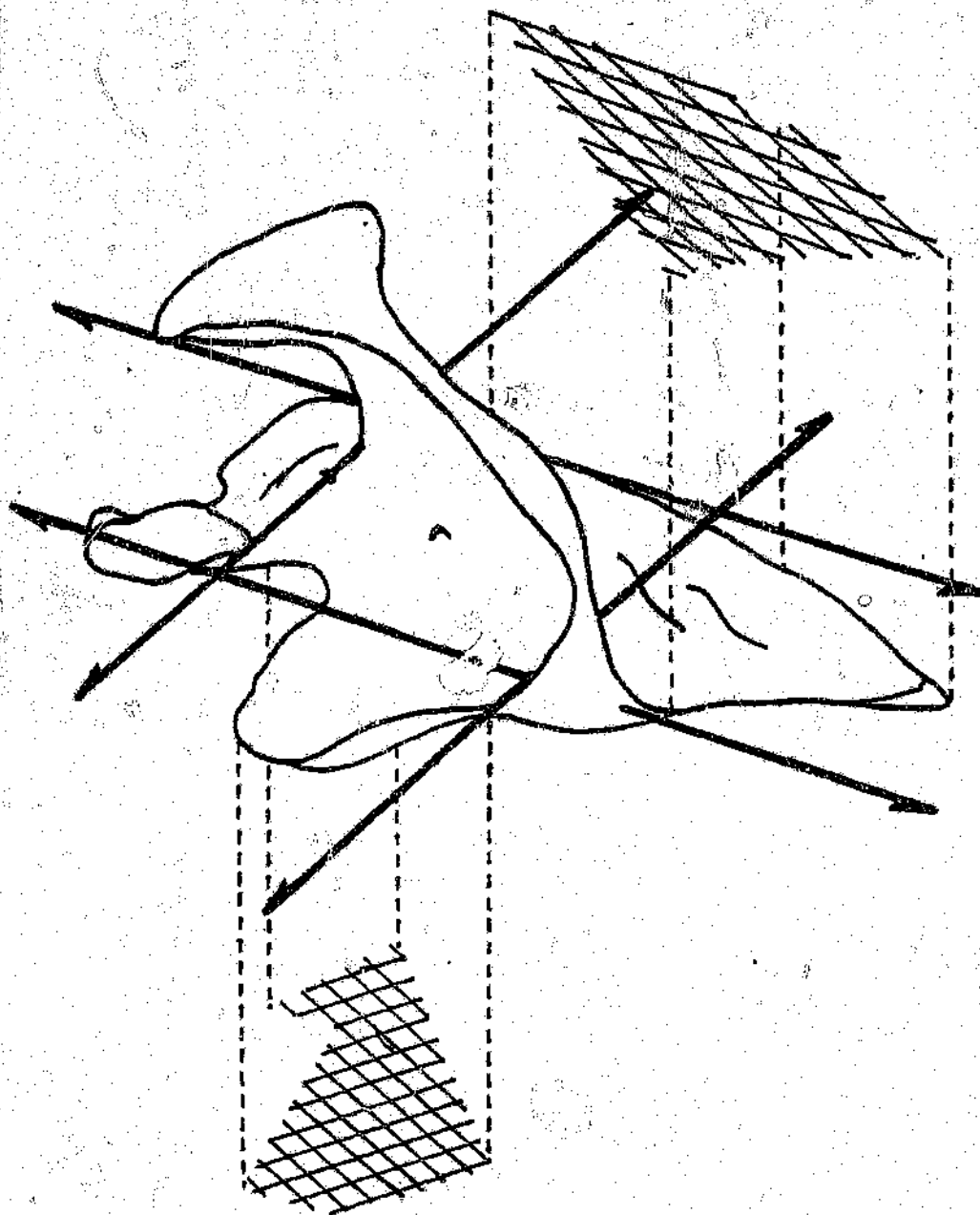
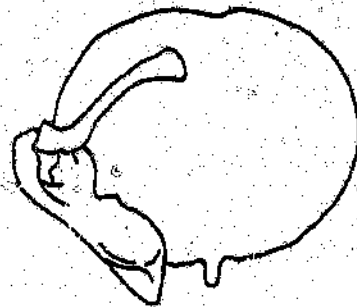


Figure 10. Diagrammatic consideration of the two-dimensionality of the areas of the infraspinous and supraspinous fossae of a human scapula when traced using the image analysis technique of scapular surface area reconstruction.

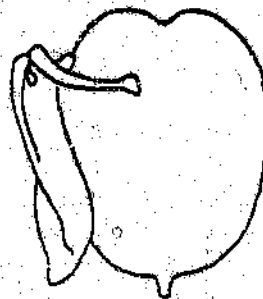


Figure 11. The position of the scapula and the clavicle on the thorax in a quadrupedal monkey and in a bipedal human, illustrated from the cranial view. Note that the blade of the scapula in the quadruped is positioned laterally on the thorax and the glenoid cavity faces anteriorly. The blade of the scapula in humans is positioned on the posterior aspect of the thorax and the glenoid cavity faces more laterally than in the quadruped. Based on illustrations of macaques and humans in Schultz (1950).

Anterior



Human



Monkey

Posterior

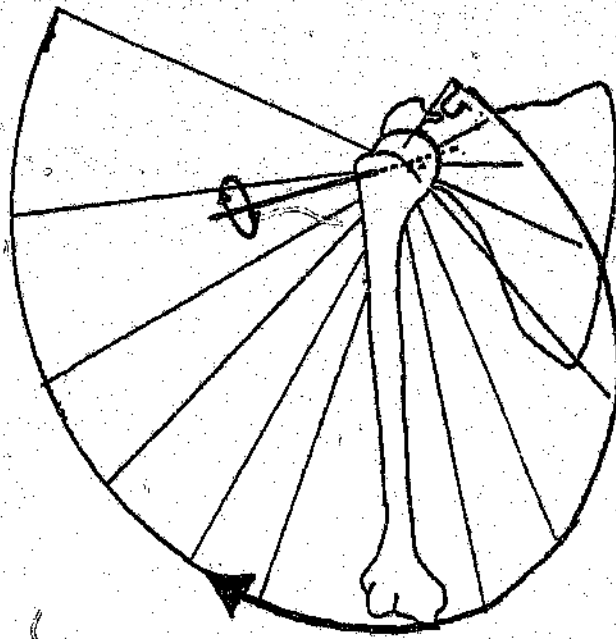


Figure 12. A two-dimensional reconstruction of the degrees of freedom of movement of the human shoulder girdle. Since the head of the humerus is offset from the shaft, spin occurs between the glenoid cavity and the humeral head but the shaft of the humerus traces part of the surface of a cone (after Williams *et al.*, 1989).

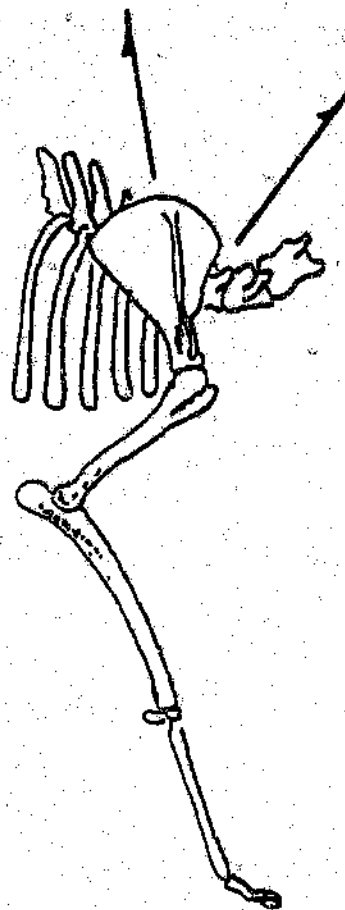


Figure 13. The thorax, scapula and forelimb of an antelope showing the morphology of a typical terrestrial quadruped. The arrows indicate the primary directions of force that pass from the forelimb through the scapula.

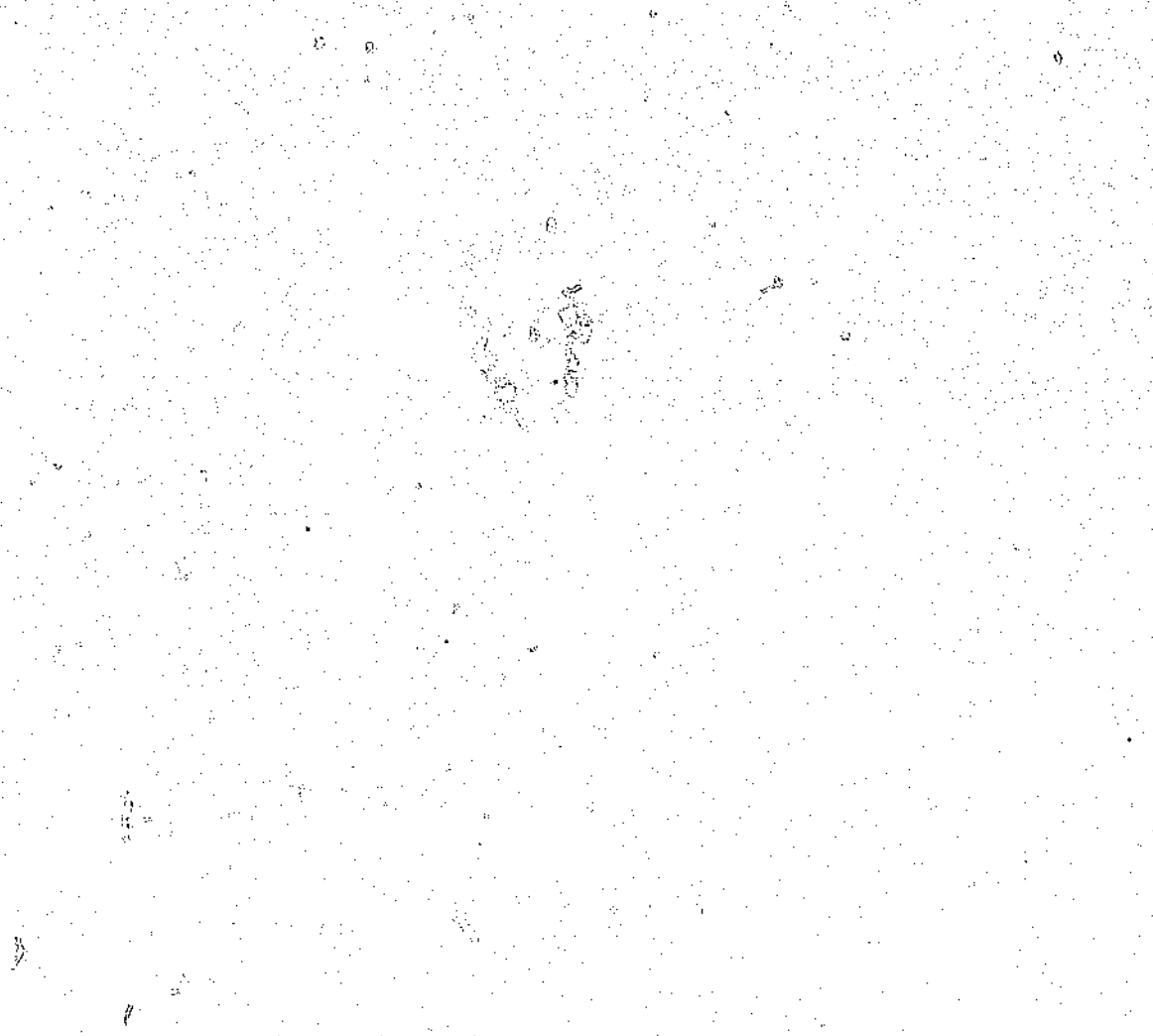
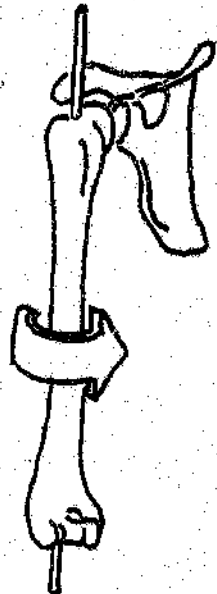
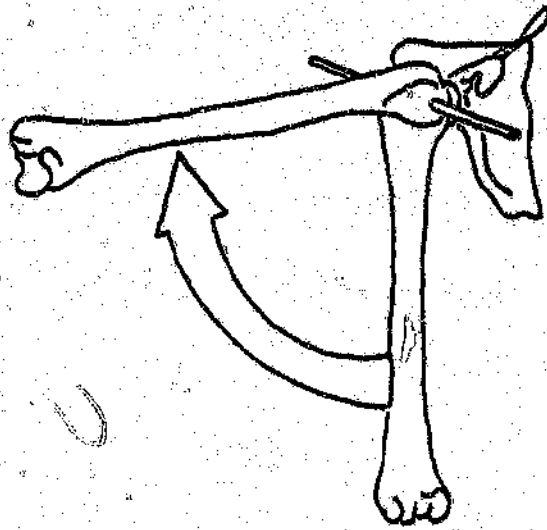
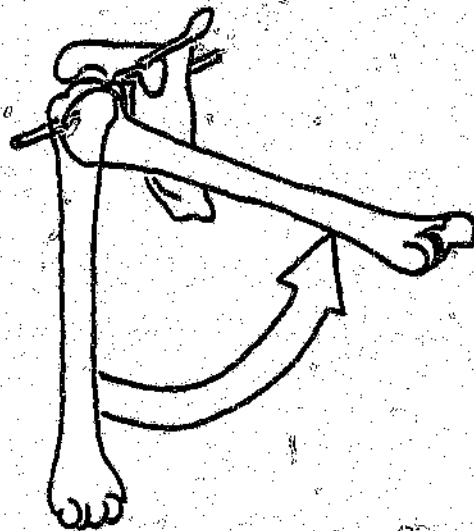


Figure 14. The three degrees of freedom in the hominoid glenohumeral joint. The three axes around which the principal movements of flexion-extension (a), abduction-adduction (b) and medial and lateral rotation (c) occur are shown. All movements of the shoulder joint are described in relation to the plane of the scapula and not to the coronal or sagittal planes of the body. Whilst many additional movements may occur at the shoulder joint these may always be resolved into components related to these three axes. Model adapted from Williams *et al.* (1989).



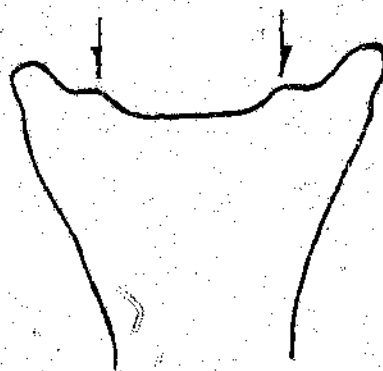


Figure 15. Diagrammatic representation of the attachment areas of the glenoid labrum on a human scapular glenoid cavity. The arrows point to the raised bony ridge that is created by the labrum at its attachment areas adjacent to the margin of the glenoid cavity. The shaded area indicates the extent of encroachment of the attachment area onto the surface.

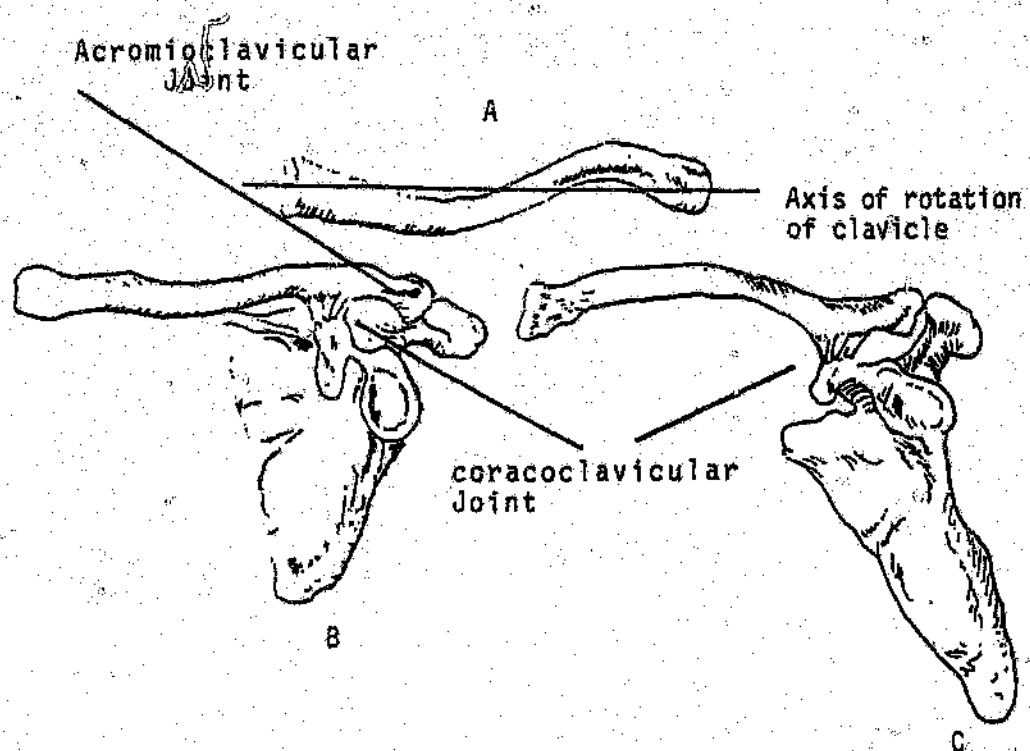


Figure 16. Rotation of the clavicle at the acromioclavicular and sternoclavicular joints in combination with the rotation and angulation of the scapula in a human. The line passing mediolaterally through the clavicle indicates the axis around which the joints allow rotation of the clavicle. Note that, while the inferior part of the body of the scapula angles cranially during rotation of the clavicle, the glenoid cavity maintains its lateral direction of orientation (after Inman *et al.*, 1944).

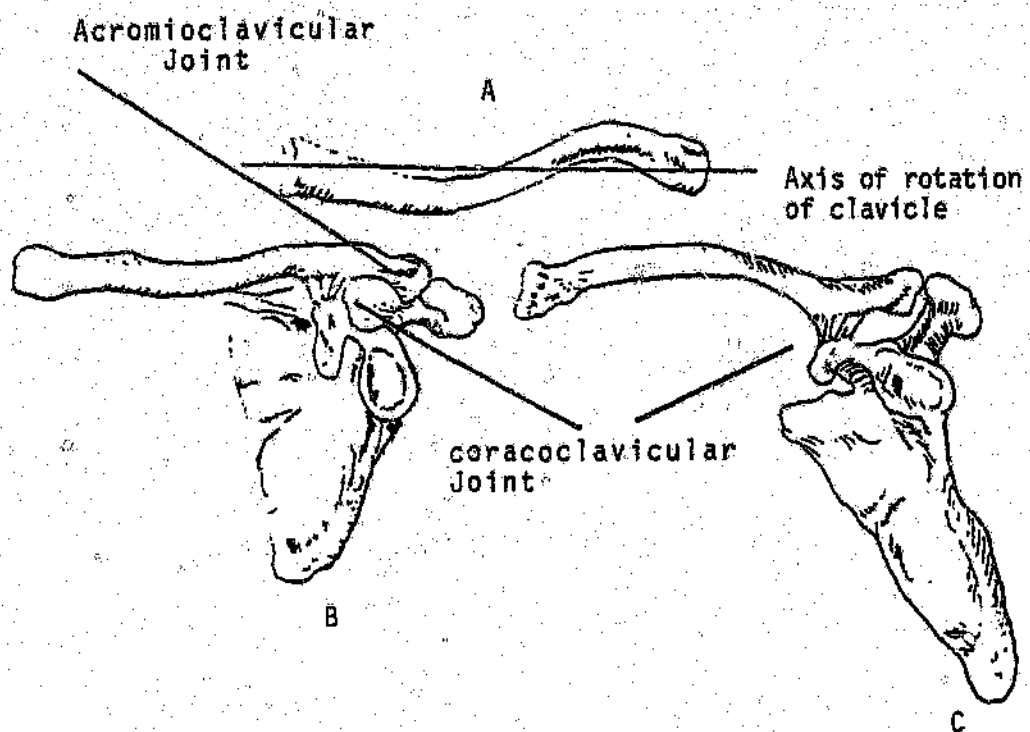
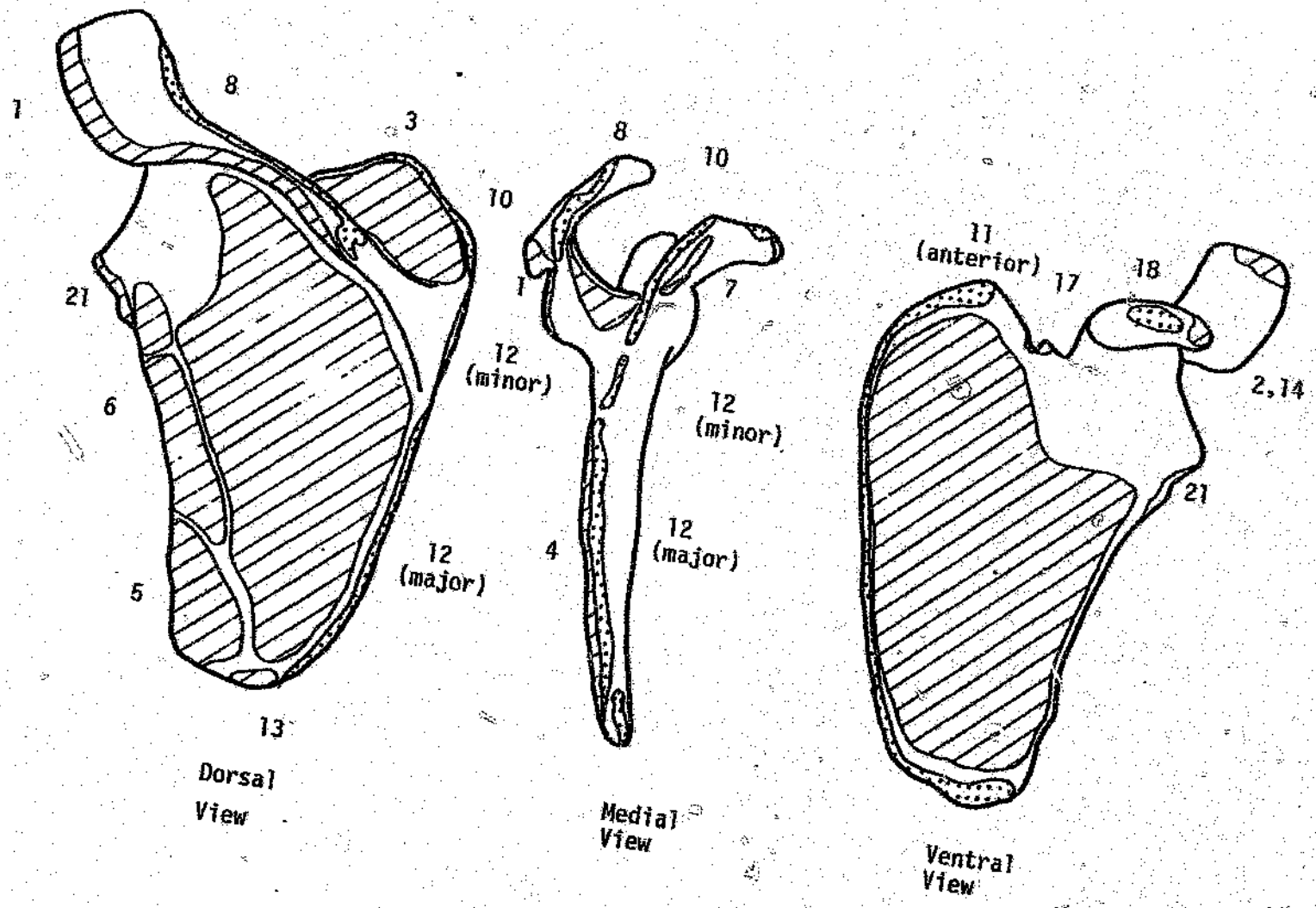


Figure 16. Rotation of the clavicle at the acromioclavicular and sternoclavicular joints in combination with the rotation and angulation of the scapula in a human. The line passing mediolaterally through the clavicle indicates the axis around which the joints allow rotation of the clavicle. Note that, while the inferior part of the body of the scapula angles cranially during rotation of the clavicle, the glenoid cavity maintains its lateral direction of orientation (after Inman *et al.*, 1944).

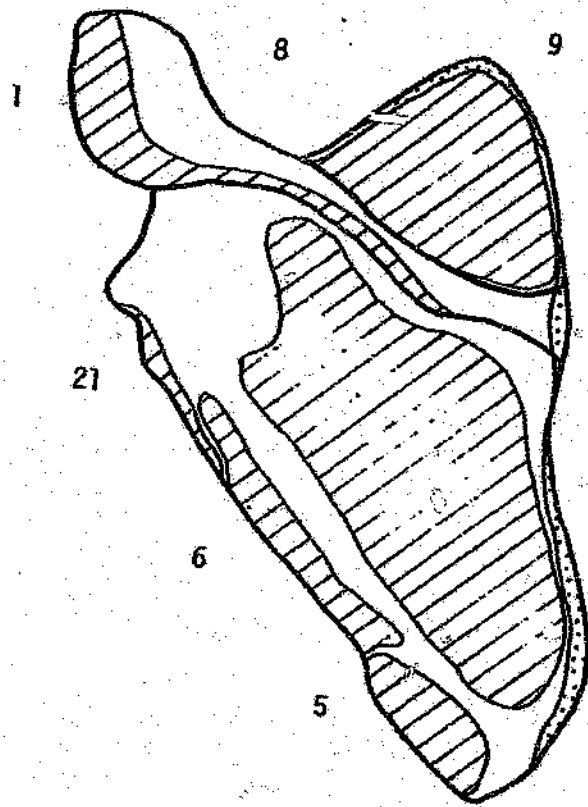
Figures 17 - 28. Muscle origins and insertions of the hominoid shoulder girdle.

1. The deltoid muscle
 2. The biceps muscle
 3. The supraspinatus muscle
 4. The infraspinatus muscle
 5. The teres major muscle
 6. The teres minor muscle
 7. The subscapularis muscle
 8. The trapezius muscle
 9. The atlantoscapularis muscle
 10. The levator scapulae muscle
 11. The serratus magnus pars cranialis muscle or the serratus anterior muscle.
 12. The rhomboid muscles
 13. The latissimus dorsi muscle
 14. The coracobrachialis muscle
 15. The subclavius muscle
 16. The atlantoclavicularis muscle
 17. The omohyoid muscle
 18. The pectoralis minor muscle
 19. The pectoralis major muscle
 20. The triceps muscle
 21. The sternocleidomastoid muscle
-

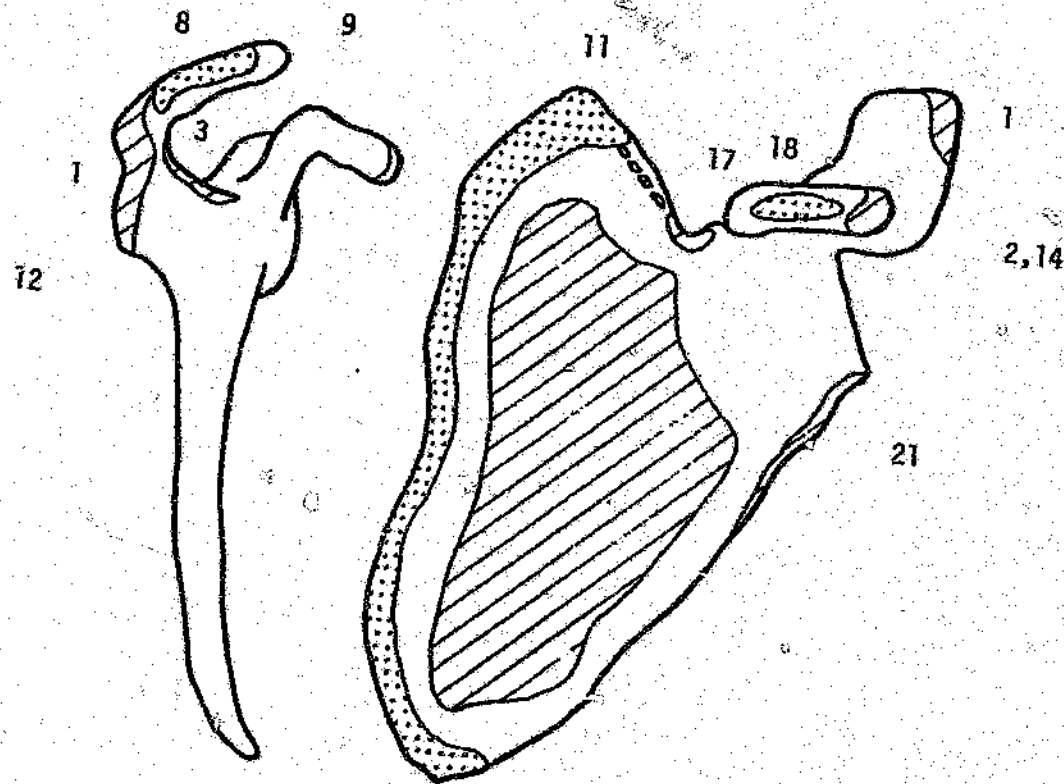
Muscle origins are marked in parallel lines, muscle insertions are marked in stippling. All bones are illustrated from the left.



The Human Scapula
Figure 17



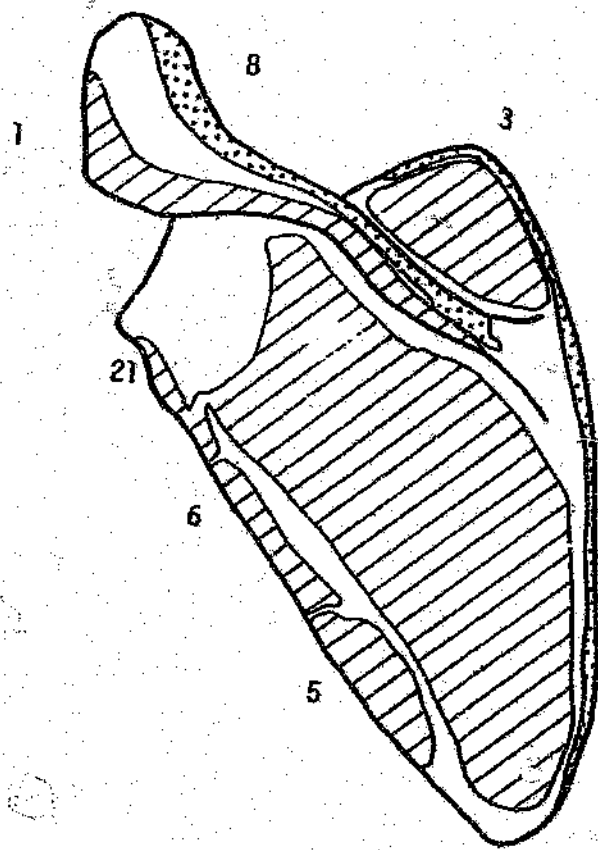
Dorsal
View



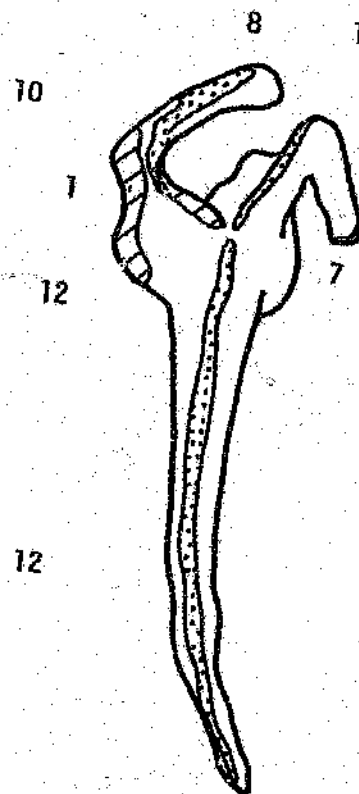
Medial
View

Ventral
View

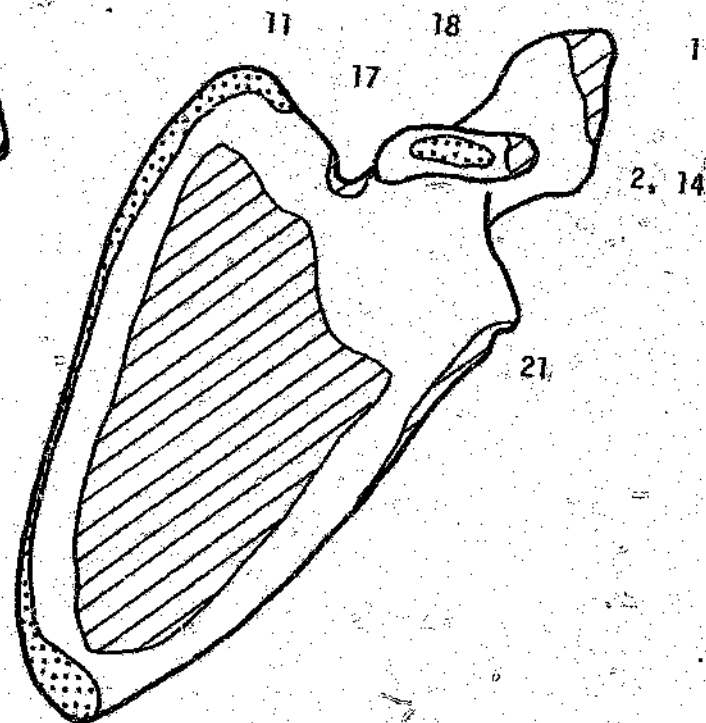
The Chimpanzee & Gorilla
Scapula
Figure 18



Dorsal
View

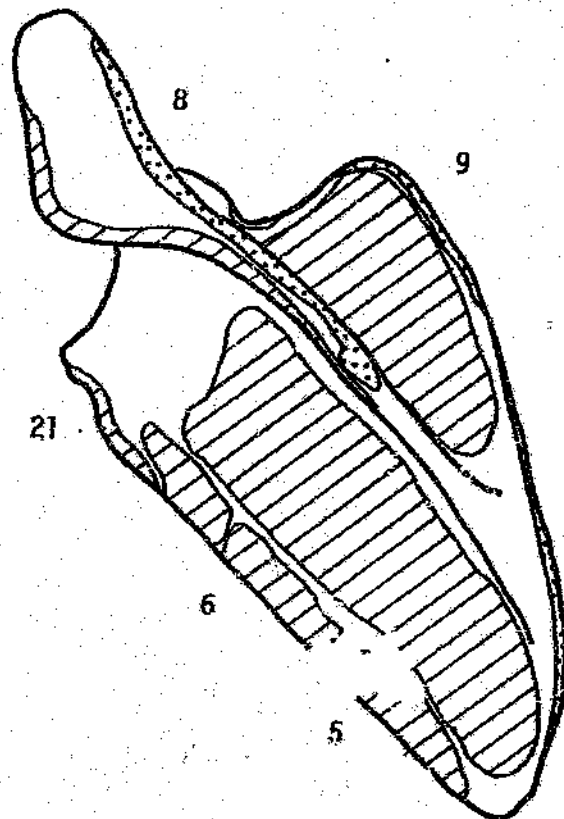


Medial
View



Ventral
View

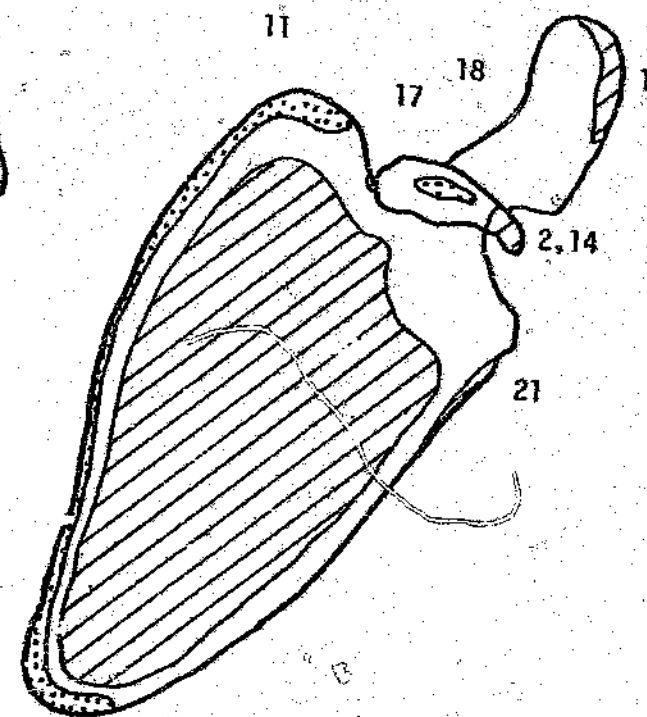
The Orang-utan Scapula
Figure 19



Dorsal View



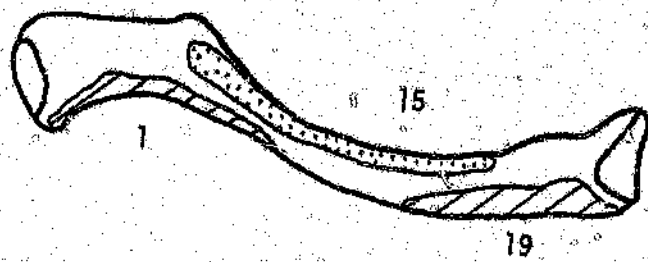
Medial View



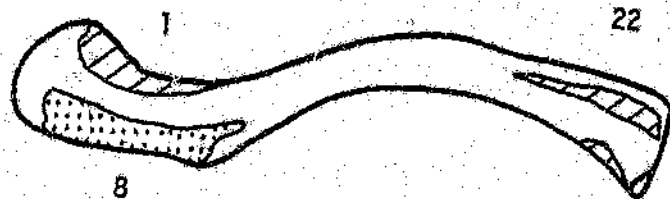
Ventral View

The Hylobatid Scapula
Figure 20

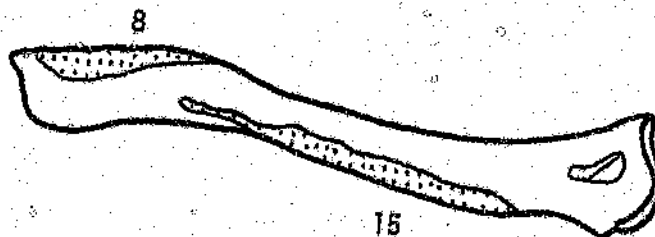
Inferior
View



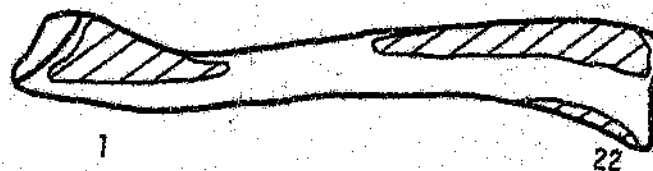
Superior
View



Dorsal
View

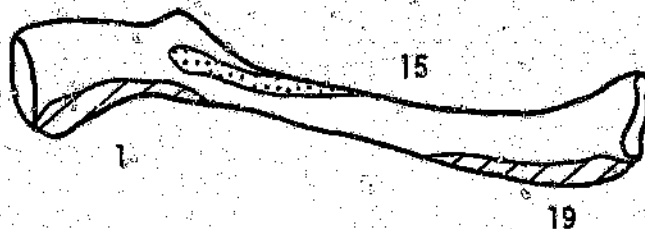


Ventral
View

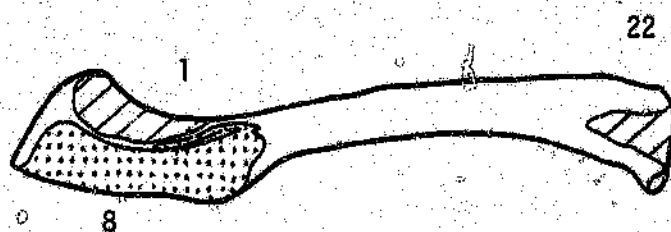


The Human Clavicle
Figure 21

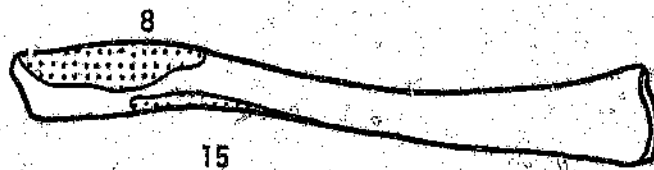
Inferior
View



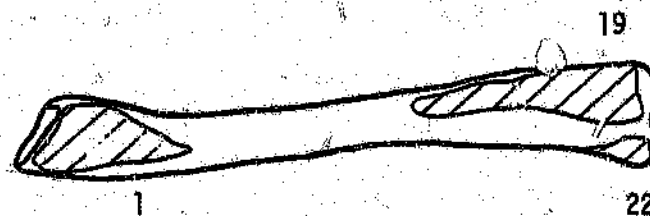
Superior
View



Dorsal
View

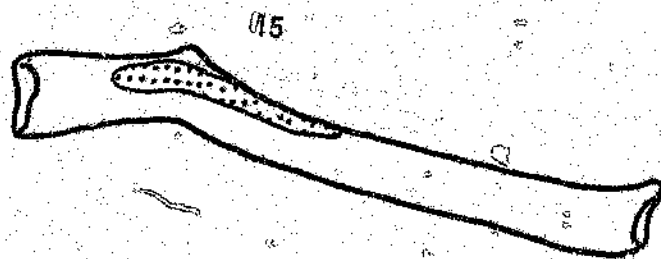


Ventral
View

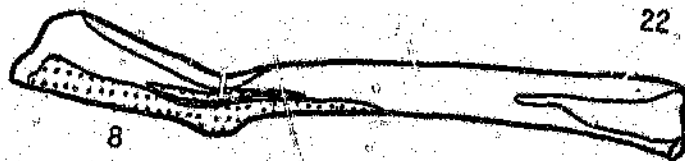


The Chimpanzee & Gorilla Clavicle
Figure 22

Inferior
View



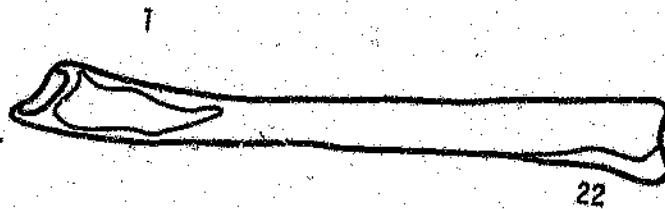
Superior
View



Dorsal
View

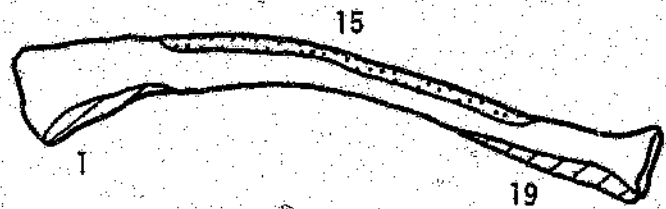


Ventral
View

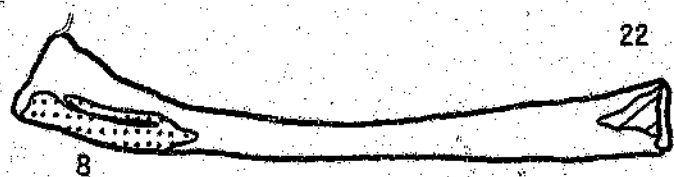


The Orang-utan Clavicle
Figure 23

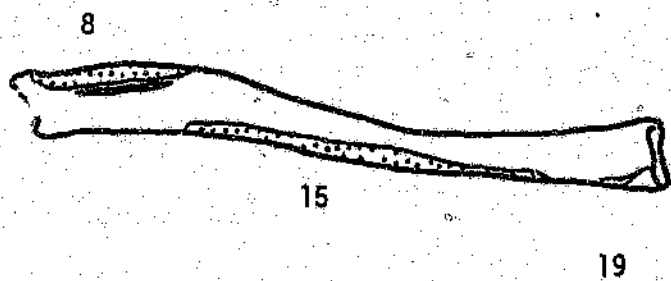
Inferior
View



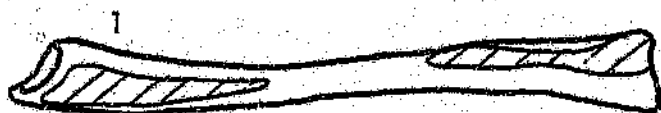
Superior
View



Dorsal
View



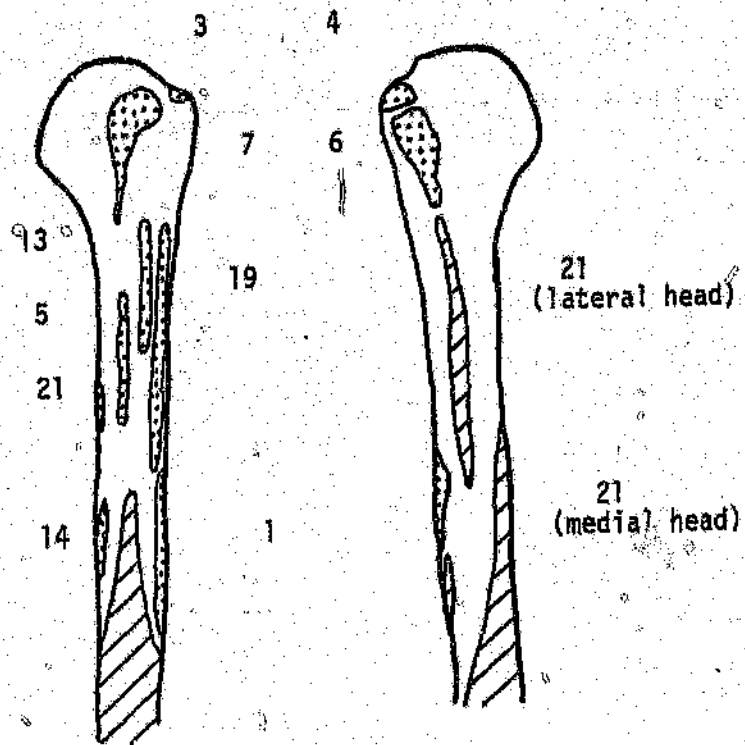
Ventral
View



The Hylobatid Clavicle
Figure 24

Anterior

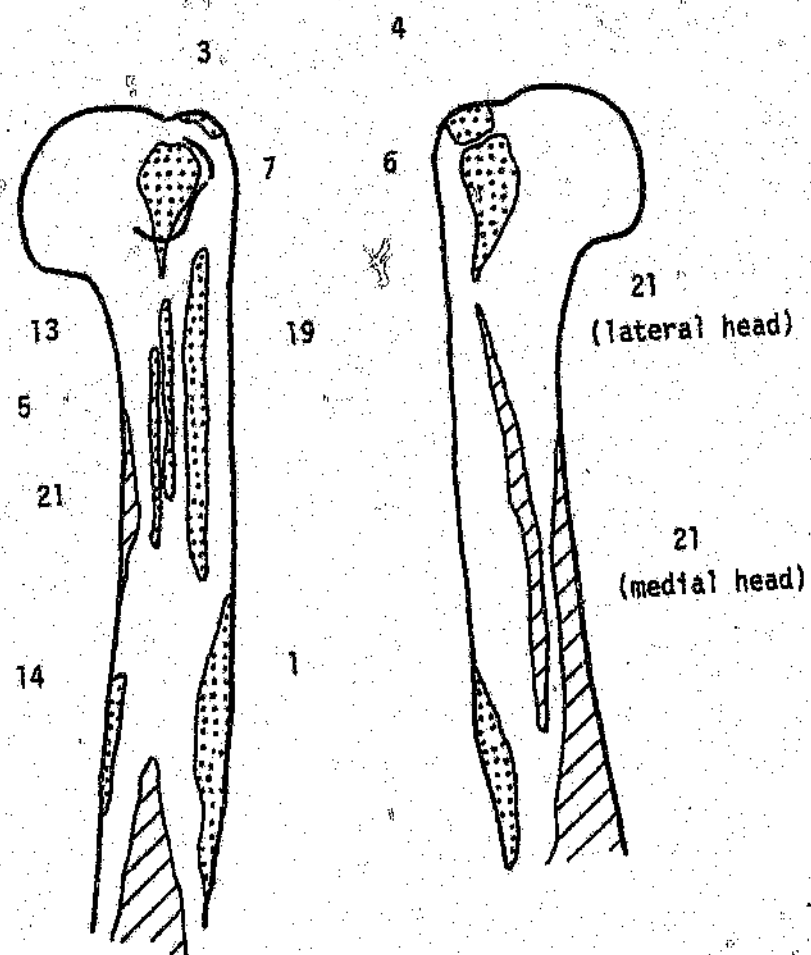
Posterior



The Human Humerus
Figure 25

Anterior

Posterior

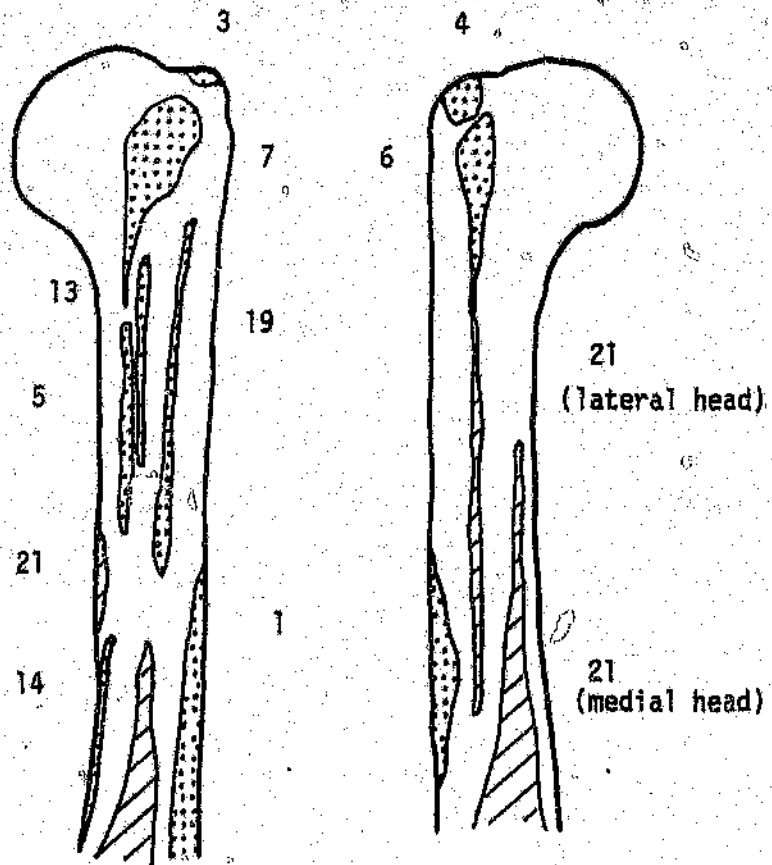


The Gorilla & Chimpanzee
Humerus

Figure 26

Anterior

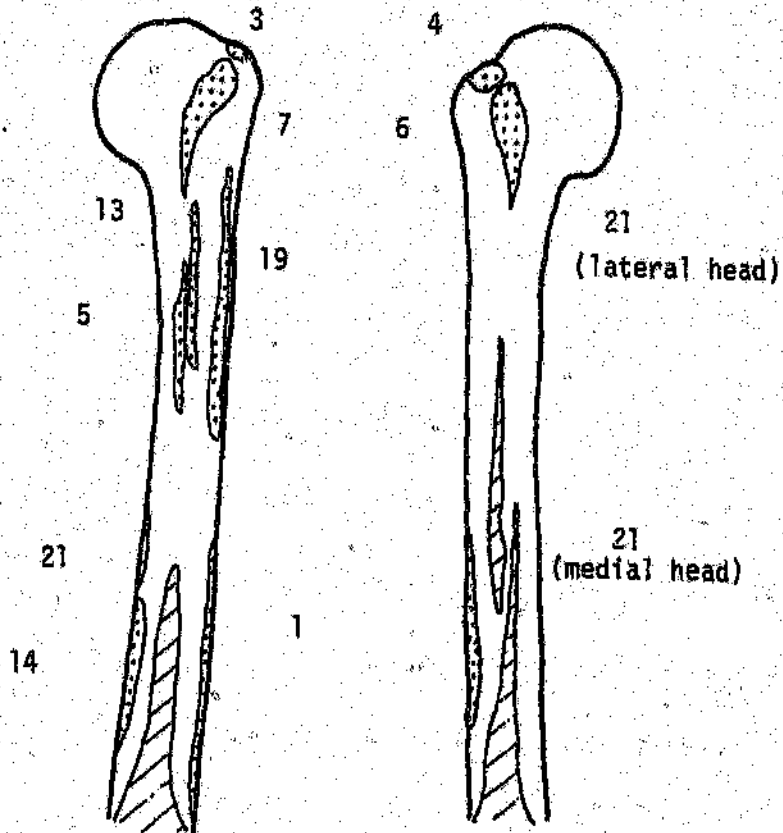
Posterior



The Orang-utan Humerus
Figure 27

Anterior

Posterior



The Hylobatid Humerus
Figure 28



Figure 29. A composite (right) hominoid scapula with morphological features illustrated and labelled. Views are dorsal (top left), ventral (top right) and lateral (lower centre).

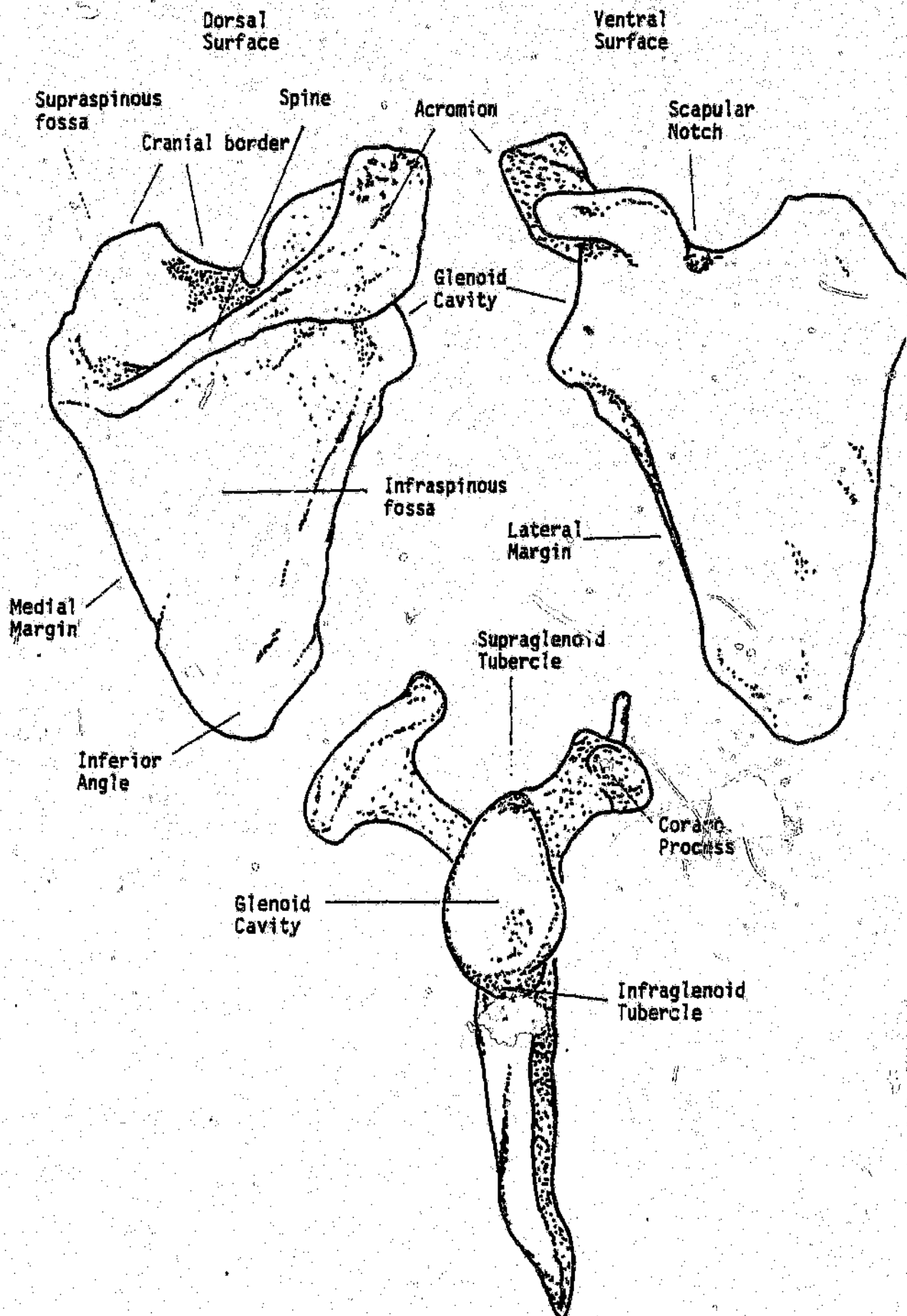


Figure 30. A composite (right) hominoid clavicle with morphological features illustrated and labelled. Views are superior and inferior.

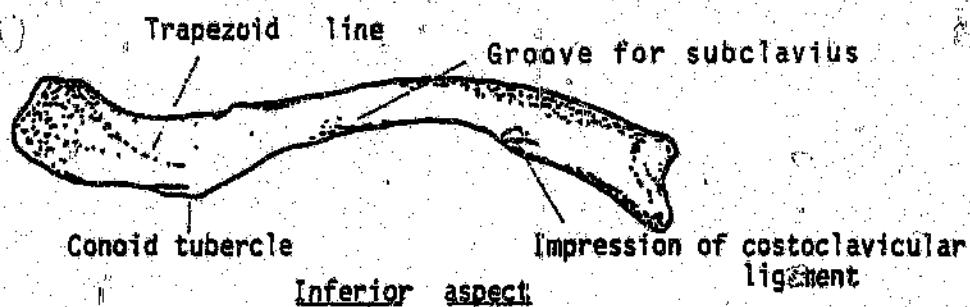
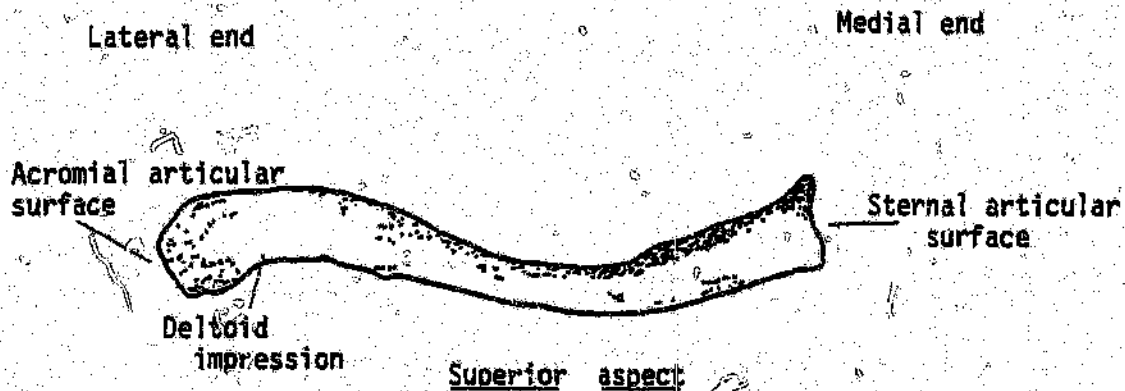


Figure 31. A composite (right) hominoid humerus with morphological features illustrated and labelled. Views are anterior, medial, posterior and superior.

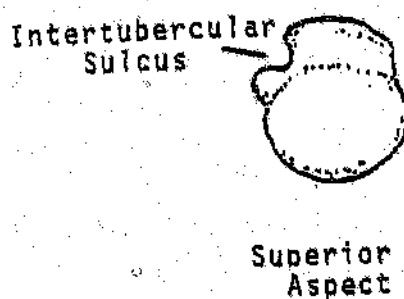
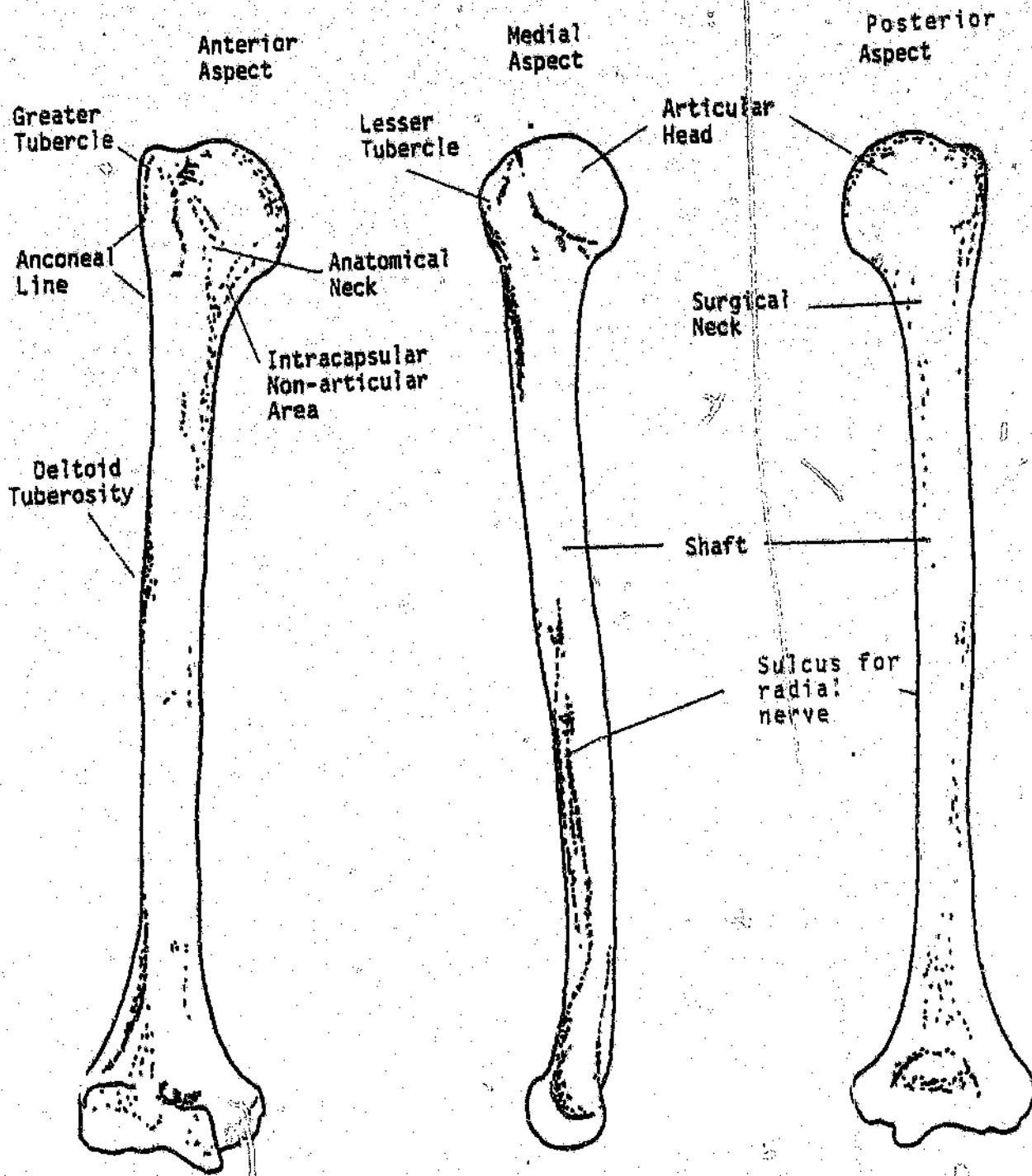
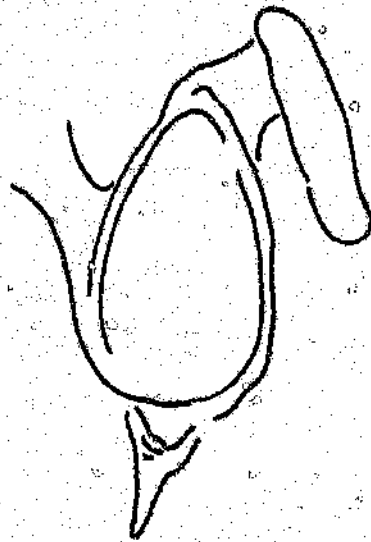


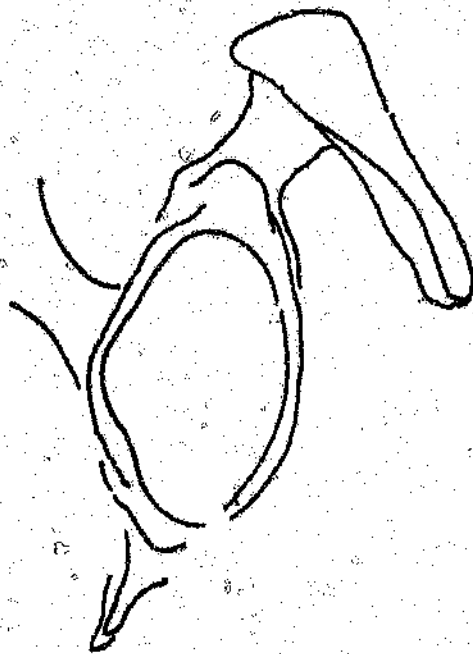
Figure 32. Shapes of the (right) scapular glenoid cavity in various hominoids. Note that the glenoid cavities of non-human hominoids tend to be more ovoid in outline than the glenoid cavity of humans. Glenoid cavities are drawn approximately to scale.



Human



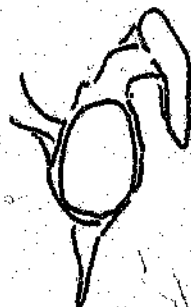
Orang-utan



Gorilla



Chimpanzee



Hylobates

Figure 33. Comparisons of glenoid index values for modern hominoid scapulae. Vertical line, sample mean; horizontal line, observed sample range; shaded rectangle, mean ± 1 standard deviation. The standard deviation for the hylobatid sample exceeds the observed range due to the small sample size used in this study.

Figure 33. Comparison of Hominoid Scapular Glenoid Shape
Glenoid Index (GB/GL x 100) *

Mod. Human

Gorilla

Chimpanzee

Orang-utan

Hylobates



* This author's data

Spinoglenoid Notch Depth vs. Glenoid Cavity Maximum Breadth In Extant Hominoids

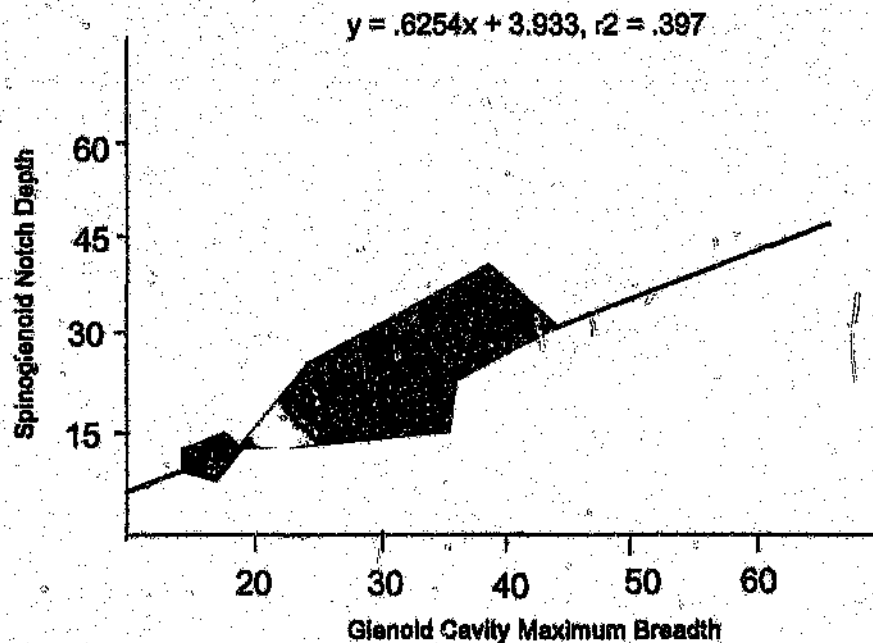


Figure 34. Bivariate plot of spinoglenoid notch depth vs. glenoid cavity maximum breadth. Shaded area indicates the observed limits of the range of variation for this relationship in the extant hominoid species examined in the present study. Data collected by the author.

Spinoglenoid Notch Depth vs. Glenoid Cavity Maximum Length

$$y = .464x + 2.098, r^2 = .577$$

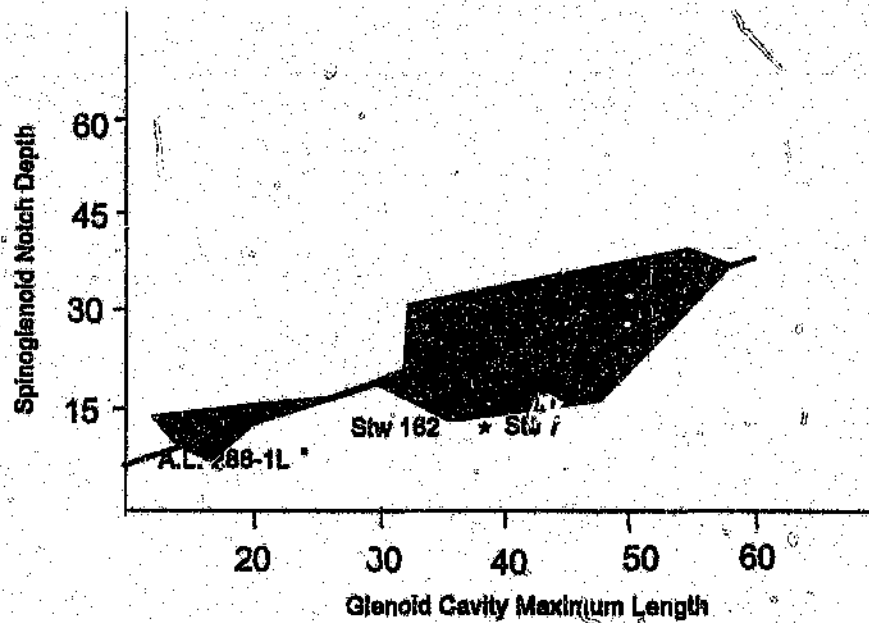


Figure 35. Bivariate plot of spinoglenoid notch depth vs. glenoid cavity maximum length. Shaded area indicates the observed limits of the range of variation for this relationship in the extant hominoid species examined in the present study. Data collected by the author.

Spinoglenoid Notch Depth vs. Glenoid Cavity Maximum Breadth In Extant Hominoids and Monkeys

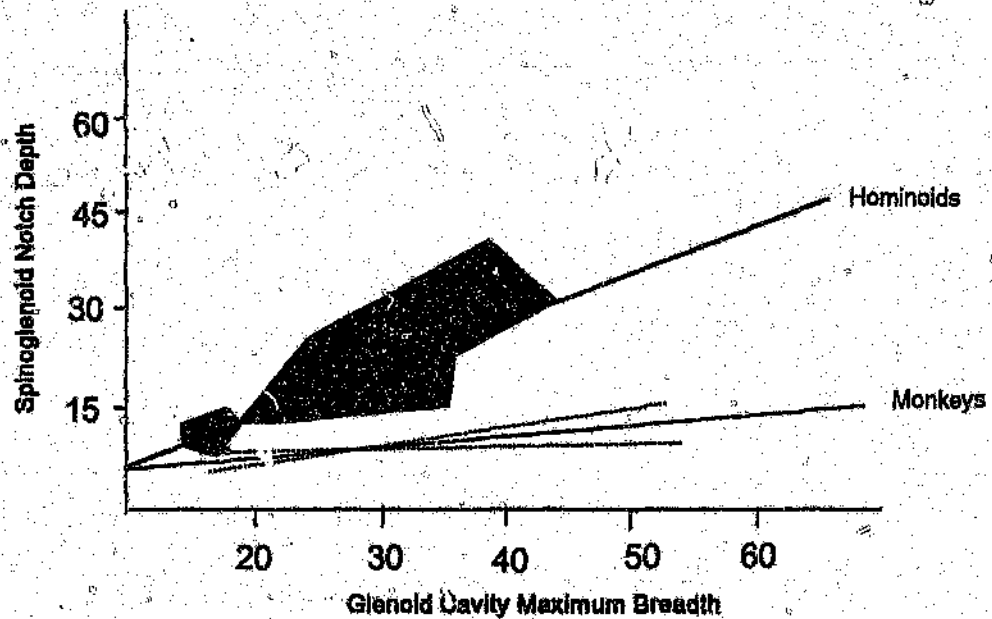
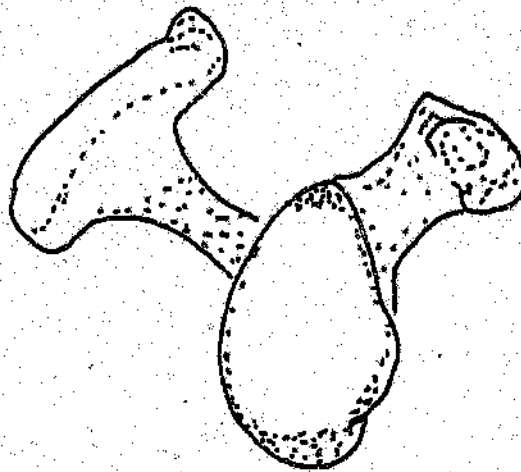
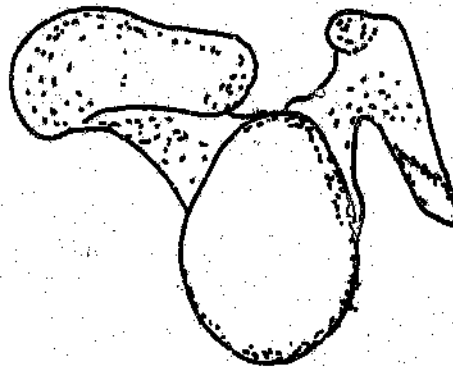


Figure 36. Bivariate plot of spinoglenoid notch depth vs. glenoid cavity maximum breadth. Shaded area indicates the observed limits of the range of variation for this relationship in the extant hominoid species examined in the present study. - Dashed lines indicate 95% confidence intervals for monkeys. Data collected by the author.



Human



Chimpanzee

Figure 37. Illustrations of the differences in orientation of the coracoid process between chimpanzee and human scapulae. Figures are drawn approximately to scale.

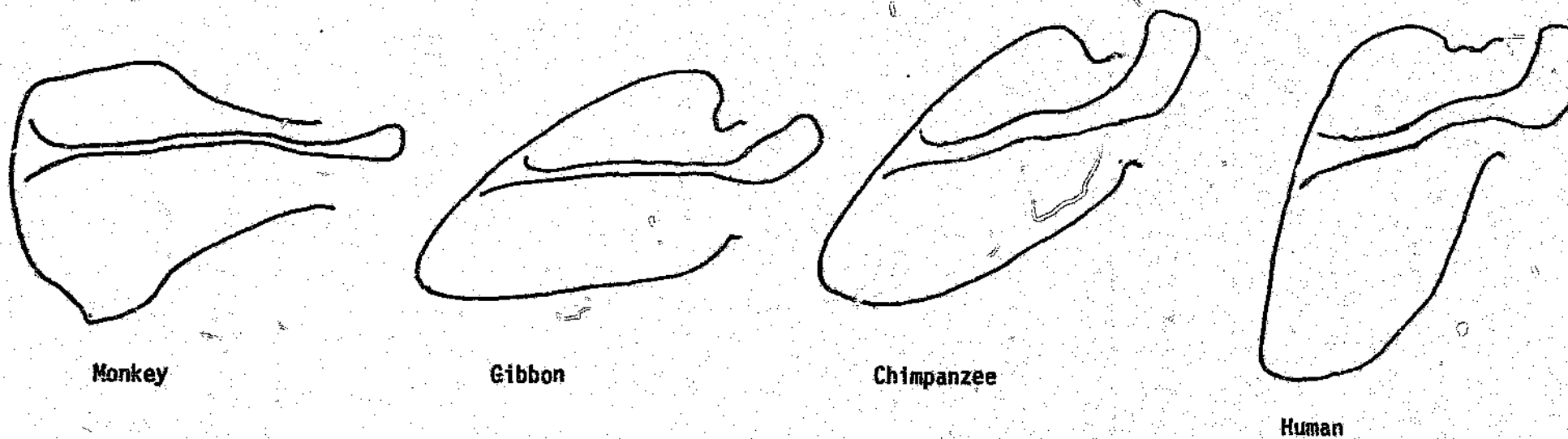


Figure 38. Comparison of the shape of the body of scapula among hominoid genera and monkeys. Note the similarity between the scapular body shape of the hylobatids and that of the monkey.

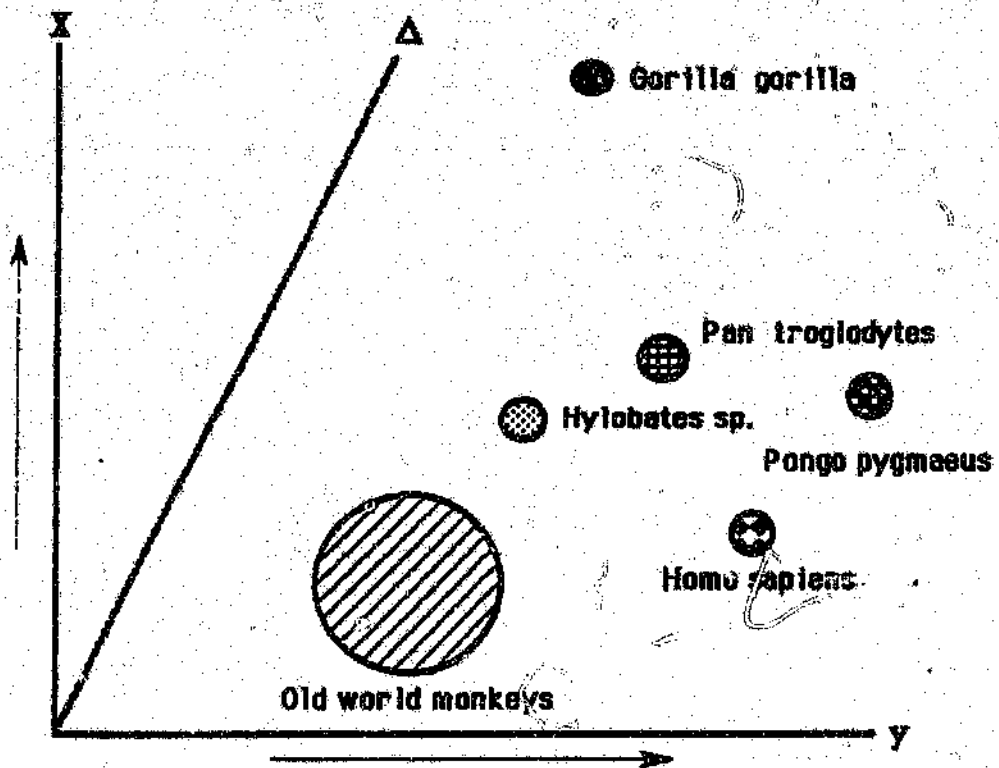


Figure 39. Bivariate plot of the supraspinous index and the infraspinous index in hominoids and Old World monkeys. x , supraspinous index; y , infraspinous index; Δ , the line of regression where the area of the supraspinous fossa equals the area of the infraspinous fossa. Modified from Roberts (1974).

Area of Infraspinous Fossa vs. Area of Supraspinous Fossa

$$y = .592x + 764.3, r^2 = .802$$

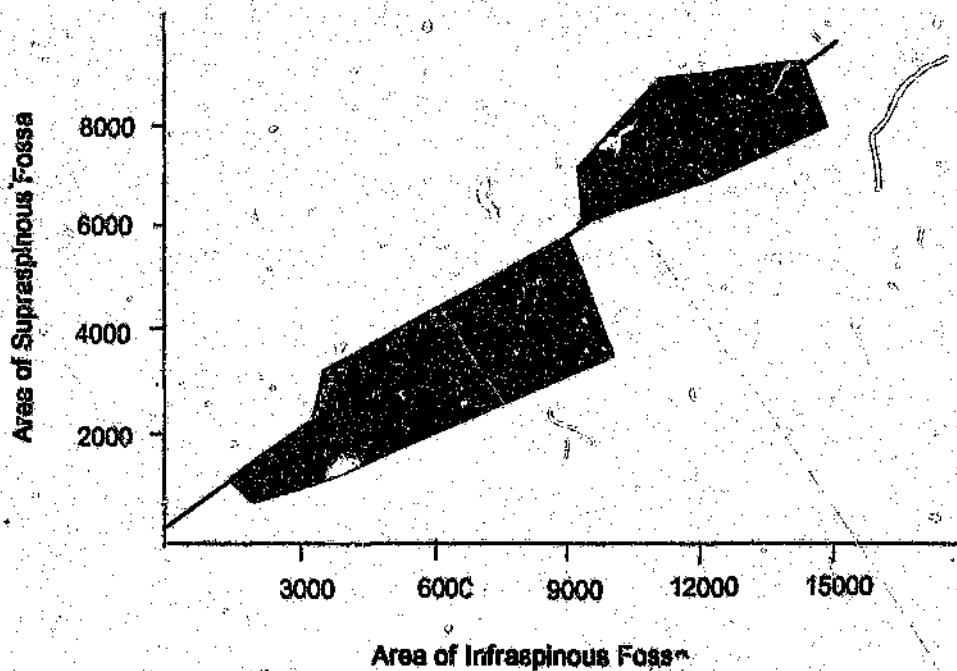


Figure 40. Bivariate plot of the area of the infraspinous fossa vs. the area of the supraspinous fossa in extant hominoids. Shaded area indicates the observed limits of the range of variation for this relationship in the extant hominoid species examined in the present study. Data collected by the author.

Area of Infraspinous Fossa vs. Area of Supraspinous Fossa (excluding the gorilla sample)

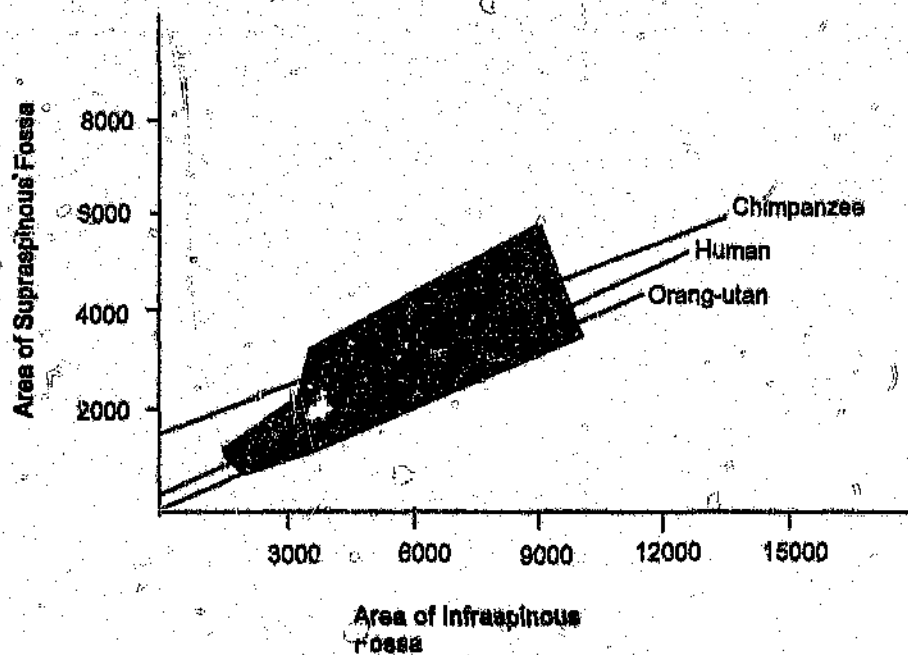


Figure 41. Bivariate plot of the area of the infraspinous fossa vs. the area of the supraspinous fossa in extant hominoids. Shaded area indicates the observed limits of the range of variation for this relationship in humans ($y = .387x + 257.027$, $r^2 = .59$), chimpanzees ($y = .319x + 1540.767$, $r^2 = .243$), and orang-utans ($y = .355x + 156.032$, $r^2 = .776$). Data collected by the author.

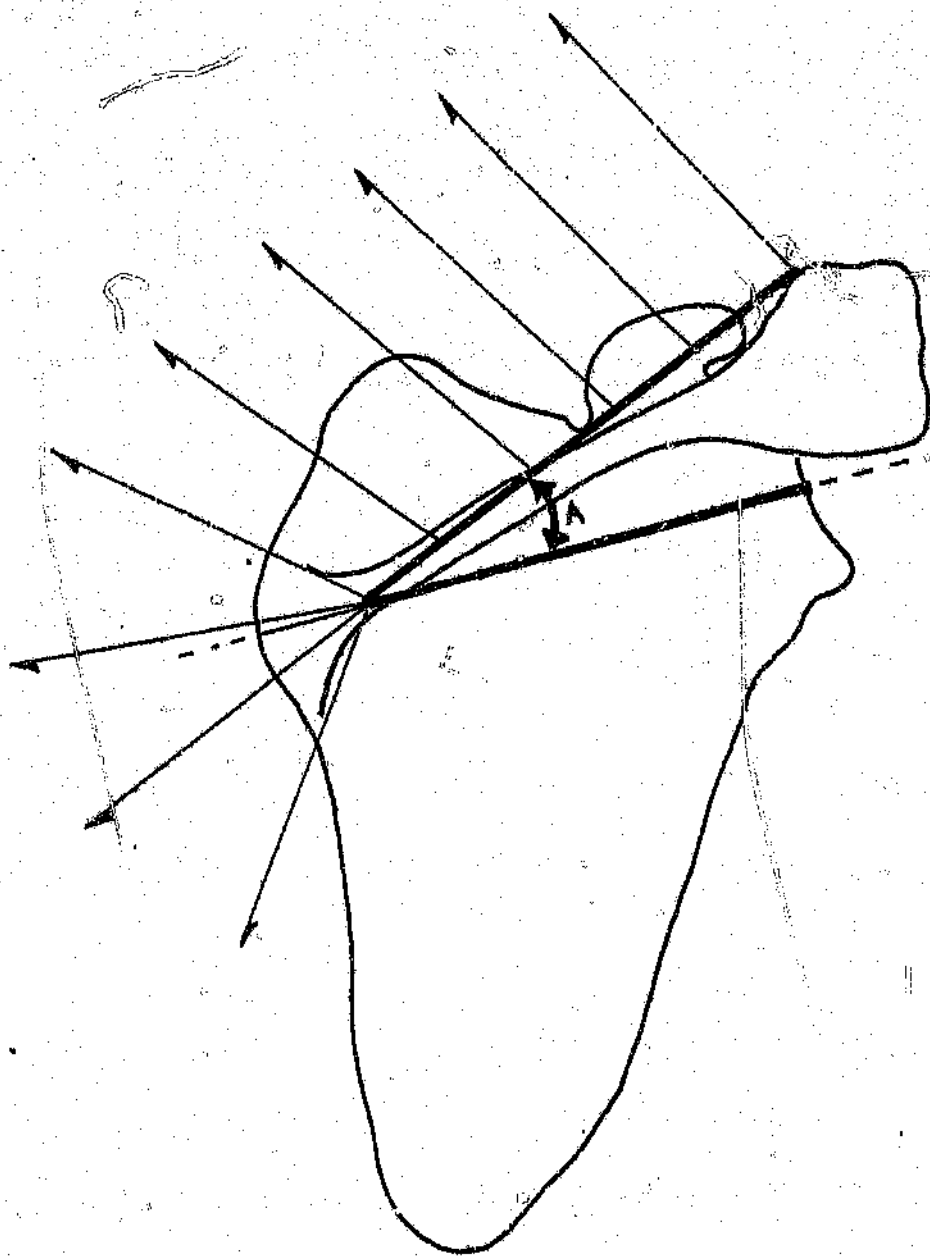


Figure 42. Illustration of the angle of insertion of the trapezius muscle in the hominoid scapula as represented by angle A. The arrows indicate the direction of forces in the muscle couple (after Oxnard, 1968c)

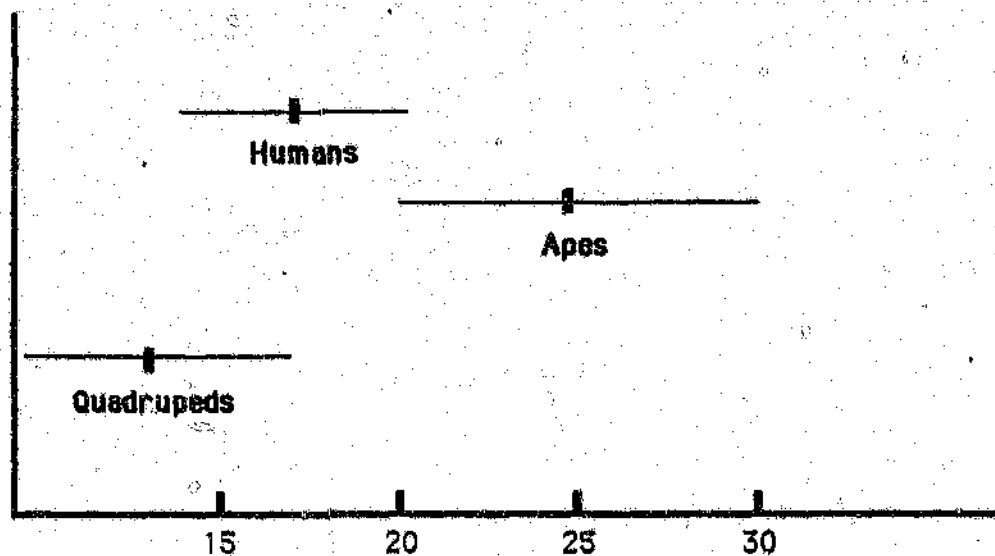


Figure 43. Calculated values for the angle of insertion of the trapezius muscle in humans, apes and quadrupedal monkeys. Vertical bar, mean; horizontal line, mean $\pm$ 1 standard deviation; x axis values in degrees (after Oxnard, 1968a.)

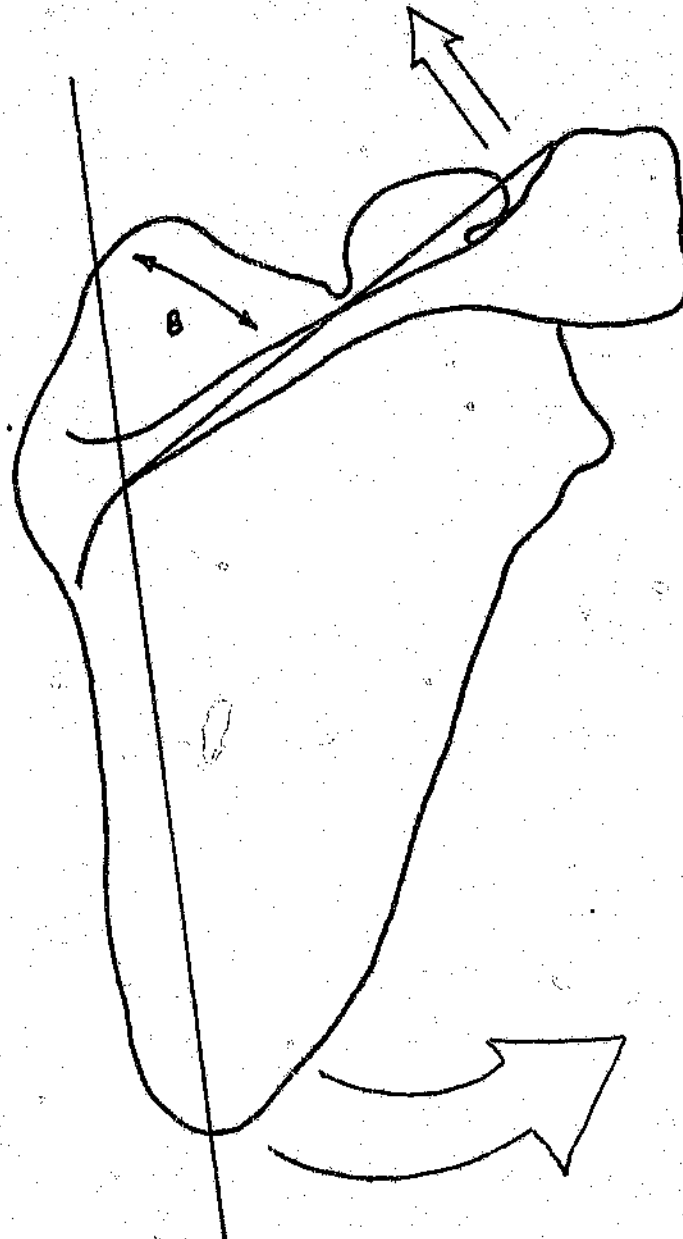
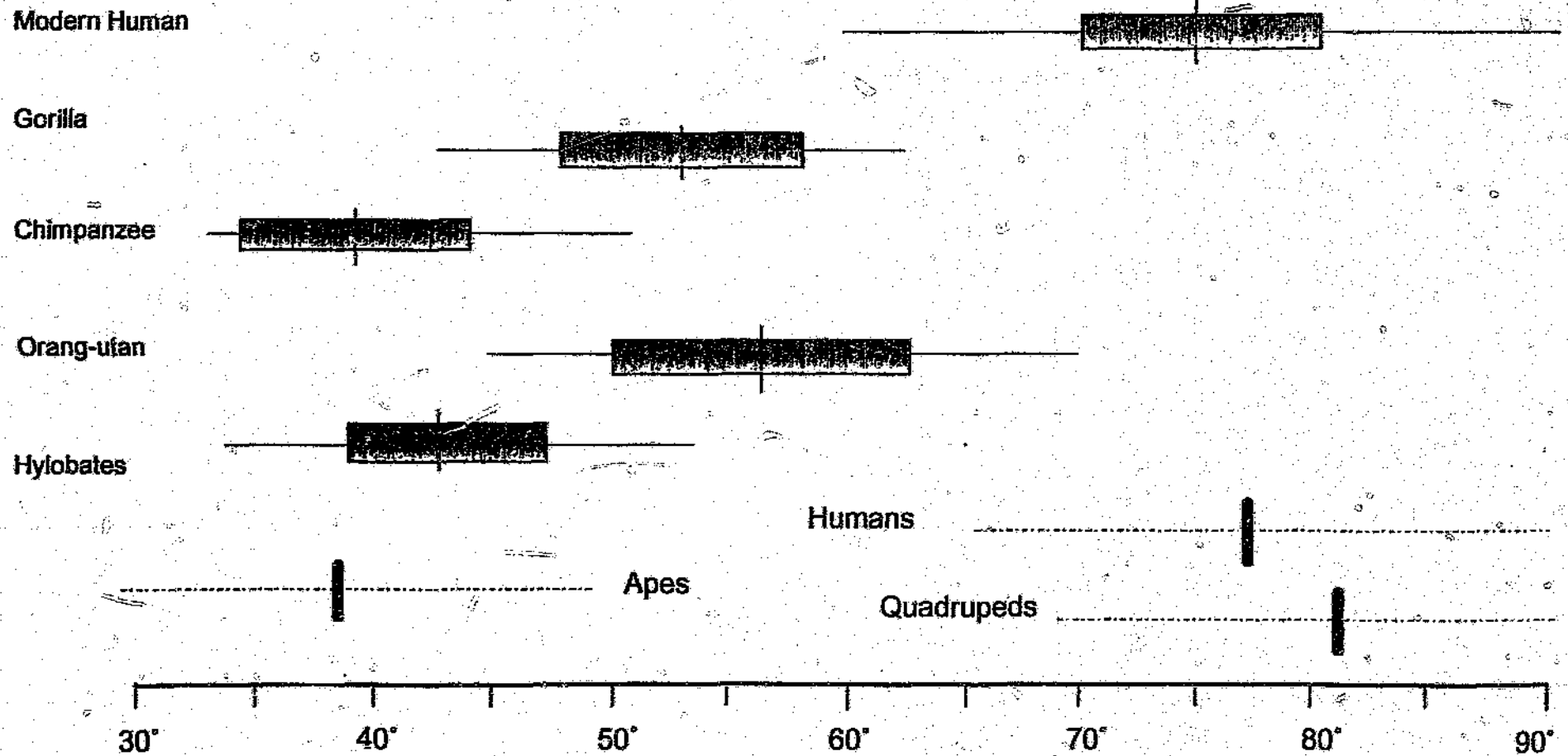


Figure 44. The orientation of components of the force couple made up of the trapezius and serratus magnus muscles (Angle B) in the scapulae of hominoids and monkeys (after Oxnard, 1968c)

Figure 45. The angulation of the trapezius / serratus magnus muscle force couple in hominoids. Data for modern humans, gorillas, chimpanzees, orang-utans and *Hylobates* (continuous line) compiled by the author. Data for apes, humans (dot- and dash-line) and quadrupeds adapted from Oxnard (1968a). Vertical line, sample mean; horizontal line, observed sample range; shaded rectangle, mean $\pm$ 1 standard deviation.

**Figure 45. Comparison of Hominoid Scapulae
Angulation of the Trapezius / Serratus Magnus Muscles Force Couple**



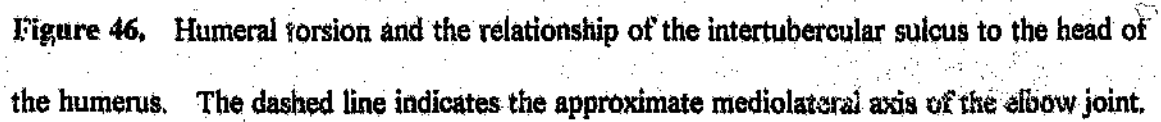


Figure 46. Humeral torsion and the relationship of the intertubercular sulcus to the head of the humerus. The dashed line indicates the approximate mediolateral axis of the elbow joint.

Modified from Aiello and Dean (1990) after Evans and Krahl (1945).



Hylobatids



Orang-utan



Human



Gorilla



Chimpanzee

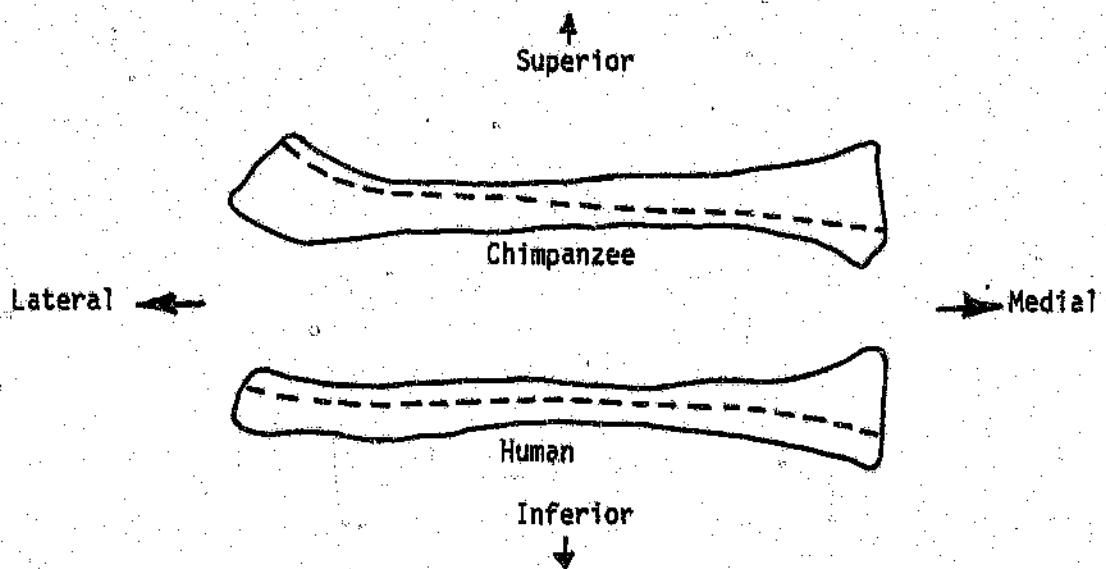


Figure 47. Anterior views of human and chimpanzee right clavicles illustrating the marked cranial twisting of the lateral end of the chimpanzee clavicle. Modified from Oxnard (1984).

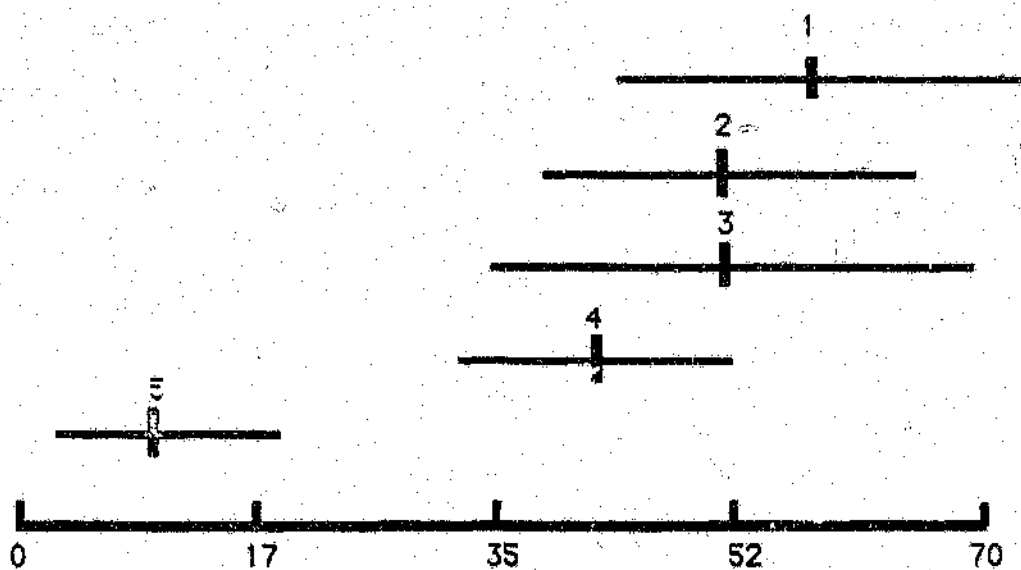


Figure 48. The angle of torsion in the clavicles of hominoids. 1, gorilla; 2, chimpanzee; 3, orang-utan; 4, gibbon; 5, human. Vertical bars, sample mean; horizontal line, mean $\pm$ 1 standard deviation. After Ashton and Oxnard (1964).

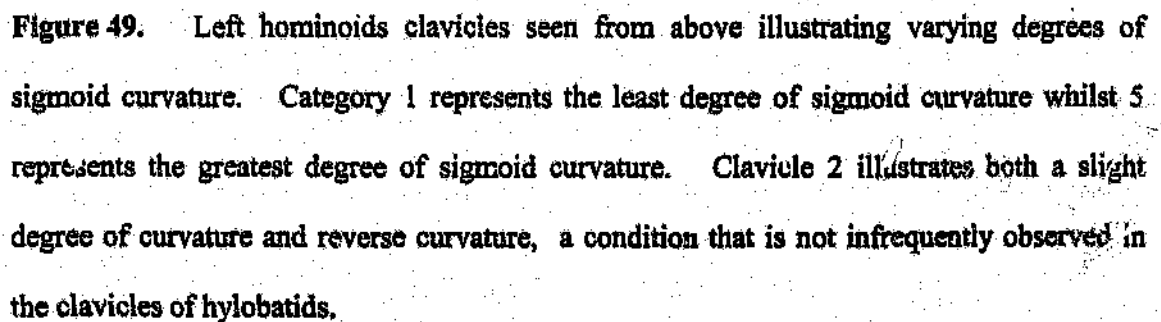
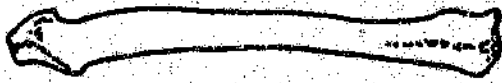
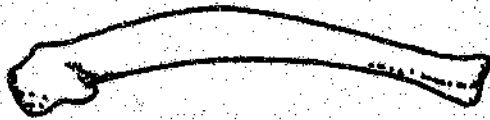


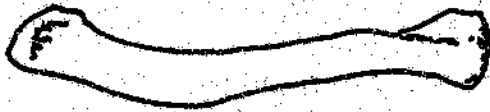
Figure 49. Left hominoids clavicles seen from above illustrating varying degrees of sigmoid curvature. Category 1 represents the least degree of sigmoid curvature whilst 5 represents the greatest degree of sigmoid curvature. Clavicle 2 illustrates both a slight degree of curvature and reverse curvature, a condition that is not infrequently observed in the clavicles of hylobatids.



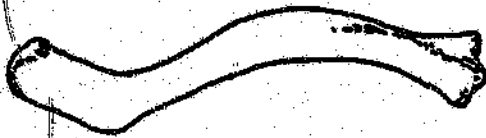
1



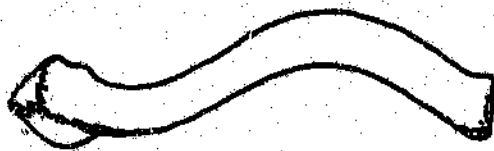
2



3



4



5

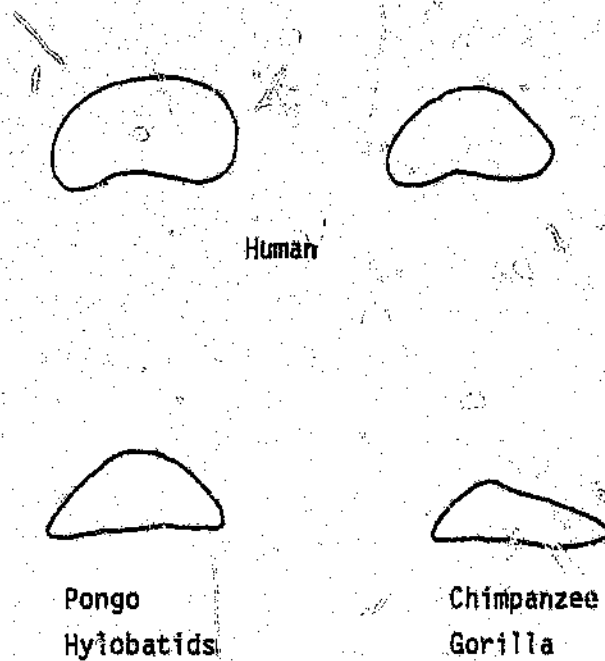
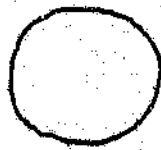


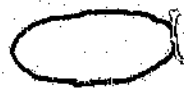
Figure 50. Cross-sectional shapes of the bodies of clavicles in hominoids. The cross-sections are taken at the approximate mid-point of the length of the clavicle. Superior surface - above; inferior surface -below.



Human



African apes



Asian apes

Figure 51. Cross-sectional shapes of the sternal end of clavicles in hominoids.

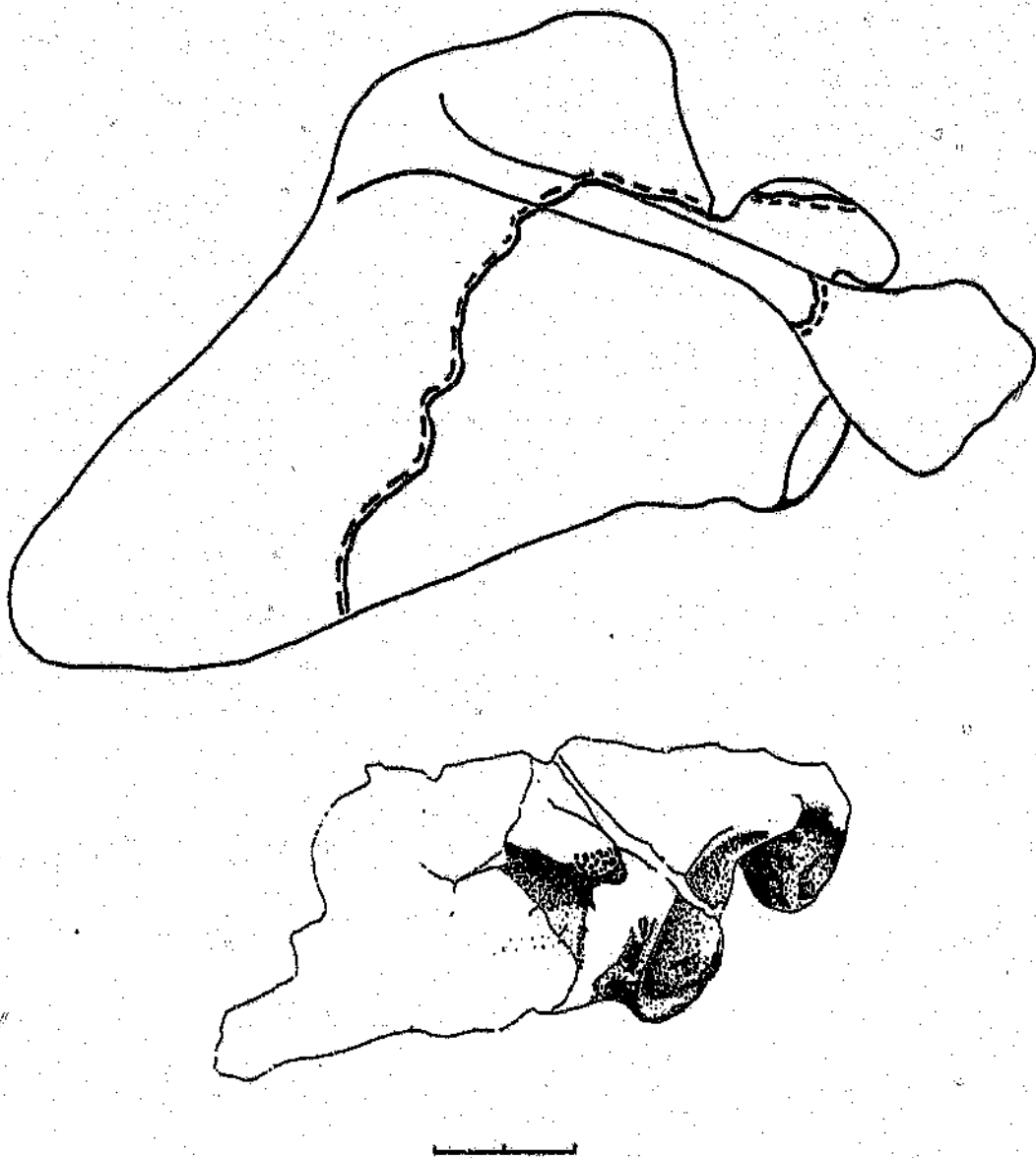
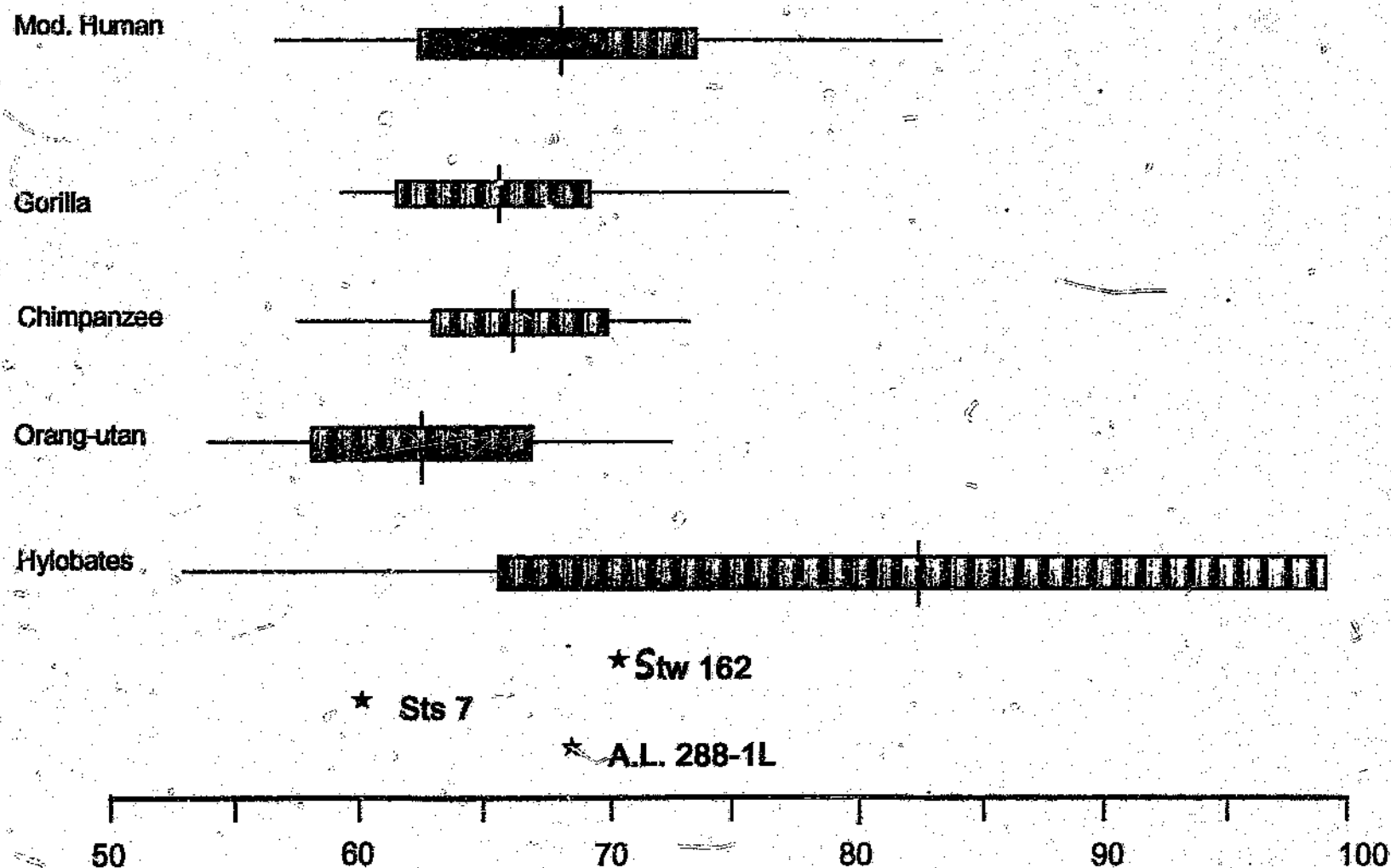


Figure 52. The Sts 7 scapula illustrating important morphological features of the dorsal surface and glenoid cavity. The dashed lines on the outline above Sts 7 illustrate the approximate completeness of the fossil compared to a whole modern human scapula.



Figure 54. Comparisons of glenoid index values for the australopithecine scapulae with corresponding values for modern humans, gorillas, chimpanzees, orang-utans and hylobatids. As discussed in the text, the glenoid length values for Sts 7 and Stw 162 are estimates, thus the actual glenoid index values for these specimens may vary slightly from those presented in this figure. Vertical line, sample mean; horizontal line, observed sample range; shaded rectangle, mean ± 1 standard deviation. The standard deviation for the hylobatid sample exceeds the observed range due to the small sample size used in this study.

Figure 54. Comparison of Hominoid Scapular Glenoid Shape
Glenoid Index (GB/GL x 100) *



* Sts 7

* Stw 162

* A.L. 288-1L

Spinoglenoid Notch Depth vs. Glenoid Cavity Maximum Breadth

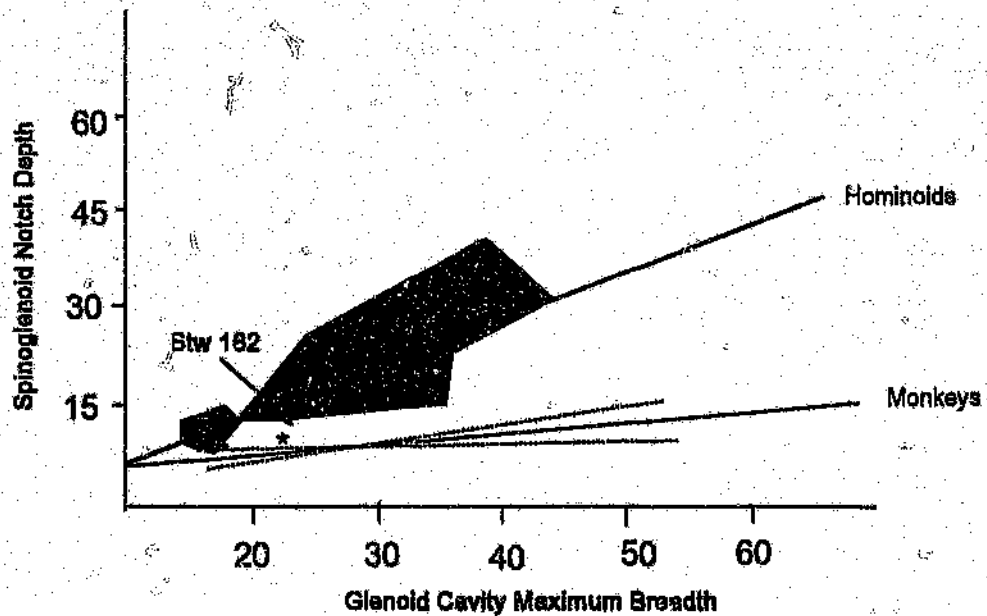


Figure 55. Bivariate plot of spinoglenoid notch depth vs. glenoid cavity maximum breadth. Shaded area indicates the observed limits of the range of variation for this relationship in the extant hominoid species examined in the present study. Interrupted lines indicate 95% confidence intervals for monkeys. * indicates position of Sts 7, • indicates position of A.L. 288-1L, arrow indicates position of Stw 162. Data collected by the author.

Spinoglenoid Notch Depth vs. Glenoid Cavity Maximum Breadth

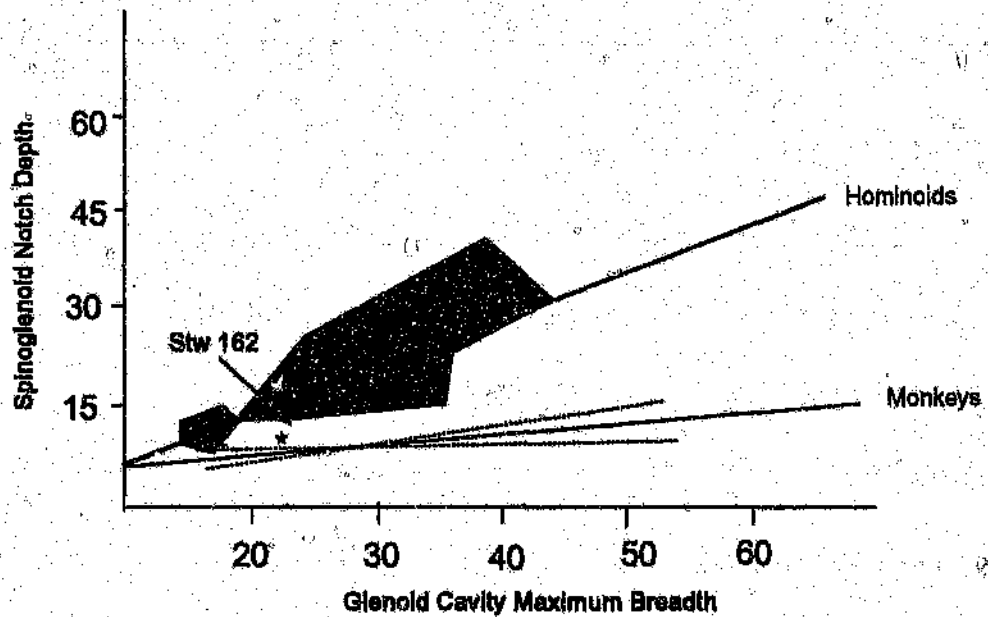
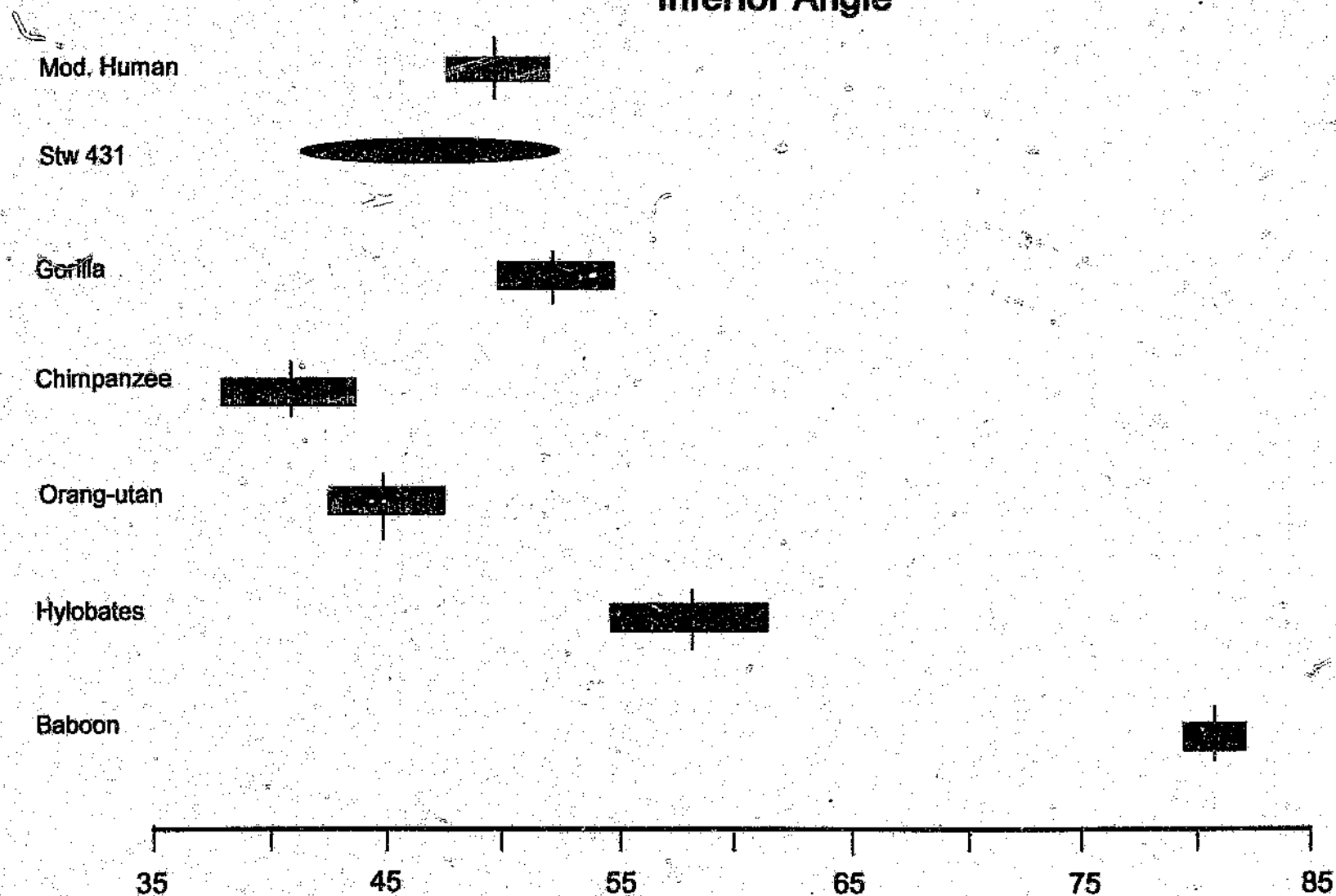


Figure 55. Bivariate plot of spinoglenoid notch depth vs. glenoid cavity maximum breadth. Shaded area indicates the observed limits of the range of variation for this relationship in the extant hominoid species examined in the present study. Interrupted lines indicate 95% confidence intervals for monkeys. ★ indicates position of Sts 7, • indicates position of A.L. 288-1L, arrow indicates position of Stw 162. Data collected by the author.

Figure 56. Comparisons of possible scapular inferior angle values for the Stw 431 scapulae with corresponding values for modern humans, gorillas, chimpanzees, orang-utans and hylobatids. As discussed in the text, the shaded circle represents this author's best guesses for Stw 431's inferior angle value based on the reconstruction illustrated in Figure 57. Vertical line, sample mean; shaded rectangle, mean $\pm$ 1 standard deviation.

**Figure 56. Comparison of Australopithecine Scapular Shape
Inferior Angle**



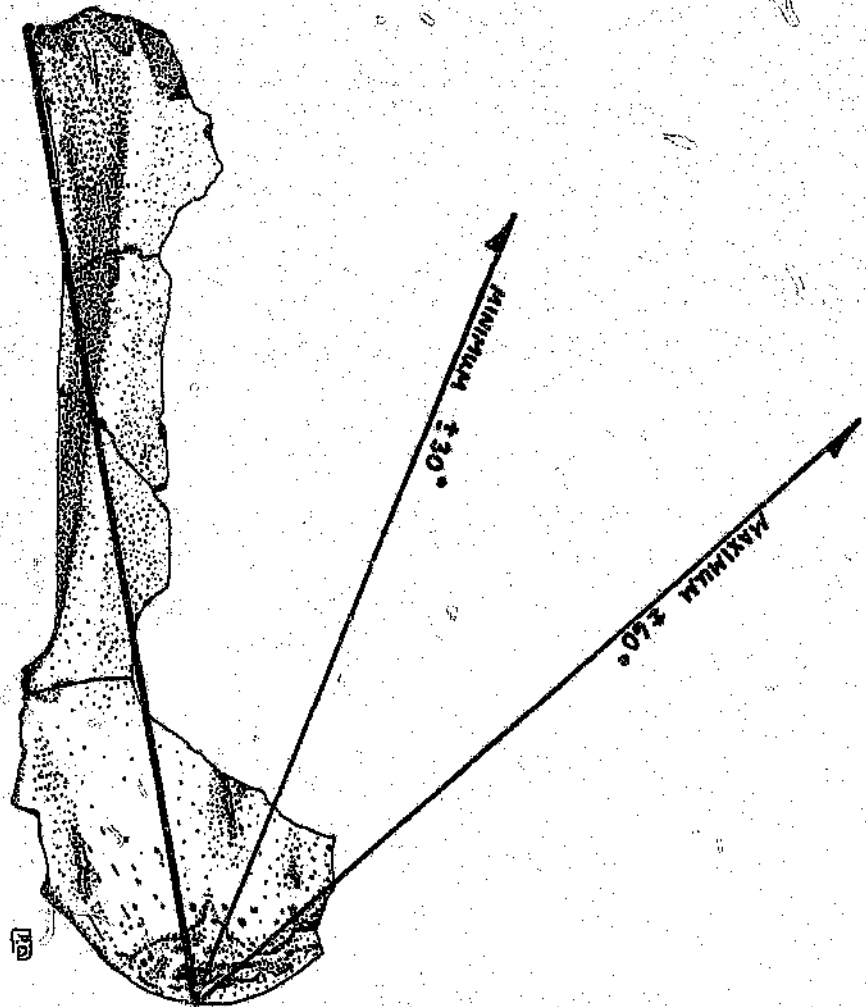


Figure 57. Diagram illustrating this author's justification for his minimum ($\pm 30^\circ$) and maximum ($\pm 60^\circ$) estimates of the inferior angle value of the Stw 431 scapula.

Figure 58. Comparisons of humeral head index values for fossil hominid humeri with the corresponding values for modern humans, gorillas, chimpanzees, orang-utans and hylobatids.

Vertical line, sample mean; horizontal line, observed sample range; shaded rectangle, mean $\pm$ 1 standard deviation.

Figure 58. Comparison of Australopithecine Humeral Shape
Humeral Head Index (HHB/HHD x 100)

Mod. Human

Gorilla

Chimpanzee

Orang-utan

Hylobates

★ Sts 7

★ Stw 517

★ A.L. 288-1L

★ Omo 119-2718

★ A.L. 333-107

70

80

90

100

110

120





Figure 59. A.L. 288-11, a, dorsal view; b, lateral view. Drawing is approximately natural size.

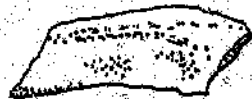


Figure 60. Right clavicular fragment, A.L. 288-1bz, inferior view. Drawing approximately natural size.



Figure 61. Right clavicle, A.L. 333x-6/9, superior view. Drawing approximately natural size.



Figure 62. Left clavicular fragment, A.L. 333-94, superior view. Drawing approximately natural size.