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Functional morphology of the hominoid shoulder, past and present

Berger, Lee Rogers

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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.

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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))

(Tafeb *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 curved 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 **OH - 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 atachment 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 <u>all</u> 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% - ?70.0% (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 (?6.7%) falls just within one standard deviation of the mean observed in Churchill and Trinkaus's sample of Neandertal scapulae (8.4% ± 1.9, n = 16) but outside one standard deviation

from the mean of the modern human sample (12.0% ± 1.6, n = 99). In contrast, the glenoid depth index calculated for **Stw 162** (?3.9%) 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 Galinet, 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.L. 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 th · 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. 132), 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".***

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 °.

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° 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 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.

7.6.2

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 degrees, 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.

7.6.4

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[illegible] 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 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 huemral 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. 288-1l** 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. 288-1l** that *A. afarensis* exhibited climbing behaviour.

The neck of the scapula of **A.L. 288-1l** 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. 288-1l** 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 axillo-glenoid value indicates that the **A.L. 288-1l** 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. 288-1L**) 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 analyis 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 clavicula, 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 pr...ssed 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; Susman *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.

7.10.1

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 inidividual 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 <u>includes</u> **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. 288-1L 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.

7.10.3

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 "protohominid". 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 (Leakey and Walker, 1988; Walker and Leakey, 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 20% 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.

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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

Table		Page
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 / HHB 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

Figure		Page
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 infraspinous and supraspinous 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 the 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 288-1L	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

Plate		Page
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
Homo sapiens			
	male	29	UW
	female	27	UW
	male	18	SI
	female	22	SI
Gorilla gorilla			
	male	3	UW
	male	12	SI
	female	5	SI
Pan troglodytes			
	male	11	SI
	female	9	SI
Pongo pygmaeus			
	male	12	SI
	female	20	SI
Hylobates species			
	male	9	SI
	female	6	SI
Symphalangus syndactylus			
	male	1	SI
	female	3	SI
Papio ursinus			
	male	16	UW
	female	12	UW
Cercopithecus aethiops			
	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[15]	277	Radiological
U.S.A.			
	1.20[16]	1000	Radiological
Czech			
	1.38[17]	3470	Radiological
Malay			
	3.00[4]	300	Radiological
Indian			
	4.30[4]	276	Radiological
Chinese			
	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, Cainbridge 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	*H. sapiens*	*G. gorilla*	*P. troglodytes*	*P. pygmaeus*	*Hylobates* 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) Atlantoscapularis 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	*H. sapiens*	*G. gorilla*	*P. troglodytes*	*P. pygmaeus*	*Hylobates* 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) Coraco-brachialis	apex of 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	*H. sapiens*	*G. gorilla*	*P. troglodytes*	*P. pygmaeus*	*Hylobates* 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) Sternocleido-mastoid	superior surface of the clavicle near the sternal end, manubrium sterni	sternal attachment more localized than in humans. V encroaches on sternal ticular 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	*H. sapiens*	*G. gorilla*	*P. troglodytes*	*P. pygmaeus*	*Hylobates* 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 ligamentum 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	*H. sapiens*	*G. gorilla*	*P. troglodytes*	*P. pygmaeus*	*Hylobates* 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
Homo sapiens				
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)**	
Gorilla gorilla				
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)**	
Pan troglodytes				
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)**	
Pongo pygmaeus				
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[3]	56.5 - 73.3	64.5	(10)	
weighted mean		**63.1**	**(39)**	
Hylobates species				
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)**	
Symphalangus syndactylus				
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)**	

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

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

Taxon	Mean of the Index Values	(n)	SD
Homa sapiens	55%	(26)	7.0
Gorilla gorilla	62%	(22)	8.0
Pan troglodytes	63%	(23)	9.0
Pongo pygmaeus	46%	(24)	8.0
Hylobates species	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*)
Homo sapiens						
	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
Gorilla gorilla						
	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
Pan troglodytes						
	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
Pongo pygmaeus						
	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
Hylobates species						
	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
Symphalangus syndactylus						
	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 x 100) Amongst Hominoidea*

Taxon	Mean of the Index Values	Observed range (*n*)	SD	CV
Homo sapiens	43.7	30.5 - 59.3 (64)	5.9	13.6
Gorilla gorilla	66.2	54.9 - 80.3 (16)	8.5	12.8
Pan troglodytes	67.6	52.8 - 93.8 (16)	10.7	15.9
Pongo pygmaeus	38.2	25.8 - 51.4 (26)	6.0	15.8
Hylobates species	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 x 100] / Anatomical Length of the Scapula) Amongst Hominoidea and Old World Monkeys*

Taxon	Observed Range (*n*)	Mean of the Index Values	SD
Homo sapiens	15.8 - 46.4 (87)	34.2	4.8
Gorilla gorilla	20.0 - 38.8 (20)	32.0	4.8
Pan troglodytes	27.1 - 46.8 (20)	36.3	5.2
Pongo pygmaeus	23.6 - 47.3 (30)	34.5	5.5
Hylobates species	19.2 - 34.5 (15)	26.5	4.3
Symphalangus syndactylus	28.3 - 34.3 (3)	31.9	3.1
Papio ursinus	-1.3 - 12.4 (28)	4.6	3.2
Cercopithecus aethiops	0.4 - 13.9 (15)	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*)
Homo sapiens					
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
Gorilla gorilla					
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
Pan troglodytes					
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
Pongo pygmaeus					
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
Hylobates species					
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
Symphalangus syndactylus					
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 (*Papio ursinus* & *Cercopithecus aethiops*)					
both sexes	139.60	4.45	3.83	124.00 - 158.00	64

The data presented this table are derived from measurments 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*
Homo sapiens	145.0	4.3	50
Gorilla gorilla	131.6	2.1	9
Pan troglodytes	126.3	2.8	11
Pan paniscus	125.9	3.4	12
Pongo pygmaeus	127.4	3.4	5

The data in this table are derived from Corruccini and Ciochon (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
Homo sapiens					
both sexes	-0.3 - -3.5	-1.7	(95)	33.2	0.6
Gorilla gorilla					
both sexes	-0.7 - -3.4	-1.9	(19)	35.9	0.7
Pan troglodytes					
both sexes	1.2 - -2.1	-0.5	(20)	48.5	0.8
Pongo pygmaeus					
both sexes	-1.3 - -4.4	-2.7	(30)	29.6	0.8
Hylobates species					
both sexes	0.3 - -2.1	-1.2	(15)	47.6	
Symphalangus syndactylus					
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
Homo sapiens				
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**	
Gorilla gorilla				
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**		
Pan troglodytes				
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**		
Pongo pygmaeus				
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**		
Hylobates species				
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**		
Symphalangus syndactylus				
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
Homo sapiens				
both sexes	9.7 - 39.9	22.8	(94)	5.5
Gorilla gorilla				
both sexes	10.3 - 30.5	18.4	(19)	6.1
Pan troglodytes				
both sexes	12.2 - 29.6	20.6	(20)	4.7
Pongo pygmaeus				
both sexes	18.0 - 46.1	26.3	(30)	6.2
Hylobates species				
both sexes	10.5 - 24.8	19.5	(15)	3.8
Symphalangus syndactylus				
both sexes	18.8 - 23.9	21.7	(4)	2.3
Monkeys (*Cercopithecus aethiops* & *Papio ursinus*)				
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)
Homo sapiens				
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.?	150
Gorilla gorilla				
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
Pan troglodytes				
both sexes[2]		141.1	5.8	65
both sexes[3]		133.9	10.9	33
both sexes[4]		128.1		12
Pongo pygmaeus				
both sexes[2]		113.1	10.2	52
both sexes[3]		119.5	12.7	14
both sexes[4]		120.3		7
Hylobates species				
both sexes[2]		113.5	10.9	80
both sexes[3]		110.7	9.7	48
both sexes[4]		112.0		10
Symphalangus syndactylus				
both sexes[3]		113.8	12.7	8

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

Table 18. *Metrical 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.L. 288-1L	25.7[b]	18.1	-	-	67.5, 70.4

[a] The two values presented for the GB, AB and GI of Sts 7 are respectively based on the measurements of this author and of Vrba (1979).

[b] The 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	AML	IA	AGA
	millimetres			
Sts 7	c12.0			120.0°
Stw 162	13.7			
Stw 431		c143.0[a]	30° - 60°	
A.L. 288-1L	10.0[b]			120.0°

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

[a]This measurement assumes that the axillary margin of Stw 431 is nearly complete at the superior point of damage.

[b]This 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
Homo sapiens				
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
Gorilla gorilla				
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
Pan troglodytes				
male	135.6 - 167.5	15[illegible]9	(11)	10.2
female	135.5 - 161.1	149.1	(9)	10.4
both sexes	135.5 - 167.5	152.5	(20)	1[illegible]
Pongo pygmaeus				
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)	10.1
Hylobates 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
Symphalangus syndactylus				
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
Stw 431	143.0*			

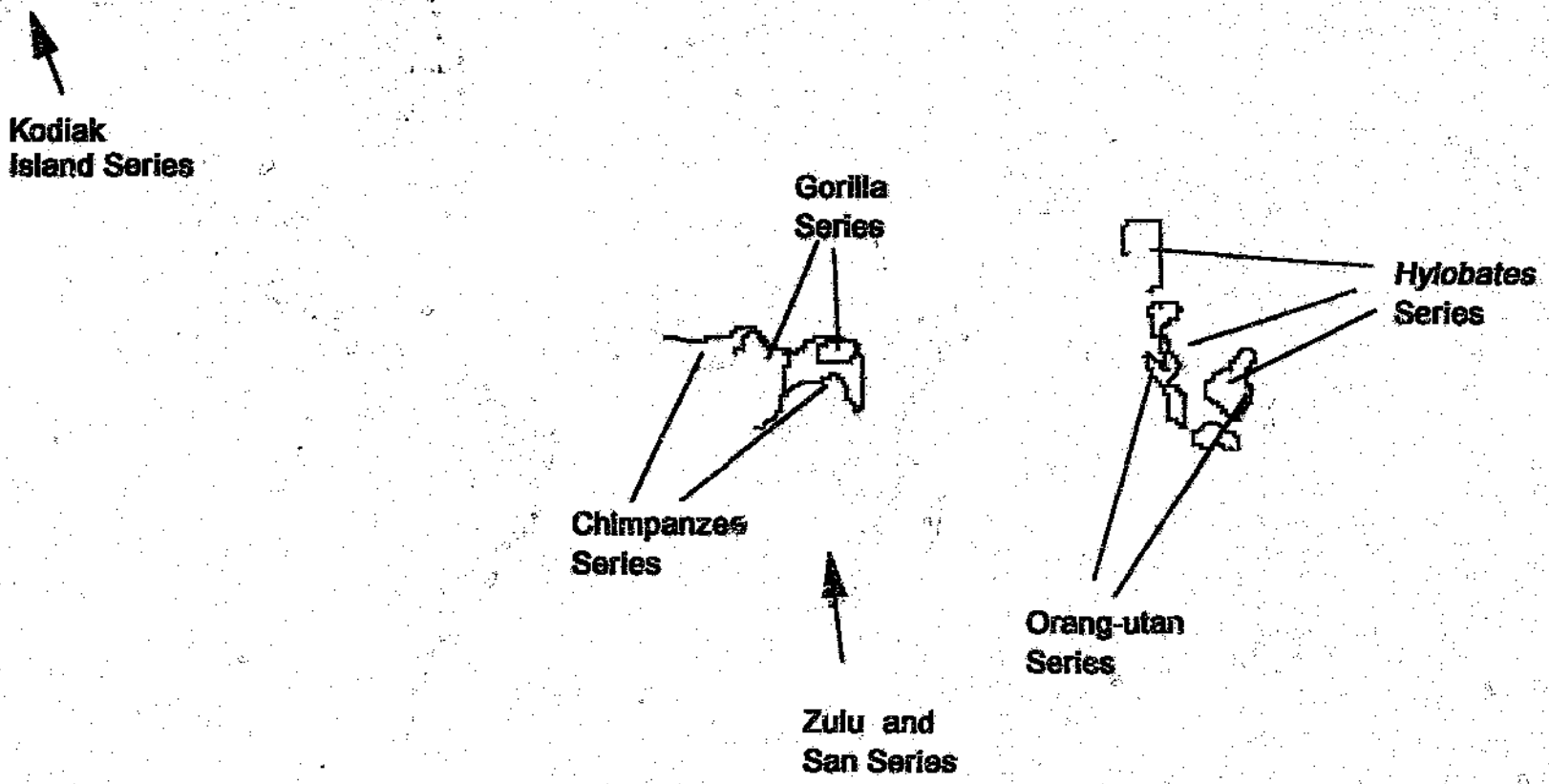
The data presented in this table were collected by the author. * As discussed in the text, the length of the axillary margin for Stw 431presented in this table represents this author's "best guess".

Table 31. *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	c6.0		
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	c34.0	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 [1]this author; [2] Johanson et al., 1982; [3]Lovejoy et al., 1982; [4]Pickford, 1973; [5]Leakey et. al., 1973.

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



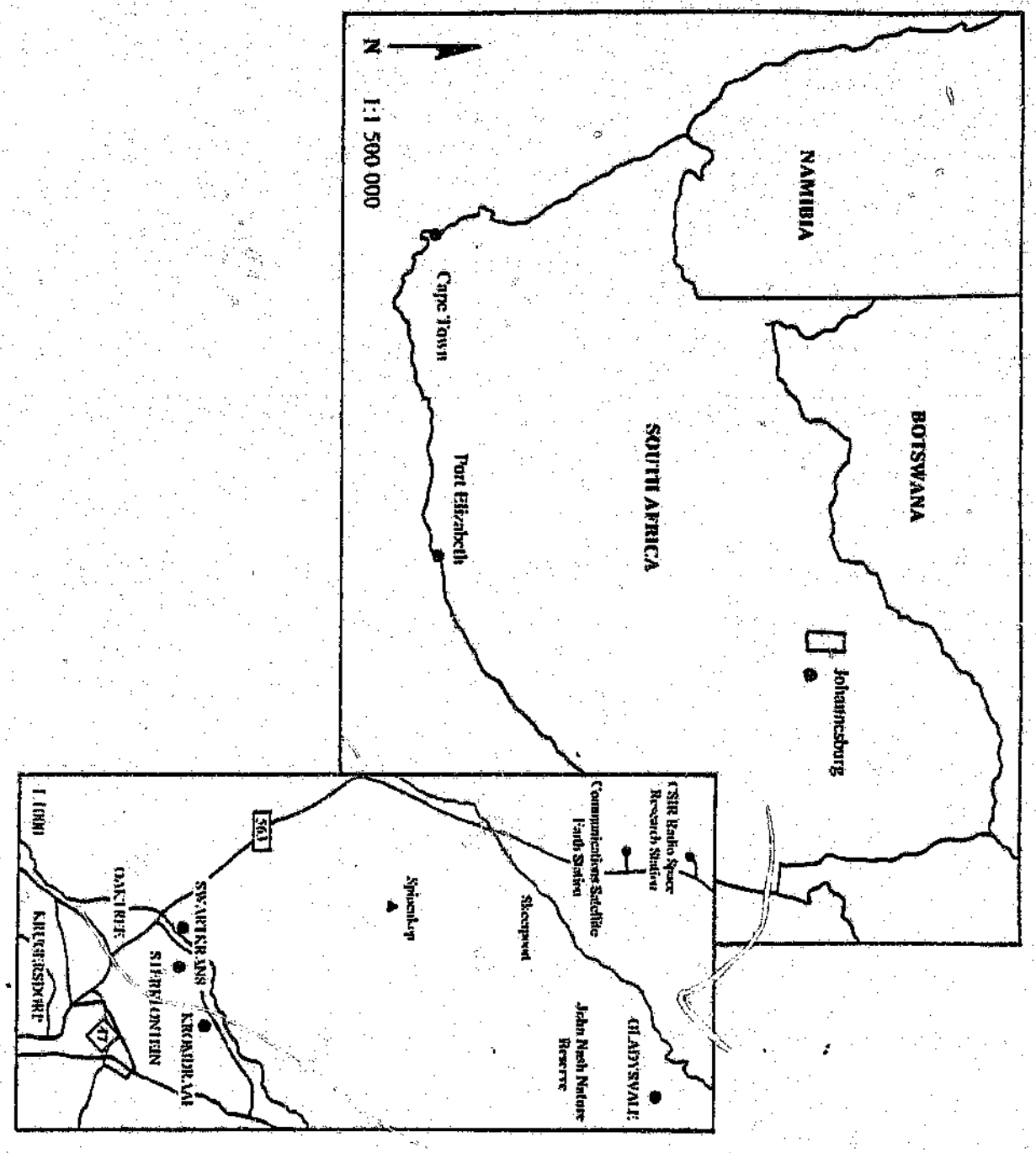


Figure 2. Map of South African early hominid fossil sites in the Krugersdorp District illustrating the position of Sterkfontein relative to other well known localities where early hominid fossils have been discovered.

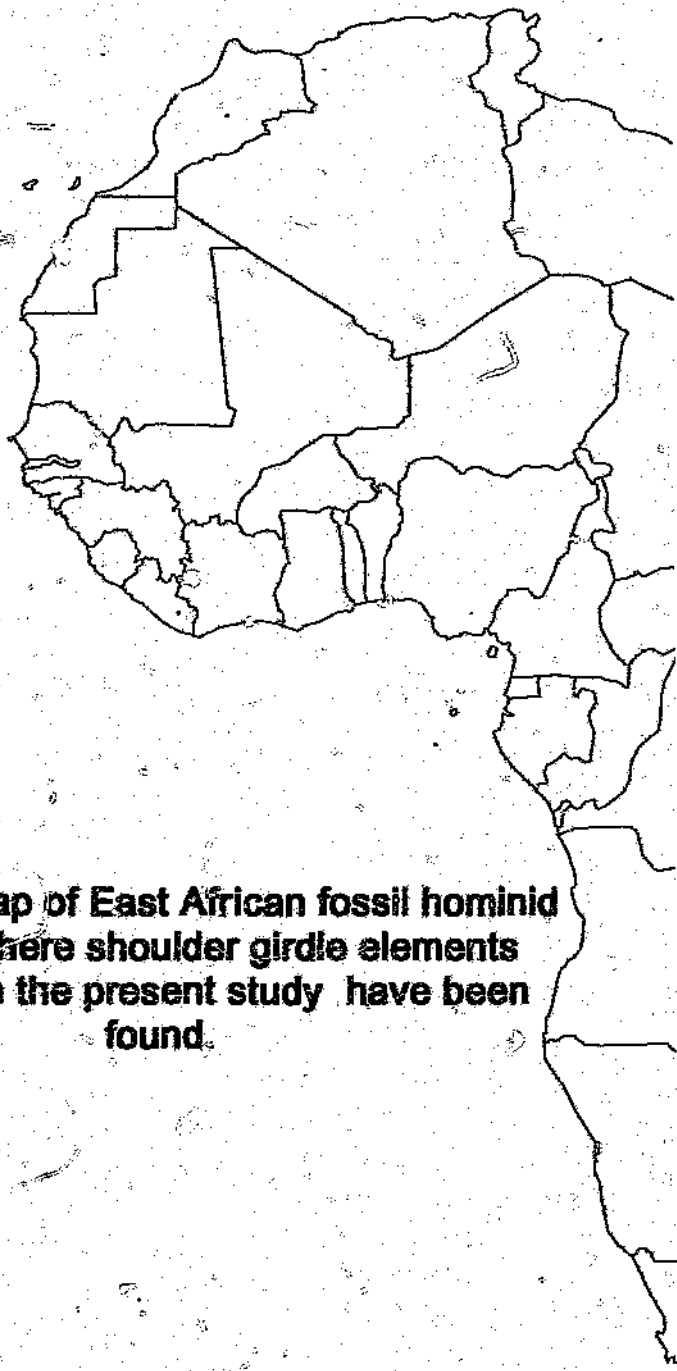


Figure 3. Map of East African fossil hominid localities where shoulder girdle elements examined in the present study have been found.

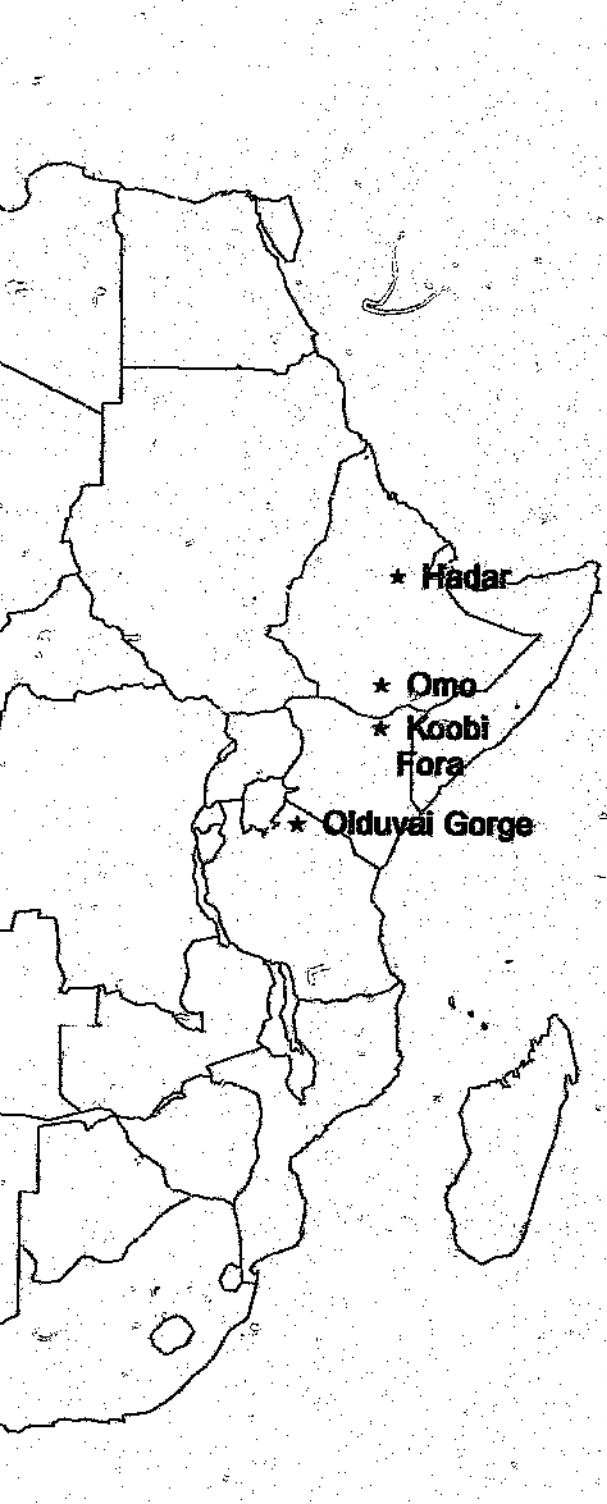
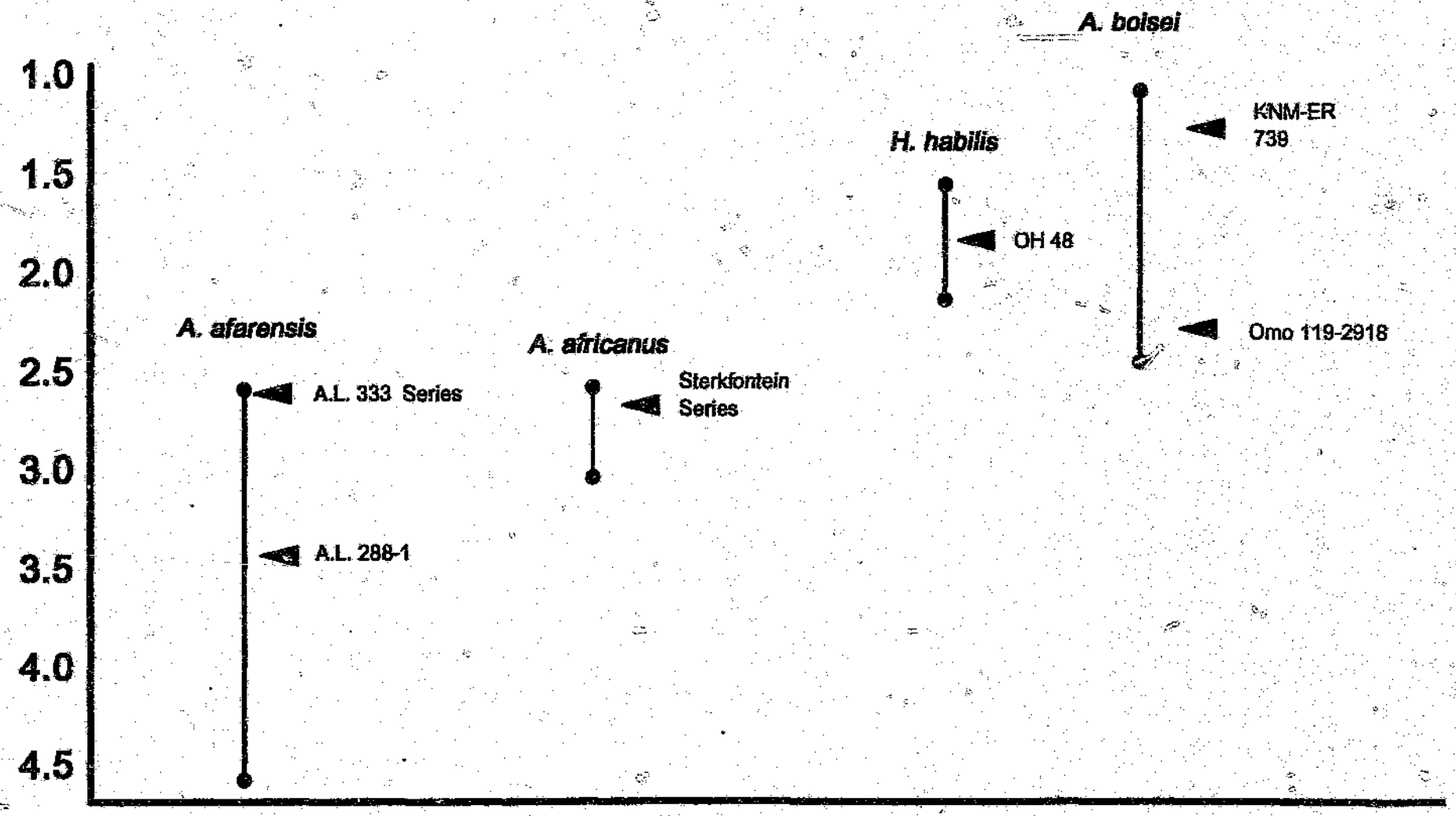

Hadar
Omo
Koobi Fora
Olduvai Gorge

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



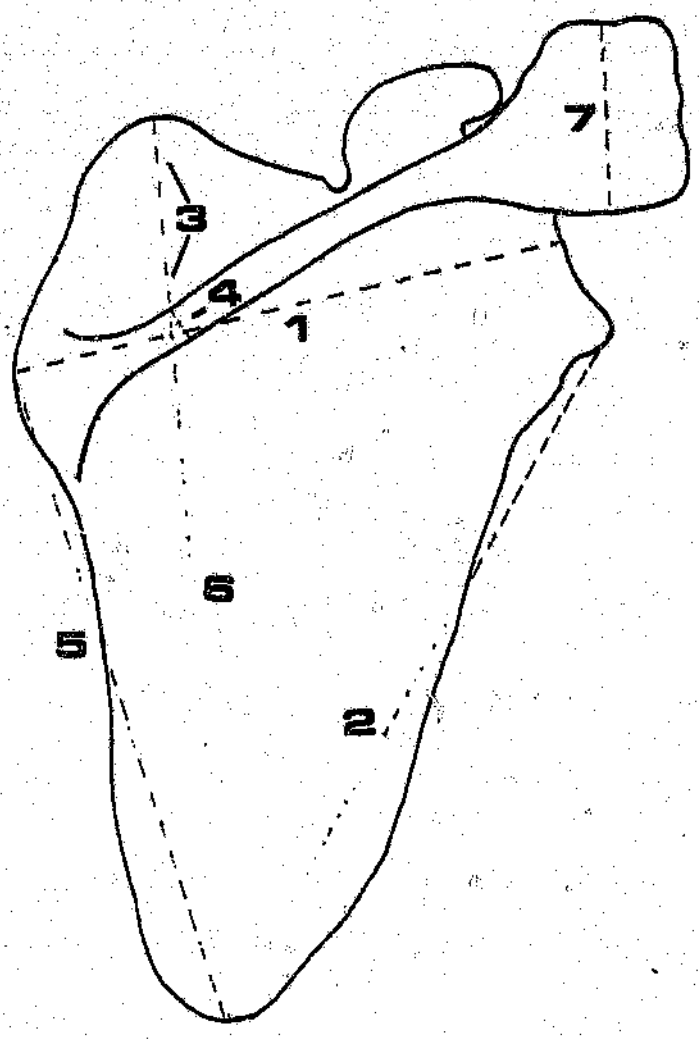


Figure 5a. Dorsal view of a human scapula illustrating landmarks and distances, as defined in the text.

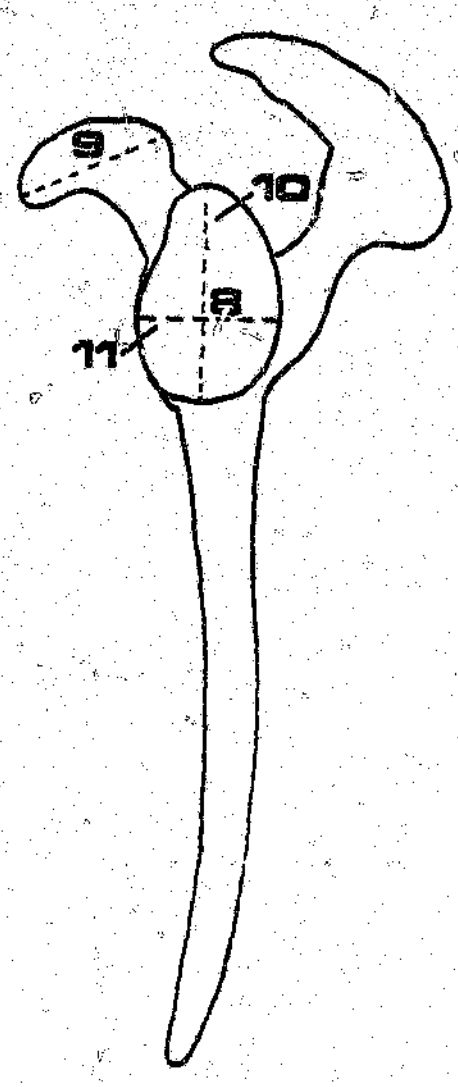


Figure 5b. Lateral view of a human scapula illustrating landmarks and distances, as defined in the text.

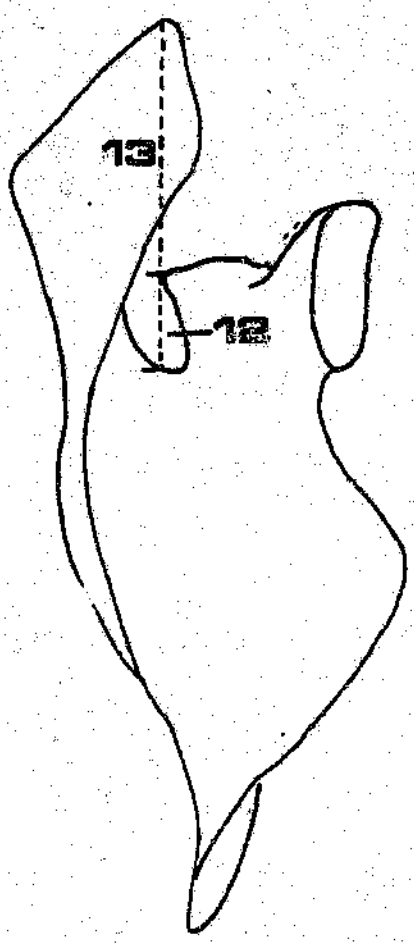


Figure 5c. Superior view of a human scapula illustrating landmarks and distances, as defined in the text.

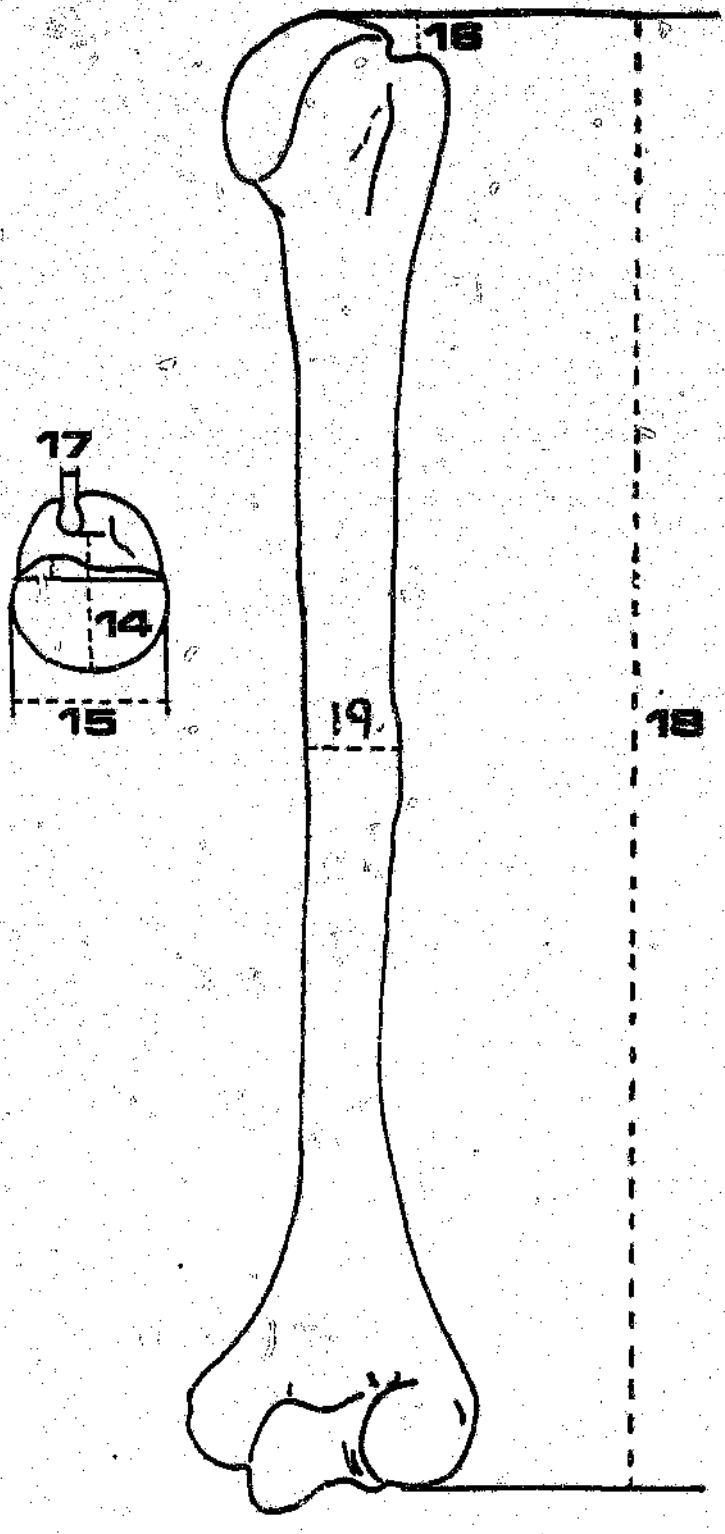


Figure 6. Superior and dorsal view of a right human humerus illustrating landmarks and distances. as defined in the text.

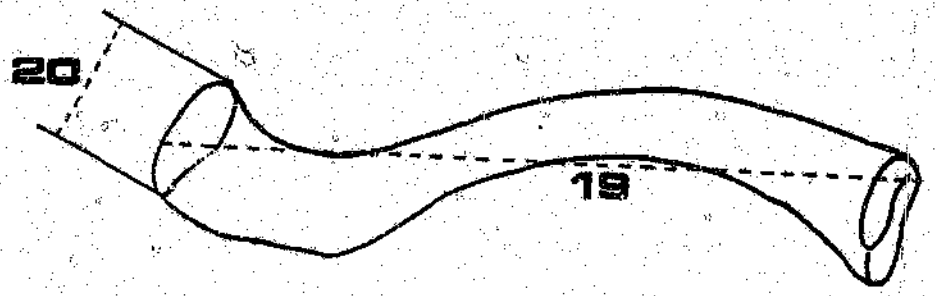


Figure 7. Inferior view of a left human clavicle illustrating landmarks and distances, as defined in the text.

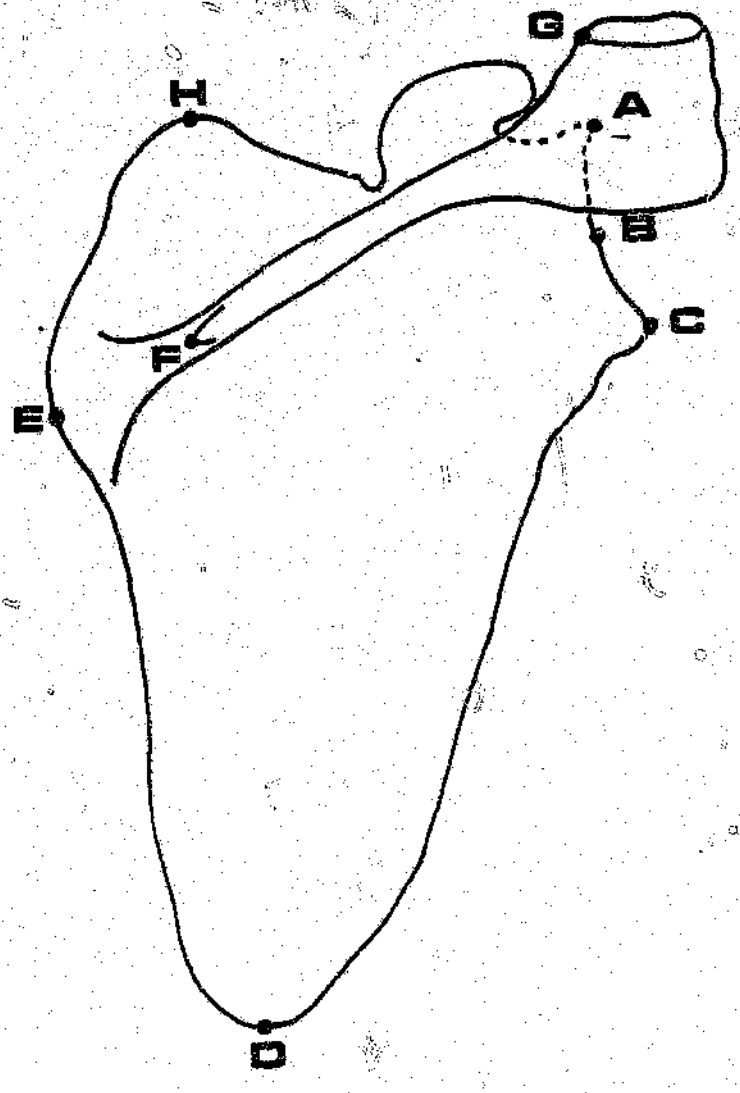


Figure 8. Dorsal view of a human scapula illustrating landmarks used in the calculation of angles. Landmarks are defined in the text.

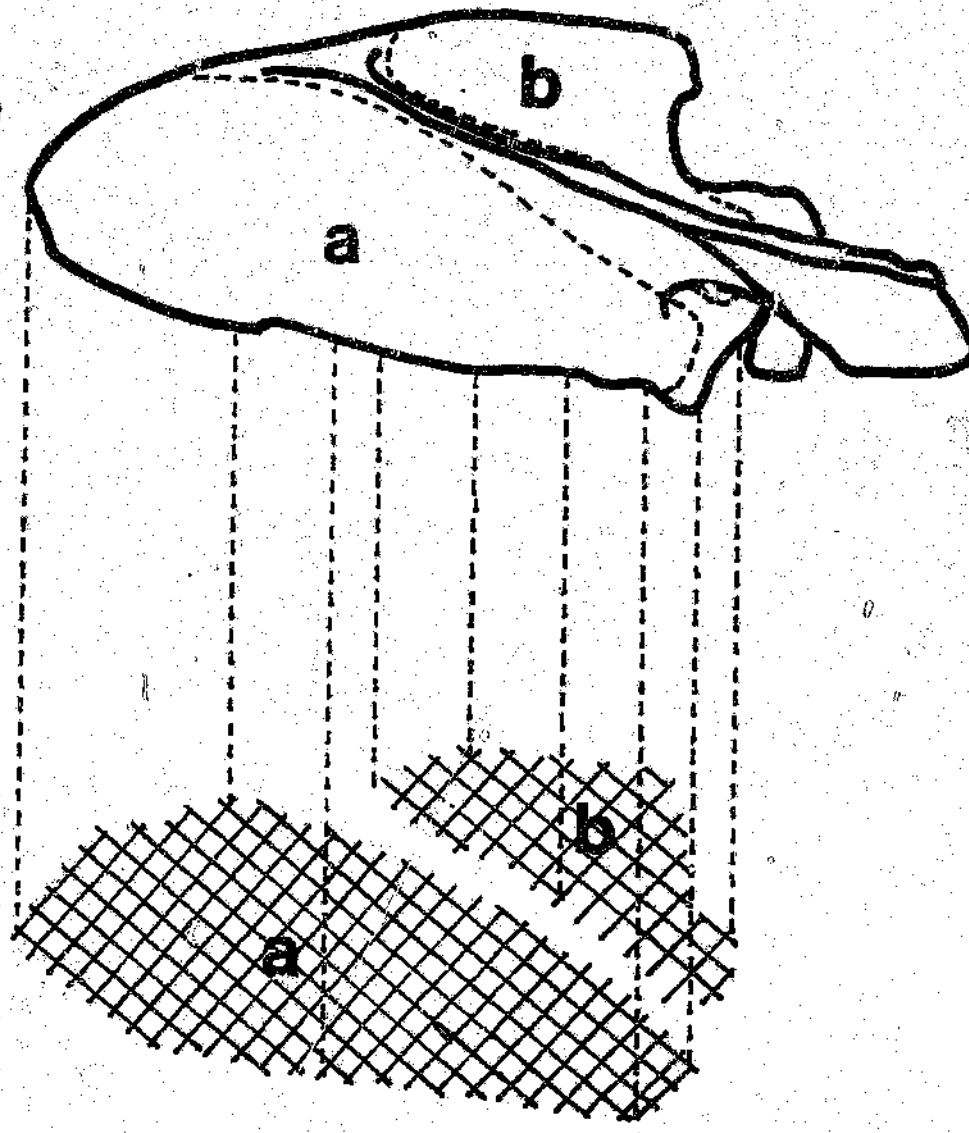


Figure 9. Two dimensional diagrammatic consideration of the areas of the infraspinous (a) and supraspinous (b) fossae traced during area calculation using the image analysis technique of scapular surface area reconstruction.

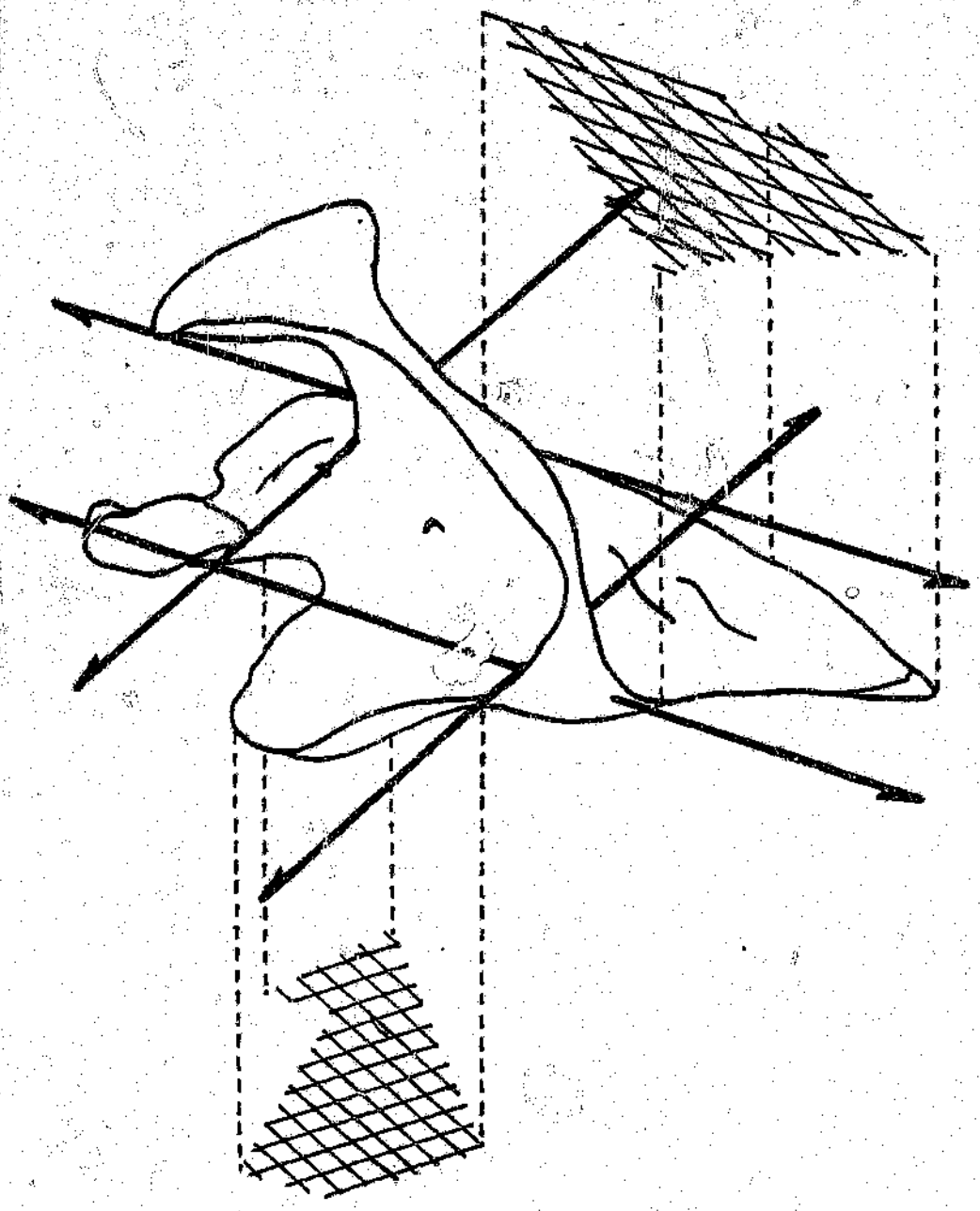


Figure 10. Diagrammatic consideration of the two-dimensionality of the areas of the infraspinous and supraspinous fossae of a human scapula when traced using the image analysis technique of scapular surface area reconstruction.

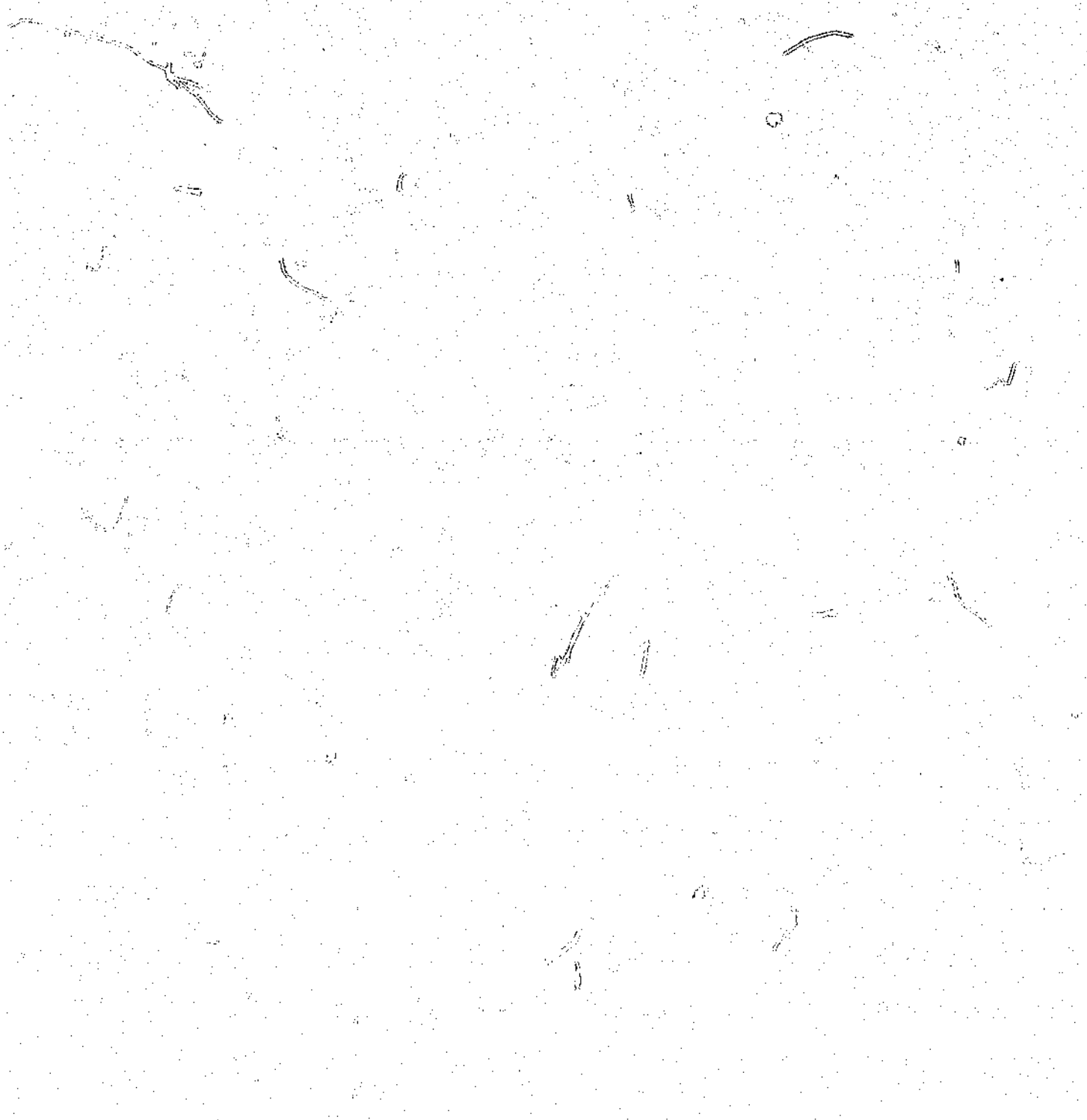
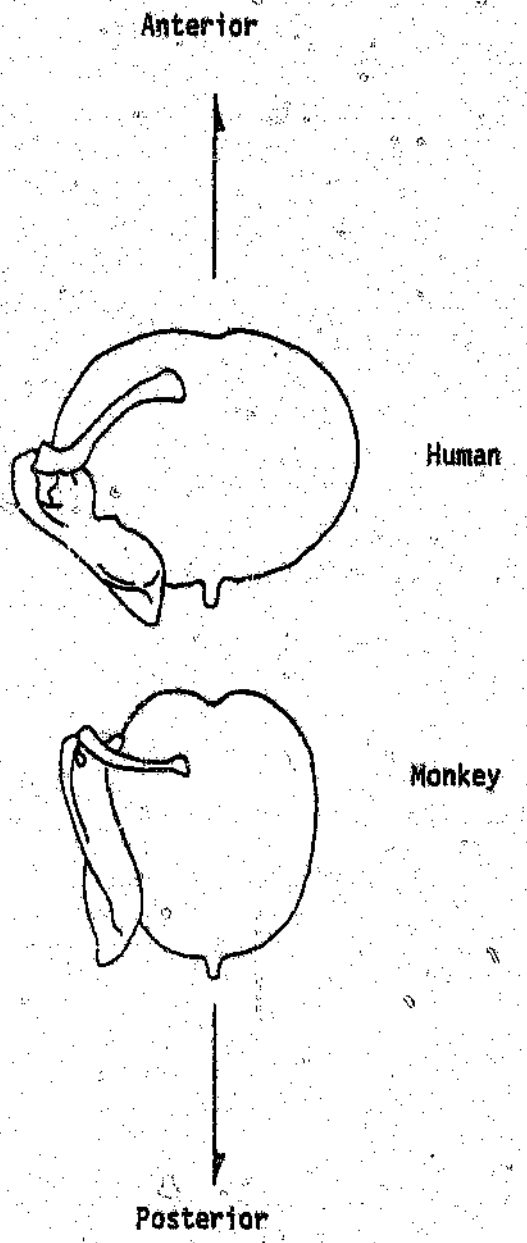


Figure 11. The position of the scapula and the clavicle on the thorax in a quadrupedal monkey and in a bipedal human, illustrated from the cranial view. Note that the blade of the scapula in the quadruped is positioned laterally on the thorax and the glenoid cavity faces anteriorly. The blade of the 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

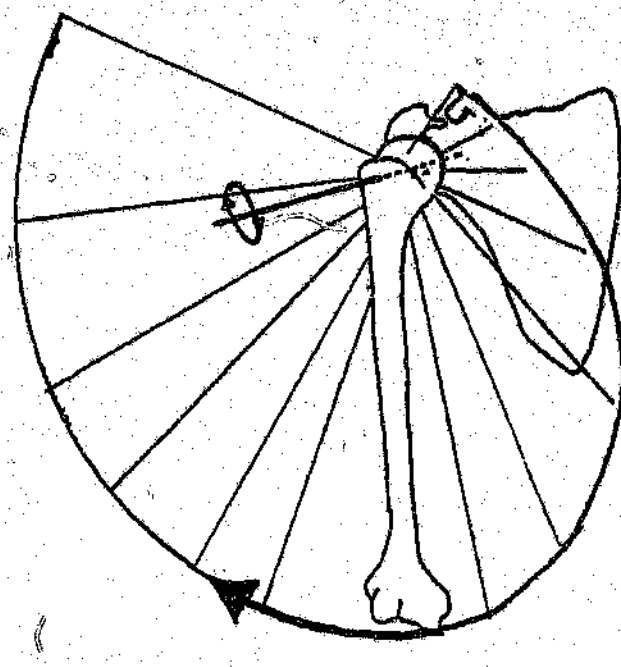


Figure 12. A two-dimensional reconstruction of the degrees of freedom of movement of the human shoulder girdle. Since the head of the humerus is offset from the shaft, spin occurs between the glenoid cavity and the humeral head but the shaft of the humerus traces part of the surface of a cone (after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

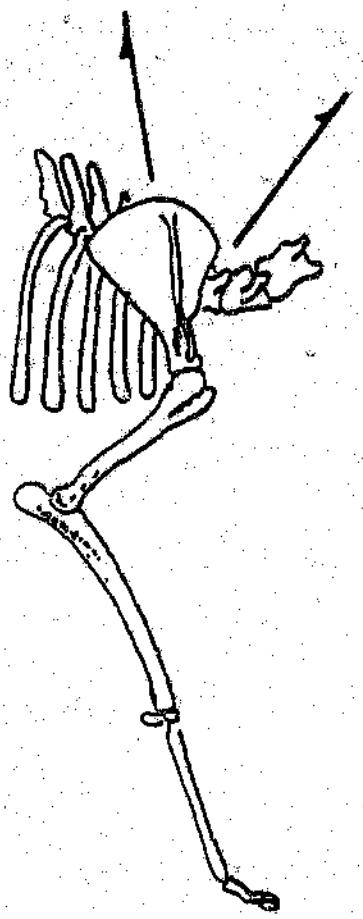
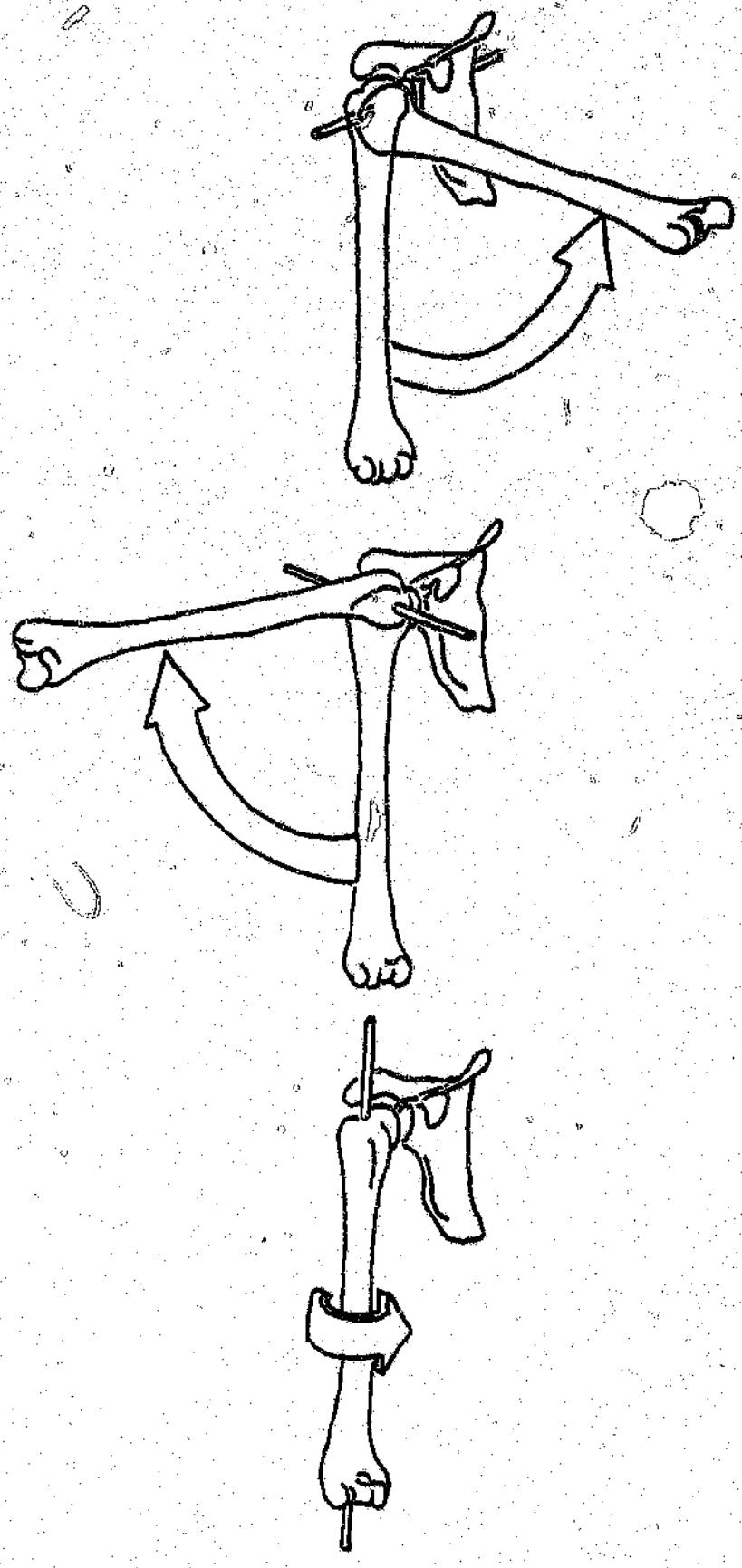


Figure 13. The thorax, scapula and forelimb of an antelope showing the morphology of a typical terrestrial quadruped. The arrows indicate the primary directions of force that pass from the forelimb through the scapula.

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).


a
b
c

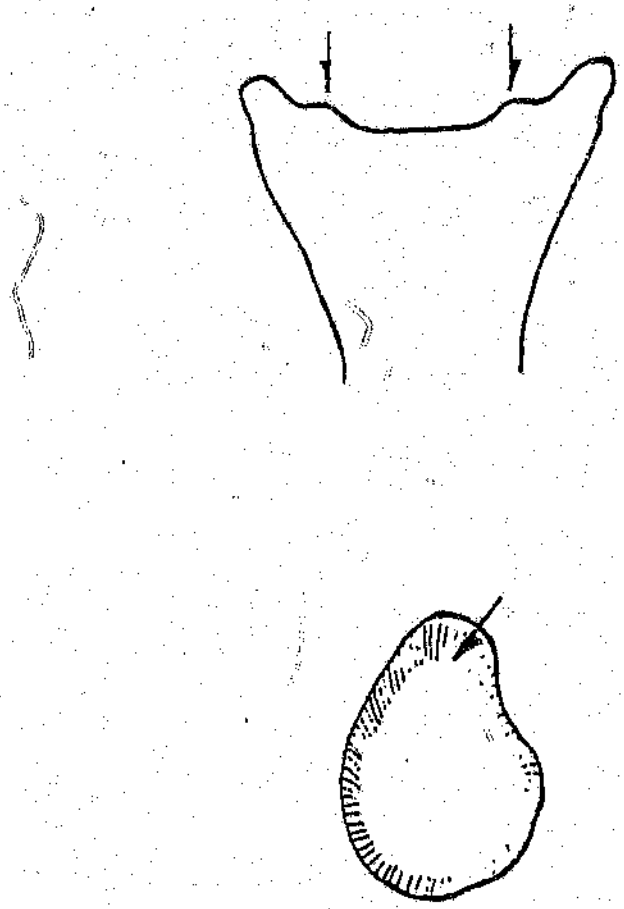


Figure 15. Diagrammatic representation of the attachment areas of the glenoid labrum on a human scapular glenoid cavity. The arrows point to the raised bony ridge that is created by the labrum at its attachment areas adjacent to the margin of the glenoid cavity. The shaded area indicates the extent of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

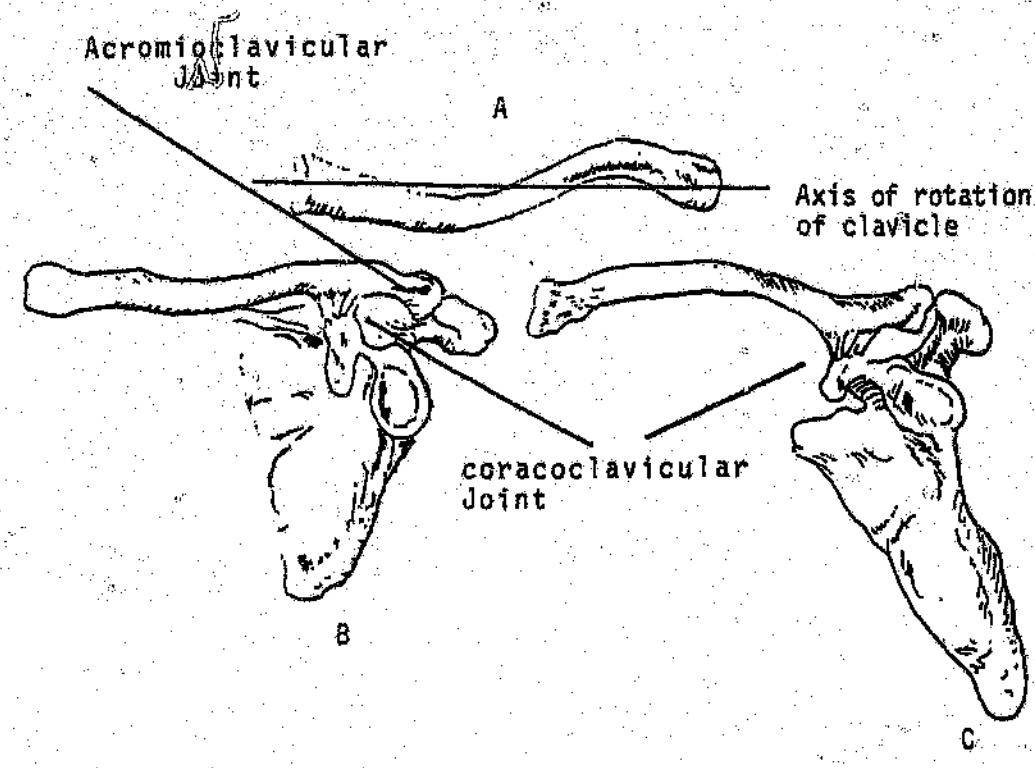


Figure 16. Rotation of the clavicle at the acromioclavicular and sternoclavicular joints in combination with the rotation and angulation of the scapula in a human. The line passing mediolaterally through the clavicle indicates the axis around which the joints allow rotation of the clavicle. Note that, 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).

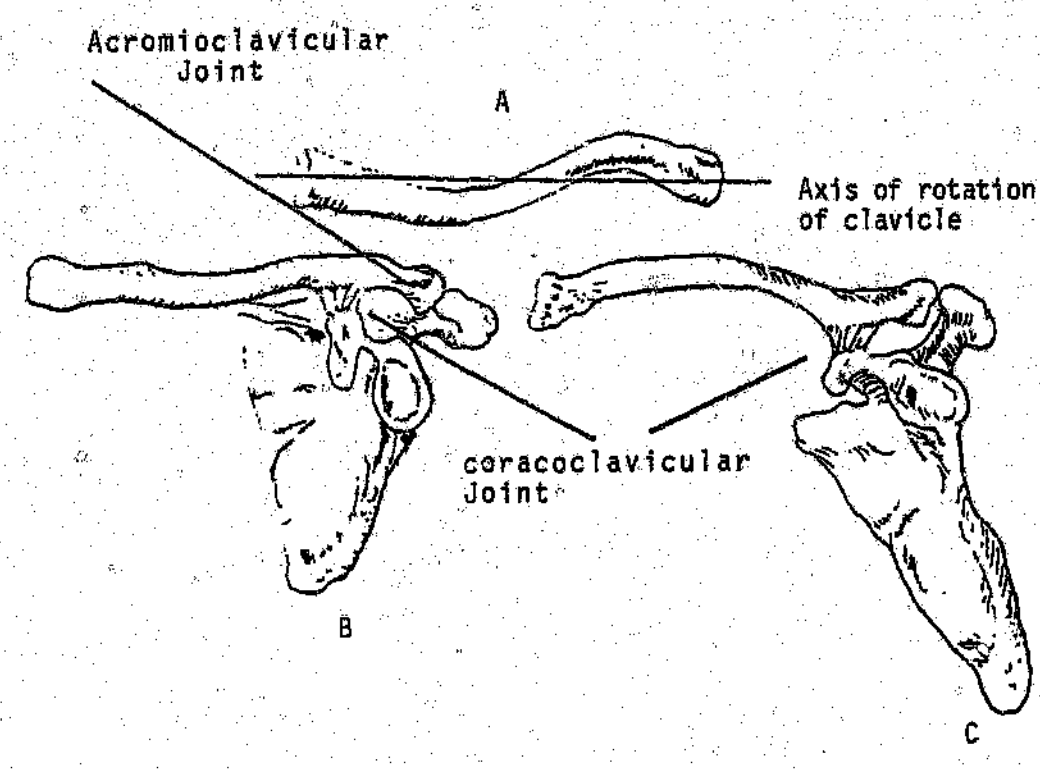
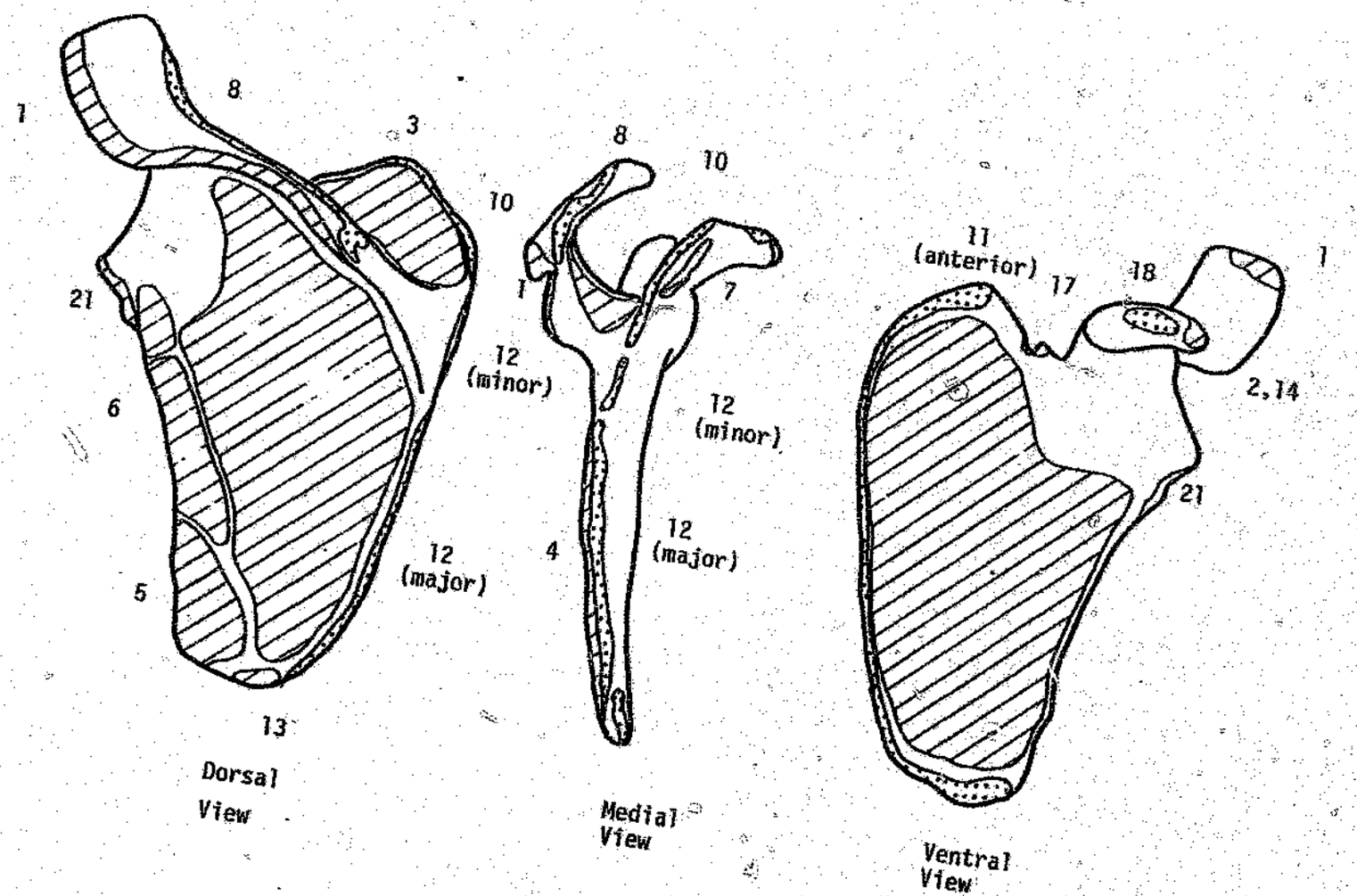


Figure 16. Rotation of the clavicle at the acromioclavicular and sternoclavicular joints in combination with the rotation and angulation of the scapula in a human. The line passing mediolaterally through the clavicle indicates the axis around which the joints allow rotation of the clavicle. Note that, 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.

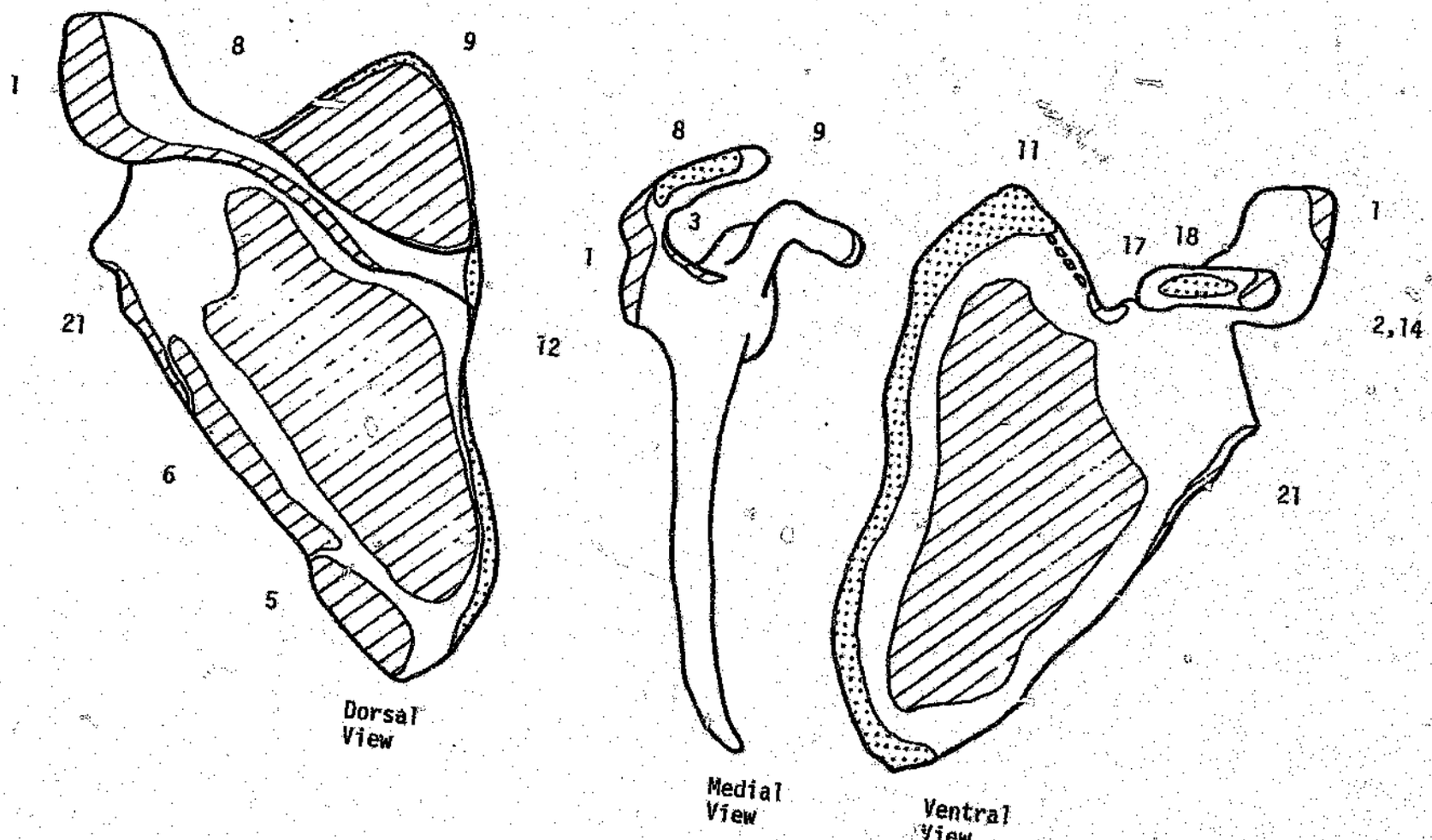
1. The deltoid muscle
2. The biceps muscle
3. The supraspinatus muscle
4. The infraspinatus muscle
5. The teres major muscle
6. The teres minor muscle
7. The subscapularis muscle
8. The trapezius muscle
9. The atlantoscapularis muscle
10. The levator scapulae muscle
11. The serratus magnus pars cranialis 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.

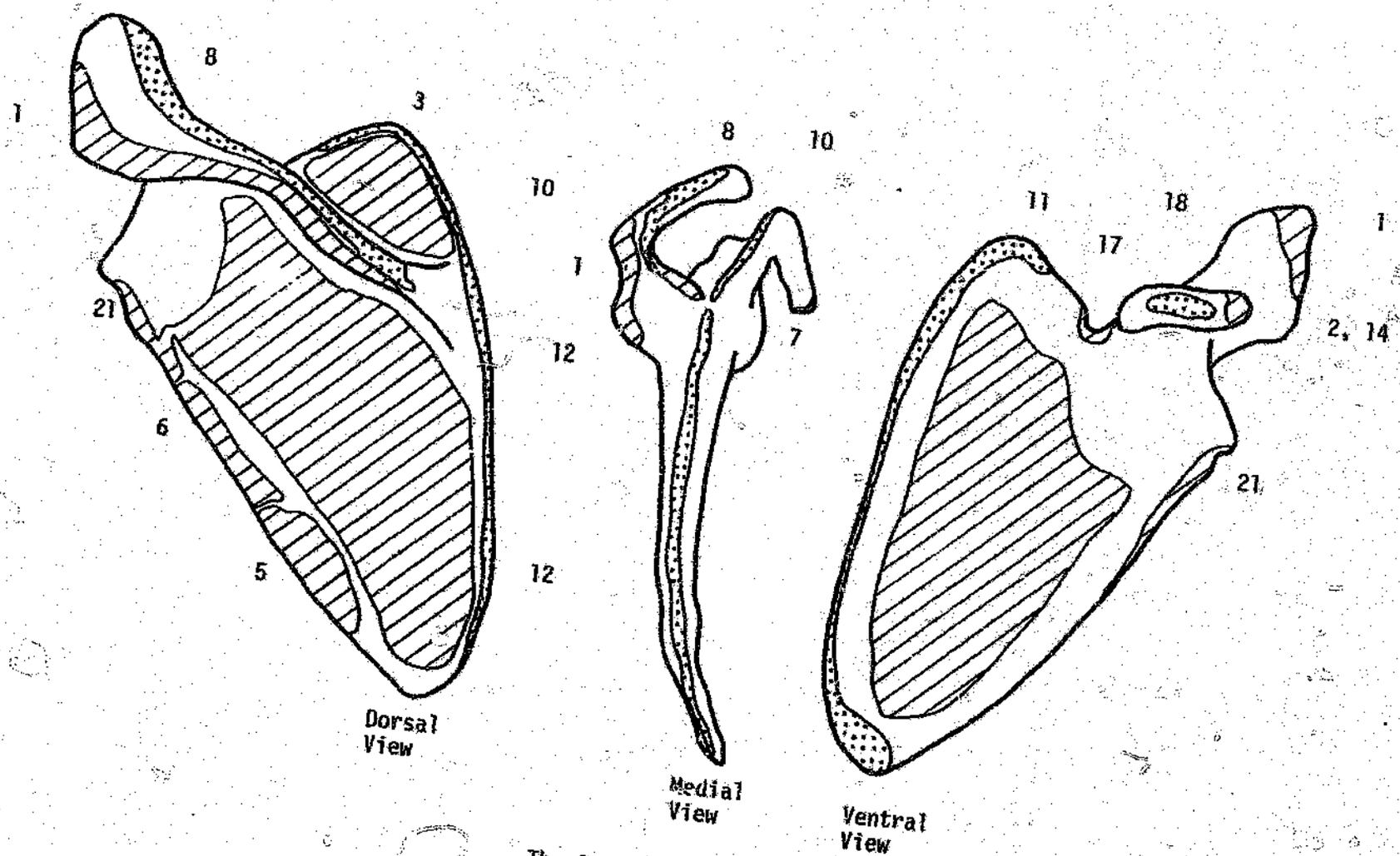


The Human Scapula

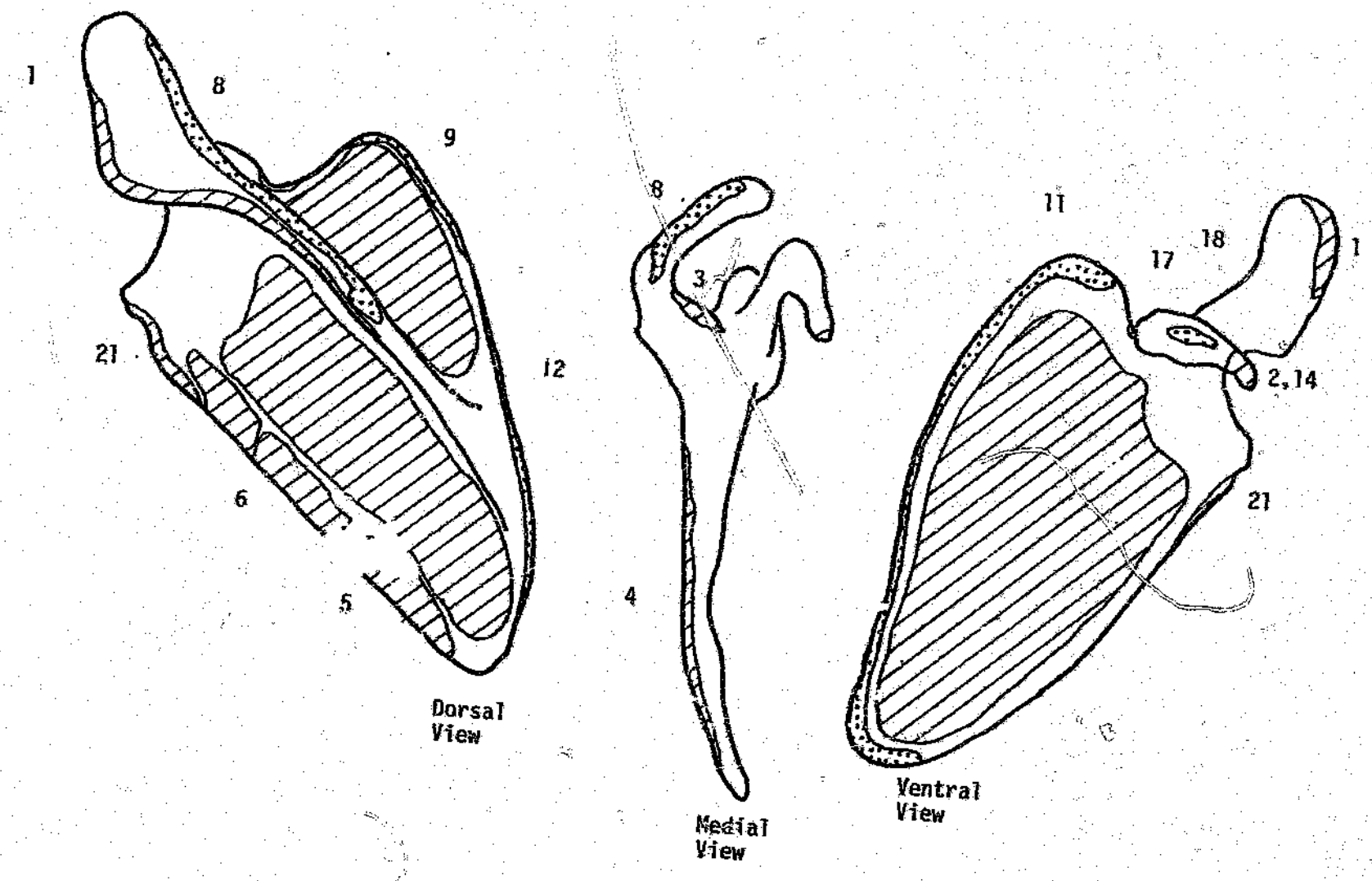
Figure 17



The Chimpanzee & Gorilla
Scapula
Figure 18

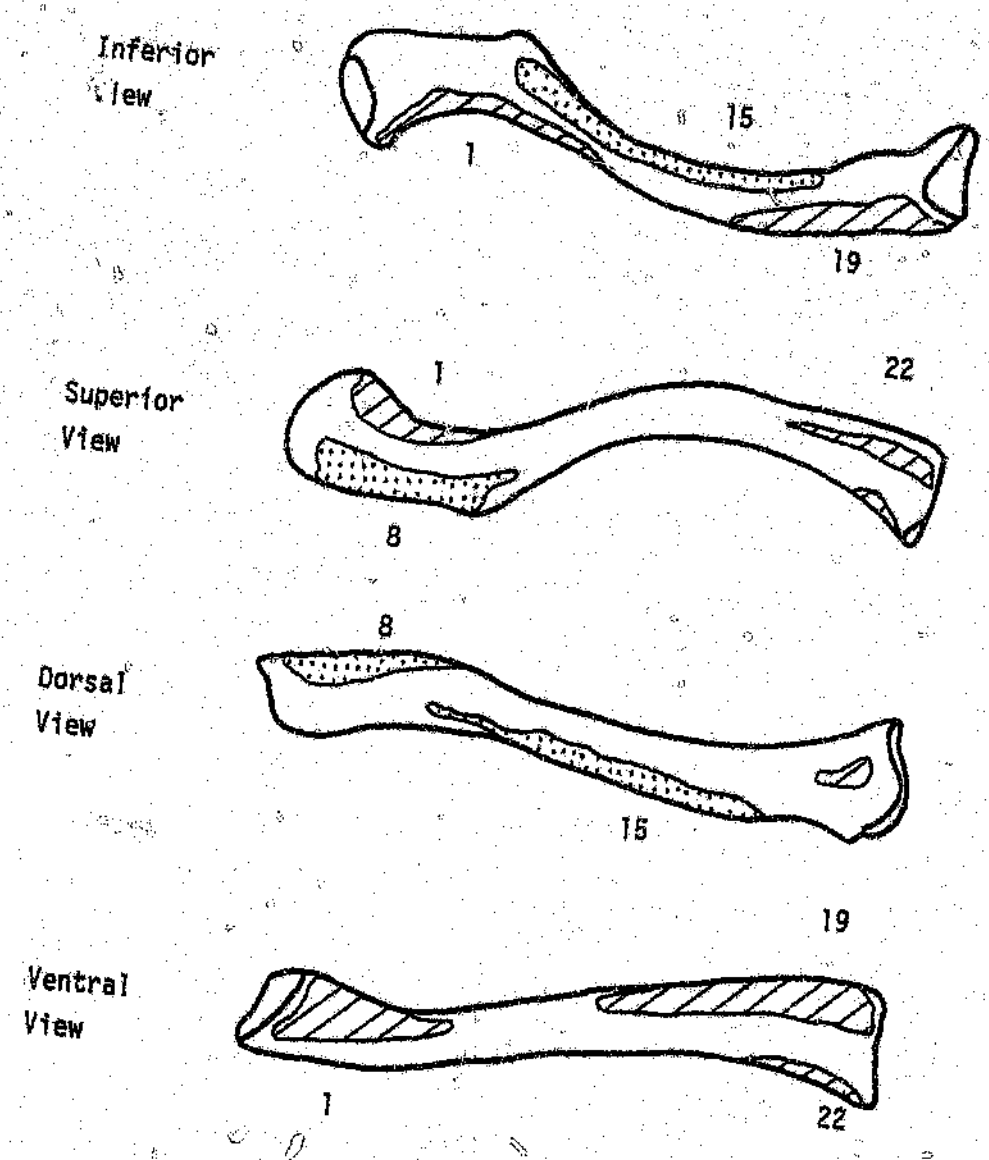


The Orang-utan Scapula
Figure 19

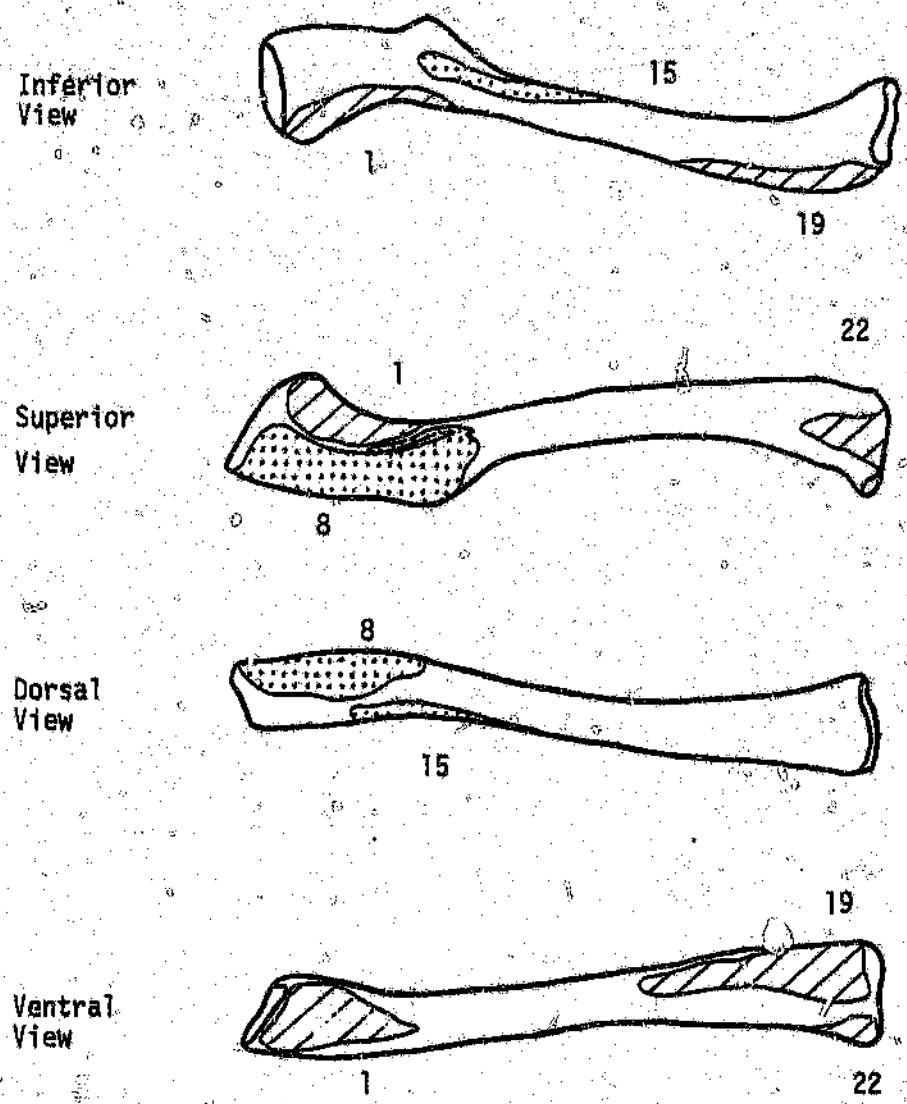


The Hylobatid Scapula

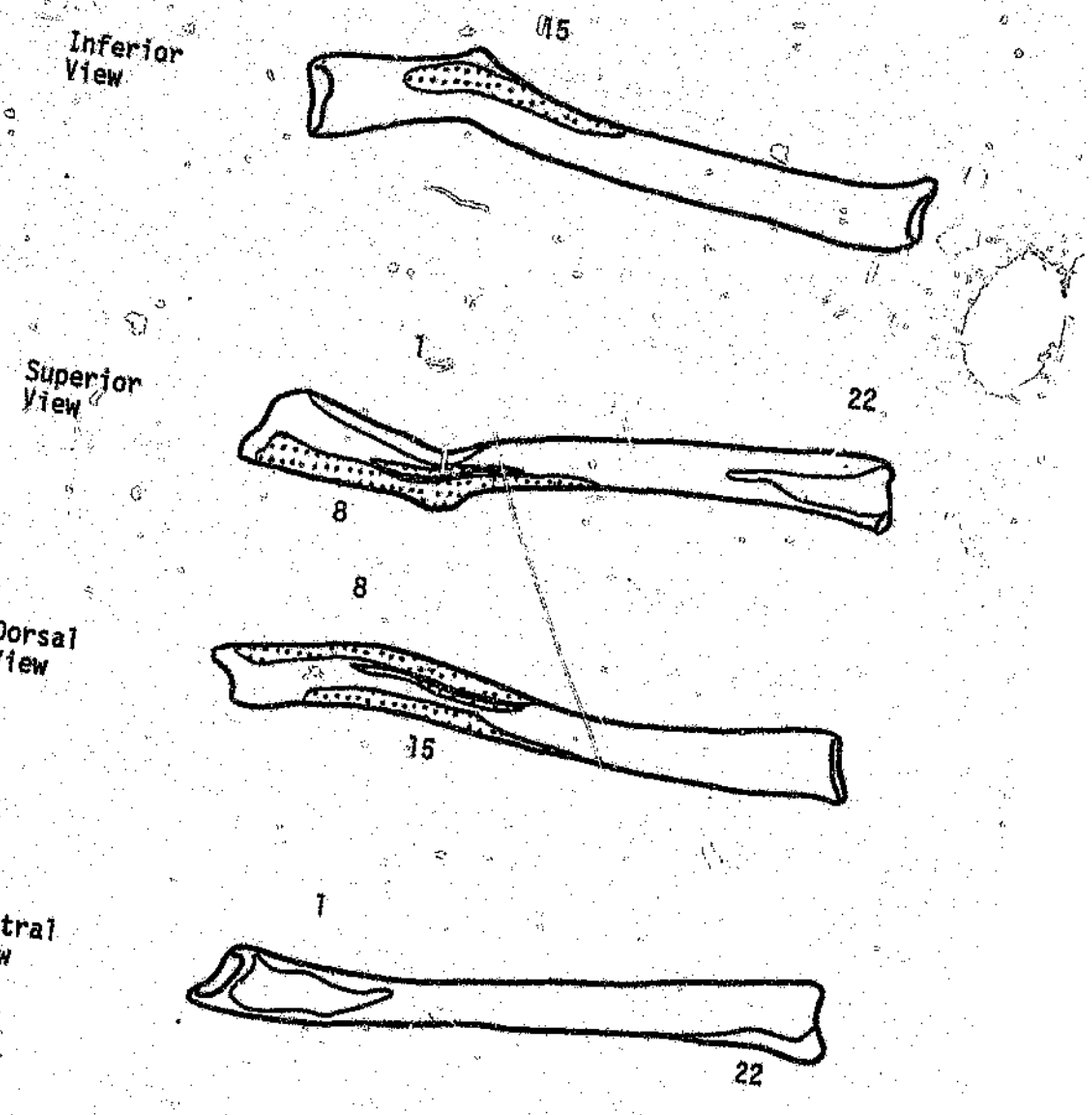
Figure 20



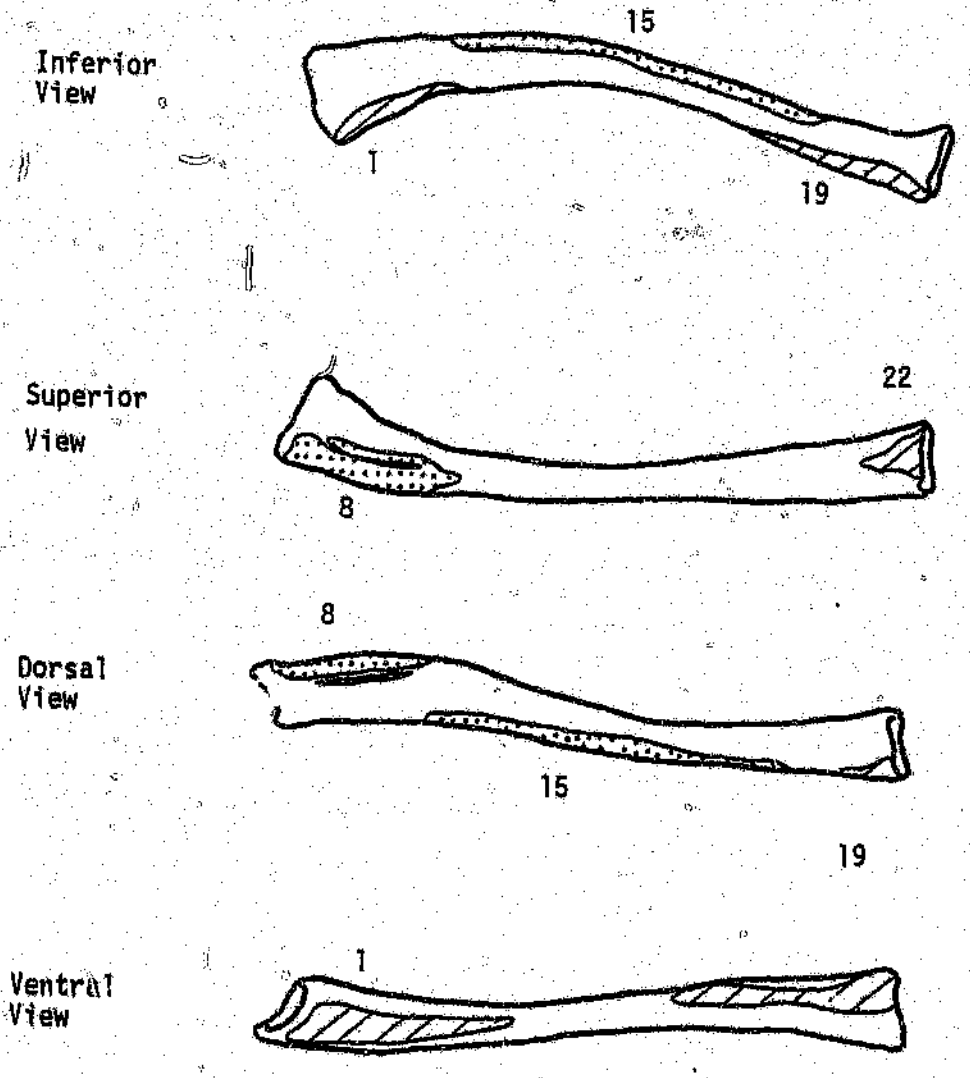
The Human Clavicle
Figure 21



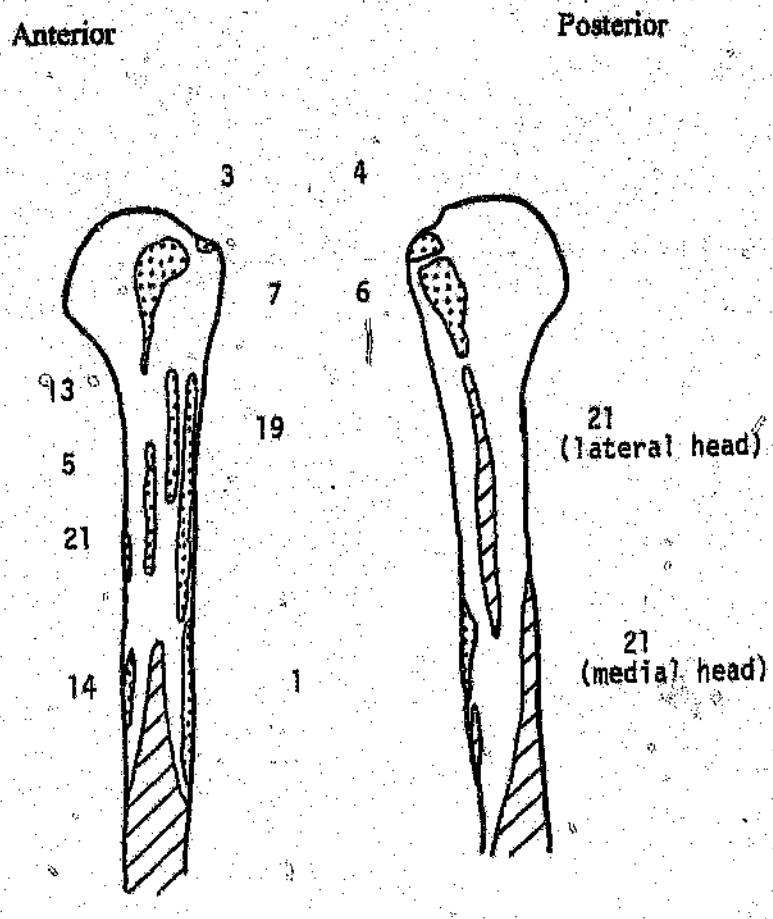
The Chimpanzee & Gorilla Clavicle
Figure 22



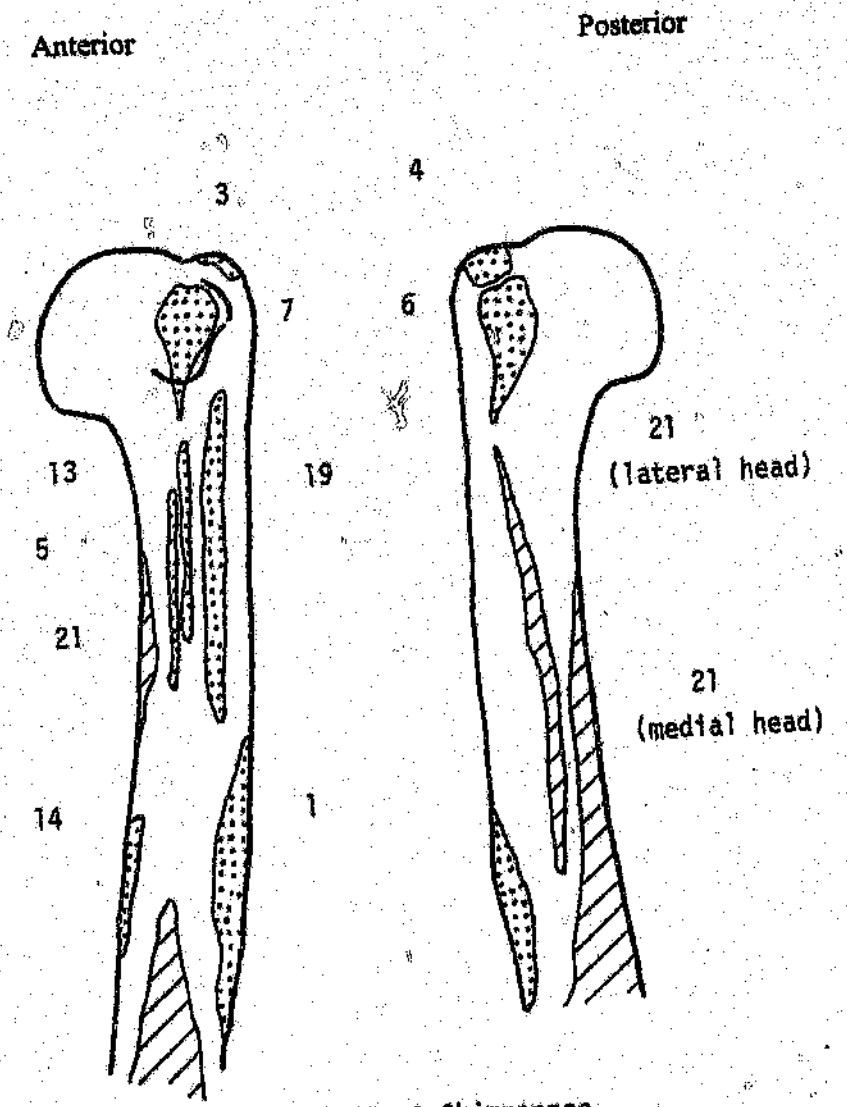
The Orang-utan Clavicle
Figure 23



The Hylobatid Clavicle
Figure 24

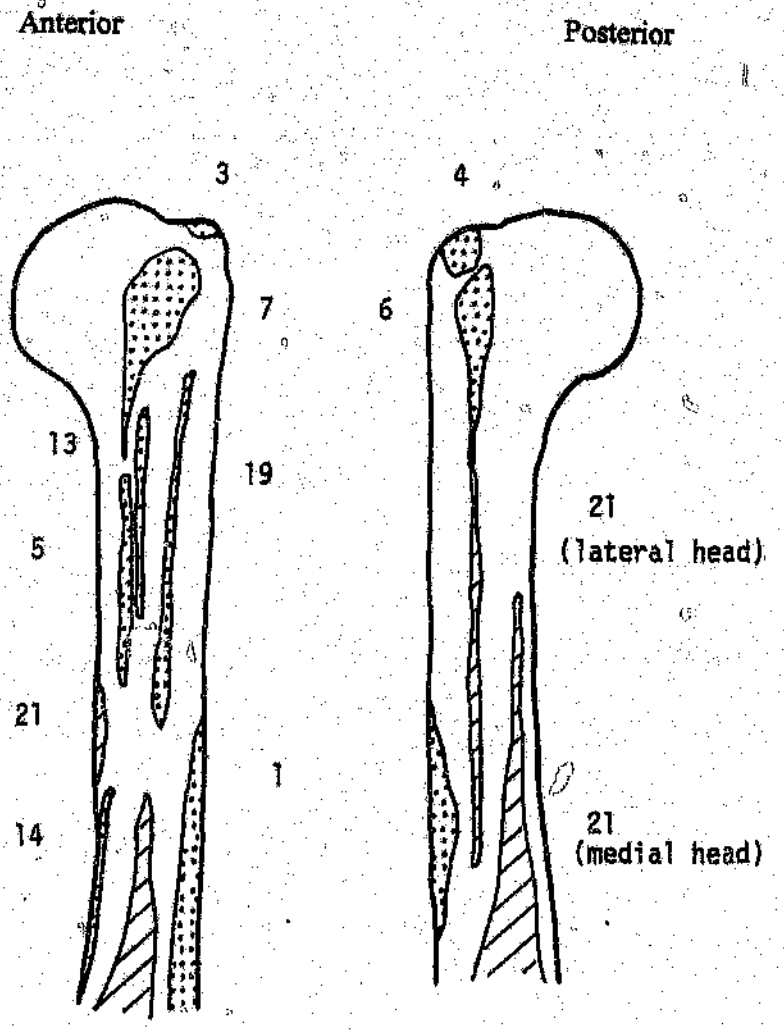


The Human Humerus
Figure 25

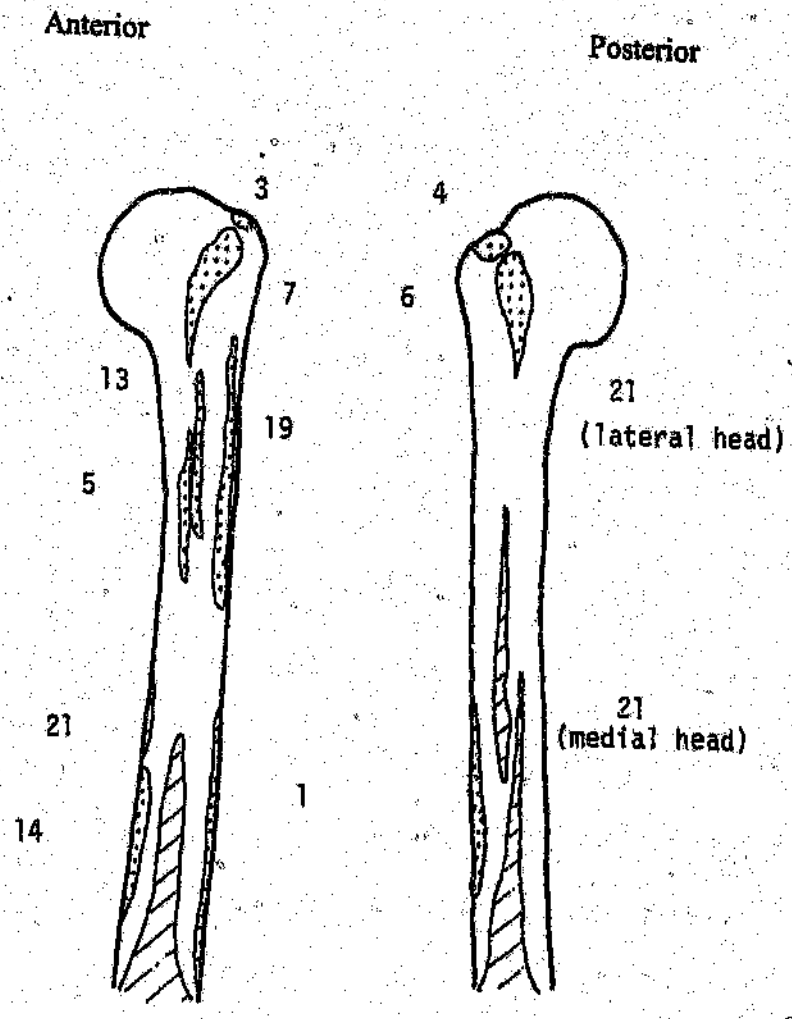


The Gorilla & Chimpanzee
Humerus

Figure 26



The Orang-utan Humerus
Figure 27



The Hylobatid Humerus
Figure 28

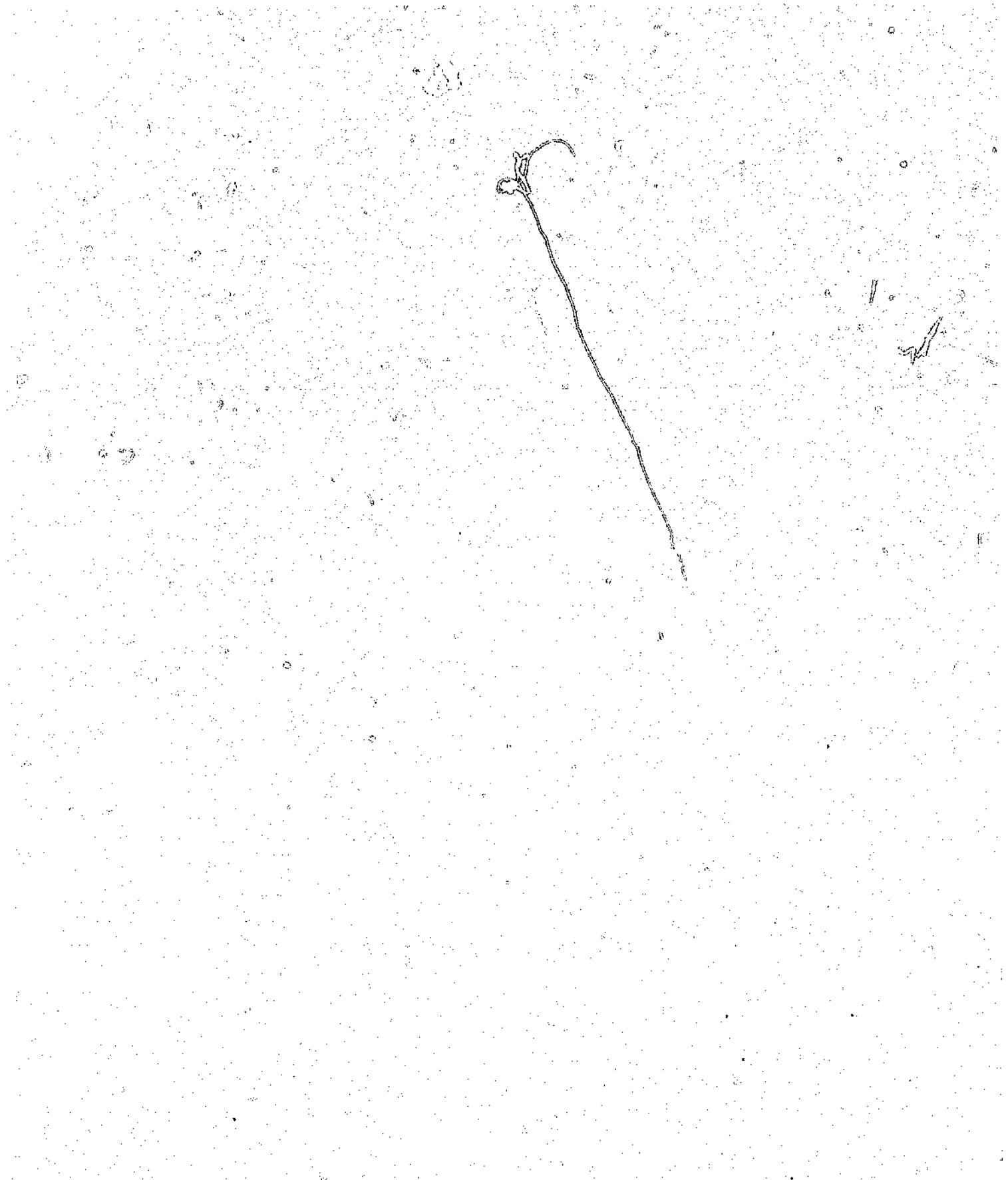


Figure 29. A composite (right) hominoid scapula with morphological features illustrated and labelled. Views are dorsal (top left), ventral (top right) and lateral (lower centre).

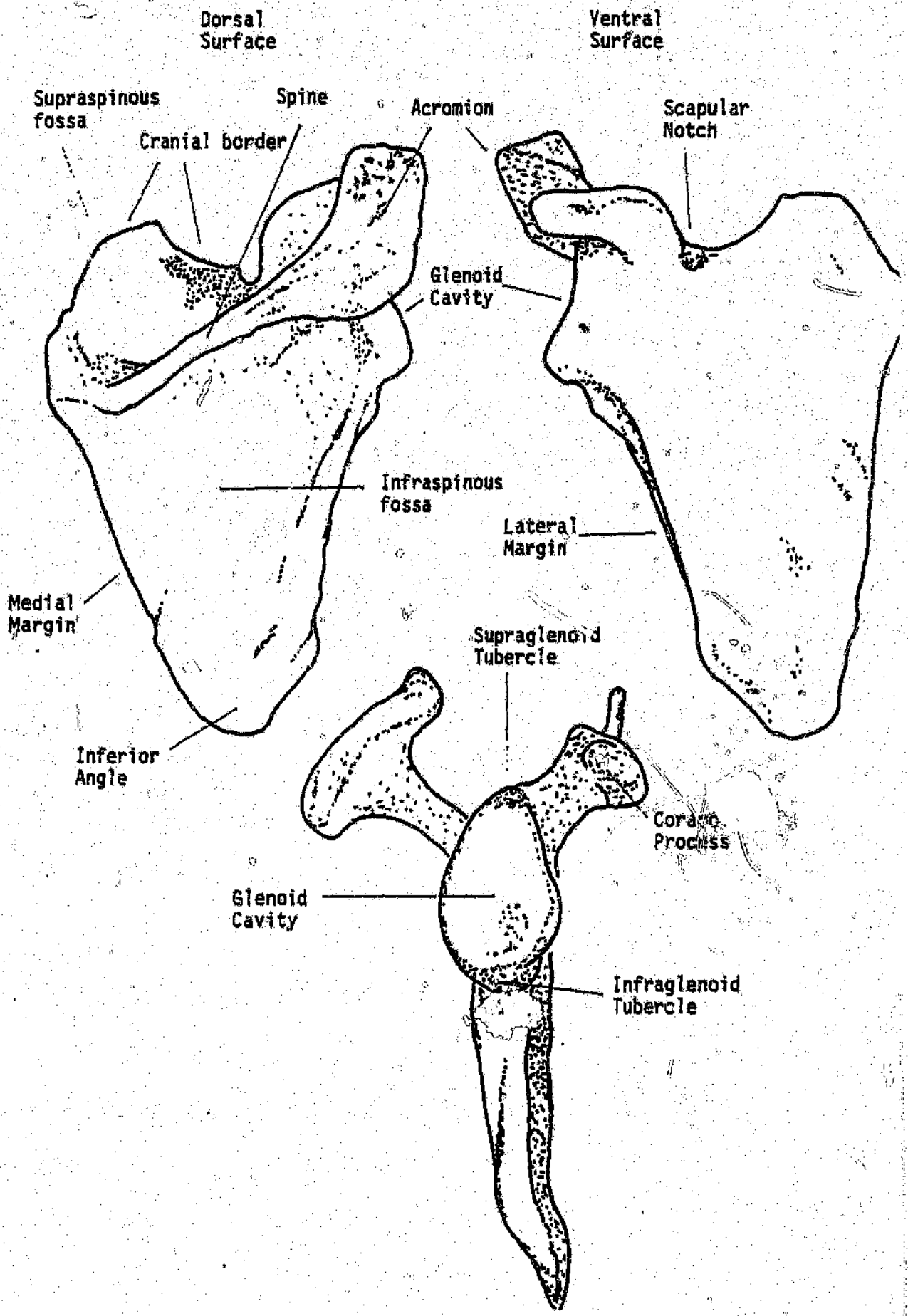

Dorsal Surface
Ventral Surface
Supraspinous fossa
Spine
Acromion
Scapular Notch
Cranial border
Glenoid Cavity
Infraspinous fossa
Lateral Margin
Medial Margin
Supraglenoid Tubercle
Inferior Angle
Coracoid Process
Glenoid Cavity
Infraglenoid Tubercle

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

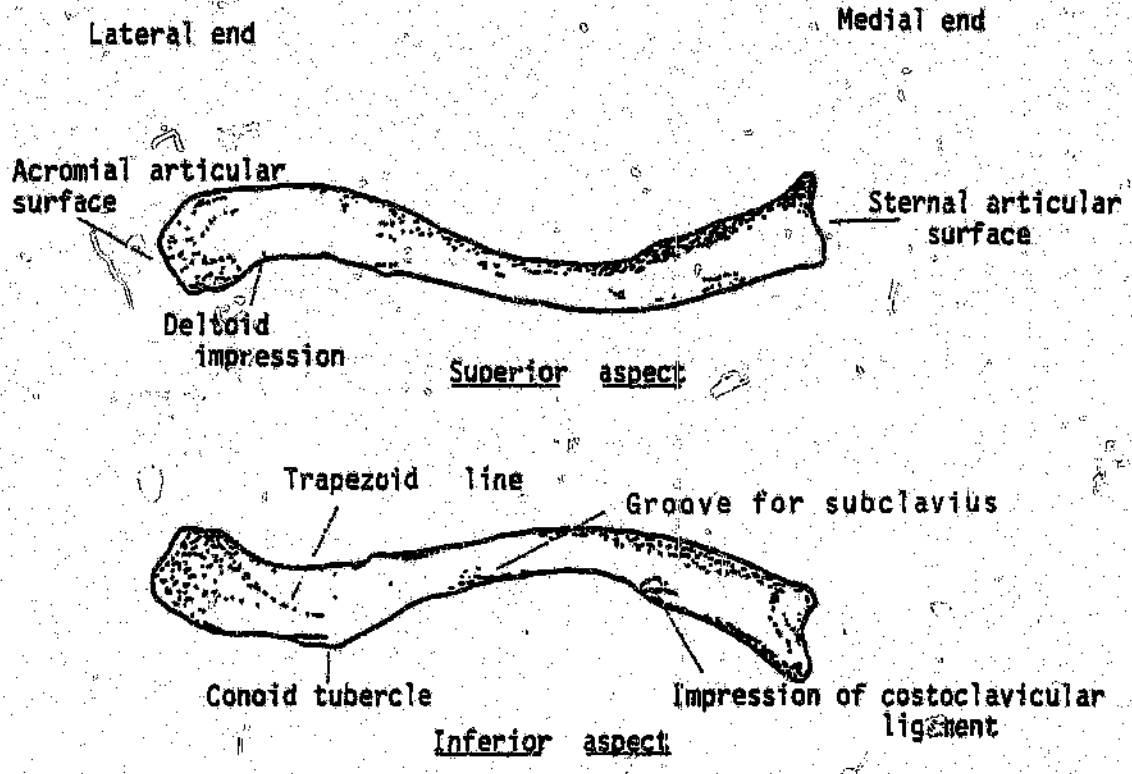

Lateral end
Medial end
Acromial articular surface
Sternal articular surface
Deltoid impression
Superior aspect
Trapezoid line
Groove for subclavius
Conoid tubercle
Impression of costoclavicular ligament
Inferior aspect

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

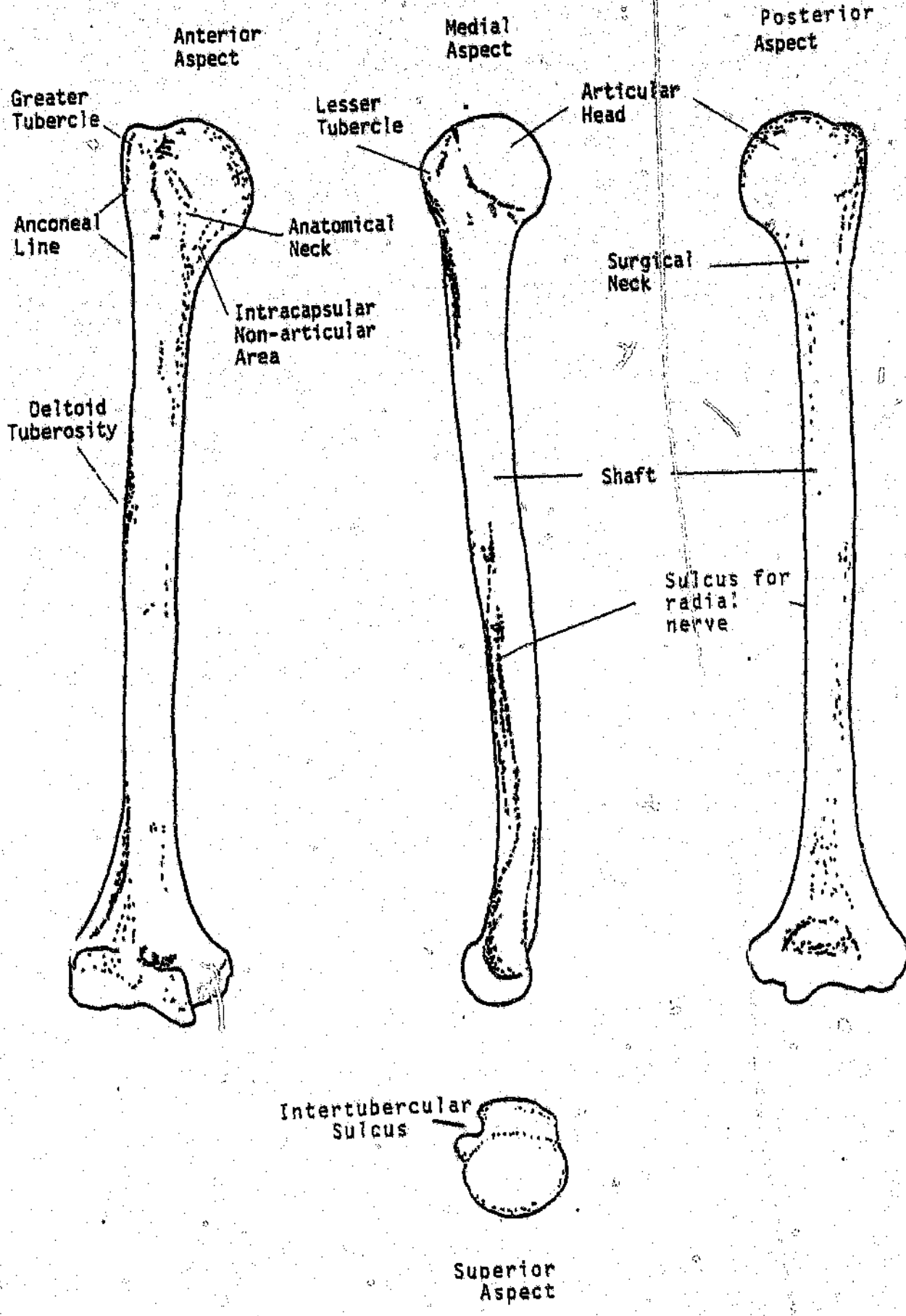
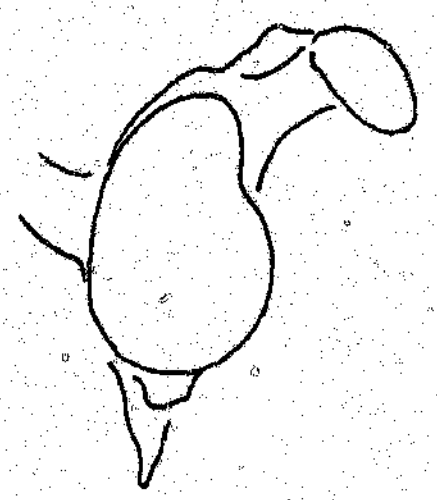
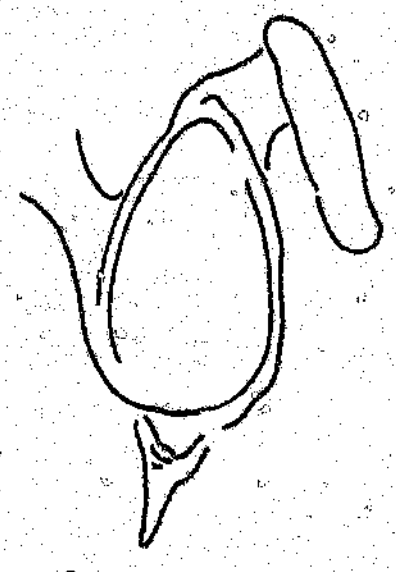

Anterior Aspect
Medial Aspect
Posterior Aspect
Greater Tubercle
Lesser Tubercle
Articular Head
Anconeal Line
Anatomical Neck
Surgical Neck
Intracapsular Non-articular Area
Deltoid Tuberosity
Shaft
Sulcus for radial nerve
Intertubercular Sulcus
Superior Aspect

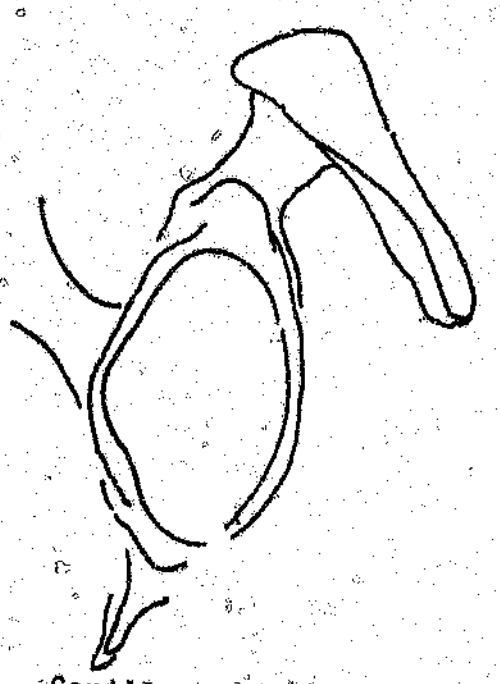
Figure 32. Shapes of the (right) scapular glenoid cavity in various hominoids. Note that the glenoid cavities of non-human hominoids tend to be more ovoid in outline than the glenoid cavity of humans. Glenoid cavities are drawn approximately to scale.



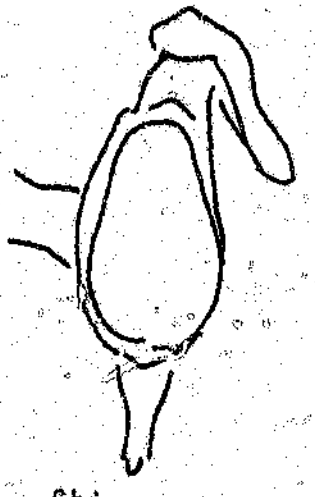
Human



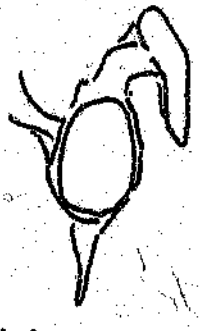
Orang-utan



Gorilla



Chimpanzee

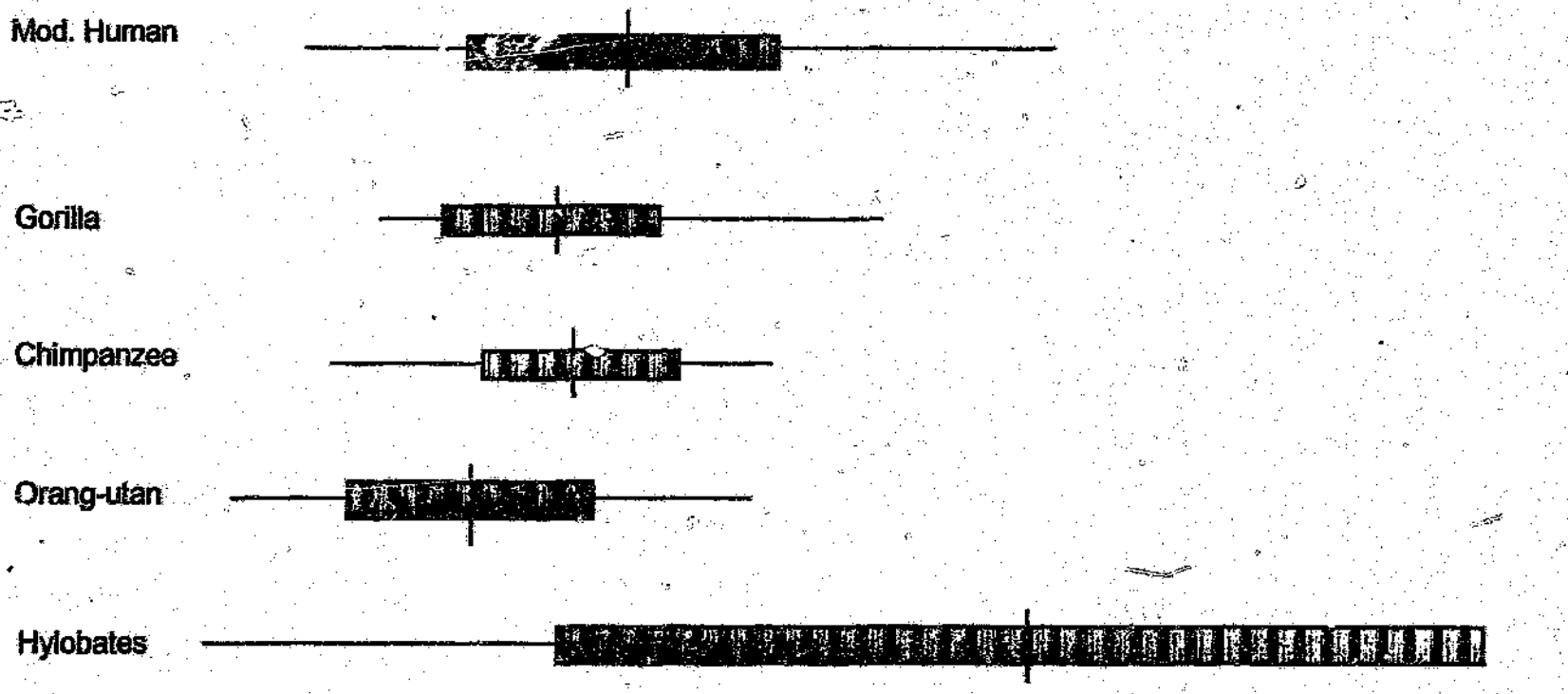


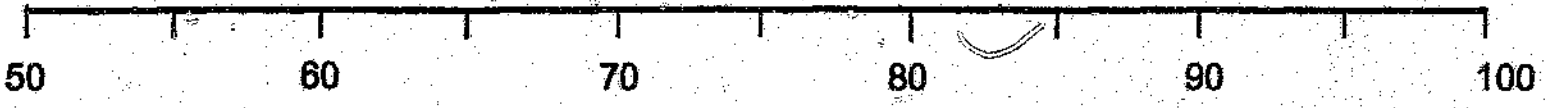
Hylobates

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) *





* This author's data

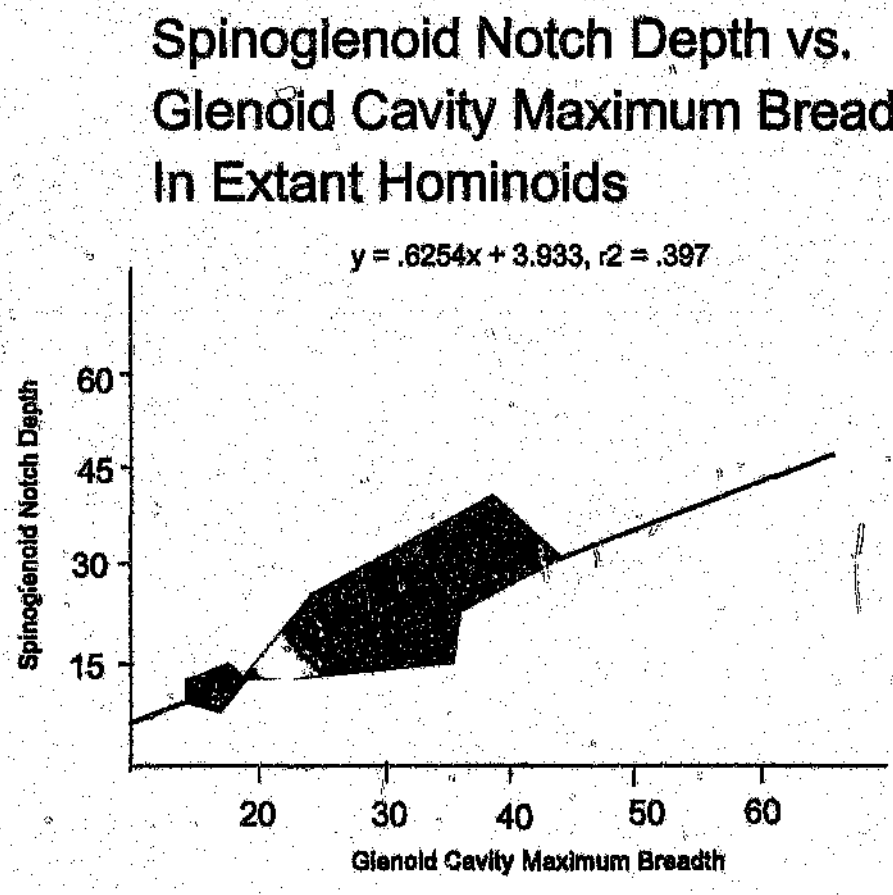


Figure 34. Bivariate plot of spinoglenoid notch depth vs. glenoid cavity maximum breadth. Shaded area indicates the observed limits of the range of variation for this relationship in the extant hominoid species examined in the present study. Data collected by the author.

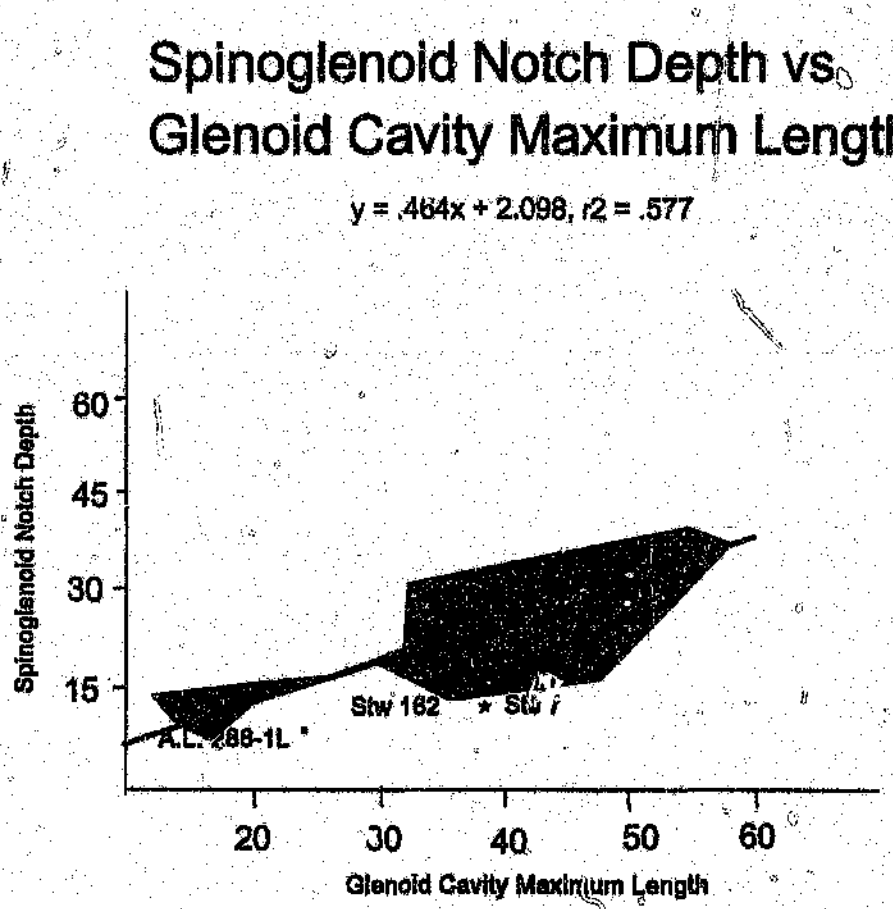


Figure 35. Bivariate plot of spinoglenoid notch depth vs. glenoid cavity maximum length. Shaded area indicates the observed limits of the range of variation for this relationship in the extant hominoid species examined in the present study. Data collected by the author.

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

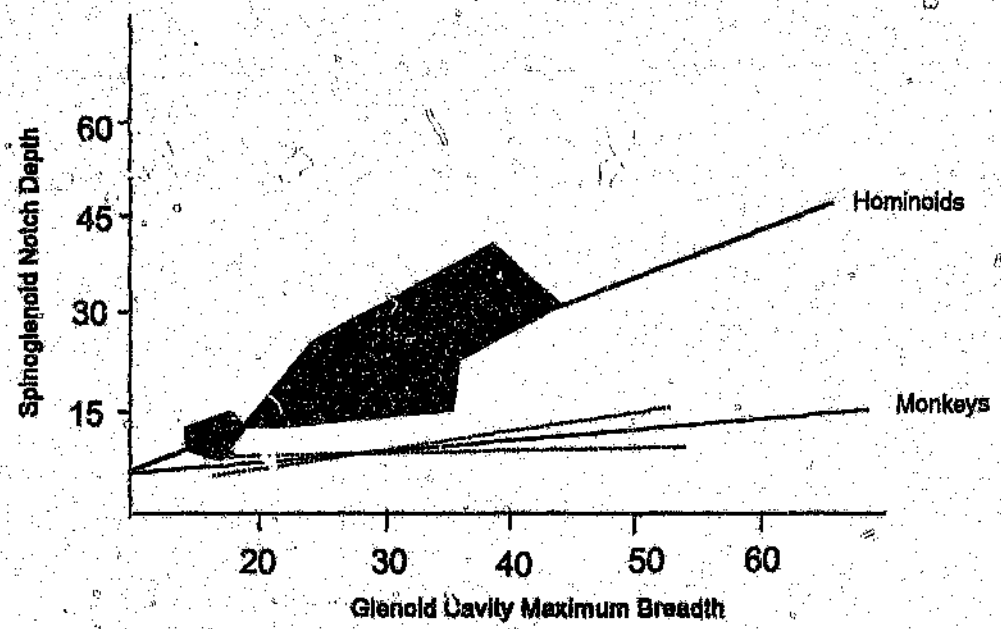
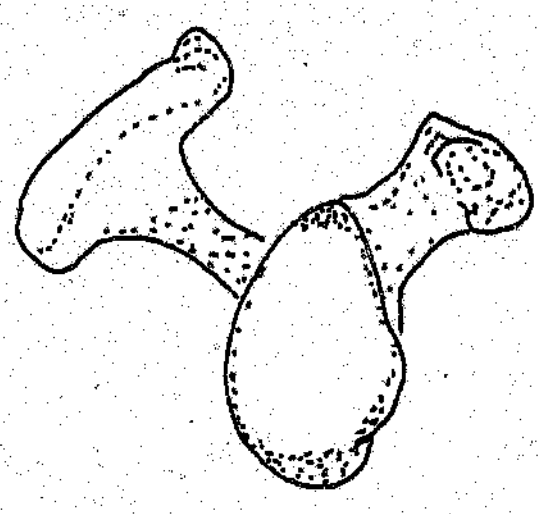
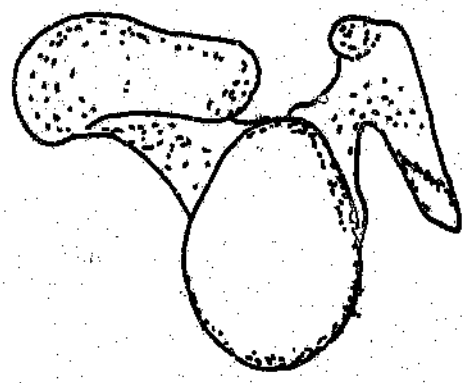


Figure 36. Bivariate plot of spinoglenoid notch depth vs. glenoid cavity maximum breadth. Shaded area indicates the observed limits of the range of variation for this relationship in the extant hominoid species examined in the present study. - Dashed lines indicate 95% confidence intervals for monkeys.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

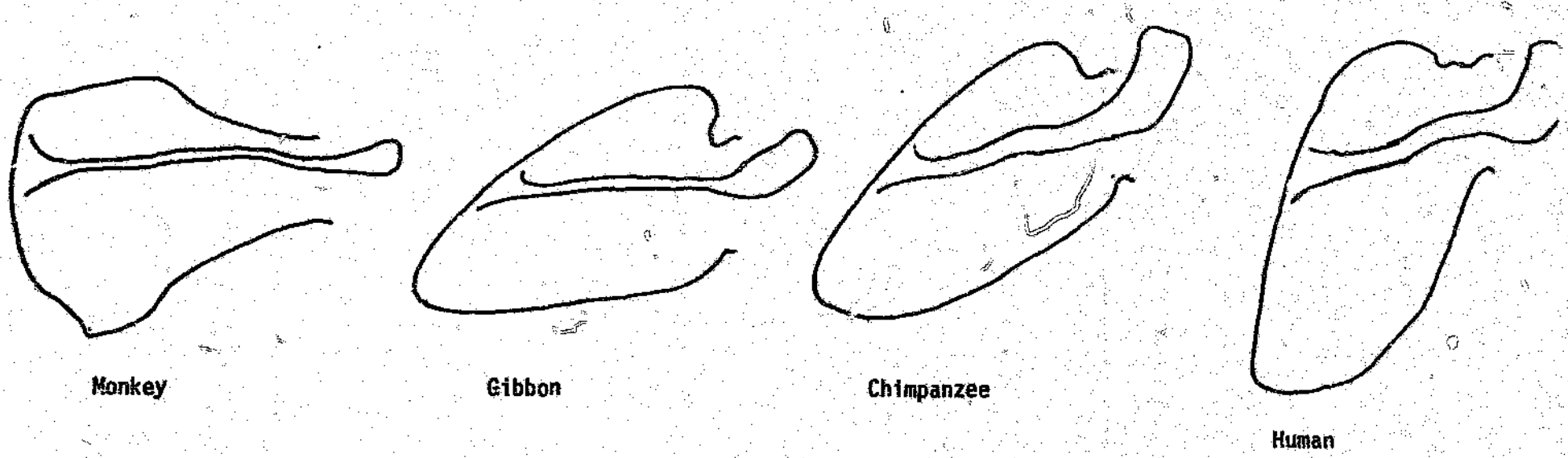


Figure 38. Comparison of the shape of the body of scapula among hominoid genera and monkeys. Note the similarity between the scapular body shape of the hylobatids and that of the monkey.

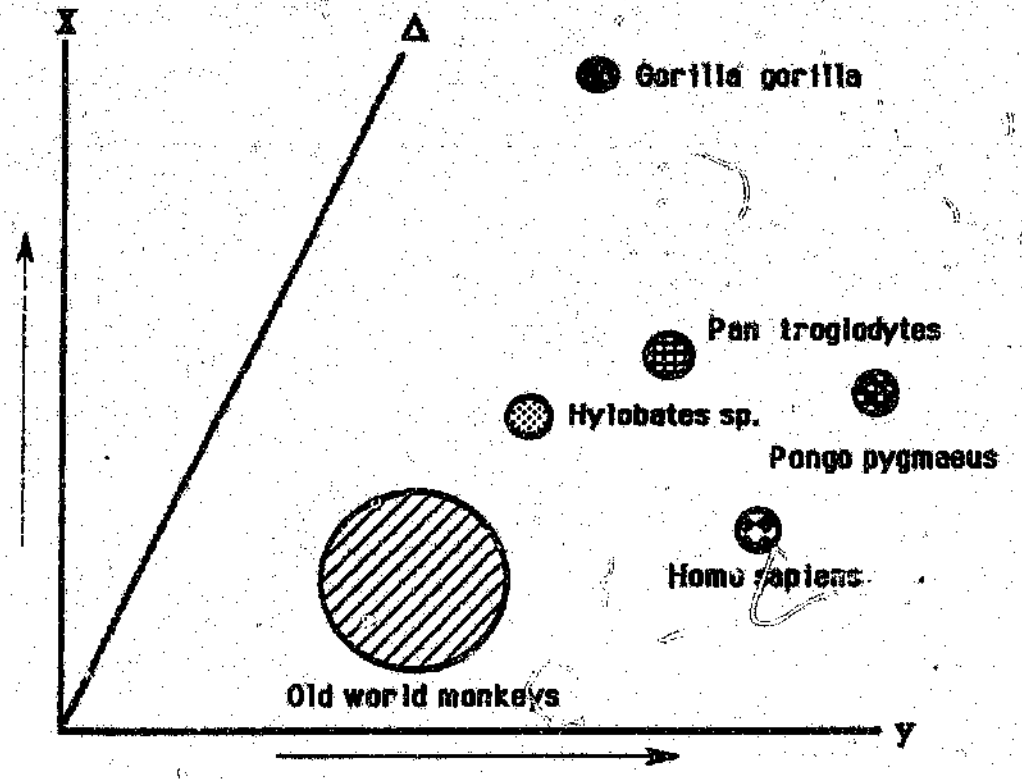


Figure 39. Bivariate plot of the supraspinous index and the infraspinous index in hominoids and Old World mokeys. x, supraspinous index; y, infraspinous index; Δ , the line of regression where the area of the supraspinous fossa equals the area of the infraspinous fossa. Modified from Roberts (1974).

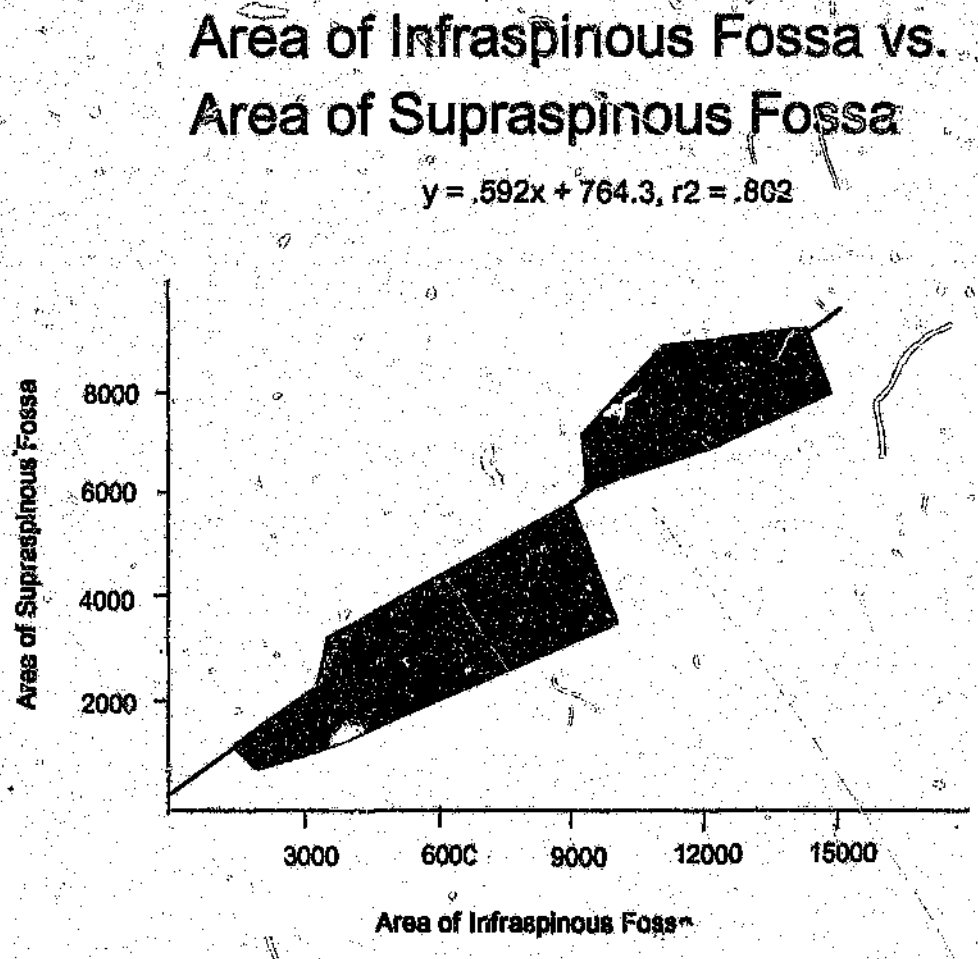


Figure 40. Bivariate plot of the area of the infraspinous fossa vs. the area of the supraspinous fossa in extant hominoids. Shaded area indicates the observed limits of the range of variation for this relationship in the extant hominoid species examined in the present study. Data collected by the author.

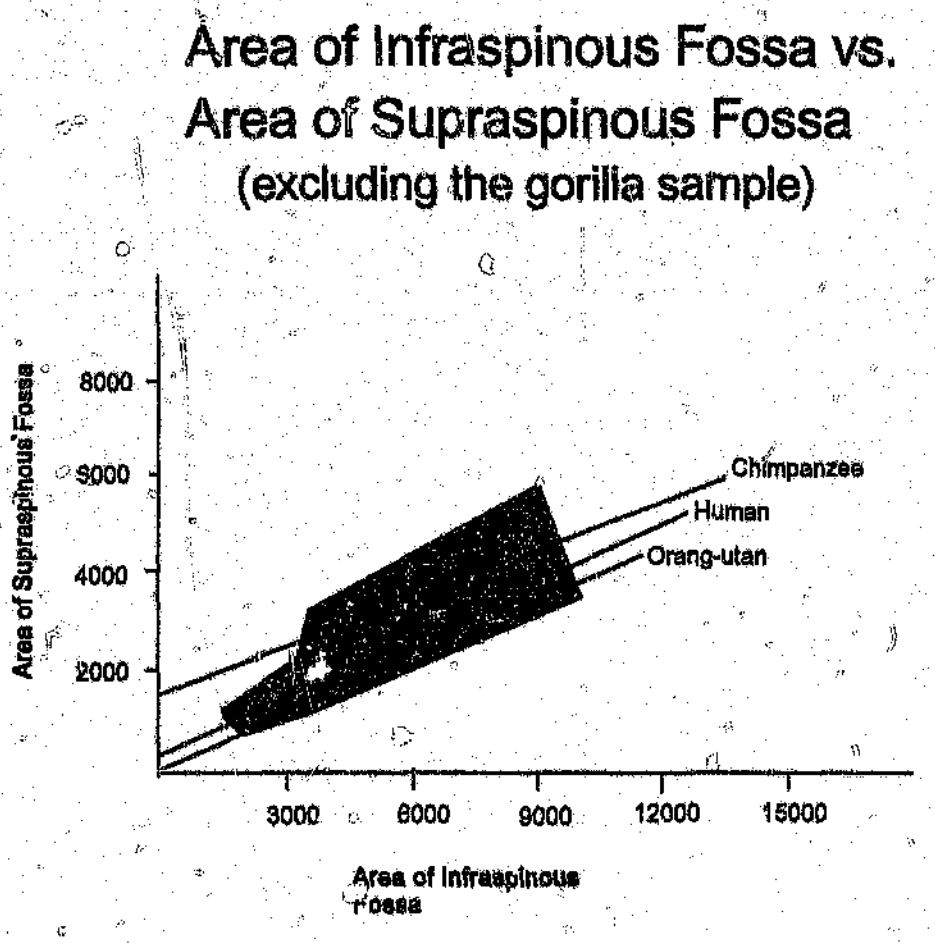


Figure 41. Bivariate plot of the area of the infraspinous fossa vs. the area of the supraspinous fossa in extant hominoids. Shaded area indicates the observed limits of the range of variation for this relationship in human s (y = .387x + 257.027, r2 = .59), chimpanzees (y = .319x + 1540.767, r2 = .243), and orang-utans (y = 355x + 156.032, r2 = .776). Data collected by the author.

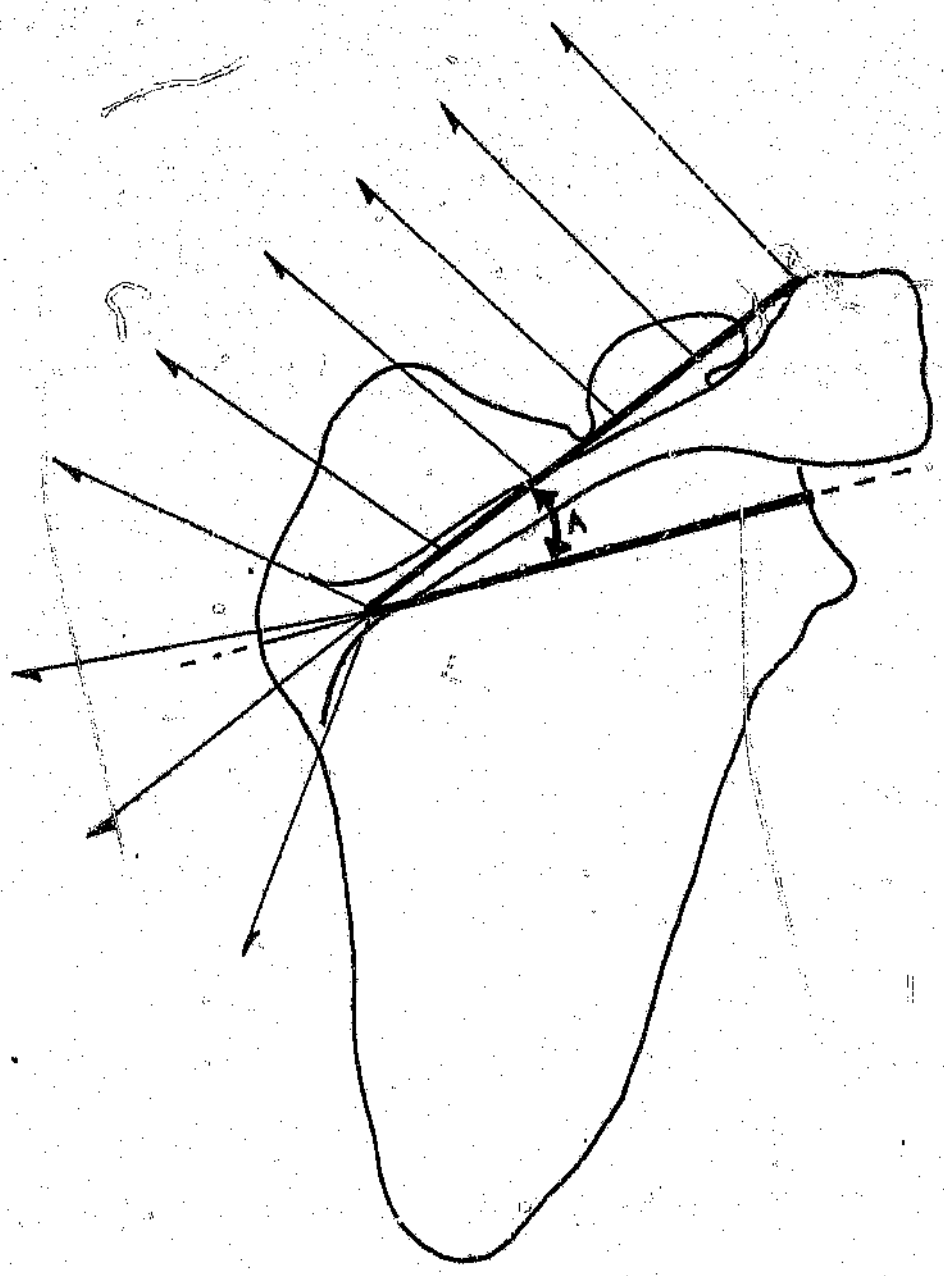


Figure 42. Illustration of the angle of insertion of the trapezius muscle in the hominoid scapula as represented by angle A. The arrows indicate the direction of forces in the muscle couple (after Oxnard, 1968c)

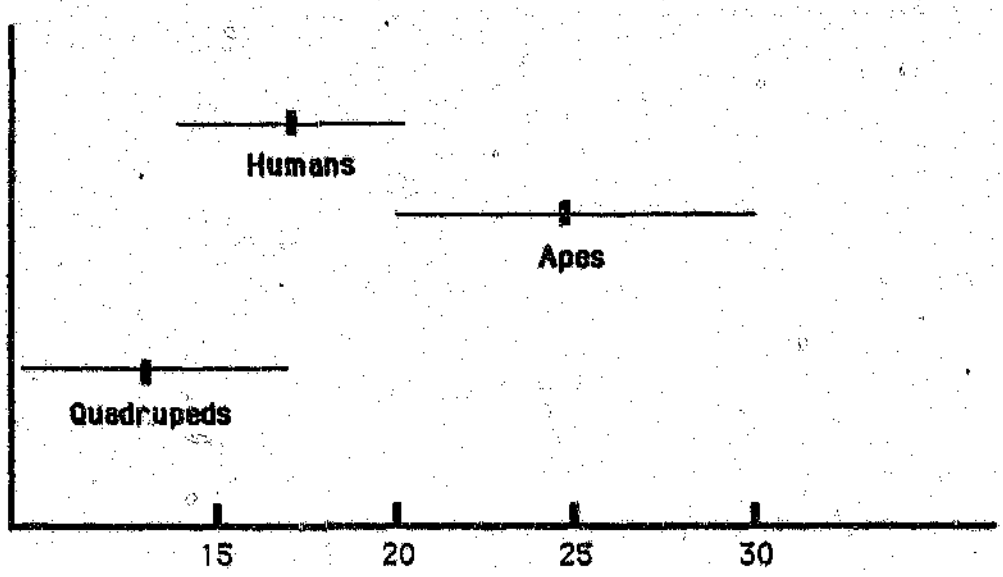


Figure 43. Calculated values for the angle of insertion of the trapezius muscle in humans, apes and quadrupedal monkeys. Vertical bar, mean; horizontal line, mean ± 1 standard deviation; x axis values in degrees (after Oxnard, 1968a)

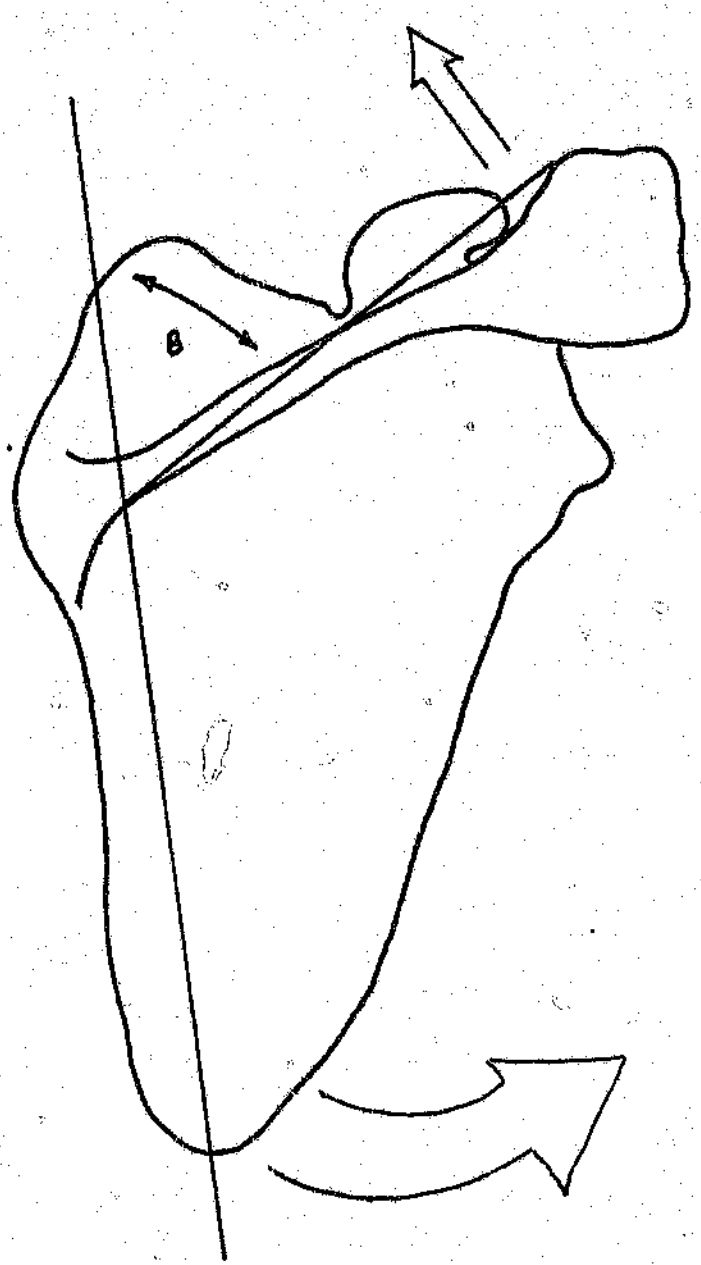


Figure 44. The orientation of components of the force couple made up of the trapezius and serratus magnus muscles (Angle B) in the scapulae of hominoids and monkeys (after Oxnard, 1968c)



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 (1968c) Vertical line, sample mean; horizontal line, observed sample range; shaded rectangle, mean ± 1 standard deviation

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

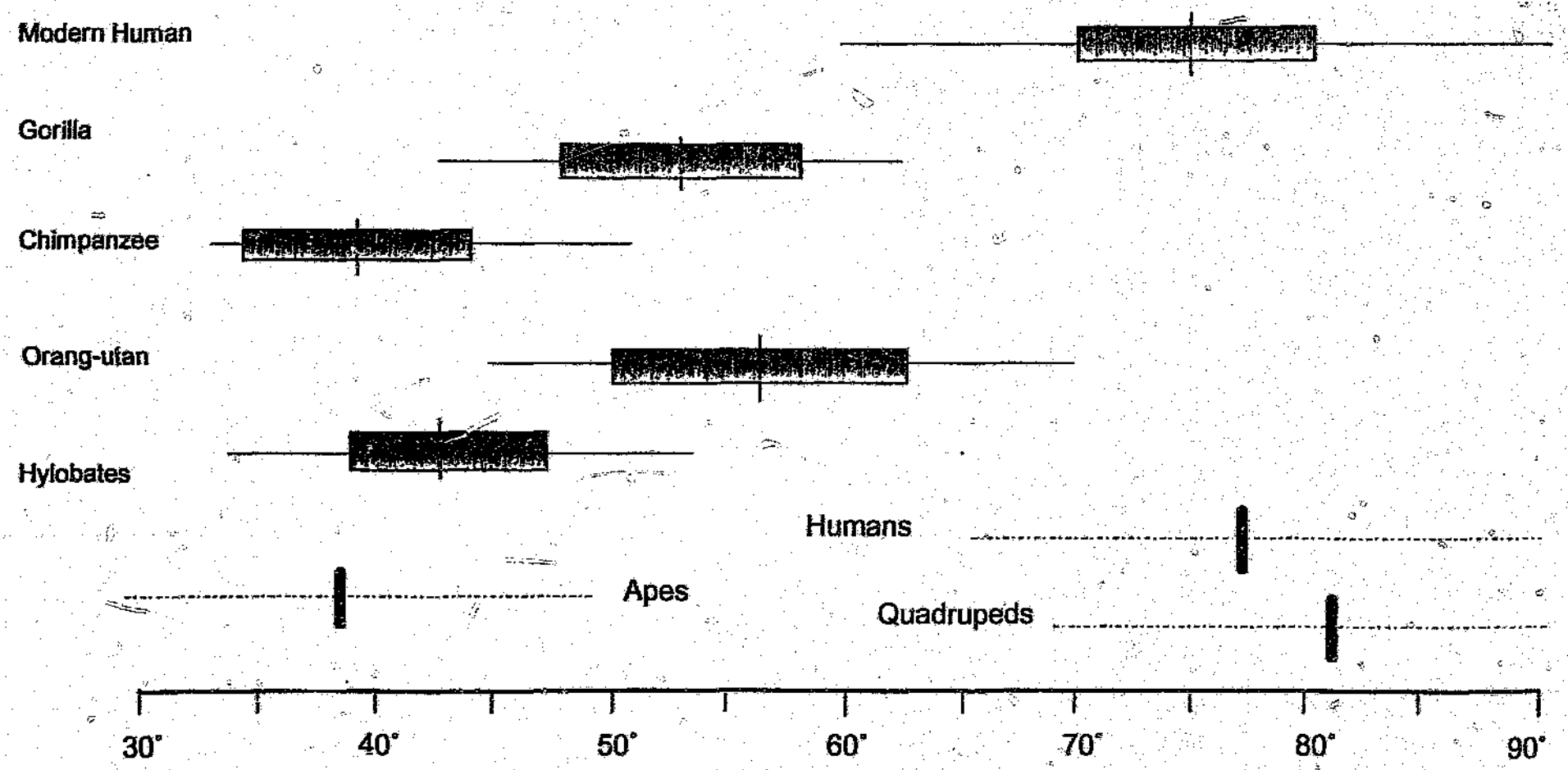


Figure 46. Humeral torsion and the relationship of the intertubercular sulcus to the head of the humerus. The dashed line indicates the approximate mediolateral axis of the elbow joint. Modified from Aiello and Dean (1990) after Evans and Krahl (1945).



Hylobatids



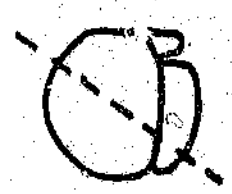
Orang-utan



Human



Gorilla



Chimpanzee

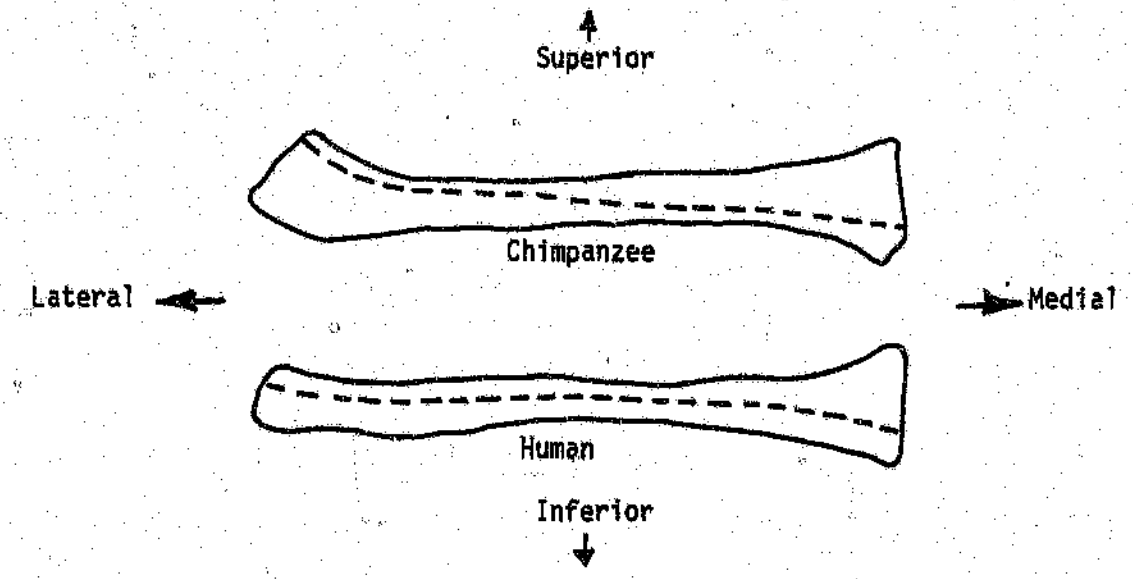


Figure 47. Anterior views of human and chimpanzee right clavicles illustrating the marked cranial twisting of the lateral end of the chimpanzee clavicle. Modified from Oxnard (1984).

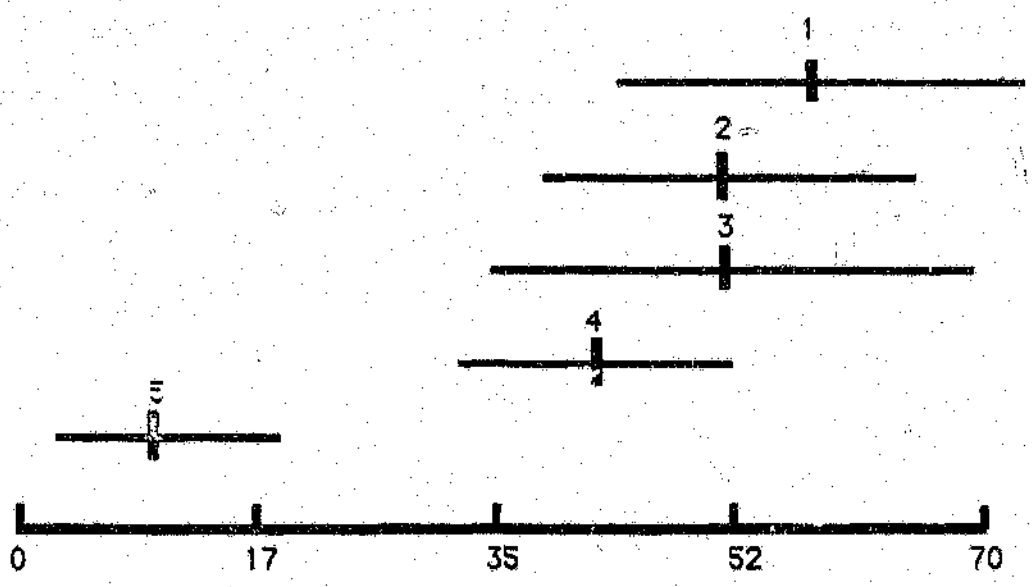
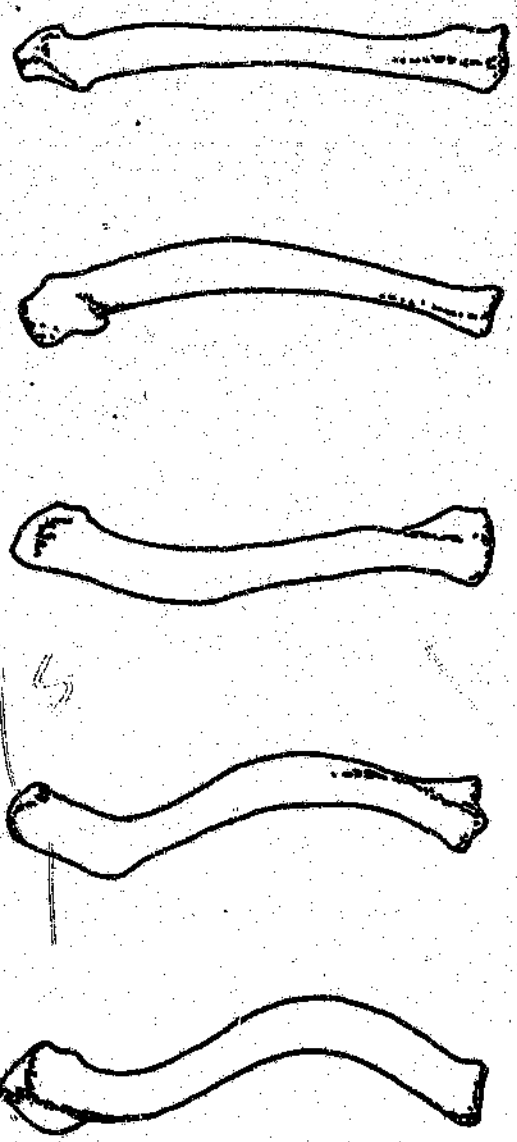


Figure 48. The angle of torsion in the clavicles of hominoids. 1, gorilla; 2, chimpanzee; 3, orang-utan; 4, gibbon; 5, human. Vertical bars, sample mean; horizontal line, mean ± 1 standard deviation. After Ashton and Oxnard (1964).

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

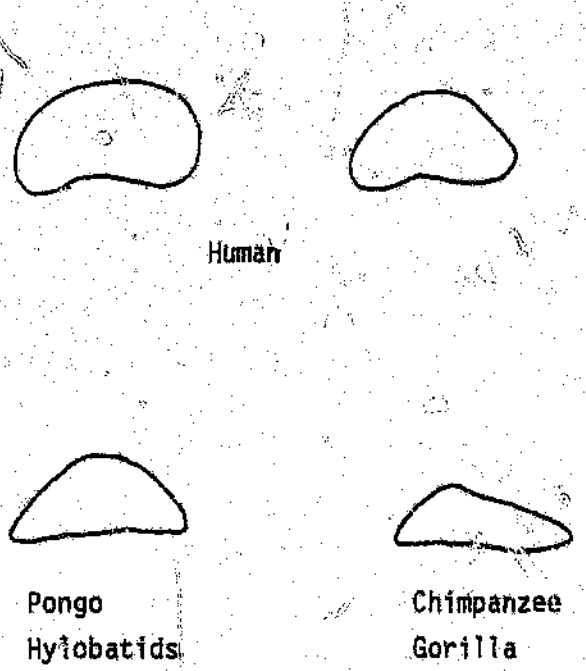


Figure 50. Cross-sectional shapes of the bodies of clavicles in hominoids. The cross-sections are taken at the approximate mid-point of the length of the clavicle. Superior surface - above; inferior surface -below.

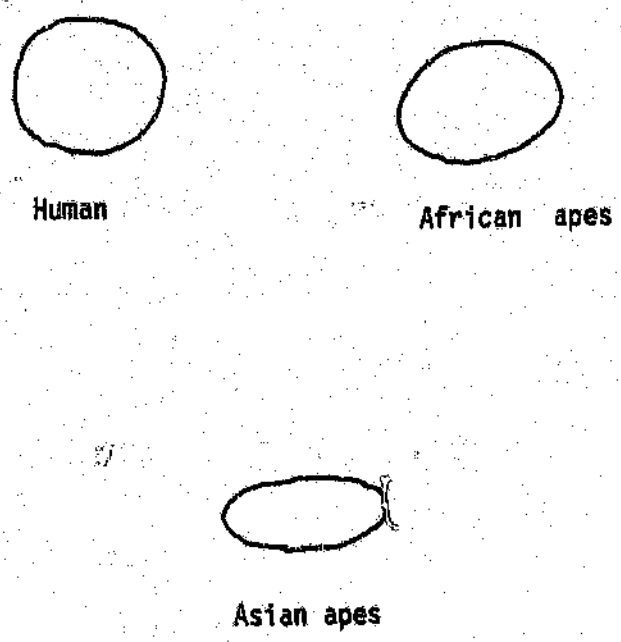


Figure 51. Cross-sectional shapes of the sternal end of clavicles in hominoids.

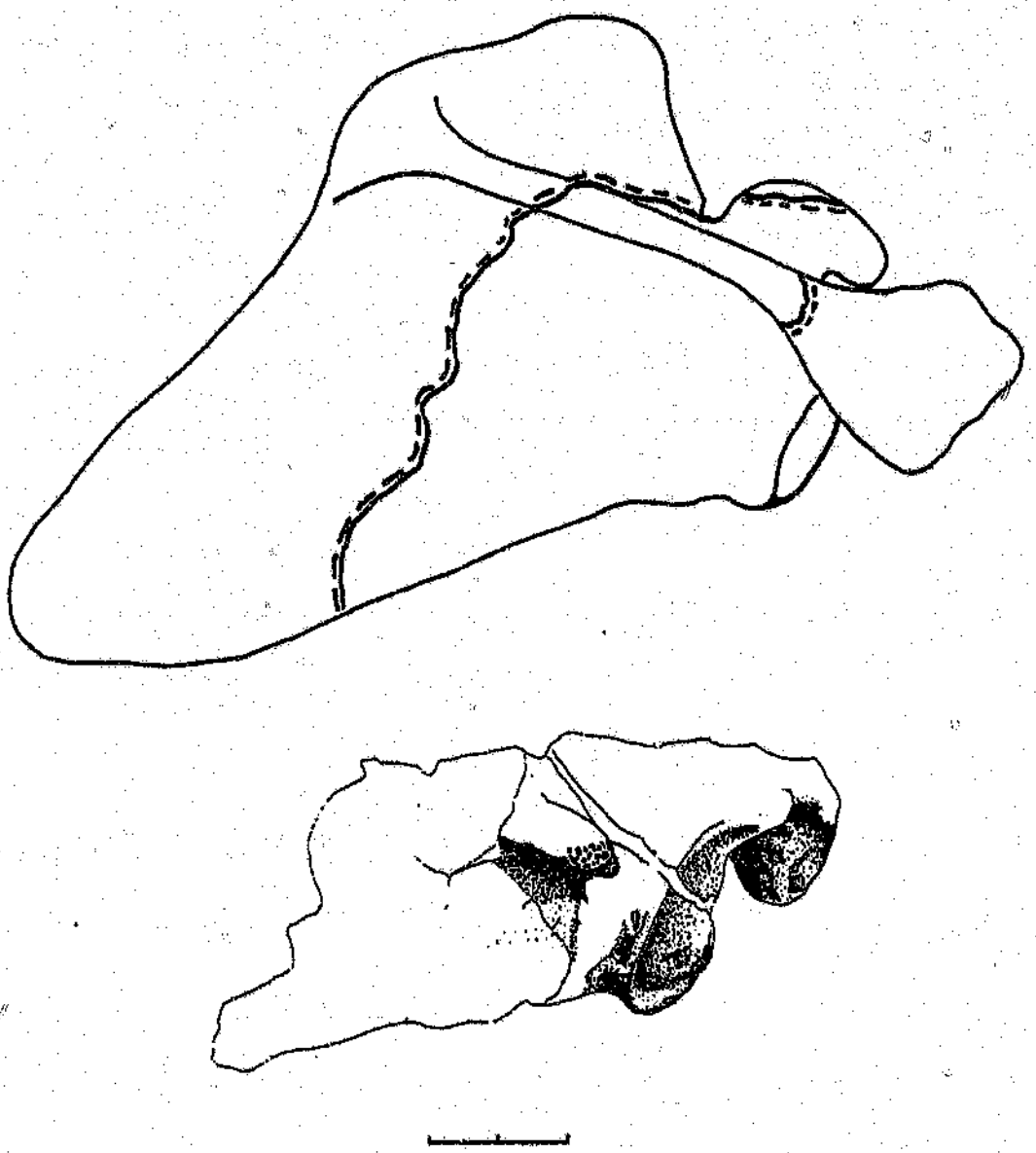


Figure 52. The Sts 7 scapula illustrating important morphological features of the dorsal surface and glenoid cavity. The dashed lines on the outline above Sts 7 illustrate the approximate completeness of the fossil compared to a whole modern human scapula.

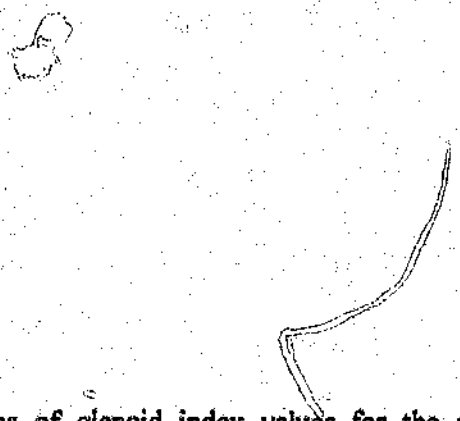
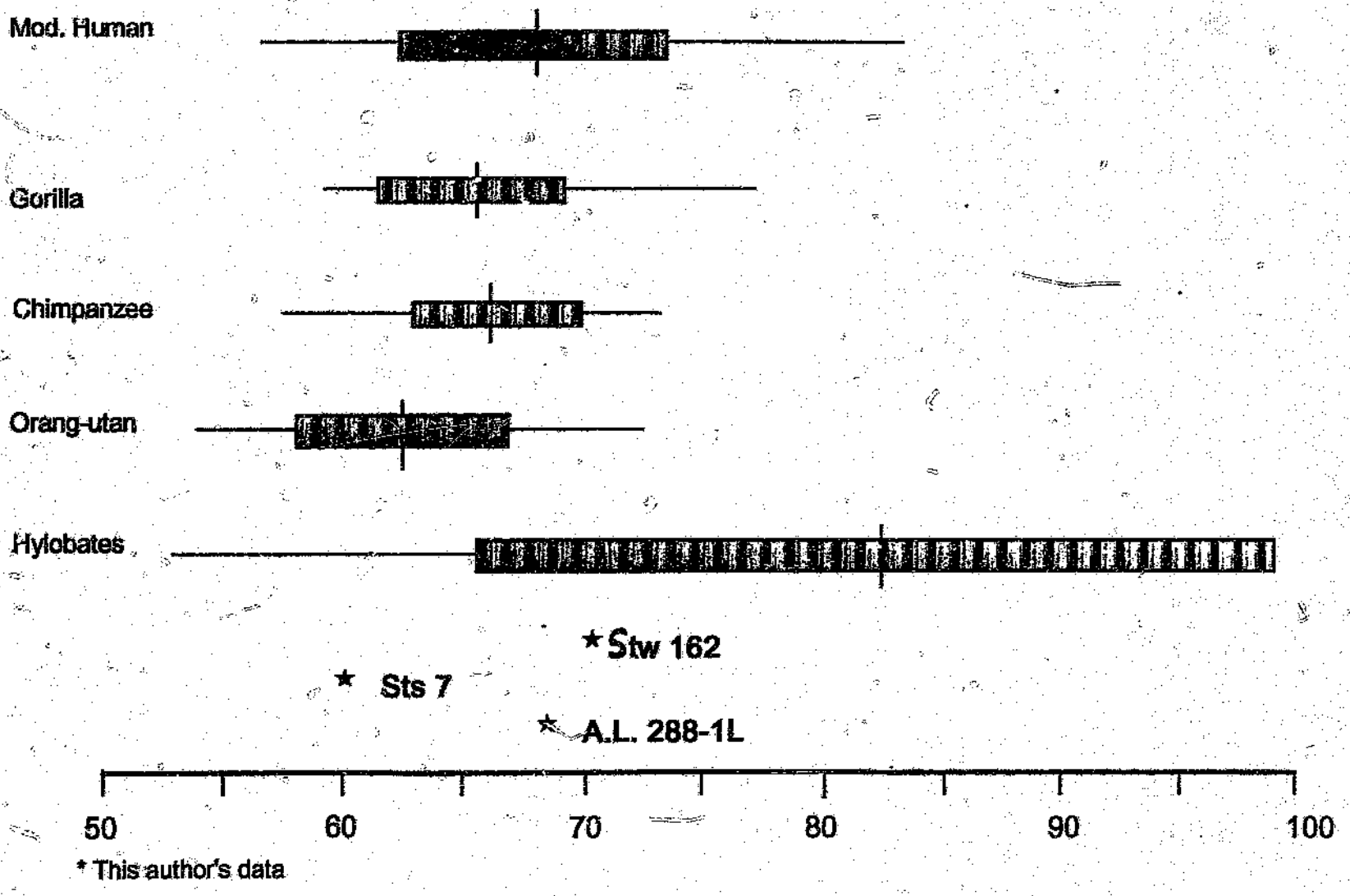


Figure 54. Comparisons of glenoid index values for the australopithecine scapulae with corresponding values for modern humans, gorillas, chimpanzees, orang-utans and hylobatids. As discussed in the text, the glenoid length values for Sts 7 and Stw 162 are estimates, thus the actual glenoid index values 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) *



* This author's data

Spinoglenoid Notch Depth vs. Glenoid Cavity Maximum Breadth

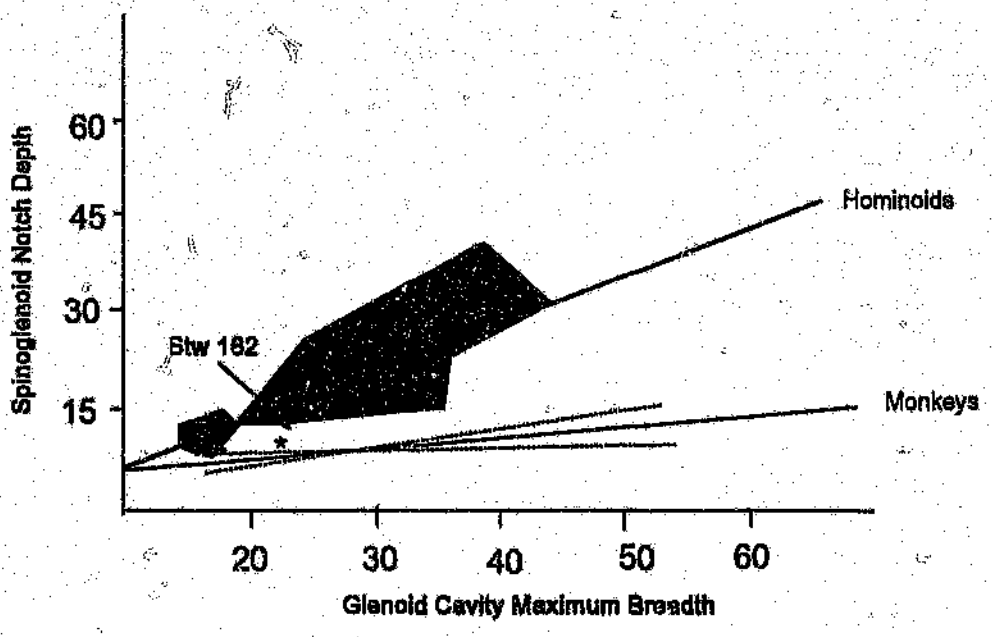


Figure 55. Bivariate plot of spinoglenoid notch depth vs. glenoid cavity maximum breadth. Shaded area indicates the observed limits of the range of variation for this relationship in the extant hominoid species examined in the present study. Interrupted lines indicate 95% confidence intervals for monkeys. * 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

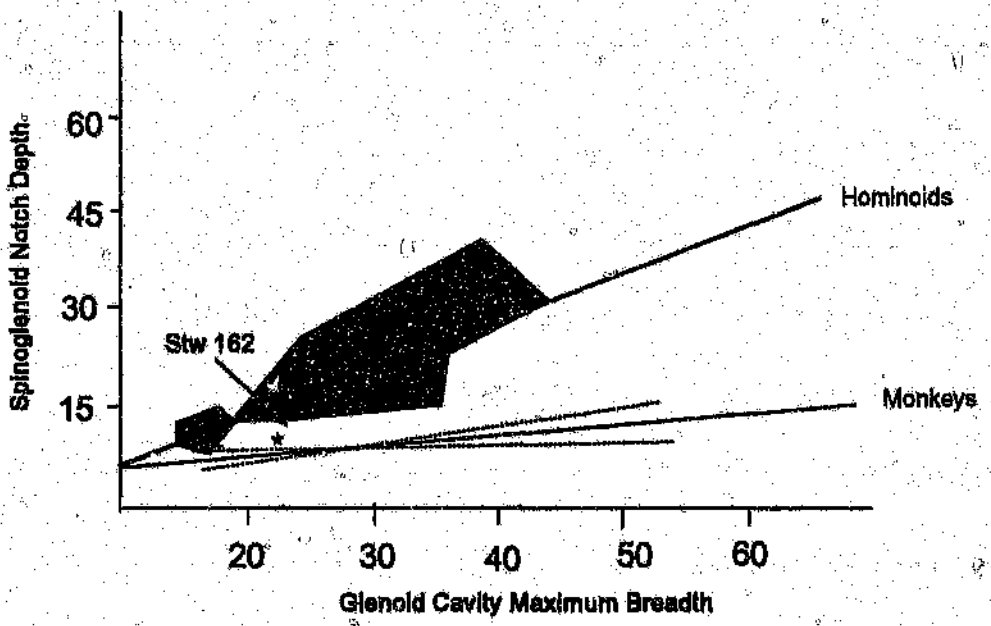
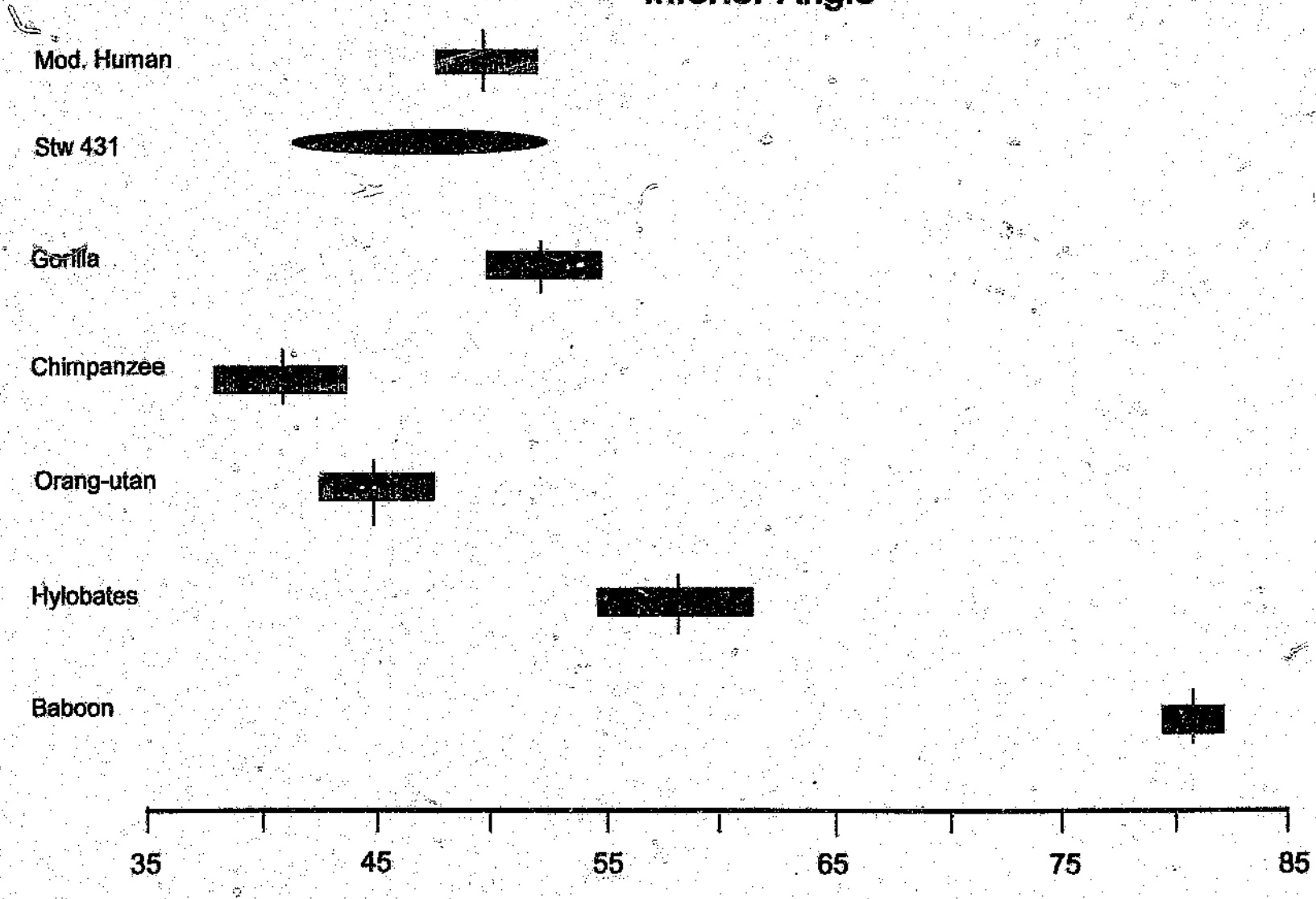


Figure 55. Bivariate plot of spinoglenoid notch depth vs. glenoid cavity maximum breadth. Shaded area indicates the observed limits of the range of variation for this relationship in the extant hominoid species examined in the present study. Interrupted lines indicate 95% confidence intervals for monkeys. ★ 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 ± 1 standard deviation.

Figure 56. Comparison of Australopithecine Scapular Shape

Inferior Angle



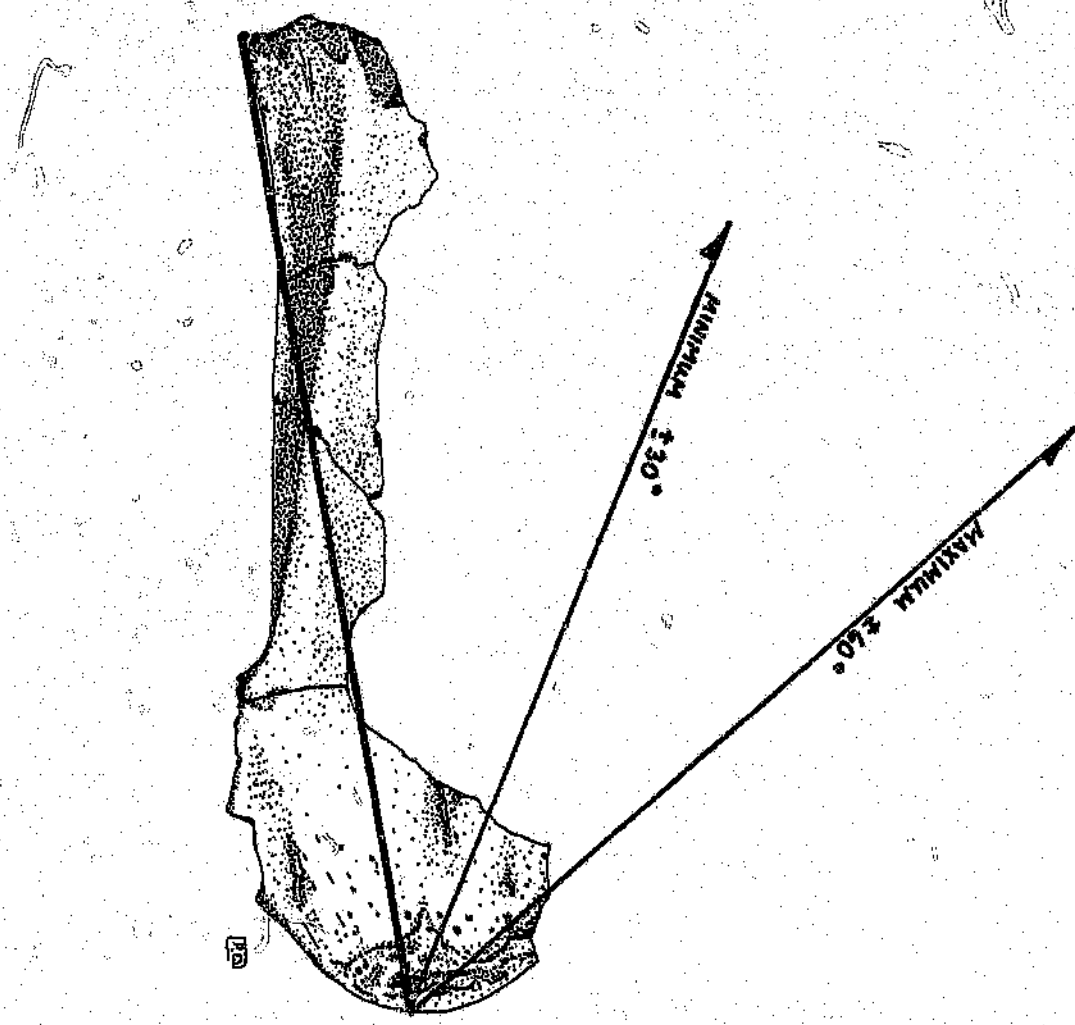


Figure 57. Diagram illustrating this author's justification for his minimum (±30°) and maximum (±60°) estimates of the inferior angle value of the Stw 431 scapula.

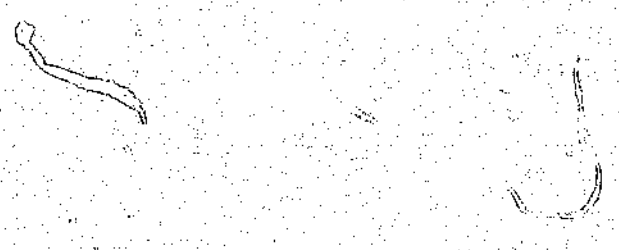
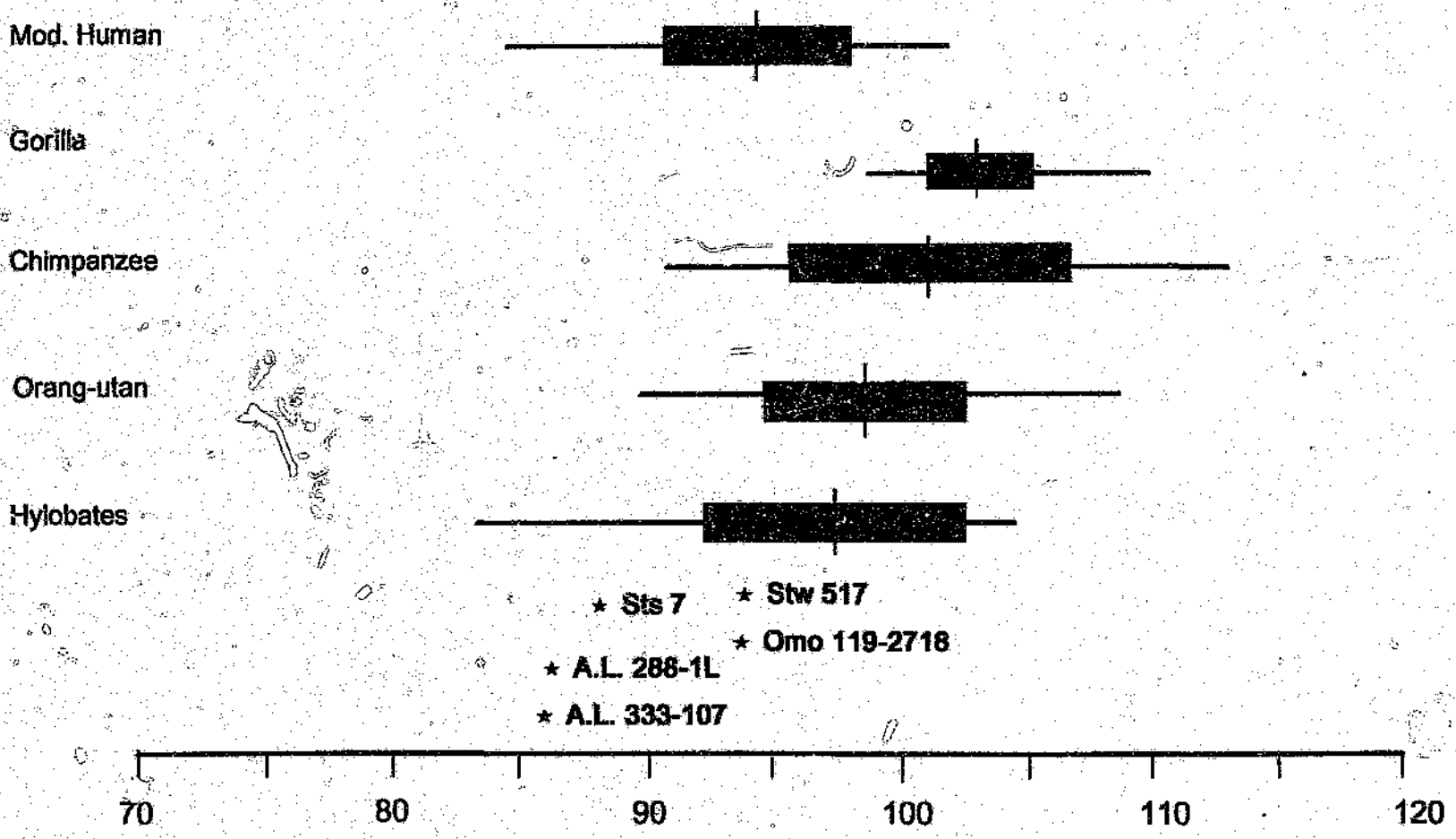


Figure 58. Comparisons of humeral head index values for fossil hominid humeri with the corresponding values for modern humans, gorillas, chimpanzees, orang-utans and hylobatids. Vertical line, sample mean; horizontal line, observed sample range; shaded rectangle, mean ± 1 standard deviation.

Figure 58. Comparison of Australopithecine Humeral Shape

Humeral Head Index (HHB/HHD x 100)



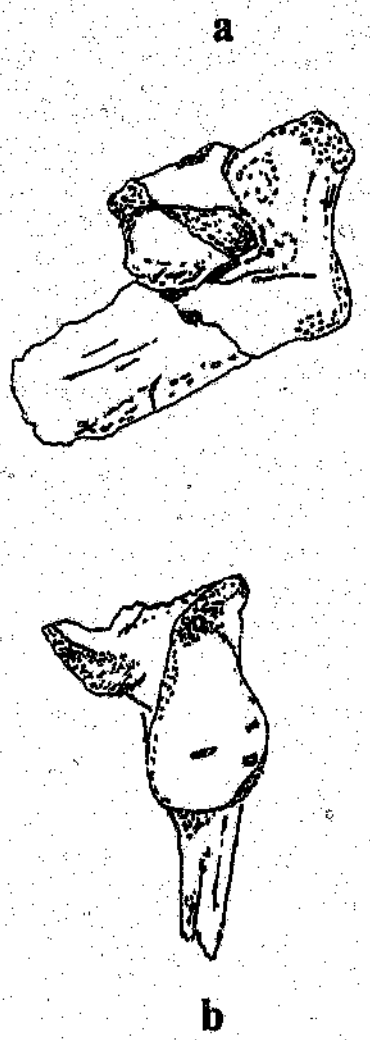


Figure 59. A.L. 288-1l, a, dorsal view; b, lateral view. Drawing is approximately natural size.

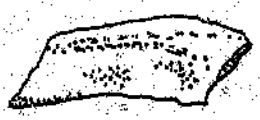


Figure 60. Right clavicular fragment, A.L. 288-1bz, inferior view. Drawing approximately natural size.



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.