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Berger, Lee Rogers

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FUNCTIONAL MORPHOLOGY OF THE HOMINOID SHOULDER, PAST AND PRESENT.

Lee Rogers Berger

Volume I

A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Doctor of Philosophy.

Johannesburg 1994

Declaration

I declare that this thesis is my own, unaided work. It is being submitted for the degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University, nor has it been prepared under the aegis or with the assistance of any other body or organization or person outside the University of the Witwatersrand, Johannesburg.

Lee R. Berger

Lee Rogers Berger

_____ day of _____, 1994

Abstract

Functional Morphology of the Hominoid Shoulder, Past and Present

by Lee Rogers Berger

This thesis presents an investigation into the functional morphology and form of the skeletal elements of the shoulder girdle of extant hominoids and extinct hominids which inhabited the African continent during the Late Pliocene and Early Pleistocene. Particular emphasis is placed on the form of the scapula, clavicle and humerus. Variation in the bony, arthrological and myological anatomy of this region in extant hominoids is examined. In light of biomechanical models resulting from this work, the bony anatomy of fossil hominid shoulder girdle elements examined and biomechanical interpretations are made.

The fossil shoulder girdle elements examined in this study are grouped into four species samples. The first sample (*Australopithecus africanus*) comprises Pliocene fossils from Sterkfontein, South Africa. The second sample (*A. afarensis*) is comprised of fossils from Hadar, Ethiopia. The third (*Homo habilis*) and fourth (*A. boisei*) samples comprise fossils from Olduvai Gorge, Tanzania, Koobi Fora, Kenya and the Omo Valley, Ethiopia. When the fossil hominid remains are sorted into species, the shoulder girdle elements may be used to construct and contrast species specific biomechanical models of the shoulder. These models explore differences in form amongst fossil

hominid species that may be related to differences in behaviour. The models may also be applied to the interpretation of systematic relationships amongst early hominids.

In order to construct models of early hominids it is first necessary to establish the movement, myology and osteology of the extant hominoid shoulder. Chapters 4,5 and 6 summarise new data and available information concerning shoulder girdle movement and form. Chapter 7 presents detailed descriptions of the fossil hominid material (n=19) available for study. This descriptive information, in combination with all of the information derived from Chapters 4 through 6, is then used to interpret, compare and contrast the functional morphology of the shoulder girdle elements of each species of early hominid. Particular emphasis is placed on those features that can be directly related to specific function. Models of the functional morphology of each of the four species are then created. Comparisons are made between individual shoulder girdle elements of the different hominid species as well as between the interpreted total morphology of each species' shoulder girdle.

The study concludes that the functional morphology of the shoulder girdle of *A. africanus* is unique amongst known hominoid models in that it possesses shoulder girdle morphology adapted to both susper ory behaviour and bipedalism. The suspensory adaptations are indicated by the overall ape-like morphology of the humeri, clavicular and head of the scapulae, whilst bipedalism is mainly

indicated by a broad, human-like inferior angle of the scapula. Several apparently primitive features are present in the *A. africanus* scapula, including a shortened scapular neck, that indicate possible ancestry from a quadrupedal form. The functional morphology of the *A. afarensis* shoulder is found to be more difficult to interpret due to poor preservation, but the hypothesised model does not differ substantially from that constructed for *A. africanus*. The few robust australopithecine (*A. boisei*) shoulder girdle elements appear to possess similar morphologies to *A. afarensis* and *A. africanus*. There are not sufficiently well preserved *H. habilis* shoulder girdle elements preserved to make meaningful interpretations about the functional morphology of this species. Due to the lack of comparable elements amongst the two larger samples (*A. afarensis* and *A. africanus*), it is not known whether the features found to be apparently unique to either species are useful as taxonomic indicators.

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Contents

		Page
	Declaration	i
	Abstract	ii
	Acknowledgements	v
Chapter 1	**The Study of the Shoulder, Past and Present**	1
1.1	Introduction	1
1.2	Background to the Present Study	2
1.3	History of Study of the Function and Morphology of the Hominoid Shoulder Girdle	7
1.4	The Application of Functional Anatomical Studies of the Shoulder Girdle to Fossil Hominids	14
1.5	Aims of the Present Study	24
1.5.1	Predictions	32
Chapter 2	**Materials**	
2.1	Introduction	35
2.2	The Extant Primate Series	38

2.2.1	Infraorder Catarrhini	38
2.2.1.1	Superfamily Hominoidea	38
2.2.1.1.1	Family Hominidae	
2.2.1.1.1.1	Genus *Homo*	38
2.2.1.1.1.1.1	Species *Homo sapiens*	38
2.2.1.1.2	Family Pongidae	43
2.2.1.1.2.1	Genus *Pan*	43
2.2.1.1.2.1.1	Species *Pan troglodytes*	43
2.2.1.1.2.2	Genus *Gorilla*	45
2.2.1.1.2.2.1	Species *Gorilla gorilla*	45
2.2.1.1.2.3	Genus *Pongo*	47
2.2.1.1.2.3.1	Species *Pongo pygmaeus*	47
2.2.1.1.3	Family Hylobatidae	49
2.2.1.1.3.1	Genera *Hylobates* and *Symphalangus*	49
2.2.1.1.3.1.1	Species *Hylobates* sp. and *Symphalangus syndactylus*	49
2.2.1.1.4	Family Cercopithecidae	51
2.2.1.1.4.1	Genus *Cercopithecus*	51
2.2.1.1.4.1.1	Species *Cercopithecus aethiops*	51
2.2.1.1.4.2	Genus *Papio*	52
2.2.1.1.4.2.1	Species *Papio ursinus*	52

2.3	The Fossil Hominid Series	54
2.3.1	Introduction	54
2.3.2	The Sites	57
2.3.2.1	Southern Africa	57
2.3.2.1.1	South Africa	57
2.3.2.1.1.1	Sterkfontein	57
2.3.2.2	East Africa	60
2.3.2.2.1	Tanzania	60
2.3.2.2.1.1	Olduvai Gorge	60
2.3.2.2.2	Kenya	61
2.3.2.2.2.1	Koobi Fora	61
2.3.2.2.3	Ethiopia	62
2.3.2.2.3.1	Omo	62
2.3.2.2.3.2	Hadar	64
2.4	Summary	67
Chapter 3	**Methods**	
3.1	Introduction	69
3.2	Anatomical Nomenclature	70
3.3	Selection of the Modern Skeletal Series	71
3.4	The Metrical Characters	72
3.4.1	Definitions of the Linear Measurements	72

2.3	The Fossil Hominid Series	54
2.3.1	Introduction	54
2.3.2	The Sites	57
2.3.2.1	Southern Africa	57
2.3.2.1.1	South Africa	57
2.3.2.1.1.1	Sterkfontein	57
2.3.2.2	East Africa	60
2.3.2.2.1	Tanzania	60
2.3.2.2.1.1	Olduvai Gorge	60
2.3.2.2.2	Kenya	61
2.3.2.2.2.1	Koobi Fora	61
2.3.2.2.3	Ethiopia	62
2.3.2.2.3.1	Omo	62
2.3.2.2.3.2	Hadar	64
2.4	Summary	67
Chapter 3	**Methods**	
3.1	Introduction	69
3.2	Anatomical Nomenclature	70
3.3	Selection of the Modern Skeletal Series	71
3.4	The Metrical Characters	72
3.4.1	Definitions of the Linear Measurements	72

3.4.2	The Angles	83
3.4.2.1	Definitions of the Angular Measurements	84
3.4.2.2	Identification of the Angle Points	85
3.4.3	Precision of the Osteometric Data	86
3.4.4	Reliability of the Measurements	87
3.4.5	Error of the Angle Measurements	88
3.5	Determination of the Areas of the Infraspinous and Supraspinous Fossae of the Scapula	88
3.6	Standardisation of the Measurement Techniques	89
3.7	Reliability of Area Determination	90
3.8	Measurement of the Fossil Hominid Material	92
3.9	The Qualitative Data	93
3.10	The Dissections	93
3.11	Photography and	

	Illustrations	94
3.12	Statistical Analysis	95
Chapter 4	**The Arthrology and Movements of Extant Hominoid Shoulders**	**96**
4.1	Introduction	96
4.2	Arthrology	102
4.2.1	General	102
4.2.1.1	Synovial Joints	104
4.2.2	The Joints of the Hominoid Shoulder Girdle	104
4.2.2.1	The Glenohumeral Joint	105
4.2.2.2	The Acromioclavicular Joint	112
4.2.2.3	The Sternoclavicular Joint	116
4.2.2.4	The Coracoclavicular Joint	120
4.2.2.5	The Scapulothoracic "Joint" or Scapular Gliding Mechanism	123
4.3	Summary	124
Chapter 5	**The Myology of the Hominoid Shoulder**	**126**
5.1	The Muscles and Muscular Forces	126

5.1.1	Introduction	126
5.1.2	The Deltoid Muscle (*M. deltoideus*)	128
5.1.3	The Biceps Muscle (*M. biceps brachii*)	134
5.1.4	The Cupraspinatus Muscle (*M. supraspinatus*)	137
5.1.5	The Infraspinatus Muscle (*M. infraspinatus*)	139
5.1.6	The Teres Major Muscle (*M. teres major*)	142
5.1.7	The Teres Minor Muscle (*M. teres minor*)	145
5.1.8	The Subscapularis Muscle (*M. subscapularis*)	148
5.1.9	The Trapezius Muscle (*M. trapezius*)	151
5.1.10	The Serratus Anterior Muscle (*M. serratus anterior*)	154
5.1.11	The Levator Scapulae Muscle (*M. levator scapulae*)	156
5.1.12	The Rhomboid Muscles	

(*M. rhomboidei*) 157

5.1.13 The Latissimus Dorsi Muscle (*M. latissimus dorsi*) 161

5.1.14 The Coracobrachialis Muscle (*M. coracobrachialis*) 163

5.1.15 The Subclavius Muscle (*M. subclavius*) 165

5.1.16 The Atlanto-Clavicularis Muscle (*M. atlanto-clavicularis*) 167

5.1.17 The Omohyoid Muscle (*M. omohyoideus*) 170

5.1.18 The Pectoralis Minor Muscle (*M. pectoralis minor*) 172

5.1.19 The Pectoralis Major Muscle (*M. pectoralis major*) 174

5.1.20 The Triceps Muscle (*M. triceps brachii*) 176

5.1.21 The Sternocleidomastoid Muscle (*M. sternocleidomastoideus*) 179

5.1.22 The Pectoralis Abdominis Muscle (*M. pectoralis abdominis*) 182

5.3 Summary 183

Chapter 6 The Skeletal Elements of the Hominoid Shoulder Girdle 186

6.1 General 186

6.2 The Hominoid Scapula 188

6.3 The Clavicle 193

6.4 The Humerus 194

6.5 The Comparative Morphology of the Bones of the Extant Hominoid Shoulder Girdle 200

6.5.1 The Scapula 200

6.5.1.1 The Articular Areas 200

6.5.1.2 The Body of the Scapula 211

6.5.2 The Proximal Humerus 225

6.5.3 The Clavicle 233

6.6 Summary 246

Chapter 7 The Anatomy of the Early Hominid Shoulder Girdle 248

7.1 Introduction 248

7.2 Specimens Referred to, or Associated With, *A. africanus* 250

7.2.1 Descriptions 250

7.2.1.1	The Scapulae	250
7.2.1.1.1	Sts 7	250
7.2.1.1.2	Stw 162	255
7.2.1.1.3	Stw 431	258
7.2.1.2	The Clavicle	261
7.2.1.2.1	Stw 431	261
7.2.1.3	The Humeri	264
7.2.1.3.1	Sts 7	264
7.2.1.3.2	Stw 328	265
7.2.1.3.3	Stw 517	268
7.3	Specimens Referred to, or Associated With, *A. afarensis*	270
7.3.1	Descriptions	270
7.3.1.1	The Scapula	270
7.3.1.1.1	A.L. 288-1L	270
7.3.1.2	The Claviculae	273
7.3.1.2.1	A.L. 288-1bz	273
7.3.1.2.2	A.L. 333-6/9	274
7.3.1.2.3	A.L. 333-94	276
7.3.1.3	The Humeri	277
7.3.1.3.1	A.L. 288-1r	277
	A.L. 288-1m	277
7.3.1.3.2	A.L. 333-87	278

7.3.1.3.3	A.L. 333-107	279
7.3.1.3.4	A.L. 333-109	280
7.4	Specimens Referred to *Homo habilis*	282
7.4.1	Description	282
7.4.1.1	The Clavicle	282
7.4.1.1.1	OH 48	282
7.5	Specimens Referred to Robust Australopithecines	283
7.5.1	Descriptions	283
7.5.1.1	The Humeri	283
7.5.1.1.1	OMO 119-2718	283
7.5.1.1.2	KNM-ER 739	286
7.6	The Functional Morphology of the *Australopithecus africanus* Shoulder Girdle	288
7.6.1	The Scapula	288
7.6.1.1	The Glenoid Area, Head, and Spine of the Scapula	289
7.6.1.2	The Axillary Margin and Body of the Scapula	315
7.6.1.3	Synopsis	323
7.6.2	The Clavicle	329
7.6.3	The Humerus	330

7.6.1.3	Synopsis	334
7.6.4	Interpretation of the Total Functional Morphology of the *A. africanus* Shoulder Girdle	336
7.7	The Functional Morphology of the *A. afarensis* Shoulder Girdle	343
7.7.1	The Scapula	343
7.7.1.1	Synopsis	348
7.7.2	The Clavicle	349
7.7.2.1	Synopsis	350
7.7.3	The Humerus	351
7.7.4	Interpretation of the Total Functional Morphological Pattern of the *A. afarensis* Shoulder Girdle	354
7.8	The Functional Morphology of the *Homo habilis* Shoulder Girdle	359
7.8.1	The Clavicle	359
7.9	The Functional Morphology of the Robust	

	Australopithecine Shoulder Girdle	360
7.9.1	The Humeri	360
7.10	Functional Anatomical and Evolutionary Relationships Among the Early Fossil Hominidae Based on the Total Morphology of the Shoulder Girdle Elements	363
7.10.1	Size Differences Amongst the *A. africanus* and *A. afarensis* Samples	364
7.10.2	Discrete Morphological Features	367
7.10.3	The Comparative Functional Morphology of the *A. afarensis* and *A. africanus* Samples	371
7.10.4	Comparison of the Functional Morphology of the Early Hominid Shoulder Girdle Elements not Associated with *A. africanus* or *A. afarensis*	403

7.10.5 The Functional Morphology of the Early Hominid Shoulder Girdle and Inferred Relationships with the Evolution of Early Hominid Behaviour 375

7.11 Conclusions 378

References 385

Tables, Figures and Plates Volume II

Chapter 1

The Study of the Hominoid Shoulder Girdle

1.1 Introduction

The choice of the shoulder girdle as an ideal anatomical area for the interpretation of the behaviour and lifestyles of early hominids stems from the recognition of basic evolutionary principles that recognise that anatomical areas which are in close contact with the environment tend to show adaptations to that environment (Darwin, 1859; Dobzhansky, 1937; Wright, 1977; Ashton et al., 1965; Oxnard, 1967a,b, 1968c, 1976; Oxnard et al., 1990; Latimer, 1991 etc.). Therefore, of all the musculoskeletal complexes in the primate body, there is probably none which shows a greater range of morphological variation and diversity related to performance requirements than the upper limb and shoulder (Inman et. al., 1944). More specifically, the shoulder girdle complex is involved in almost every act of locomotion performed by primates, modern humans being the only living exception to this rule.

Since musculoskeletal functional complexes such as the shoulder girdle are in direct contact with the external environment, adaptations in the functional morphology of these complexes should be good indicators of the environment to which they had originally adapted(Oxnard et al., 1990; Latimer, 1991).

1.2 Background to the Present Study

The functional complexity of the shoulder girdle is readily evident and has been dealt with in detail by several researchers (Miller, 1932; Inman et al., 1944; Ashton and Oxnard, 1963; Ashton et al., 1965; Oxnard, 1967a,b, 1968c, 1972, 1976; Ciochon and Corruccini, 1976; Oxnard et al., 1990 etc.). It is therefore not the purpose of the present study to further elaborate on these complexities. Rather, this study attempts to apply the results of these previous studies, in combination with morphological and functional analyses conducted by the author on extant primates, to the shoulder girdles of fossil

hominids. This method is chosen with the hopes of identifying morphological characters and character complexes that might be associated with particular early hominid lifestyles and behaviour. Furthermore, the resulting information will be used to address questions of the taxonomy and phylogenetic relationships of early hominids, in addition to defining their adaptive strategies.

Insomuch as early hominid studies are concerned, this research was begun and conducted during a critical period in the study of African Plio-Pleistocene hominids. Whilst fossil hominid remains are still being recovered in relatively large numbers from the ancient lake and river beds of East Africa and several of the South African cave sites are producing a consistent supply of early hominid fossils, the intense race to find more "new" and "older" hominid fossils that characterised the 1970's and 1980's has slowed. Much of the emphasis on exploration that marks this period has been replaced by a recognition of the need to describe and analyse the large amounts

of hominid material recovered during the past two decades.

At the time the present study was initiated there were some 19 elements of adult, early hominid shoulder girdles available for study. Much of this material, if analysed at all, had only been preliminarily described. Some of the material, in particular the most recently recovered specimens from the Sterkfontein site in South Africa had not been previously described. In addition, this study represents the first time a researcher has had available two relatively large samples of shoulder girdle elements from two (apparently) distinct species of early hominid. This was largely due to the recovery of numerous shoulder girdle specimens from Sterkfontein that have been attributed to the species *A. africanus* (Tobias 1985-1991, PARU reports). These South African early hominid specimens are closely comparable in age and "gracility" to the fossils that were discovered in Hadar, Ethiopia during the middle and late 1970's and which have been attributed to *A. afarensis*. Therefore, this

investigation has also attempted to examine the evolution of the hominoid shoulder girdle complex with the hope of elucidating meaningful evolutionary trends and / or phyletic relationships in the development of the shoulder complex in the Plio-Pleistocene hominids.

Whilst many studies have been conducted on the form and function of the extant primate shoulder girdle, and some have applied studies of the modern hominoid shoulder girdle to fossil hominid remains (Campbell, 1966; Oxnard, 1968a,b, 1969; Senut, 1978, 1981a,b, 1982, 1984, 1989; Lovejoy, 1976, 1978, 1981; Vrba, 1979; Lovejoy et al., 1982a; Stern and Susman, 1983; Senut and Tardieu, 1985; Susman et al., 1985; Larson and Stern, 1986), none has attempted an exhaustive functional study of the fossil hominid shoulder girdle. While one might question our ability to interpret function in such a manifestly complex region as the shoulder girdle from fragmentary fossil remains, the potential results of such are of critical importance to our understanding of the lifestyles of these early hominids.

Nevertheless, while the skeletal elements of the early hominid shoulder girdle are better represented than ever before, a reconstruction of the whole functioning shoulder girdle, or even of single elements of the shoulder girdle, of these extinct forms requires more than simply this fragmentary skeletal foundation. This is because the functional operation of the shoulder girdle is expressed in not only an osteological complex but also in an arthrological and myological complex.

It was therefore necessary to include in this study an examination of the major soft tissues of the shoulder complex of selected living primates in order to enable the osteological anatomy of the fossilised shoulder girdle elements to be examined. Detailed treatments of the anatomy and function of the shoulder girdle of some living hominoids are available (Inman et al., 1944; Ashton and Oxnard, 1963; Stern et al., 1977; Stern and Susman, 1981, 1983; Jungers and Stern, 1983; Susman, 1983; Susman et al., 1984, Larson and

Stern, 1986; Larson, 1988; Oxnard et al., 1990; Susman and Stern, 1991 etc.) and provide the framework from which the soft tissues of the early hominid shoulder girdle can be deduced and reconstructed. The best studied of these modern hominoid forms is *Homo sapiens*, a species which may be considered the most likely candidate to be the closest living relative of the early Pleistocene hominids. In addition, this study is fortunate in having available for examination the cadavers of chimpanzees, which may be as closely related to the early to mid-Pliocene hominids as *Homo sapiens* is to these earlier forms.

1.3 History of Study of the Function and Morphology of the Hominoid Shoulder Girdle

The study of the form of the hominoid shoulder girdle dates back at least to the middle of the 19th century when most efforts concentrated on the explanation of variation in individual bones. The scapula received the most attention as it was

perceived to exhibit a high degree of morphological variation amongst humans whilst also presenting a host of anomalies for study. From the late 1850's, through the mid-twentieth century, numerous studies of variation in form of the bony elements of the shoulder girdle were conducted (Mivart, 1868; Gruber, 1861; Flower 1870; Poirier, 1890, 1911; Parsons, 1898; Hrdlicka, 1910, 1914, 1916, 1929, 1937; Martin, 1928; Vallois, 1924, 1926a,b, 19[illegible]; Miller, 1932). However, most of the above studies were concerned only with morphology and few examined the function associated with the observed variations in bone structures.

The relative dearth of functional studies conducted on the shoulder girdle during this early period was primarily due to the lack of availability of an unbiased method for establishing the function of the muscles in the shoulder region. It was not until the studies by Inman *et al.* (1944) which applied the results of electromyographic (EMG) studies of muscles of the shoulder to infer osseous morphology of the

region, that relationships between form and function in the shoulder could be hypothesised.

As Inman *et al.* noted in 1944:

> ***The scapula in the living form is suspended, as it were, in space by the muscles acting upon it, and it is therefore not surprising that this bone should reflect more clearly than any other the changes which have been brought about by more specialized functional demands.***

Possibly the greatest contribution of the study by Inman *et al.* (1944) was the first objective proof that the variation in shapes observed between the bones of the shoulder girdle of apes, monkeys and humans were indisputably related to differences in muscular shapes and actions that are "brought about by more specialised functional demands" (Inman et al.,

1944, p. 2). From this research onwards, studies of the form and function of the shoulder girdle of primates would take a new direction. Anatomical studies of the shoulder girdles of primates such as those of Ashton and Oxnard (1963, 1964) Ashton et al. (1963) and Oxnard (1963, 1967, 1968c, 1972), would be based on associating morphological variations with specific functions and behaviour. Unfortunately, these studies amongst others, would over-simplify primate locomotion by categorising it into "modes" of locomotion that have since proved inadequate for detailed functional anatomical studies (see below).

In the 1970's and 1980's, mainly due to the advent of easily accessible computers that were able to synthesise larger data bases, studies of the functional morphology of the shoulder girdle tended to use complex, multivariate statistics to associate variations in morphologies with variations in performance demands (Oxnard, 1972, 1973a,b, 1976,1986; Corruccini and Ciochon, 1976; Oxnard et al., 1981). However, even during this period the methods used by many researchers for

their multivariate analyses were questioned(see Wood, 1978). Many recent studies have begun to recognise that form is not as easily related to function as had been originally thought (see Oxnard et al., 1990; Susman and Stern, 1991). This recognition is due to the results of EMG studies of specific muscles and studies of behaviour and lifestyles of wild primates that have shown that classification of the "modes" of locomotion or any attempt to relate bony morphologies to single function almost certainly does not represent the realities of a primates' complex locomotor repertoire (see Oxnard et al., 1990; Susman and Stern, 1991 for a review). The results of this recognition have led recent researchers in two directions and these are detailed below.

A few researchers, most notably C.E. Oxnard et al.(1990), have attempted to use complex, multivariate studies to more accurately relate a primate's total behavioural "lifestyle" to its anatomy. Oxnard et al. (1990) have highlighted the problems associated with the use of the

"dominant behaviour terminology" which has characterised most attempts at locomotor classification. Recognition of the extreme complexity of behaviour and posture of extant primates, largely due to studies by Ashton and Oxnard (1964), Napier and Napier (1967), Oxnard (1967, 1975, 1983), Fleagle (1976, 1979), Charles-Dominique (1977), Hunt (1990, 1993) etc., has led to the abandonment of such single-minded attempts at primate locomotor classification.

More recent studies have attempted to redefine the way in which we classify locomotion in primates by quantifying the relationship between morphology and primate habitat use, body size and food acquisition (see Oxnard *et al.*, 1990 for an overview). However, the accumulation of quantitative data on these aspects of primate ecology is extremely time consuming and the data are difficult to interpret once in hand.

Most recently, Oxnard *et al.* (1990) have proposed an alternative method of primate

locomotor classification to the dominant behaviour terminology method. Oxnard's proposed method involves the multivariate analysis of a primate species' total lifestyle. While the method appears sound and the initial study results were promising, the method has yet to be applied extensively to hominoids.

In contrast to Oxnard's methods, several recent examinations of fossil and modern primate postcranial elements have tended to use character analyses and direct form-to-function comparisons in their exploration of primate functional anatomy (Latimer, 1991; McHenry, 1991; Susman and Stern, 1991). These studies use the results of positional behavioural studies of living primates such as those of Hunt (1990, 1993) and of EMG studies of muscular activity, to associate the form of bones with their function. These studies have resulted in the recognition that many specific areas of the bony anatomy of primates may be directly associated with certain behaviour. This latter, descriptive approach is used in the present study for the following reasons: first, the results of

complex locomotor and behavioural studies on extant hominoids are not yet available; second, our ability to apply "total" lifestyle interpretations to the fossil hominids is limited by the lack of detailed information on environment, physiology, and social behaviour in the fossil record.

1.4 The Application of Functional Anatomical Studies of the Shoulder Girdle to Fossil Hominids

The application of functional anatomical studies of the shoulder girdle to the early hominid record began with the discovery of the Sts 7 shoulder girdle complex at Sterkfontein in 1945 (Broom and Schepers, 1946). It was this discovery that led several authors to recognise that the upper limbs of the australopithecines may not have been as derived toward the modern human condition as the pelvis and lower limbs (Broom and Schepers, 1946). However, shoulder girdle specimens remained elusive in the fossil record and between 1946 and 1972 only one other

early hominid shoulder girdle element (OH 7) had been discovered (L.B.S Leakey et al., 1964); a clavicle of *Homo habilis*. Consequently, during the latter part of this period Sts 7 was placed under intensive scrutiny. The opinion of most researchers was that the morphology of Sts 7 was as similar to that of extant apes as to humans but different from any single locomotor form observed in extant apes (Coon, 1962; Campbell, 1966; Oxnard, 1968a,b; Robinson, 1972; Ciochon and Corruccini, 1976; Senut, 1978, 1982, 1989, 1990; Vrba, 1979; Latimer, 1991). Whilst these similarities led many scientists to hypothesise that the common ancestor of humans and apes shared a similar form of locomotion (Tuttle, 1975, 1977), the results of more recent studies of the locomotion of wild primates and of the comparative morphology of this region suggest that a more generalised (?suspensory) form of forelimb-dependent locomotion was practised by the common hominoid ancestor (Stern et al., 1977; Prost, 1980; Fleagle et al., 1981; Tuttle, 1981, 1984; Sarmiento, 1985; Hunt, 1990, 1993 etc.).

Within the abovementioned evolutionary scenario, modern apes have retained the upper limb morphology suitable for dependence on forelimb dominated climbing behaviour. This morphology has been replaced, however, in humans by morphology which is (presumably) adapted for precision manipulation and tool use. Thus the variations in shoulder girdle morphology seen between the apes and humans are hypothesised to be due to the upper-limb of apes being adapted for locomotion, while that of humans has been, for the most part, freed from this task (see Latimer, 1991 for a discussion).

By the early 1970's Koobi-Fora in Kenya, and the Omo and Hadar in Ethiopia began yielding more fossil hominid shoulder girdle elements. At Hadar alone, no less than 9 fossil shoulder elements were recovered in the period 1973 - 1976 (Senut, 1978, 1980; Johanson *et al.*, 1978, 1980a,b, 1982; Lovejoy *et al.*, 1982a,b). By the late 1970's and early 1980's, the initial descriptions of this material were begining to appear in the literature (Senut, 1978, 1981;

Johanson *et al.*, 1982; Lovejoy *et al.*, 1982a,b) and the results of preliminary analyses indicated that the functional morphology of the gracile australopithecine shoulder girdle was, as had been suspected from the shoulder girdle morphology of Sts 7, in many ways as, or more similar, to extant ape morphology than it was to that of modern humans (Senut, 1978, 1981, 1982; Larson and Stern, 1986).

In contrast to the above, during this same period, there appeared in the literature a tendency to "humanise" the behaviour and locomotion of early hominids. In particular, studies conducted on the lower limbs by Brace (1979), Wolpoff (1983a,b) and Lovejoy (1981) tended to examine early hominid locomotion and behaviour as an extension of modern human bipedalism. The frustration of authors such as Zihlman and Tanner (1978), Senut (1978, 1981), Vrba (1979) Tardieu (1981) and Larson and Stern (1986) amongst many others who recognised critical differences in the total postcranial morphology of early hominids, was evident throughout this

period. The aformentioned "humanising" studies tended to emphasise similarities between the postcranial morphology of australopithecines and humans and de-emphasise the differences.

However, there has been a recent resurgence of recognition that there are fundamental features in the postcranial morphology of early gracile australopithecines that distinguish them from living humans. Numerous studies conducted during the 1970's and the early and mid-1980's (e.g. Day, 1978; Senut, 1978, 1981, 1982,1989; Vrba, 1979; Tardieu, 1981; Jungers, 1982; Jungers and Stern, 1983; Schmid, 1983; Stern and Susman, 1983; Susman, 1983; Rose, 1984; Susman et al., 1984; Senut and Tardieu, 1985; Larson and Stern, 1986) and more recent studies (Berge, 1991; Latimer, 1991; McHenry, 1991; Preuschoft and Witte, 1991; Rose, 1984, 1991; Schmid, 1991; Susman and Stern, 1991; Hartwig -Schrerer, 1993 etc.), suggest that some components of the behaviour and locomotor repertoires of these early hominids were not as humanlike as was previously thought (Dart, 1959;

Day, 1978; Brace, 1979; Wolpoff, 1980; Lovejoy, 1981; Morgan, 1982; Parker, 1987).

Models for the "modes" of locomotion of australopithecines that have been developed based on the post-cranial morphology (primarily the hands, elbow joint, pelvis, knee joint and feet) vary greatly but, as outlined by Senut (1991), they may be grouped into two main categories: climbing and non-climbing. Within these categories are at least 8 models for the exact form of locomotion australopithecines undertook. Senut summarised the categories as follows:

Climbing Models

1) The "chimpanzee-like brachiator" model
   (Keith, 1923; Gregory, 1928; Tuttle, 1969)
2) The "knuckle-walking" model
   (Washburn, 1967)
3) The "gibbon" model
   (Tuttle, 1981)
4) The orang-utan model
   (Stern, 1976)

5) The "semi-brachiator" model

(Napier, 1963)

Non-Climbing Models

1) The "bonobo" model

(Zihlman, 1985)

2) The Cercopithecoidea terrestrial quadruped model

(Delmas, 1972; Hotton et al., 1984)

3) Sitting as an origin for bipedalism

(Wood Jones, 1964; Jolly, 1970; Napier, 1970; Heim, 1979; Wrangham, 1980)

The varying categories of locomotion are self-explanatory. However, for a comprehensive review of the individual categories see Senut (1991, p. 247-248). What is most important to note is that all of the above-mentioned models imply locomotor behaviour that involves use of the upper limbs. Thus, examination of the functional morphology of the shoulder girdle of fossil australopithecines should allow these various models to be tested. On the other hand, the

functional morphology and locomotor capabilities of robust australopithecines have recently been assessed to be much more comparable to humans or the chronologically contemporaneous members of the genus *Homo* than they are to apes and this morphology should be discernible in the shoulder girdle (Susman, 1988a,b, 1993; Susman and Brain, 1988). Nevertheless, despite the discovery of the large Hadar hominid sample, and our increasing knowledge of the postcranial morphology of the various species of Plio-Pleistocene hominid, we still have no clear picture of what the exact form(s) of locomotion of these early australopithecine species were.

During the late 1970's and the early- to mid-1980's, discussions concerning australopithecine locomotion were centred around the postcranial morphologies of the hominids from Hadar since this represented the most complete sample yet discovered. By the late 1980's and the early part of the 1990's, the number of studies conducted on the functional morphologies of any species of early hominid shoulder girdle had

declined significantly, since almost no new, well preserved fossil hominid shoulder girdle material was described. The few studies that were conducted specifically on the extant primate shoulder girdle were almost wholly multivariate attempts to associate the morphologies of the bones of the region with the recently recognised complex lifestyles of living primates (Oxnard, 1976; Oxnard et al., 1981; Oxnard et al., 1990). Also during this period great efforts were being made in exploring the origins, and reasons for the origins, of hominid bipedalism since fossil evidence from Plio-Pleistocene hominids has indicated that the pelvis and lower limbs are already capable of a form of sustained terrestrial bipedalism (Rose, 1976, 1984, 1991; Rodman and McHenry, 1980; Wrangham, 1980; Lovejoy, 1981; Senut and Tardieu, 1985; Day, 1986; Parker, 1987; Eickhoff, 1988; Montgomery, 1988; Hunt, 1990; Latimer, 1991). However, these explorations were forced to rely primarily on indirect evidence rather than on direct evidence, since late Miocene proto-hominids are conspicuous by their absence.

It was within this environment that in late 1989 the author was presented by Professor P.V. Tobias with the opportunity of analysing several recently recovered hominid shoulder girdle elements from the Sterkfontein site as part of the ongoing analyses of hominid materials. During preparatory researches into the functional morphology of the hominoid shoulder joint for the purpose of the aforementioned analysis, it was brought to this author's attention that there was also a need to synthesise the functional and comparative anatomical work that had been conducted on the hominoid shoulder girdle. The last such comprehensive attempts had been made for these skeletal elements nearly 60 years prior (Inman et al., 1944) and for the myology, nearly 30 years ago (Ashton and Oxnard, 1963). In addition, the results of that preliminary research led the author to recognize that there was potential for answering some of the behavioural and taxonomic questions that had arisen from functional morphological studies of other more complete areas of the early hominid postcranial

skeleton. Latimer (1991, p. 172) has effectively summarised the importance of functional morphological studies of the early hominid upper limb and shoulder girdle. He notes:

> *"The upper limb, however, is not under immediate selection pressures related to bipedality and in this sense can be considered largely independent of this evolutionary transition. Moreover, in an animal whose survival depends upon effective climbing behaviours and whose hindlimb has lost virtually all arboreal function, one can expect to see clear and easily recognized climbing adaptations in the upper limb. This is especially true in view of the forelimb dominance that characterises even the most terrestrial of extant apes."*

1.5 Aims of the Present Study

This work aims to provide a detailed comparison of the anatomy and functional morphology of the extant hominoid shoulder girdle, to describe the morphology of the early hominid shoulder girdle fossils and to assess the functional morphology of the early hominid shoulder girdle with the hopes of interpreting behaviour and exploring issues of taxonomy. As a

result of the above analyses, this work will also evaluate previous hypotheses as to the functional morphology, behaviour and taxonomy of the early hominids that are based on assessment of postcranial morphology. Therefore, it is necessary to outline previous assessments and interpretations of early hominid behaviour, and these are presented below as a series of testable hypotheses.

Hypothesis 1: The shoulder girdle of "gracile" australopithecines possesses adaptations to arboreal locomotion not found amongst modern humans:

Since Broom first described the **Sts 7** scapula and humerus (Broom *et al.*, 1950), most authors have supported the suggestion that the *A. africanus* shoulder was adapted for climbing and suspensory behaviour (Campbell, 1966; Oxnard, 1968; Senut, 1978, 1980, 1982,1988-1989,1989, 1991; Vrba, 1979; Senut and Tardieu, 1985). This same conclusion was reached when shoulder girdle specimens of *A. afarensis* were examined (Senut,

1978; 1980, 1982, 1989, 1989; Stern and Susman, 1983; Senut and Tardieu, 1985; Larson and Stern, 1986). Thus the general consensus among researchers has been that both species of gracile hominid possessed adaptations in their shoulder girdles to arboreal behaviour.

The exact definition of the upper limb locomotor behaviour of *A. africanus* has varied depending on the examiner. Broom et al. (1950) felt that the upper limb of *A. africanus* is most similar to that of orang-utans and this indicated that the australopithecines were capable arborealists. Oxnard (1968, 1969) proposed that the upper limb of *A. africanus* was unlike any extant primates but he indicated that the species probably practiced a locomotor behaviour most similar to that observed in the "highly arboreal orang-utan". Senut (1978, 1980, 1990) and Vrba (1979) amongst others, suggest that the shoulder girdle morphology of *A. africanus* possessed adaptations to climbing and suspensory behaviour.

The *A. afarensis* shoulder girdle morphology is known from the **A.L. 288-1** (Lucy) shoulder girdle and a few fragmentary clavicular and proximal humeral specimens from the **A.L. 333** site at Hadar. The functional morphology of these specimens has been preliminarily examined by Senut (1978, 1980, 1991), whilst Larson and Stern (1986) have briefly examined a few aspects of the morphology of the **A.L. 288-1L** scapula. These preliminary assessments of the shoulder girdle of *A. afarensis* suggest that this species shares features with ape morphology that may indicate adaptations to climbing and/or suspensory behaviour.

Hypothesis 2: The shoulder girdle of "robust" australopithecines possessed adaptations to arboreal locomotion not found amongst modern humans.

The known upper-limb evidence for arboreal adaptations in the shoulder girdle morphology of the robust australopithecines (*A.* (*Paranthropus*) *robustus*, *A. aethiopicus* and *A.* (*P.*) *boisei* is

minuscule. The only scapular material undamaged enough to give clues as to the functional morphology of the shoulder girdle is a scapular spine fragment (part of the partial skeleton **KNM-ER 3735**) (Leakey et al., 1988). A small glenoid fragment associated with **KNM-ER 1500** (also attributed to *A. boisei*) is so badly damaged as to be of little value in a morphological analysis (Leakey and Walker, 1988; Grausz et al., 1988) However, there are two proximal humeri that have been associated with robust australopithecines, **KNM-ER 739** and **OMO 119-2718** which are in relatively good condition.

As all of the above specimens suggest large, heavily muscled shoulders, the general consensus is that the east African robust hominids, *A. boisei* and *A. aethiopicus*, had shoulders well suited to climbing and suspensory behaviour (Senut, 1978; Walker et al., 1987; R.E.F.,Leakey et al., 1988).

Hypothesis 3: The shoulder girdle of early *Homo* possesses adaptations to arboreal locomotion.

The O.H. 7 clavicle 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 it may share some morphological similarities with modern ape clavicles (Napier, 1965; Oxnard, 1969).

The only other shoulder girdle specimen that is attributed to the earliest species of *Homo* is the humerus of the very fragmentary partial skeleton **O.H. 62**, attributed to a small female *Homo habilis* (Asfaw *et al.*, 1987; Johanson *et al.*, 1987). As with the **O.H. 7** clavicle, this specimen presents tantalising evidence that the intermembral index of this species of early *Homo* may have been more ape- than human-like (Johanson *et al., 1987*; Hartwig- Scherer, 1993).

Hypothesis 4: Morphological differences between the shoulder girdles of early hominids are sufficient to distinguish among taxonomic units

Hypothesis 5: Morphological differences between the shoulder girdles of early hominids are sufficient to make phylogenetic inference.

Due to the relative paucity of comparable samples of fossil hominid shoulder girdles, the value of this region as a taxonomic and phylogenetic indicator in early hominids is understudied. However, the new fossil hominid shoulder girdle material from Sterkfontein described in this thesis, makes the comparison of two relatively large fossil hominid shoulder girdle samples possible.

Differences in the functional anatomy of locomotor related skeletal complexes have been frequently used to assess systematic and phylogenetic relationships in the fossil record. In particular, the study of fossil primates has benefited from the observations of differences in functional anatomy (see Szalay and Delson, 1979; Senut and Tardieu, 1985 etc.). Senut and Tardieu (1985) have used differences in parts of the postcranial morphology (the knee and elbow joints)

of the Hadar australopithecines to illustrate the probability of two functionally distinct morphotypes, and thus most probably two species, being present in the sample.

By examining features of a skeletal region that may be related to different "modes" of locomotion, or different specific behaviour, one should be able recognise taxonomically unique adaptations, or modifications. In particular, since all the early hominid species appear to be performing a similar form of terrestrial locomotion, namely facultative bipedalism (e.g. Rose, 1976, 1984; Wrangham, 1980; Rodman and McHenry, 1980; Lovejoy, 1981; Gomberg and Latimer, 1984; Senut and Tardieu, 1985; Latimer et al., 1987; Hunt, 1990a,b; Latimer, 1991; Rak, 1991 etc.), the functional morphology of the shoulder girdle may prove useful in differentiating these forms, or at least differentiating species specific locomotor adaptations or modifications. In addition, Fleagle (1988) has observed that many of the modifications of the musculoskeletal system that are related to locomotor differences are

influenced by the ancestry of the group being considered. Thus, when forms show similarities in function in one part of their anatomy differences may be due to differences in ancestry.

Recognition of the above is particularly critical to the study of early hominid evolution, since much discussion has centered around the phylogenetic relationships of the Plio-Pleistocene hominids (White et. al., 1981; Skelton et al., 1986; Grine, 1988 etc.). In particular, there is considerable debate concerning the phylogenetic relationships of *Australopithecus africanus*, *A. afarensis* and the earliest members of the genus *Homo* (White et al., 1981; Tobias, 1991b; Wood, 1991, 1992 etc.).

1.5.1

Predictions

If hypotheses 1-3 are accepted then a series of predictions may be made. Firstly, one would expect that the morphology of the shoulder girdle in these fossil hominids would bear significant

resemblances to that of extant arboreal apes. Secondly, the attachment areas for muscles associated with abduction, adduction and extension of the forelimb would be enlarged over those found in modern humans, since enlargement of these muscles and muscle groups characterises those apes that practice extensive arboreal behaviour. Thirdly, the morphology of the shoulder girdle should allow exclusion of certain forms of specialised upper limb dependent locomotor behaviour since these presumably have characteristic features that may be identified. Finally, the reconstructed soft tissue and anatomy of the bony morphology of the shoulder girdle region should be found to be non-restrictive and offer a wide freedom of movement, as one would assume that this is an essential requirement to an animal practicing generalized suspensory and/or climbing behaviour.

Concerning Hypothesis 4, one may predict that if *A. afarensis* is ancestral to *A. africanus*, the latter species will not possess any primitive characters in its shoulder girdle morphology that

are not also present in the *A. afarensis* shoulder girdle morphology. Likewise, the shoulder girdle of early *Homo* should not possess primitive features that are not present in its proposed australopithecine ancestor. One might also suggest that there would be strong grounds for exclusion of a species as a potential ancestral form if it violated any part of the above prediction.

Finally, if the species of early hominid were practising species-specific locomotor behaviour linked to the upper limbs, then these behavioural differences should be observable as morphological differences in the bones of the shoulder. One would therefore also expect to be able to infer differences in the percentage of time allocated to arboreal behaviour.

Chapter 2

Materials

2.1 Introduction

It is the purpose of this chapter to briefly examine the skeletal materials used in this thesis and also examine the ecology, behaviour and locomotion of the modern primates from which the skeletal materials are derived. While it is beneficial in a morphometric or descriptive analysis to describe the function of a morphological complex in relation to a specific primate species' "mode" of locomotion, the application of a rigid classification of primate locomotor behaviour, based on our knowledge of primate behaviour at the time of this study, is most probably impossible. Oxnard *et al.* (1990) have highlighted the problems associated with the use of the "dominant behaviour terminology" which has characterised most attempts at locomotor

classification and these are discussed in Chapter 1. As a result of studies such as Oxnard's, the author has chosen not to utilise specific primate locomotor classifications in this investigation except where absolutely necessary. Where morphology can be related to a specific function, and that function is specific to a certain behaviour in an extant primate species, then its implication for specific locomotor classification will be discussed.

The skeletal elements of the shoulder girdle from six extant species of Hominoidea and two species of Cercopithecoidea are examined to represent a diverse array of locomotor behaviour and a diversity of body sizes. Classifications of these species follow the taxonomy of the primate order as outlined in Jolly (1972). Hominoids comprise a majority of the sample since the living species which comprise this group are presumably the most closely related of living primates to the extinct hominid species under study. However, whilst modern hominoids exhibit a considerable diversity of locomotor behaviour,

none utilise extensive pronograde quadrupedalism. Since forms of quadrupedalism appear to have been the modes of locomotion of many Miocene hominoids (see Szalay and Delson, 1979, for a review), modern quadrupeds are included in this study as this particular mode of locomotion may have significant bearing on early hominid locomotor behaviour. The short descriptions and discussions which follow are intended to give the reader general ecological and behavioural information on the extant primate species examined whilst also describing the variety of "modes" of locomotion of each species. A list of all the modern specimens examined in the present study is given in Table 1.

In addition to the above, the geological and temporal derivation of the fossil hominid material under study is described in this chapter, since the context whence such material is recovered may lead to insights into systematics, phylogeny and behaviour of these extinct forms. A list of all the fossil shoulder-girdle elements examined in the present study is given in Table 2.

2.2 The Extant Primate Series

2.2.1 Infraorder Catarrhini

2.2.1.1 Superfamily Hominoidea

2.2.1.1.1 Family Hominidae

2.2.1.1.1.1 Genus *Homo*

2.2.1.1.1.1.1 Species *Homo sapiens*

The study of the shoulder girdle complex of modern humans is particularly relevant to the study of the early hominid shoulder complex, since modern humans represent the only extant primates that practise terrestrial bipedalism as their primary mode of locomotion. In the present study the human skeletal series is derived from three populations: South African Zulu, southern African San and an archaeological collection of Native Americans.

The Native American series is derived from the repatriated collection of Koniag and

Pre-Koniag skeletons formerly held at the Smithsonian Institution. The specimens were originally recovered by Ales Hrdlicka between 1931 and 1936 from a large burial midden near Uyak Bay, Kodiak Island, Alaska (Smithsonian records) (Figure 1).

It is believed that the Pre-Koniags represent one of the earliest migrations of Asian peoples into North America. This population is therefore related only slightly to the later immigrants, the Alaskan Eskimo peoples, but is closely related to the Algonquin peoples of the Bering Sea region (Smithsonian records). The Pre-Koniag are thus more similar culturally and physically to the earliest American Indian inhabitants of the Northwest Coast than to the "classic" Eskimo (Aleut) peoples of Alaska and the Arctic region.

The Pre-Koniags were primarily marine hunter-gatherers, making a living from the exploitation of the marine fishes and mammals that are abundant on the Kodiak Island coastline.

Approximately 300 years ago, they were replaced or driven out of Kodiak Island by the Koniag peoples. Physically the Pre-Koniag peoples most likely resembled the less "mongoloid"-featured Northwest Coast tribes to which they almost certainly gave rise.

The Koniag peoples examined in the present study are true "Eskimos", resembling the Eskimos from the Aleutian Islands in basic physical makeup and culture. They do not appear to be related in any way to the earlier Pre-Koniag peoples, but rather represent a complete replacement of the earlier culture sometime in the early 1600's. They lived on Kodiak Island from the early part of the 17th century until they abandoned their living sites at the same time as, or shortly after the arrival of the Russians in the 18th Century. Their culture was that of the modern Eskimo peoples across Alaska and the Bering Sea region, surviving chiefly as marine-dependent hunter-gatherers (Smithsonian Records).

21 male skeletons and 15 female skeletons were examined in the present study.

The Zulu series, from which a sample of 50 skeletons (25 male, 25 female) was derived, are members of one of the largest nationalities or "tribes" in southern Africa. The Zulu nation has its origins in tribal warfare in southern Africa that occurred in the early 1800's (Edgerton, 1988). The original tribe that bore the "Zulu" name was one of the numerous Bantu-speaking peoples which lived in the northern part of Natal in what is now known as Zululand or Kwazulu. The Zulu empire was created after a remarkable leader (Shaka), rose to power using a new form of close combat warfare. During the middle and late 19th century, the Zulus were at war with the English and Boers. During this period, hundreds of thousands of Zulus died or were displaced across southern Africa. After the end of the wars with the Boers and English, the Zulus settled in what is now called Zululand. Because it was the practice of the conquering Zulu nation to incorporate the conquered into the Zulu culture,

the population is most probably genetically very diverse (Edgerton, 1988). Thus the Zulu series used in this study is only considered a population group in the loosest sense.

The Zulu skeletons were obtained primarily from cadaver-derived material held in the ***Raymond Dart Collection of Human Skeletal Specimens,*** in the Department of Anatomy and Human Biology at the University of the Witwatersrand. Individuals were identified as Zulu by information obtained from the catalogue of human skeletal specimens held in the department.

The 11 specimens (8 male, 3 female) representing the Bushman peoples used in this study are part of the cultural group "Bushman" or San, (see Tobias, 1978) but do not include representatives from the allied Khoikhoi or "Hottentot" groups. At one time the San peoples were apparently scattered across much of southern Africa, and Bushmen have been encountered along the south-central and southeastern coast from as early as the 15th century (Inskeep, 1978), but

it was not until 1682, when the early Cape Dutch settlers encountered "true" bushmen, or inland hunter-gatherers and herders, that a distinction was made between the peoples of differing means of subsistence.

The physical features of the San have been described as being paedomorphic, the adults being small in stature and retaining "infantile anatomical features" (Tobias, 1978). Tobias (1978) reports that while the average heights recorded for San men and women have increased over the past century by as much as 10 centimetres, the average height for males is still less than 162 centimetres and females around 152 centimetres.

2.2.1.1.2 **Family Pongidae**

2.2.1.1.2.1 **Genus *Pan***

2.2.1.1.2.1.1 **Species *Pan troglodytes***

20 shoulders (11 male, 9 female) of *Pan troglodytes* were examined in his study. The

chimpanzee is the most geographically widespread of the pongids. Its distribution has historically been recognized as spanning most of central Africa, from Senegal to Tanzania (Figure 1). Chimpanzees are catholic in habitat preferences, occupying a variety of ecological zones ranging from dry savannah to tropical rainforest. They are probably the best studied of all the apes (see Goodall, 1989 for a review).

The chimpanzee may be considered both terrestrial and arboreal in its habits (Reynolds , 1985; Goodall, 1965; Susman, 1984; Ghiglieri, 1984; Hunt, 1990, 1993). Whilst arboreal, chimpanzees practise diverse modes of locomotion including arm-swinging (brachiation), a variety of suspensory behaviours, slow climbing and quadrupedalism (Susman, 1984; Hunt, 1990). While terrestrial, chimpanzees primarily employ a form of quadrupedal locomotion where the weight of the upper-limbs and body is borne on the middle phalanges of the 3rd and 4th digits.

The main foods of the chimpanzee are fruits and leaves, but they commonly augment this diet with insects and small mammals. Males may reach weights around 90kg, but in the wild rarely exceed 40kg. Females are smaller, averaging 30kg in the wild.

The skeletal series examined in the present study is derived from populations originating in Senegal, Zaire, the Central African Republic, the People's Republic of the Congo and Tanzania.

2.2.1.1.2.2 **Genus *Gorilla***

2.2.1.1.2.2.1 **Species *Gorilla gorilla***

The gorilla inhabits the west and central tropics of Africa (Figure 1). There are three recognised subspecies that are considered to maintain geographical isolation (Harcourt, 1984). Skeletal elements from two of the subspecies, the western lowland gorilla (*Gorilla gorilla gorilla*) and the mountain gorilla (*Gorilla gorilla beringei*) are examined in the present study.

Gorillas show a preference for secondary herbaceous forests and their modern distribution is therefore limited by diminishing habitat. Gorillas may be considered primarily folivorous. They are the largest of all living primates, wild males averaging around 170kg. However, wild weights of as much as 200kg have been recorded (Schaller, 1963). Female gorillas are considerably smaller than the males, averaging around 90kg (Napier and Napier, 1985).

Gorillas employ true "knuckle-walking" while terrestrial. In this form of locomotion, all the weight of the upper limbs and body is supported on the middle phalanges (Hunt, 1990). They are one of the most terrestrial of all primates with adults rarely climbing trees (Schaller, 1963). Nevertheless, gorillas are efficient slow climbers during their infrequent climbing sessions. Gorillas are known to engage in brief, infrequent bouts of bipedalism. It is unlikely that adult gorillas perform true brachiation in the wild but they may exhibit

limited arm-swinging behaviour (Schaller, 1963).

15 male and 5 female gorilla shoulders were examined in the present study. The gorilla skeletal series examined in the present study was obtained from a population in the Virunga volcanoes, south-western Uganda as well as Nigeria, Cameroon, Gabon and the Congo.

2.2.1.1.2.3 **Genus *Pongo***

2.2.1.1.2.3.1 **Species**

Pongo pygmaeus

There are two recognised living subspecies of orang-utan, *Pongo pygmaeus pygmaeus* and *Pongo pygmaeus abelli*. Historically their geographical distribution has been confined to the islands of Borneo and Sumatra (Figure 1). Both subspecies have been extensively studied in the wild and they have been found to exhibit similar behaviour (MacKinnon, 1974). They live mainly in upland forest area, where they subsist on fruits but also eat new leaves, shoots and

bark. Orang-utans' home ranges are small, extending over approximately 70 ha. Day ranges do not usually exceed 300m (MacKinnon, 1974; Galdikas, 1985; Fleagle, 1988). Adult males typically extend over much larger home ranges that overlap those of several females.

Orang-utans are extremely sexually dimorphic, the males averaging 120 kg and being approximately twice the size of the females (Napier and Napier, 1985). The limbs of the orang-utan show extreme specialisation for a life of suspensory behaviour. Their forelimbs are very long, ending in hooklike hands with long curved fingers and a short thumb. Their legs are very short, but mobile, ending in prehensile, handlike feet that have long curved digits and a short hallux.

Females and young are almost exclusively arboreal, only rarely descending to the ground (Sarmiento, 1985). Males travel on the ground more frequently, but usually only to change trees. Arboreally, the orang-utans typically use a

slow-quadrumanous climbing where their hands and feet are used interchangeably to pull them through the upper canopy (Sarmiento, 1985). Whilst on the ground they move quadrupedally with their hands held in fists (Mackinnon, 1974). Only rarely do they engage in brachiation, and then only when fleeing danger.

12 male and 20 female orang-utan shoulders were examined in the present study.

2.2.1.1.3 **Family Hylobatidae**

2.2.1.1.3.1 **Genus *Hylobates* and *Symphalangus***

2.2.1.1.3.1.1 **Species *Hylobates* species and *Symphalangus syndactylus***

The hylobatids, or gibbons, are the smallest and numerically most successful of the living apes. Species of gibbons are found throughout the

vast evergreen forests that run from India to Southern China, as well as Borneo, Java and Sumatra and the nearby islands (Figure 1). Considering their extremely wide range and diversity of habitats, the gibbon's behaviour, ecology and morphology are remarkably uniform (Chivers, 1984). Gibbons are generally grouped in three categories: the siamangs, the concolor gibbons, and the lar gibbons. The greatest morphological differences are found in the two species, *Hylobates concolor* and *Symphalangus syndactylus*, that exist sympatrically in the forests of Malaysia (Chivers, 1984). In the present study, all the specimens classed as *Hylobates* sp. are members of the *"concolor"* group (a more informal grouping of several species of hylobatids (Chivers, 1984), but not all are members of the species *Hylobates concolor*.

Gibbons are in many ways the most primitive of the apes, retaining many morphological features found in cercopithecids. They may also be considered the most specialised of all the hominoids in their locomotor behaviour. Gibbons

are the most suspensory of all the primates, moving almost exclusively by two-armed brachiation and quadrumanous climbing. The smaller species of hylobatids use rapid ricochetal brachiation in which they throw themselves from tree to tree. The larger siamang travels mainly by slow, pendulum-like, arm over arm brachiation (Fleagle, 1988). Gibbons are the only primates other than humans that do not include quadrupedalism in their locomotor repertoire.

15 Hylobates sp. (9 male, 6 female) and 4 Siamang (1 male, 3 female) shoulders were examined in the present study.

2.2.1.1.4 **Family Cercopithecidae**

2.2.1.1.4.1 **Genus *Cercopithecus***

2.2.1.1.4.1.1 **Species *Cercopithecus aethiops***

The vervet monkey is the most widespread of the guenon species, being distributed throughout sub-Saharan Africa. Although extremely catholic,

being found in almost all environments, its habitat preference is reported to be woodland savannah and gallery forests (Jolly, 1985; Napier and Napier, 1985). It is the most terrestrial of all guenons (20% of all locomotion), frequently leaving the trees to forage on the ground (Struhsaker, 1978). Vervet monkeys are predominantly quadrupedal even whilst arboreal, with leaping and other forms of locomotion making up less than one-quarter of their total locomotor activities. They subsist on almost any food, including small invertebrates.

Sexual dimorphism in the vervet is not as pronounced as in baboons. Total length excluding the tail averages 450-650 mm in both sexes. Female vervet monkeys average around 1440g in body weight and males about 2200 g (Napier and Napier, 1985).

2.2.1.1.4.2 **Genus *Papio***

2.2.1.1.4.2.1 **Species**

Papio ursinus

The chacma baboon is one of five allopatric species of savannah-dwelling baboons in Africa. The behaviour and ecology of this species is one of the best documented of any of the African monkeys (see Jolly, 1972 and Fleagle, 1988 for reviews). They are found in almost every environment in sub-Saharan Africa. Their primary mode of locomotion may be considered to be terrestrial, pronograde, quadrupedal walking and running. They usually seek shelter in trees or cliffs for sleeping and resting. Their main foods are ripe fruits, roots and tubers, grass seeds, leaves and acacia gums, as well as the occasional small mammal or invertebrate.

The chacma baboon lives in large, socially complex troops ranging from thirty to more than eighty members. The troops occupy extremely large home ranges which often exceed 4,000 ha in area. A troop may travel more than 5 km per day during foraging. Sexual dimorphism is pronounced in the species. Males are reported to weigh on average 31 kg, and females around 27 kg (Fleagle, 1988).

Twenty-eight specimens of *Papio ursinus* were examined in this study. All the specimens are in the Department of Anatomy and Human Biology, University of the Witwatersrand.

2.3 The Fossil Hominid Series

2.3.1 Introduction

The present study is primarily concerned with the reconstruction of the functional morphology of early African hominids. The relative paucity of fossil shoulder girdle specimens which have been recovered from Plio-Pleistocene deposits highlights the taphonomically fragile nature of this anatomical region.

Only two Plio-Pleistocene hominid bearing localities have yielded more than a few well-preserved shoulder girdle specimens and all of these are currently assigned to a single lineage of "gracile" australopithecines. In

contrast, only two shoulder girdle specimens attributed to the so-called "robust" australopithecines are well enough preserved to warrant morphological comparison. The remainder of the fossil shoulder girdle specimens referred to the robust lineage of australopithecines are either too fragmentary to make meaningful functional interpretations, exhibit pathological conditions which alter or obscure their morphology, or are those of juveniles (Day, 1976, 1978; McHenry, 1991 etc.). The same is true for most specimens attributed to early members of the genus *Homo* (Day, 1976, 1978; Walker *et al.*, 1982; Leakey and Walker, 1985; Johanson *et al.*, 1987; Walker and Leakey, 1993 etc.) and there is only one published adult specimen which is sufficiently preserved to enable functional morphological comparisons to be made (Day, 1991). The fossil series examined in the present study are derived almost wholly from two geographic regions, eastern and southern Africa, and span around 2.2 million years of time, from about 4.0 mya. to about 1.8 mya.

The southern African fossil sample is comprised exclusively of specimens from Member 4 at the Sterkfontein site, South Africa. The east African material is derived primarily from the formations at Hadar, Ethiopia. Isolated shoulder girdle specimens have also been recovered from sites in the Omo, Ethiopia, at Koobi Fora, Kenya, and at Olduvai Gorge, Tanzania. The chronological position of the various fossils is presented after the general description of the material.

The attribution of certain specimens to a particular taxon is useful for examining phyletic relationships. Where the individuals represented by fossil shoulder girdle elements are classified in this study, except where indicated, this author has chosen to accept the most commonly held view of classification at the time of writing.

2.3.2

The Sites

2.3.2.1 Southern Africa

2.3.2.1.1 South Africa

2.3.2.1.1.1 Sterkfontein

(Figure 2)

The early hominid remains recovered from Sterkfontein are found in two of the six members recognised in the Sterkfontein Formation (Partridge, 1982): Member 4 where specimens representing the species *Australopithecus africanus* have been recovered, and Member 5 where specimens of *Homo habilis* have been recovered, as well as at least two stone industries (Kuman, in press).

In 1947 R. Broom and J.T. Robinson discovered the head and proximal shaft of a right humerus, a fragmentary right scapula, a partial vertebra and assorted rib fragments in close association with a crushed mandible in part of the Sterkfontein deposit known then as the Type Site (Broom and

Robinson, 1947; Broom *et al.*, 1950), and corresponding to the subsequently recognised Member 4. Due to its size and stage of dental wear, the mandible was identified as that of an old, adult male *Plesianthropus transvaalensis* Broom (= *Australopithecus africanus* [see Robinson, 1954]). Because of the close association of the postcranial remains to the mandible, they have been considered as belonging to the same individual and thus given the collective catalogue number of **Scs 7** .

Seven additional specimens of shoulder girdle material have been recovered by P.V. Tobias and A.R. Hughes since the excavations at Sterkfontein were renewed in December, 1966. **Stw 162** is a left scapular fragment recovered in 1983 by A.R. Hughes and members of the excavation team from grid square Aa / 49 at a depth of 5' 2" - 6' 2" . It has been assigned to Member 4 (Tobias, 1984; R.J. Clarke, pers. comm.). The **Stw 328** specimen is a fragment of a right proximal humerus recovered in 1985 by Hughes from Grid Square U / 42, 9' 0" - 10' 4" (Tobias, 1986) and has been

assigned to Member 4 (Clarke, pers. comm.). The **Stw 431** specimens are the lateral one-half of a right clavicle, and the axillary margin and inferior angle of a right scapula. These specimens are part of an adult partial skeleton which has been assigned to the species *Australopithecus africanus* (Toussaint *et al.*, in preparation). The specimens were recovered from grid squares R/45 and Q/45 at a depth of 21' 11" - 25' 6" in 1986 by A.R Hughes and members of the Sterkfontein field team (Tobias, 1987). **Stw 517** is a fragmentary left proximal humerus. The specimen was recovered in 1988 from grid square k/40 at a depth of 20'0" - 21' 4". It has been assigned to member 4 (Clarke, pers. comm.). Whilst undeniably fragmentary, in shape and morphology all of these more recently recovered specimens are certainly attributable to the Hominoidea. Since this study recognises only a single species of *Australopithecus* from Member 4, it is most reasonable to attribute these specimens to the hominid species *Australopithecus africanus*.

The age of the Sterkfontein Member 4 deposit has been established primarily by faunal correlation with east African sites (Cooke, 1963; Simpson, 1971; Maglio and Cooke, 1978; Partridge, 1982; Vrba, 1982; Delson, 1984, 1988; McKee, 1991, 1993; Partridge and Watt, 1991; Berger, 1993; McKee *et al.*, in press). Faunal dating of Sterkfontein Member 4 indicates an age for the deposit at around 2.8 to 2.4 mya.

2.3.2.2 East Africa

2.3.2.2.1 Tanzania

2.3.2.2.1.1 Olduvai Gorge

(Figure 3)

Olduvai Gorge is a (rift) canyon in the Serengeti Plain north of lake Eyasi and west of Ngorongoro Crater. In 1960 a nearly complete left clavicle, **OH 48**, was discovered by L.S.B. Leakey in the FLK NN Site in Bed 1 at Olduvai Gorge, Tanzania (L.S.B. Leakey, 1960). L.S.B. Leakey *et al.* (1964) and Tobias (1991b) have tentatively attributed the specimen to the taxon *Homo habilis* because of its association on the

same site with cranio-dental remains of at least four individuals attributed to this species (Tobias, 1991b, pp. 541 - 544 and M. Leakey's Appendix 1, same volume).

The sediments in Bed 1 where the specimen was recovered have been dated by Argon/Argon methods to around 1.7 - 1.8 mya (Hay, 1976).

2.3.2.2.2 **Kenya**

2.3.2.2.2.1 **Koobi Fora**

(Figure 3)

Hundreds of fossils of early hominids have been recovered from sites at and around Koobi Fora, East Lake Turkana in northern Kenya since R.E.F. Leakey initiated excavations there in 1968 (Leakey, 1971; Leakey *et al.*, 1972; Leakey, 1972; Leakey, 1976 etc.). To date, only a small number of fragmentary shoulder girdle elements have been recovered despite extensive surveys and excavations. The first shoulder girdle specimen was discovered in 1970. **KNM-ER 739** is a large right humerus with the shaft and distal end

preserved, but missing the head. It was recovered from the Chari Tuff and is dated to around 1.53 (Feibel *et al.*, 1989). The specimen has tentatively been attributed to the genus *Australopithecus* (Leakey, 1971; Leakey *et al.*, 1972; Day and Leakey, 1974; Day et al., 1976).

KNM-ER 1473 is the proximal portion of an adult right humerus and the articular surface of the humeral head recovered from the Upper Burgi Member (Leakey, 1973; Day et al., 1976), dated to 2.6 - 2.8 mya (Brown *et al.*, 1985).

The most recently reported find is a small scapular spine fragment associated with the partial skeleton **KNM-ER 3735** (Leakey et al., 1989), but the author has been unable to obtain a cast of this small specimen and no formal description has been given.

2.3.2.2.3 **Ethiopia**

2.3.2.2.3.1 **Omo**

(Figure 3)

The Omo sites, situated in the south-west of Ethiopia, have been geologically and palaeontologically explored since early French expeditions prospected the region in 1932-1933. Hominid material has been recovered from the Omo region since the late 1960's.

There are numerous recognised formations within the Omo deposits but only the Shunguru has yielded shoulder girdle elements of early hominids. The geochronology and member succession at Omo have been established by both Argon-Argon dating and faunal succession (Coppens, 1975; Coppens and Howell, 1976; Maglio and Cooke, 1978; Bonnefille *et al.*, 1987; Churcher, 1992). Members are lettered from oldest to youngest (e.g. Member A, B, C...etc.).

Only one shoulder girdle element, a left proximal humerus and shaft labelled **OMO 119 - 2718**, has been reported from any of the Omo sites (Senut, 1978). The specimen was recovered from Member D in the Shungura Formation and has been dated to approximately 2.5 mya (Brown *et al.*,

1985). This specimen has been attributed to the genus *Australopithecus* (Senut, 1978) and most probably to the species *Australopithecus aethiopicus* (Kimbel et al., 1988).

2.3.2.2.3.2 **Hadar**

(Figure 3)

Between 1973 and 1977 the international Afar Research Group recovered numerous remains of fossil hominids and associated fauna from the Hadar Formation, central Afar, Ethiopia (Johanson *et al.* 1978; Johanson *et al.*, 1982). Included in the finds is a 40% complete skeleton, **A.L. 288-1**, popularly dubbed "Lucy". The parts of the skeleton referred to in this study are the right scapula (**A.L. 288-1L**), right clavicle (**A.L. 288-1Bz**), and left and right proximal humeri (**A.L. 288-1r** and **A.L. 288-1m**, respectively). These specimens were described by Johanson *et al.* (1982). Additional observations and measurements were made by the author using casts supplied by the ***Institute of Human Origins***. The partial skeleton is attributed to the species *A. afarensis*

by Johanson *et al.* (1979) and is dated to 2.6 - 2.9 mya (Brown, 1982).

During the 1974-1977 field seasons several fragments of upper limb material were recovered from Hadar including the following shoulder girdle material: a left clavicular fragment (**A.L. 333-94**), a right clavicular shaft (**A.L. 333X-6/9**), a left proximal humerus (**A.L. 333-87**), a right proximal humerus (**A.L. 333-107**), and a right humeral shaft (**A.L. 333-109**). The descriptions used in the present study are taken primarily from Senut (1978) and Lovejoy *et al.* (1982).

There remains considerable controversy as to the age of the hominid fossils from Hadar. Some scientists have placed the specimens recovered from the 333 site around 4.0 mya (White and Harris, 1977; Cooke, 1978; Harris and White, 1979), but it is more likely that the specimens are closer to 3.3 mya in age.

Some investigators consider that the substantial amounts of fossil hominid material at

Hadar represent two species of hominid being represented in the sample, a "robust" and a "gracile" variant (Johanson and Taieb, 1976; Johanson *et al.*, 1976, Olsen, 1981; Coppens, 1981, 1982, 1983a,b; Senut, 1978; 1981a, b; 1982; Senut and Tardieu, 1985; Tardieu, 1979, 1982, 1983). However, it seems that a majority of authors have settled on the single-species hypothesis and assigned all the specimens to a single highly sexually dimorphic species *Australopithecus afarensis*. Kimbel (1985), and Kimbel and White (1988) have since reported that there is little doubt that only one species of *Australopithecus* is found in the Hadar sample. Nevertheless, the taxonomic affinities of the Hadar sample are still an area of much debate (Tobias, 1980, 1988b; Tardieu, 1981; White *et al*. 1981; Senut and Tardieu, 1985; Zihlman, 1985; McHenry, 1988; McHenry, 1991; Hartwig-Scherer, 1993). Some authors include *A. afarensis* within the species *A. africanus* though as a separate subspecies, whilst others recognise a probable second species at Hadar (e.g. Tobias, 1988a, b; Tardieu, 1981; Zihlman, 1985; Senut and Tardieu, 1985). However,

most continue to regard *A. afarensis* as a morphologically distinct species (e.g. Aiello, 1981; Johanson *et al.*, 1982b; Jungers, 1982; Jungers and Stern, 1983; White, 1985; Skelton *et al.*, 1986; McHenry, 1988,1991,1993; Hartwig-Scherer, 1993, etc.). For the purposes of the present analysis, all of the australopithecine material from Hadar is considered to belong to one species *A. afarensis*.

2.4

Summary

The metrical and non-metrical analysis of the extant osteological material used in this thesis is based upon data collected from the measurements of the scapulae, clavicles and humeri of 251 individuals representing 8 species of primates. The skeletal specimens are derived from the collections of the Department of Anatomy and Human Biology, University of the Witwatersrand, Johannesburg, the Transvaal Museum, Pretoria, and the Smithsonian Institution, Washington D.C.

In addition to the modern skeletal sample, 20 early hominid shoulder girdle fossils are examined. Each species' chronological position is summarised in Figure 4. In this thesis, all of the Pliocene specimens from Hadar are referred to the species *Australopithecus afarensis*. The specimens derived from Member 4, Sterkfontein are referred to *A. africanus*. The single specimen from Olduvai Gorge is referred to the species *Homo habilis*. One specimen from the Omo and two from Koobi-Fora are not placed in any particular species but are referred to the genus *Australopithecus*.

Chapter 3

Methods

3.1 Introduction

Measurements used in this study were chosen, in part, on the basis of those used in previous biomechanical, functional, anatomical and morphometric studies of the scapula, clavicle, and humerus. Particular emphasis was given to the studies conducted by Vallois (1924, 1926a,b,1927, 1928, 1932), Schultz (1930, 1937), Olivier (1951), Ashton and Oxnard (1963,1964), Oxnard (1967, 1969, 1972, 1975, 1983, 1990), Corruccini and Ciochon (1976), Serut (1978), Vrba (1979), Sarmiento (1985), and Churchill and Trinkaus (1990). Wherever applicable, the definitions of the measurements or angles, as described by Martin (1928) or Martin and Saller (1957), are adhered to except where more recent literature suggests otherwise. In addition, measurements not found in Martin (1928) or Martin and Saller (1957) but

accepted by more recent studies are included. In this chapter, the etymology of the name of each measurement is given following its definition.

3.2 Anatomical Nomenclature

Anatomical nomenclature used in the descriptions of the modern skeletal series, as well as for the fossil hominid series follows, where possible, that found in the fifth edition of the *Nomina Anatomica* (1980). In most cases the English equivalents of the Latin forms have been used.

Whilst many of the anatomical terms used in this study are readily found in anatomical texts such as Swindler and Wood (1973), Grays Anatomy (Williams *et al.*, 1989), or Tobias *et al.* (1988), others are more obscure. Therefore, where necessary, these terms are defined in the text.

3.3

Selection of the Modern Skeletal Series

In most cases selection of modern individual bones was confined to adult specimens on which complete sets of data could be taken, except in the case of the Alaskan Indian population from the Smithsonian Institution. This series was derived from excavated material and many of the specimens exhibited postmortem damage. Any specimens that were believed to have suffered antemortem injury, or exhibited bone pathology or other abnormalities, were discarded in favour of visibly normal material.

In general, specimens representing captive animals were rejected in favour of field collected wild specimens. The only exceptions are the series of *Papio ursinus* and *Cercopithecus aethiops*. A majority of the skeletons in these two samples originated from populations of captured wild animals that had been used in medical research by the *South African Institute for Medical Research* (SAIMR). These

animals were held in captivity by the SAIMR for varying lengths of time before being sacrificed. Selection from these samples were especially strict and any skeleton which exhibited possible damage (even if most likely postmortem) were not used in this study.

3.4 The Metrical Characters

3.4.1 Definitions of the Linear Measurements

1. **Anatomical length of the scapula** (Figure 5a, No. 1) (measurment 2: Martin and Saller, 1957, p. 528) - This measurement is taken from the midpoint of the dorsal margin of the glenoid cavity to the midpoint of the vertebral end of the scapular spine. Broca (1878) named this measurement the "morphological breadth". This measurement has also been called the "scapular breadth" (Hrdlicka, 1942, p. 375), the "breadth of the scapula" (Hrdlicka, 1952, p. 171), the "scapula morphological length" (Montagu, 1960, p. 68;

Corruccini and Ciochon, 1976, Figure 1A, p. 22), and the "maximum breadth" (Bass, 1971, 1979, 1987, p. 117). Nevertheless, the definition of the measurement has remained largely the same.

2. **Length of axillary margin** (Figure 5a, No. 2) - This measurement is taken from the most caudal point on the glenoid margin of the scapula's glenoid cavity to the most caudal point on the inferior angle of the scapula (Measurement 3: Martin and Saller, 1957, p. 529). This measurement differs from that of Oxnard (1969, Figure 1, p. 320), who uses the most caudal marking of *m. serratus magnus* (vel anterior) as his inferior point. A majority of authors do not use Oxnard's definition but adhere to the definition used in this study (see Vrba's 1979 discussion on this matter, pp. 120 -122). To make the results obtained by the present study more broadly comparable, the more consistently used definition of this measurement has been adhered to.

3. **Anatomical breadth of supraspinous fossa** (Figure 5a, No. 3) - This measurement is taken

from the point of intersection of the line defining the *anatomical breadth of the scapula* (Measurement 6, this chapter) and the line defining the *anatomical length of the scapula* (Measurement 1, this chapter) to the most cranial point of the cranial angle (Measurement 6a: Martin and Saller, 1957, p. 529) .

4. **Anatomical breadth of the spine of the scapula** (Figure 5a, No. 4) - This measurement is taken across the spine of the scapula at the point where the *anatomical breadth of the supraspinous fossa* (measurement 3) intersects the superior margin of the spine. At this point a measurement is taken from the most cranial to the most caudal point on a line perpendicular to the axis of the spine. This measurement is equivalent to Corruccini and Ciochon's (1976, Figure 1A, p. 22) "spine thickness".

5. **Anatomical breadth of infraspinous fossa** (Figure 5a, No. 5) (Martinand Saller, 1957) - This measurement is taken from the midpoint of the vertebral end of the spine of the scapula to the

most caudal point on the inferior angle. This measurement is also known as the "infraspinous height", or "infraspinous length" of the scapula (Broca, 1878) and the "infraspinous fossa breadth" (Montagu, 1960, p. 70; Corruccini and Ciochon, 1976, Figure 1A, p. 22).

As early as 1886, Turner had expressed reservation about the use of this measurement because of the great fluctuation in accuracy of measurement that is a result of the bend of the scapular spine and consequent displacement of the location of the point at the spine's vertebral border. Dorsey (1887) subsequently noted that the use of the *anatomical breadth of the scapula* as a comparative measurement did "not seem worthy of much consideration". Although many later researchers have concurred with Dorsey's sentiment, the measurement has continued in use in recent literature (see Martin and Saller, 1957; Olivier, 1960; Ashton and Oxnard, 1963; Oxnard, 1969; Corruccini and Ciochon, 1976; Bass, 1971, 1979, 1987). Hrdlicka (1942, pp. 375 - 383) has indicated the need for this measurement to be

"supplemented by something more reliable". Nevertheless, most recent morphometric studies of the scapula have included this measurement under the name "Length of infraspinous line" (Bass, 1971, 1979, 1987, p. 118).

6. **Morphological breadth of the scapula** (Figure 5a, No. 6) (Montagu, 1960, p. 68) - This measurement is taken from the most caudal point on the inferior angle to the most cranial point on the superior angle. This measurement has been known as "length of the scapula" (Broca ,1878; Martin and Saller, 1957, measurement 1, p. 528), "scapula total height" (Hrdlicka, 1952, p. 170), and "Maximum length" of the scapula (Bass, 1971,1979,1987, p. 116) .

7. **Acromion width** (Figure 5a, No. 7) (Martin and Saller (1957) measurement 9 (p. 530))- This measurement is defined as the maximum acromial width measured perpendicular to the estimated long axis of the acromion (Corruccini and Ciochon, 1976, Figure 1A, p. 22).

8. **Depth of the scapular glenoid cavity** (Figure 5b, No. 8) - This measurement is taken from a point which lies on the line created by the length of the glenoid cavity measurement (measurement 10), perpendicular to the point of greatest depth of the glenoid cavity. This follows closely the definition of glenoid fossa maximum depth (GFD) by Churchill and Trinkaus (1990, p. 149). It is equivalent to Martin and Saller's (1957) measurement 14.

9. **Length of the coracoid process** (Figure 5b, No. 9) (Measurement 11: Martin and Saller, 1957, p. 530) - This measurement is taken from the most anterolateral point of the coracoid process to the most posteromedial extension of the coracoid process (see also Corruccini and Ciochon, 1976, Figure 1B, p. 22).

10. **Length of scapular glenoid cavity** (Figure 5b, No 10) (Measurement 12: Martin and Saller, 1957, p. 530) - This measurement is taken from the most cranial point on the (glenoid) margin of the glenoid cavity of the scapula, to the most caudal

point on the (glenoid) margin of the glenoid cavity. Vallois (1932) uses the "most elevated point" of the superior projection of the glenoid to identify the superior point of this measurement. This measurement has also been labelled "glenoid height" by Corruccini and Ciochon (1976, Figure 1B, p. 22), and "scapular glenoid fossa maximum length" by Stewart (1962), although disagreements as to the exact definition of this measurement abound in the literature (Churchill and Trinkaus, 1990, p. 149; Stewart, 1954, p. 98; Bass, 1971, 1979, 1987, p. 123).

10b. **Glenoid cavity articular length** (Figure 5b) - This measurement follows the definition given in Churchill and Trinkaus (1990, p. 149) and is defined as the "maximum craniocaudal distance in a coronal plane between the outermost edges of the line of attachment of the glenoid labrum " (GAL: glenoid articular length).

11. **Breadth of the glenoid cavity** (Figure 5b, No. 11) (M. 13: Martin and Saller, 1957, p. 530) - This measurement is taken as the diameter at the

point of greatest width taken perpendicular to the axis of the glenoid length measurement. Stewart (1962) refers to this measurement as the "scapular glenoid maximum breadth".

12. **Spinoglenoid notch depth** (Figure 5c, No. 12) (Corruccini and Ciochon, 1976, Figure 1C, p. 22) - This measurement is defined as a chord taken from the most posterolateral border of the glenoid cavity to the most medial point in the spinoglenoid notch , the chord being parallel to the *morphological length of the scapula* .

13. **Acromion projection** (Figure 5c, No. 13) - This measurement is taken as the projected maximum lateral extent of the acromion as measured from the most medial point in the spinoglenoid notch parallel to the morphological length, to the most lateral point on the acromion process (Corruccini and Ciochon, 1976, Figure 1A, p. 22).

14. **Humerus mediolateral head diameter** (Figure 6) (Martin, 1928; M. 12a, p. 102) - This measurement is taken from the intertubercular sulcus floor to

the most medially projecting point on the humeral head perpendicular to the longitudinal axis of the humerus.

15. **Humerus anteroposterior head diameter** (Figure 6) (Martin, 1928; M.10) - This measurement is taken from the most anterior to the most posterior point on the articular surface of the head of the humerus adjacent to the greater and lesser tubercles and perpendicular to the *humerus mediolateral head diameter*.

16. **Greater tubercle/head projection height** (Figure 6) (Corruccini and Ciochon, 1976, M.15, pp 22 - 23) - This measurement is the perpendicular distance between the most superior point on the greater tubercle and the horizontal plane through the most superior point on the humeral head articular surface. .

17. **Intertubercular sulcus width** (Figure 6) - This measurement is taken as the minimum horizontal distance between the internal crests of the greater and lesser tubercles (Measurement 13,

Figure 1E, p. 22 - 23; Corruccini and Ciochon, 1976).

18. **Greatest length of humerus** (Figure 6) (M.1, Martin and Saller, 1957, p. 532) - This measurement is taken from the most cranial point of the humeral head to the deepest point point of the trochlea. It is measured with an osteometric board.

19. **Humerus mid-shaft circumference** (Figure 6) (Measurement 7a: Martin, 1928, p. 1011)- This measurement is taken at the mid-point of measurement 18 with a standard anthropometric tape. The measurement is usually found to lie a few millimetres above the lower margin of the deltoid tuberosity (Singh and Bhasin, 1968, p. 107).

20. **Greatest Length of clavicle** (Figure 7) (M.1: Martin and Saller, 1957, p. 527- This measurement is taken from the most medial point on the sternal facet to the most lateral point on the acromial facet of the clavicle. In the present

investigation this measurement is taken using sliding callipers. However several authors prefer to take this measurement with an osteometric board (Montagu, 1960; Bass, 1971, 1979, 1987).

21. **Clavicle sternal facet length** (Figure 7) (M.2: Martin and Saller, 1957, p. 527) - This measurement is taken from the most superior point to the most inferior point on the sternal facet of the clavicle (see also Corruccini and Ciochon, 1976, measurement 18, Figure 1D, pp. 22 - 23).

22. **Humeral torsion** - This is taken as a direct measurement of the angle between two imaginary lines. One line passes through the axis of the trochlea (Evans, 1973;Martin, 1928). The other line is drawn through the axis of the humeral head. Thus, a humeral head with the axis forming a right angle with the distal trochlear axis would show a torsion value of 90 degrees, whilst medial

rotation of the distal joint would give torsion values higher than 90 degrees.

3.4.2

The Angles

The four angles measured on the scapula are contained by connecting the following points (Figure 8) : (A) cranial extremity of the long axis of the glenoid cavity; (B) intersection of the base of spine with the glenoid cavity; (C) caudal extremity of the long axis of the glenoid cavity; (D) most caudal point on the inferior angle; (E) midpoint of intersection of base of spine with vertebral border; (F) most medial marking of the trapezius muscle; (G) lateral extremity of insertion of the trapezius muscle on the spine (roughly equal to the medial extremity of the acromial articular facet); (H) most cranial marking of the serratus magnus muscle (vel anterior).

3.4.2.1

Definitions of the Angular Measurments

Angle A-C-D is the angle between the glenoid cavity and the lateral margin of the scapula, and represents the angulation of the shoulder joint surface. The intersection of line G-F and B-E approximates the angulation of the crest of the spine and represents the angulation of the insertion of the trapezius muscle. Angle C-D-E is the inferior angle of the scapula. This measurement of the inferior angle differs from that of Oxnard (1969) in that his Point 4 (Oxnard, 1969, fig. 1, p. 320) does not correspond to point D in this study but represents the most caudal marking of the serratus magnus muscle (vel anterior), while point D in this study is the more frequently used point (e.g. Martin and Saller, 1957,1959; Corruccini and Ciochon, 1976; Vrba, 1979). The intersection of the lines D-H and F-G creates the angle between the spine and long axis of the medial margin of the scapula. This angle has been used by Ashton *et al.* (1965) and Oxnard (1969) to approximate the

position of the serratus magnus muscle on the scapula.

3.4.2.2

Identification of the Angle Points

The points that define the angles were identified by projection using a dioptrograph. The scapulae were positioned with the ventral surface facing downwards. Points C, D, and H were supported at an equal height of 5 cm by plasticine placed on the base board of the dioptrograph. The points, once identified through the eyepiece, were transferred to a sheet of cartridge paper. Lines were drawn through the points creating the angles described. All angles were measured to the nearest one-half degree using a standard protractor. This method differs from that of Oxnard who laid a sheet of perspex over the specimen and recorded points on the perspex for later transfer to a separate paper sheet (Oxnard, 1969, p. 320). An earlier method of angle measurement employed the use of an underlying sheet of cartridge paper onto which points were

projected (Ashton and Oxnard, 1963, Figure 1, p. 54). The method of projection of points by the dioptrograph appears to be at least as reliable as both of the earlier methods due to the consistent positioning of the eyepiece for identification of points .

3.4.3

Precision of the Osteometric Data

Except where noted, all linear measurements were taken with a set of sliding dial callipers except for the measurements of total length of the humerus (Measurement 18), which was taken with an osteometric board, the measurement for depth of the glenoid fossa (Measurement 8), which was taken with co-ordinate callipers, and the humeral mid-shaft circumference (Measurement 19), which was taken with a standard anthropometric tape. All measurements taken with dial callipers were recorded to the nearest 0.1 mm. Measurements taken with the osteometric board were recorded to the nearest 0.5. Measurements taken with the co-ordinate callipers were taken to the nearest

0.2 mm. Measurements taken with the standard anthropometric tape were recorded to the nearest 1.0 mm. All measurements and identifications of the bony points for measurement have been performed by the author over a period of approximately two years.

3.4.4 Reliability of the Measurements

The reliability of measurement, was assessed after the completion of the linear measurements on the skeletal specimens. From the completed series 11.6 % of the total were selected randomly for re-measurement. The repeated measurements were tested against the original data collected using paired t-tests. The results obtained indicated that the values for any repeated measurement within species did not differ significantly from the original value ($p < 0.05$).

3.4.5

Error of the Angle Measurements

Angle measurments were repeated on 20 scapulae during the course of the investigation. The absence of significant error was demonstrated by means of a paired t-test. The results obtained indicated that the values for any single repeated measurement did not differ significantly from the original value ($p < 0.05$).

3.5

Determination of the Areas of the Infraspinous and Supraspinous Fossae of the Scapula

Area determination of the fossae of the scapulae was limited to those specimens in the University of the Witwatersrand Department of Anatomy and Human Biology, where image analysing equipment was available and to those specimens at the Smithsonian Institution that were photographed by the author. Area determination was calculated using a Kontron-Bildanalyse Videoplan system run on a DOS compatible computer. Video reproduction

for analysis was accomplished using an Ikegami video camera.

The area determined by this method is not that of the actual bone surface area but represents the area of a plane which lies between the margins of the lateral and medial borders and inferior and superior angles (Figure 9). The author tried, and in most cases succeeded, to include only the relative muscle attachment areas on the dorsal surface contained within the supraspinous and infraspinous fossae of the scapula (Figure 10).

3.6 Standardisation of the Measurement Techniques

Initially 10 pairs of scapulae, claviculae, and humeri were examined and measured to familiarise the observer with the measurement techniques. Measurement was continued until the intra-observer variation in measurement was less than 5 % for each of the measurements.

3.7

Reliability of Area Determination

Because of variations in the morphology of the surface of the scapula, particularly in regions that do not possess definitive borders such as the area of the scapular neck, inconsistencies in area determination resulted. To reduce error during tracing of a particular region for area determination, attempts were made to follow only lines of muscular attachment visible on the surface of the bone. However, the curvature of the fossae of the scapula presents difficulties when area determination is attempted by any method which converts the three dimensionality of the surface into a two dimensional view (Figure 10). The image analysis method of area determination used in this study is not an exception. Despite attempts at insuring that a scapula's fossa lay in the horizontal plane, when the curved blade of the fossa is converted into a two-dimensional surface through image reproduction on the screen of the image

analyser, some part of the absolute area contained in the convexity of the fossa surface is lost.

It is therefore necessary to approach the results and reliability of the image analysis method of area determination with a great deal of caution and not consider it as an effective method for bone surface or muscle attachment area determination. Its effectiveness lies in its ability to act as an index of absolute size and relative size of the scapula when one examines interspecific and intraspecific variation.

Reliability of the area measurements was assessed by repeating the area determination of 10 scapulae. The absence of systematic error was confirmed by means of a paired t-test. The results obtained indicated that the value for any single repeated measurement did not differ significantly from the original value ($p < 0.05$).

3.8

Measurement of the Fossil Hominid Material

The method of linear measurement of the fossil specimens follows that described in this chapter for the measurement of modern material. However, in numerous cases where the described measurement cannot be completed because of damage to the fossil, yet the author felt that a reasonable estimate of the original measurement could be made, a "best guess" was recorded. These estimates, or "best guesses" , are indicated as such in the description of each fossil along with the actual measurement taken of the damaged region of the fossil specimen. The letter "c" in front of a measurement value indicates that there may be some imprecision involved in the measurement. In addition, linear measurements of important morphological features have been taken for completeness. All measurements in the fossil descriptions are expressed in millimetres unless otherwise stated.

3.9

The Qualitative Data

The non-metrical characters comprise primarily those for which no quantitative data are provided or for which quantitative measurement is beyond the scope of this investigation. Wherever possible the clearest and most precise comparative morphological terminology is used. However, in some cases where the use of comparative terminology is unwieldy the author has used common and easily visualised analogies.

3.10

The Dissections

The shoulder regions of seven specimens representing 2 of the taxa (humans and chimpanzees) examined in the present study were dissected in the Department of Anatomy and Human Biology, University of the Witwatersrand. Dissection procedures follow those described for humans in the fifth edition of *Man's Anatomy* (Tobias *et al.*, 1988), and for non-human

primates, those illustrated and described in *An Atlas of Primate Gross Anatomy* (Swindler and Wood, 1973) and those used by Ashton and Oxnard (1963).

3.11

Photography and Illustration

Black and white photographs of selected specimens which are held in foreign museums were taken to assist with identification of morphological features characteristic of the species that are not obtainable in South Africa. The plates of the fossil specimens were taken in the Department of Anatomy and Human Biology, University of the Witwatersrand by Mr. P.M. Faugust. Illustrations of the original fossil specimens were drawn to scale by Mr. P. Quinney and by the author.

Drawings of the casts of the fossil material were made by the author. Additional plates of the casts of the fossil specimens not available for original photography were made by Mr. P. Quinney

or by the author. All other illustrations, tables, plates etc. were made by the author.

3.12

Statistical Analysis

Statistical analysis was conducted on a Macintosh SE and a DOS compatible PC using the 1990 version of Abacus Concepts, StatView II statistical analysis software, as well as the 1992 version of CSS Statistica by StatSoft. Since the main goal of this study is to examine the normal morphology, function, and dimensions of the shoulder complex, it was decided to restrict the statistics used to those of a descriptive nature.

Chapter 4

The Arthrology and Movements of Extant Hominoid Shoulders

4.1 Introduction

The morphological differences observed between the scapulae, clavicles and humeri of primates are primarily related to variations in the performance demands placed upon the upper limb by differing locomotor behaviour (Miller, 1932; Ashton and Oxnard, 1963; Roberts, 1974; Oxnard et al., 1990). It is thus to be expected that the more similar the requirements of the locomotor behaviour in related groups of animals, the more similar will be the morphology and shape of the region.

Humans, and to a lesser extent apes, have freed their upper limbs from the demands of quadrupedal behaviour. Hence, apes and humans exhibit a far greater range of upper limb mobility than their truly quadrupedal cousins. The

exceptions to this rule are those prosimian primates (some leaping lemurs and tarsiers) that habitually practise the form of locomotion known as vertical clinging and leaping. In addition, the shoulders of some of the more acrobatic, arboreal New World monkeys exhibit a relatively high degree of freedom of movement (Erikson, 1963).

The greater mobility of the shoulder girdles of apes and humans is largely due to the scapulae of these groups being situated more on the dorsal aspect rather than on the sides of the rib cage (Schultz, 1947) (Figure 11). This positioning of the scapulae in the hominoids allows nearly the full range of motion at the glenohumeral joint to be achieved. In addition, certain osteological features of the scapula, such as the relatively round, wide and flattish glenoid cavity of humans and apes, compared to the elongated, narrow and more deeply concave glenoid cavities of monkeys, have been shown to give a greater range of mobility to the humeral head (see Chapter 6). However, this greater degree of freedom is

achieved at the cost of some structural stability.

The hominoid shoulder is a highly mobile complex operating in practically all three dimensions and it has the largest degree of freedom of movement of any osteo-dependent mechanism in the hominoid body (Inman *et al.*, 1944). The great mobility is due to the presence of no fewer than four joints, all of which are involved in the movements of the shoulder complex. These four joints are the glenohumeral joint (*articulatio (capitis) humeri*), the acromioclavicular joint (*articulatio acromioclavicularis*), the sternoclavicular joint (*articulatio sternoclavicularis*) and the scapulothoracic joint or scapulothoracic gliding mechanism. These joints work togeth r to provide the brachium with an almost 360 degree cone of movement (Figure 12).

The primary functions of the joint systems of the shoulder girdle are to furnish a platform, in the form of the glenohumeral joint, from which

the joint complex provides a field of motion for the lever in the system, the humerus. Most of the anatomical variation observed in the shoulder girdle of modern primate groups is due to morphological restrictions or freedoms granted to this field of motion. The restrictions and freedoms are a result of adaptations to differing forces placed on the complex in the performance of various locomotor activities. However, despite this, the variation in the anatomical configuration of the joints of the shoulder girdle between the different species of extant hominoids is minimal. This is surprising given the variability of upper limb locomotor behaviour that may be observed in this superfamily (see also Chapter 2).

Modern hominoids perform a variety of activities that require the upper limb to operate in three dimensions. Hominoids in particular are dependent on the ability to control precisely the movements of the arm, forearm, hand and fingers in the performance of many manipulative activities and locomotor behaviours. To

successfully perform a wide range of manipulative activities, accurate positioning of the hand in space is critical. Logically, the accurate positioning of the hand in space is highly dependent on the accurate positioning of the forearm and arm to which it is attached. Since the humerus acts as the lever in the shoulder complex, the ability to position the upper limb accurately is intimately linked to the range of motions allowed at the shoulder joint. Consequently, the degree to which some manipulative behaviours can be efficiently performed is also linked directly to the field of mobility allowed by the four primary joints of the shoulder girdle complex.

To allow this wide choice of potential movements, the whole of the shoulder girdle complex is suspended primarily by soft tissues that arise from the head, neck and thorax. Thus, anterosuperior support is through the highly mobile, but strong, sternoclavicular joint (see the discussion below). The cervical spine and occiput assist in suspension of the complex by

the upper trapezius, levator scapulae and sternocleidomastoid muscles.

Electromyographical (EMG) studies of human shoulders indicate that when the upper limb is in the anatomical position there is no electrical activity in the supporting muscles mentioned above (Bearn, 1961). Support is therefore provided by a combination of passive muscular restraint and by the tension in the sternoclavicular joint. Furthermore, the scapula is attached to and in essence hangs from the lateral end of the clavicle by the coracoclavicular ligament and the superior part of the capsule of the acromioclavicular joint.

Roberts (1974) has claimed that most quadrupedal animals rely substantially on the skeletal strength of the shoulder complex to provide stability since the humerus applies force directly to the superiorly positioned scapula (Figure 13). Thus quadrupeds utilise their limbs primarily in two dimensions, whereas hominoids use

their upper limbs in three dimensions. Therefore, to maintain the structural integrity of the joint, hominoids require additional muscular support to stabilise their shoulder joints (Larson and Stern, 1986).

Below may be found a discussion of the morphology of each of the four primary joints of the shoulder girdle of extant hominoid species. Later in this chapter the described morphology is related to locomotor oriented functions.

4.2 Arthrology

4.2.1 General

Joints are articulations which are formed when two or more bones are united by fibrous, elastic or cartilaginous tissue either alone or in combination. Three primary groups of joints are typically recognised and are named according to their characteristic structural features. These joint types are fibrous (*articulationes*

fibrosae), cartilaginous (*articulationes cartilagineae*) and synovial joints (*articulationes synoviales*). The present study is primarily concerned with the last group, which is the joint type most associated with movement.

4.2.1.1

Synovial Joints

Synovial joints are the commonest joints of the extremities and offer the greatest degree of movement. Synovial joints are generally characterised by five components: a joint cavity (*cavitas articularis*), a joint capsule (*capsula articularis*), synovial fluid (*synovia articularis*) and articular cartilage (*cartilago articularis*) and the bony surfaces that participate. The blood supply of synovial joints is provided by an arterial and venous network that usually originates from one or more parent trunks lying near the joint.

Lymphatic vessels also are present in synovial membrane and this accounts for the rapid removal

of proteins and substances invasive to the joint capsule (Bauer *et al.*, 1940; Gardner, 1950). Synovial joints are innervated by peripheral and muscular branches of nerves that cross or lie in the vicinity of the joint.

4.2.2

The Joints of the Hominoid Shoulder Girdle

There are typically three or four joints in the hominoid shoulder girdle: the glenohumeral joint, the acromioclavicular joint, the sternoclavicular joint, and the inconstant coracoclavicular joint. In addition, some authors suggest that the scapulothoracic gliding mechanism might be considered a *de facto* joint. The movements and morphologies of these structures will be discussed in detail in the following five sections.

4.2.2.1

The Glenohumeral Joint

The hominoid glenohumeral joint has been described as a ball and socket joint, but it is not as freely mobile as an ideal ball and socket joint would be. Rotation of the head of the humerus does not occur solely as rotation around a central axis since this would result in severe dislocation of the axis spatially. Rather, rotating movement takes place within the joint capsule, accompanied by inferior displacement (or gliding down) of the head of the humerus (the ball) within the glenoid cavity (the socket). Additional restrictions on freedom of movement occur as glenoid cavity breadth is reduced in relation to length, thus creating a glenoid cavity that is more pyriform in shape. This morphological situation is normally observed in the more terrestrial, quadrupedal primates and the reverse is true of the more acrobatic, arboreal forms (Inman et al., 1944). In addition, the humeral head itself restricts freedom of movement as it is not a complete sphere nor in most cases

is its contour perfectly spherical. Thus the humeral head of quadrupedal hominoids and those species that do not experience a wide range of movement is less spherical in shape, whereas, in apes and humans, groups that enjoy a higher degree of freedom of movement in the upper limb, the humeral head articular surface is more spherical. However, because of these morphological adaptations to increased mobility, skeletally the joint is weakest in apes and humans and these groups must rely primarily on surrounding muscles and ligaments for structural stability (Roberts, 1974; Larson and Stern, 1986). In contrast, the more terrestrial quadrupeds depend primarily on skeletal support in the joint for structural security with corresponding restraints on freedom of rotation in the shoulder girdle.

There are typically three degrees of freedom in the glenohumeral joint of the hominoids (Figure 14), but as has already been mentioned, they do not operate to the same degree as in a classic ball and socket joint (Fahlstrom, 1981). Skeletal restrictions in degrees of freedom in the

glenohumeral joint are only partially due to the shape of the glenoid cavity. The potential degree of freedom of this joint is also affected by other skeletal structures such as the protuberance of the lesser and greater tubercles at the head of the humerus, and the body and thorax, which prevent complete spherical adduction. The degree of freedom exhibited by the glenohumeral joint also depends on the morphology and shape of the proximal humerus and the shape of the glenoid fossa. The glenoid shape creates "end" or "locking" positions for the humeral tubercles. In addition, the length of the humerus and the shape of the thorax may affect freedom of movement. Thus a two-dimensional image of the range of motion of the glenohumeral joint, at least in humans, is more like one-half of a large circle with a distinct ovoid shape (Figure 12). In other non-human hominoids, and in any animal that possesses a glenohumeral joint, the degree of freedom of movement of the joint will also vary with several muscular and skeletal factors.

Kinematic studies on humans have shown that the humeral head is held precisely in the centre of the glenoid fossa except at extremes of movement (Howell *et al.*, 1988). Even at the most extreme ranges of movement, the humeral head remains within 1 mm of the centre of the glenoid cavity (Poppen *et al.*, 1976; Howell *et al.*, 1988). Thus, although the form of the glenohumeral joint does not match that of the traditional ball and socket joint, the mechanics of the joint are nearly identical to those of the more constrained ball and socket joint (Fahlstrom, 1981). More recent studies indicate that these precise ball and socket kinematics are provided by the constraining effect of the glenoid labrum which significantly deepens the socket of the glenoid cavity fossa (Howell and Galinet, 1989a,b).

The glenohumeral joint itself is surrounded by a fibrous capsule which attaches medially to the head of the scapula outside the glenoid labrum (*labrum glenoidale*). The glenoid labrum attaches on the actual articular surface of the glenoid cavity. While there is some debate on the role of

the glenoid labrum, it is generally agreed that the labrum is a fibrocartilaginous structure that provides additional depth to the glenoid cavity and thus increases the socket-like effect of the joint (Howell and Galinet, 1989a,b; Chadwick *et al.*, 1990). The glenoid labrum also encroaches onto the root of the coracoid process and it includes within its margins the superior attachment of the long head of the biceps muscle. Laterally it has strong attachments to the anatomical neck of the humerus except infero-medially where it descends onto the humeral shaft. In general, the labrum is structurally weak, but its architecture allows for an extremely wide range of movement and considerable distraction of the bones. Amongst modern hominoids the attachment area of the glenoid labrum forms a raised bony rim typically visible just inside the glenoid cavity margin (Figure 15). While the morphology of this attachment area varies to a considerable degree amongst hominoids, it can be generalised that larger, more heavily muscled animals possess a more pronounced attachment area.

The capsule of the glenohumeral joint is supported by the tendons of infraspinatus muscle and. the teres minor muscle posteriorly, supraspinatus muscle anteriorly, and the long head of triceps inferiorly. These tendons, excluding the long head of triceps, blend with the fibrous capsule to add additional active support and create what is known as the rotator cuff. The long bicipital tendon traverses the joint capsule in a synovial sheath and continues laterally into the intertubercular sulcus, attaching at the anatomical neck of the humerus. The entire mechanism acts as a barrier to guard against displacement of the humeral head during external rotation.

There are three glenohumeral ligaments (*ligamenta glenohumeralia*) which offer additional support and security to the fibrous capsule of the shoulder joint and these attach to the supercmedial edge of the glenoid margin. The superior glenohumeral ligament travels along the medial edge of the bicipital tendon and attaches laterally above the lesser tubercle of the

humerus. The middle glenohumeral ligament attaches to the inferior portion of the lesser tubercle, and the inferior extends to the lowest part of the anatomical neck of the humerus. The inferior glenohumeral ligament arises from the area of the infraglenoid tubercle, reinforcing the area between the origin of the long head of the triceps muscle and the subscapularis muscle, and attaches to the surgical neck of the humerus.

The coracohumeral ligament (*ligamentum coracohumerale*) arises medially from the lateral part of the base of the coracoid and passes laterally to insert into the greater tubercle of the humerus. It blends on its deep surface and posterior edge with the capsule of the joint and the tendon of the supraspinatus muscle. It is important in checking rotation of the humeral head and preventing downward subluxation of the head of the humerus (Steindler, 1955; Basmajian and Bazant, 1959).

A synovial membrane lines the capsule of the joint and covers most of the anatomical neck of

the humerus. Between the superior and middle ligaments is the opening for the superior subscapular bursa. Innervation of the joint is by branches of the circumflex, suprascapular and lateral thoracic nerves and occasionally from the stellate or other sympathetic ganglia (Gardner, 1950).

4.2.2.2

The Acromioclavicular Joint

The acromioclavicular joint is a synovial planar joint and is the articulation between the convex, oval facet on the acromial end of the clavicle and a concave area on the medial margin of the acromion process. These two articular surfaces create a joint line that is oblique and slightly curved. This curvature permits the acromion, and thus the scapula, to glide forward or backward over the lateral end of the clavicle, thus protecting against dislocation at the glenohumeral joint by keeping the glenoid fossa continually facing the humeral head. Forces transmitted through the forelimb will tend to

drive the acromion process under the lateral end of the clavicle. Stability in the region is not in the joint itself but in accessory soft tissues and ligaments that surround the joint (Hall, 1965).

The joint is surrounded by a fibrous capsule that completely encases the articular margins. Above the joint, intertwined with the trapezial and deltoid aponeuroses and extending between the acromion and lateral end of the clavicle, is the acromioclavicular ligament (*ligamentum acromioclaviculare*), which offers support to, and strengthens, the upper aspects of the fibrous capsule. The major ligamentous support structure of the joint is the coracoclavicular ligament (*ligamentum coracoclaviculare*) which binds the clavicle to the scapula. The coracoclavicular ligament can be divided into two components, the trapezoid (*ligamentum trapezoideum*) and conoid (*ligamentum conoideum*) ligaments. The coracoclavicular ligament is situated medial to, but separate from the acromioclavicular joint. It offers the most efficient means of soft tissue

support by preventing dislocation of the joint at the contact point of the clavicle and acromion (Salter *et al.*, 1990). The two major parts of the coracoclavicular ligament are functionally and anatomically distinct but they share a border. Anteriorly there is a space between the ligaments that is filled with fat and often, in man and the great apes, lodges a bursa. A second ligament, the coraco-acromial ligament, attaches to the anterior and inferior undersurfaces and near the articular facet of the acromion process. It forms a hood over the head of the humerus that may help prevent upward subluxation of the head of the humerus and it also appears to be a significant stabiliser of the joint (Hall, 1965).

The potential movements of the acromioclavicular joint are described relative to the position of the scapula or, in the case of movements of the scapula, to the dorsal thorax. In humans the freedom of movement is about 30 degrees (Kapandji, 1982), but any movement at the joint is combined with axial rotation of the clavicle (Inman *et al.*, 1944) (Figure 16). By

simultaneous rotation at the sternoclavicular joint, about 60 - 70 degrees of scapular rotation is allowed (Hall, 1965; Kapandji, 1982). The nature of this joint allows angulation of the scapula in almost any direction.

Spin, rotation and angulation all occur at the acromioclavicular joint. Extreme spin and angulation tense the coracoclavicular ligament while spin alone tightens the entire capsule through spiralization. Additional rotation at the acromioclavicular joint is allowed by rotation at the sternoclavicular joint (Steindler, 1955; also see below). The middle and proximal capsular structures that surround the acromioclavicular joint appear to restrain external rotation of the upper limb, the middle glenohumeral ligament acting as the main check of external rotation from 0° to 60° of abduction (Ferrari, 1990).

The acromioclavicular joint is extremely important in all movements of the shoulder girdle, not only because it transmits force between the clavicle and acromion process, but also because it

contributes to total arm movement (Steindler, 1955; Hall, 1965). The principal role of the acromioclavicular joint in more arboreal primates is to permit continued lateral rotation of the scapula after 100 degrees of abduction, at which point further acromioclavicular movement is restrained by the sternoclavicular ligaments (Kapandji, 1982; Peat, 1986). The two major movements of the acromioclavicular joint are a gliding movement as the shoulder joint flexes and extends, as well as an elevation and depression movement that conforms to changes in the positional relationship between the scapula and humerus during abduction (Frankel and Nordin, 1980, Peat, 1986). The joint is innervated by the suprascapular nerve.

4.2 2.3

The Sternoclavicular Joint

The sternoclavicular joint is a planar synovial articulation but its function most closely resembles that of a restricted ball and socket articulation. The articular surfaces lack

congruity and about half of the medial end of the clavicle typically protrudes above the shallow sternal socket. The sternal surface of the medial end of the clavicle has a small, superior non-articular region where an intra-articular disc attaches.

The sternal end of the clavicle is surrounded by a fibrous capsule with ligaments encasing the whole area. This capsular and ligamentous structure acts to strengthen the joint and bind the clavicle to the sternum, first rib and its costal cartilage. The articular disc (*discus articularis*), along with the costoclavicular ligament (*ligamentum costoclaviculare*), are the principal structures that stabilise the joint and resist medial displacement of the clavicle, thereby limiting the clavicular component of arm movement (Hall, 1965; Williams *et al.*, 1989).

The fibrocartilaginous articular disc is nearly circular and completely divides the joint space into two separate cavities. It attaches superiorly to the upper part of the sternal end of

the clavicle and passes inferiorly between the articular surfaces to attach at the first costal cartilage, being peripherally woven into the joint capsule. This mechanism allows the disc to act like a hinge, contributing to the total range of the joint's movement. The disc also acts to stabilise the joint when forces pass medially through the clavicle to the axial skeleton during upper limb movement.

The joint capsule which surrounds the sternal end of the clavicle is supported by the anterior and posterior sternoclavicular ligaments (*ligamentum sternoclaviculare anterius* and *ligamentum sternoclaviculare posterius* respectively) and two accessory ligaments: the interclavicular (*ligamentum interclaviculare*) and costoclavicular ligaments (*ligamentum costoclaviculare*). The sternoclavicular ligaments pass inferiorly and medially from the sternal end of the clavicle to the anterior and posterior aspects of the manubrium sterni.

The interclavicular ligament passes over the superior aspect of the sternoclavicular joint, joining the sternal ends of the two clavicles. It provides stability to the superior aspect of the joint (Steindler, 1955). The costoclavicular ligament is adjacent to and probably forms part of the sternoclavicular joint capsule (Cave, 1961). It is formed in two layers, anterior and posterior, which are separated by a bursa. Fibres from the anterior layer pass inferiorly and medially to the sternum. Fibres from the posterior layer pass inferiorly and laterally to the sternum.

Movement at the sternoclavicular joint allows for elevation and depression of the clavicle, as well as protraction and retraction of the clavicle (Peat, 1986). In addition, the joint allows for rotation of the clavicle around the axis of the shaft of the bone (Figure 16), as well as rotation about the fulcrum of the costoclavicular ligament in horizontal and vertical planes (Hall, 1965). The sternoclavicular joint is innervated by the

medial suprascapular nerve and the nerve to subclavius.

4.2.2.4

The Coracoclavicular Joint

When present as a rare anatomic variant, the coracoclavicular joint is a true synovial joint possessing a capsule, synovial-lined space and hyaline articular cartilage. When present, the joint lies between facets of the superior surface of the coracoid and the inferior surface of the clavicle close to the lateral end of the groove for subclavius (Figure 16). If present, the joint facets may be difficult to identify in skeletal material, but there is often a bony protuberance (conoid tubercle) which extends from the clavicle towards the coracoid. However, absence of this conoid tubercle does not preclude the existence of a true joint, nor is it known whether the presence of a rudimentary conoid tubercle indicates the presence of a true joint (Cockshot, 1979).

The coracoclavicular joint has been often overlooked in both standard anatomical texts as well as more specialised scientific literature. As noted by Gruber as early as 1861, this neglect is due to the difficulty in assessing the joint area on dry bone and also to the rarity of the joint. In addition, the area where the joint typically occurs is often divided by a bursa that, when accompanied by metaplasia of the trapezoid ligament to fibrocartilage, may simulate a true joint (Jaltvka, 1957; Lewis, 1959; Cockshot, 1958, 1979).

The reported occurrence of the coracoclavicular joint in human subjects depends greatly on whether the study was conducted by dissection, radiological methods, or osteological studies, dissection being the only certain way to identify the presence of a true joint (Table 3). Both the radiological studies and the osteological studies mentioned below generally record the presence of a coracoclavicular joint when a "pronounced" conoid tubercle (pronounced = roughly + 2.0 mm) is observed. In six studies utilising

bilateral dissections of shoulders in a variety of human populations, presence of the joint was recorded in approximately 13.0 % of all shoulders, with a recorded range of observed occurrence amongst all human populations of 2.6 - 33.0 %, (n = 610) (Gruber, 1861; Poirier, 1890; Schlyvitch, 1937; Abe, 1964; Pillay, 1967; Fischer *et al.*, 1971). In radiological studies of the human shoulder conducted from chest films, the recorded occurrence frequency of the joint based on twelve studies of various populations world-wide was approximately 3.0 % of all shoulders with a recorded range of 0.04 - 21.0 %; (n = 26,161) (Ponde and Silveira, 1938; Nutter, 1941; Wertheimer, 1948; Moore and Renner, 1957; Cockshot, 1958, 1979; Jaluvka, 1959; Pillay, 1967; Oikawa and Hatafuku, 1970; Fischer, 1971). In seven osteological studies of the human clavicle a pronounced coracoid process, possibly indicating the presence of a true joint, was noted in approximately 4.0 % of the human population with a recorded range of 0.3 - 9.9 % . In the present study the presence of a pronounced coracoid process was recorded in approximately 12.0 % of

all chimpanzee and gorilla clavicles and 16.0 % of all orang-utan clavicles.

Most authors feel that the presence of this joint offers no extra stability to the shoulder, nor does it appear to create any restriction of movement in the shoulder (Cockshot, 1979). However, Sarrafian (1983) has linked the presence of the joint to the lateral stability of the clavicle, since he assumes that the joint must in part add a component of dislocation resistance.

4.2.2.5

The Scapulothoracic "Joint" or Scapular Gliding Mechanism

There is some debate whether the scapular gliding mechanism should be regarded as a joint or whether it should simply be seen as the riding of the anterior surface of the scapula on the posterolateral surface of the thoracic cage (Peat, 1986; Williams *et al.*, 1989). It certainly does not meet the definition of a classic joint.

The scapula is without any ligamentous attachments to the thorax. The thorax is separated from the scapula by the subscapularis and serratus anterior muscles, which contact and glide over each other during movement of the scapula. The scapula is thus permitted a wide range of movement during movements of the shoulder. These movements include protraction, retraction, elevation, depression, and rotation, all around a variable axis, perpendicular to its flat surface (Frankel and Nordin, 1980; Williams *et al.*, 1989).

4.3

Summary

The modern hominoid shoulder girdle is characterised by the presence of three or four synovial joints and the scapulothoracic gliding mechanism. These structures allow the three bones of the girdle an extremely wide range of movement.

The morphological variation of the joint structures and variation in the potential range of

movement of the shoulder girdle among modern species of hominoids is surprisingly limited. However, in general the more arboreal hominoids possess relatively more gracile joint structures that trade some strength for added flexibility. The more terrestrial hominoids exhibit more robust joint structures that reduce overall flexibility but provide considerably greater strength.

Chapter 5

The Myology of the Extant Hominoid Shoulder

5.1 The Muscles and Muscular Forces

5.1.1 Introduction

The muscular system is composed of contractile units of varied morphology that are energised by voluntary and involuntary electrical impulses from the nerves. The smallest functional cell unit of the muscular system is the muscle fibre. These muscle fibres are typically classified into three types: smooth, cardiac and striated and the present study is concerned only with the last.

The actions of many shoulder girdle muscles in non-human hominoids have not been sufficiently studied. The present investigation relies mainly on the reported actions of muscles based on electromyographical (EMG) studies conducted on human and ape subjects as well as on kinematic

studies of muscular actions where these are available.

This chapter is a compendium of the results of EMG and kinematic studies that have been conducted on the actions of the muscles of the shoulder girdle in hominoids. It also includes a brief description of the anatomy of, and variation observed in, the musculature of the extant hominoid shoulder girdle region. The results of this study provide a framework from which to build a model of the soft tissues of the fossil hominid shoulder girdle.

Twenty-one skeletal muscles that are primarily responsible for the movements of the hominoid shoulder girdle exhibit muscle markings on the bones of the shoulder girdle at their areas of origin and insertion, since only those muscles that leave discernible muscular markings on bones may be studied in fossil specimens. To simplify reading, a description of each muscle is given and variations among the hominoid species are discussed. Finally, the muscle's actions,

including variations in actions, are described. It should be noted that the general descriptions are of the human condition. While some of the following information was obtained from dissections of human and ape cadavers conducted during the present study, most of the information presented is derived from the literature. Figures 17 - 28 illustrate the muscle attachments on the bones of the shoulder girdles of the extant hominoids that are discussed in the text.

5.1.2

The deltoid muscle (*M. deltoideus*)

5.1.2.1

General

The deltoid muscle is a thick triangular muscle that has its origins on the caudal aspect of the scapular spine, the most lateral aspect and upper surface of the acromion process and the ventrolateral one-third to one-quarter of the clavicle. It descends inferolaterally to attach along the shaft of the humerus creating the

prominent deltoid tuberosity. It is multipennate and is comprised of three divisions: the anterior head (*pars clavicularis*), which take a fleshy origin from the attachment area on the clavicle; the middle head (*pars acromialis*), which arises via several tendons from the lateral attachment on the acromion process and the aponeurosis which overlies this region of the muscle, and the posterior head (*pars spinalis*), which takes a fleshy origin along the caudal edge of the scapular spine. The middle head inserts by a short tendon into the distal part of the deltoid tuberosity. The anterior and posterior heads converge to insert by tendinous fibres on the ventral and dorsal aspects of the deltoid tuberosity, at the sides of the attachment of pars acromialis.

5.1.2.2

Variation

The deltoid muscle reaches its largest relative size in the hylobatids (Ashton and Oxnard, 1963). The great apes have deltoid

muscles which are almost as large as those of the hylobatids, whilst humans exhibit the relatively smallest deltoid muscles amongst hominoids (Ashton and Oxnard, 1963). Within the ape group, the insertion of the deltoid muscle into the humerus usually occurs about one third of the way down the humeral shaft. Its insertion may be identified as the deltoid tuberosity. In humans, insertion on the humerus occurs as in the apes.

Ashton and Oxnard (1963) report that separation of the deltoid heads by fibrous raphes is consistently found among all the anthropoid apes. Separation of the heads by fibrous raphes was found in the two chimpanzee specimens dissected by the author.

Extensive variation has been observed among the hominoid species in the origin of the pars clavicularis of the deltoid muscle. In chimpanzees and gorillas the pars clavicularis consistently arises from the lateral third of the clavicle as in humans (Raven, 1950; Ashton and Oxnard, 1963, Swindler and Wood, 1973). In

orang-utans the origin tends to extend over the lateral half of the clavicle (Sonntag, 1923, 1924; Ashton and Oxnard, 1963). In modern humans the anterior head arises as in the African apes (Williams *et al.*, 1989; Tobias, *et al.*, 1938).

5.1.2.3

Actions

All recent EMG studies of the deltoid indicate that, when one examines the activity of the muscle, it must be considered as three separate parts (Tuttle and Basmajian, 1978a,b; Basmajian and de Luca, 1985; Larson and Stern, 1986). EMG studies on chimpanzees indicate that the anterior deltoid is most active during movements that involve flexion of the upper limb, such as cross-body or forward reaches, climbing and arm-swinging (Larson and Stern, 1986, p. 177, see also Chapter 2, this study). Activity increases as the hand is supinated during these movements (Inman *et al.*, 1944; Basmajian and de Luca, 1985), whereas during active pronation the anterior deltoid is in the "null" electrical position in

cross-body or forward reaches (Larson and Stern, 1986, p. 177). However, in orang-utans, the activity level of the anterior deltoid is low during all reaching activities (Tuttle and Basmajian, 1978a,b). The anterior deltoid in humans and apes is reported to assist in rotary torque and support of the arm (Larson and Stern, 1986). In apes, the muscle has been shown to assist in the downward swing of the arm during pendular arm-swinging (Larson and Stern, 1986). Pendular arm-swinging has been defined by Larson and Stern (1986) as a rapid form of suspensory locomotion where the body is suspended from a nearly vertical supporting upper limb. During locomotion, the swinging limb is swept downward and then upward in an arc, and the trunk behaves much like a pendulum hanging beneath the supporting hand.

The middle deltoid is recognised as a powerful abductor. When acting alone its line of pull abducts the arm in the plane of the scapula. It is reportedly active in all voluntary reaches and its activity has been shown to be unaffected by

pronation or supination (Larson and Stern, 1985; Basmajian and De Luca, 1985). In addition, activity is recorded in the middle deltoid during all arm-swinging behaviour (Larson and Stern, 1985, 1986). These arm-swinging behaviours include nonpendular forms that differ from pendular arm-swinging in that the body pivots approximately 180° around the axis of a nearly vertical supporting arm (Larson and Stern, 1985).

Amongst chimpanzees, the posterior deltoid exhibits no activity during elevation of the forelimb (Larson and Stern, 1986, p. 177). In contrast, during experiments conducted on orang-utans and humans, Tuttle and Basmajian (1978) have recorded high levels of activity in the posterior deltoid during elevation of the forelimb. The posterior deltoid is also active during the second half of the support phase of pendular arm-swinging, when it adds propulsive power (by retraction and adduction of the humerus) and during the first half of the swing phase during lowering of the forelimb (Larson and Stern, 1986).

5.1.2.4

Innervation

Innervation of the deltoid muscle is by the axillary nerve.

5.1.3

The Biceps Muscle (*M. biceps brachii*)

5.1.3.1

General

The biceps muscle arises from the scapula by long (*caput longum*) and snoi. (*caput breve*) heads. The long head of biceps arises from the supraglenoid tubercle. Its tendon runs across the superior part of the humeral head and emerges from the shoulder joint capsule through the intertubercular groove where it is held in place by the transverse humeral ligament and part of the tendon of insertion of the pectoralis major muscle. The short head of biceps arises with coracobrachialis from the lateral aspect of the coracoid process. Its fibres descend to fuse

with the long head of biceps in the area around the distal one-third of the humerus. The muscle passes deep and forms a short tendon that inserts into the posterior part of the radial tuberosity on the radius. Medially the biceps tendon gives off the bicipital aponeurosis (*aponeurosis musculi bicipitis brachii*) which blends with the antebrachial deep fascia. Through a thickened part of the deep fascia of the forearm, the insertion of biceps is extended into the posterior border of the ulna.

5.1.3.2

Variation

In approximately eighty adult human cadavers dissected at the University of the Witwatersrand Medical School in 1992, Professor J.C. Allan observed bilateral bicipital aponeuroses in 100% of the specimens (Prof. J.C. Allan, pers. comm.). In addition, bilateral bicipital aponeuroses were observed in the two chimpanzees dissected by the author. In gibbons the short head of biceps commonly arises from the superior part of the

humerus and almost immediately fuses with the long head (Miller, 1932). There is no reported variation in this muscle amongst other hominoids.

5.1.3.3

Actions

The biceps muscle is a powerful flexor and supinator of the forearm and both heads are active in flexion of the shoulder joint (Basmajian and Latif, 1957). The short head of biceps, in combination with coracobrachialis, is a flexor of the whole shoulder joint. The long head of biceps assists in holding the head of the humerus against the glenoid cavity thereby resisting dislocating forces.

5.1.3.4

Innervation

Innervation of the biceps brachii muscle is from the musculocutaneous nerve.

5.1.4

The supraspinatus muscle (*M. supraspinatus*)

5.1.4.1

General

The supraspinatus muscle originates from the medial two thirds of the supraspinous fossa of the scapula. Its area of origin includes the region of the suprascapular notch where some of its fibres arise from the fascia covering the subscapularis muscle. The fibres of the supraspinatus muscle travel laterally to converge on a tendon adhering to the capsule of the shoulder joint, this tendon inserting into the most superior part of the greater tubercle.

5.1.4.2

Variation

There is little reported variation in the morphology of this muscle among the hominoid species and no variation from the above was observed in this author's dissections. However,

Miller (1932) reports that orang-utans exhibit relatively narrower supraspinatus muscles than in other hominoid groups.

5.1.4.3

Actions

With the deltoid muscle, the supraspinatus muscle is a powerful abductor of the arm. It also assists in keeping the head of the humerus in position, preventing it from being pulled upwards against the acromion process and deltoid muscle.

EMG studies of the supraspinatus muscle in chimpanzees and orang-utans (Tuttle and Basmajian, 1978a; Larson and Stern, 1986) indicate that the supraspinatus is active at the beginning of almost all reaches, activity that decreases as the reach progresses. This holds true for all reaches save for posterolateral reaches where there is no reduction of the supraspinatus muscle's activity level. Correspondingly, activity

increases after completion of the reach as the forelimb begins its return to the "null" electrical position. In addition, the supraspinatus muscle is active during arm-swinging and is particularly involved in the beginning of brachial elevation, before the release of the hand (Larson and Stern, 1986, p. 182). This activity decreases after the middle of the swing phase.

5.1.4.4

Innervation

Innervation of the supraspinatus muscle is by the suprascapular nerve.

5.1.5

The infraspinatus muscle (*M. infraspinatus*)

5.1.5.1

General

The infraspinatus muscle originates from the medial two-thirds of the infraspinous fossa. It passes superiorly and laterally to insert on

the middle facet of the greater tubercle of the humerus.

5.1.5.2

Variation

In humans this muscle reaches its greatest width relative to its length (Miller, 1932). There is fusion of the muscle's fibres with the teres minor muscle (Williams *et al*., 1989). This infraspinatus/teres minor combination passes into a tendon that inserts distally on the greater tubercle of the humerus. Besides this variation observed in humans, there is little reported variation in the anatomy of infraspinatus among the hominoid species. No variation from the hominoid pattern was noted during the dissections conducted by the author.

5.1.5.3

Actions

The primary function of the infraspinatus muscle is to assist the teres minor muscle in

rotating the arm laterally. The muscle is also important in keeping the head of the humerus in place during abduction.

EMG studies of the chimpanzee infraspinatus muscle by Larson and Stern (1986, p. 178) establish that this muscle is active in all reaches and is also an important stabiliser of the glenohumeral joint. Its activity level progressively increases through the middle of each reach, while it is lowest during posterolateral reaches. In addition, infraspinatus is highly active during arm-swinging behaviour as a supporting muscle and it exhibits increasing activity through the middle of the swing (Larson and Stern, 1986, p. 182).

5.1.5.4

Innervation

Innervation of the infraspinatus muscle is from the suprascapular nerve.

5.1.6

The teres major muscle (*M. teres major*)

5.1.6.1

General

The teres major muscle has its origin on the dorsal surface of the scapula. It arises as fleshy fibres from the inferior angle and by tendinous fibres superiorly along the lateral margin of the scapula. Both sets of fibres pass craniolaterally in front of the humerus to insert along the entire crest of the lesser tubercle (medial lip of the intertubercular groove) of the humerus. Insertion begins just below the distal limit of the insertion of the subscapularis muscle. The middle third of the insertion lies medial to the attachment of the latissimus dorsi muscle to the intertubercular groove of the humerus.

5.1.6.2

Variation

The morphology of this muscle differs little among the hominoid groups. However, the great apes typically possess a much reduced area of attachment for the fleshy origin, while the tendinous attachment tends to be positioned higher on the lateral margin of the scapula than is seen in humans. In humans the area of fleshy attachment is somewhat enlarged compared to that of the apes. In contrast, the length of the tendinous insertion along the lateral margin of the scapula is much reduced in humans. The muscle mass is usually less strongly developed in humans compared to the condition in the apes (Miller, 1932).

Ashton and Oxnard (1963) report that in several specimens of the Pongidae examined in their study, fleshy fibres are received from the latissimus dorsi muscle near the insertion on the humerus. No additional fleshy fibres were noted in the chimpanzees dissected by the author. The

lower edges of the tendons of the teres major and latissimus dorsi muscles are commonly fused in humans (Miller, 1932; Ashton and Oxnard, 1963; Williams *et al.*, 1989; present investigation).

5.1.6.3

Actions

The teres major muscle is mildly active during almost all movements of the upper limb, but is vigorously active only when assisting in maintaining the static position of the shoulder under stress, or when the shoulder is in positions of active resistance (Kamon, 1966; Basmajian and De Luca, 1985). Larson and Stern (1986) report that in chimpanzees, the teres major muscle is inactive during all voluntary reaches, but it is important in assisting the active lowering of the forelimb during the first half of the swing phase in pendular arm-swinging. In both chimpanzees and gibbons, the teres major muscle is involved in providing propulsive power during the second half

of the support phase in pendular arm-swinging (Jungers and Stern, 1983; Larson and Stern, 1986).

5.1.6.4

Innervation

Innervation of the teres major muscle is by the lower subscapular nerve.

5.1.7

The teres minor muscle (*M. teres minor*)

5.1.7.1

General

In humans the teres minor muscle has its origin on a flat strip along the superior two thirds to one-half of the axillary margin of the scapular dorsum. It also arises from an aponeurotic lamina separating it from the infraspinatus and teres major muscles. At its origin, it is often pierced by the circumflex vessels that traverse the groove in the lateral border of the scapula. It ascends laterally. Its

more superior fibres end in a tendon that is first adherent to the capsule of the shoulder joint and then inserts into the lowest facet on the greater tubercle of the humerus. Its inferior fibres insert into the shaft of the humerus immediately distal to the greater tubercle and lateral to the proximal end of the origin of the lateral head of triceps.

5.1.7.2

Variation

Little variation is reported in the morphology of this muscle among the various non-human hominoid groups and none was noted in the dissections conducted during the present investigation. However, in humans the teres minor muscle attains its greatest extent of scapular origin (Miller, 1932). In this species it is often fused with the infraspinatus muscle.

5.1.7.3

Actions

The teres minor muscle acts in conjunction with the subscapularis and infraspinatus muscles as the inferior part of the force couple that abducts the humerus (Inman *et al.*, 1944). The EMG studies of the teres minor muscle of the chimpanzee by Larson and Stern (1986) ard of the orang-utan by Tuttle and Basmajian (1978a), indicate that the teres minor muscle is inactive during all voluntary arm raising behaviours, but is active during rotation and adduction. Low levels of activity in the teres minor muscle were reported in chimpanzees during reaches which involve lateral rotation of the flexed arm. However, the EMG activity is nullified if there is active pronation during this movement (Larson and Stern, 1986, p. 178).

The observed participation of the teres minor muscle in rotation and adduction is supported by the recording of a sharp increase in activity just before the chimpanzee grasps the support at

the end of the swing. It assists in adding propulsive power to the second phase of pendular arm-swinging in chimpanzees (Larson and Stern, 1986).

5.1.7.4

Innervation

Innervation of the teres minor muscle is by the axillary nerve.

5.1.8

The subscapularis muscle (*M. subscapularis*)

5.1.8.1

General

The subscapularis muscle has its origin in the subscapular fossa. Its fibres travel laterally and converge into a single tendon that adheres to the medial part of the capsule of the glenohumeral joint and inserts into the lesser tubercle of the humerus and its crest.

5.1.8.2

Variation

Little variation has been observed in the anatomy of the subscapularis muscle among the Hominoidea. One exception is that in humans, the muscle attains its greatest scapular attachment (Miller, 1932).

5.1.8.3

Actions

Subscapularis assists the infraspinatus and teres minor muscles to act as the inferior force couple during abduction of the humerus (Inman *et al.*, 1944). Tuttle and Basmajian (1978a,b) report that in orang-utans, the onset and increase of muscle activity in subscapularis occurs during reaching activities that involve medial rotation at the shoulder. In chimpanzees, Larson and Stern (1986) report that subscapularis acts as a powerful medial rotator of the arm during climbing.

The subscapularis muscle has been divided into upper, middle and lower portions by Larson and Stern (1986) in their EMG studies of the chimpanzee shoulder. The upper portion is active in all reaches except those which involve extreme lateral rotation of the forelimb. Activity does not begin until the middle of the reach and decreases with active pronation or supination during the reach. The middle portion is only minimally active during the end of a reaching behaviour, most likely as a result of medial rotation of the arm that occurs at the end of each reach. Activity levels increase if marked pronation is involved during the reaching behaviour. The lower portion of the subscapularis muscle is inactive during reaching but is active during marked pronation (Larson and Stern, 1986).

5.1.8.4

Innervation

Innervation of the subscapularis muscle is by the subscapular nerve.

5.1.9

The trapezius muscle (*M. trapezius*)

5.1.9.1

General

The trapezius muscle is a large, triangular muscle originating from the ligamentum nuchae, the spines of the seventh cervical and all the thoracic vertebrae and the ligamenta supraspinalia. The most cranial fibres run caudolaterally to attach to the lateral end of the clavicle and the superolateral aspect of the acromion. The intermediate fibres run laterally from the vertebral column and insert into the acromion and along the cranial border of the scapular spine. The most caudal fibres run cranially, becoming continuous with a short aponeurosis that inserts into a large tubercle. The tubercle is located near the medial end of the caudal lip of the scapular spine.

5.1.9.2

Variation

Most of the variation in morphology of trapezius observed between the hominoid species occurs in the relative thickness of the muscle as well as in the direction of the muscle fibres. In humans the cranial part of the muscle is no thicker than the caudal part and some of the more cranial fibres attach to the lateral end of the clavicle. In the great apes the cranial part of the muscle reaches its largest relative proportions and its fibres pass laterally to the intermediate and lateral parts of the clavicle, acromion and the lateral part of the scapular spine. In apes the clavicular attachment is heavier and wider than in humans. The variations in orientation of the muscle fibres are due to differences in the position of the scapulae among the various hominoid species (Miller, 1932; Ashton and Oxnard, 1963; see also Chapter 4, this volume). There is rarely a nuchal origin for this muscle in *Pan* (Swindler and Wood, 1973). However, the origin of the muscle sheet does not

often extend to the last thoracic vertebra (Miller, 1932). In gibbons, the muscle commonly has only a slight occipital origin (Miller 1933).

5.1.9.3

Actions

The trapezius muscle is active during elevation and retraction of the shoulder and during flexion and abduction of the humerus. It also assists in raising the arm by preventing downward dislocation of the humerus (Yamshon and Bierman, 1948). The trapezius is in a null electrical condition when the shoulder girdle is in a relaxed upright posture and thus does not actively assist in support in this position (Fernando - Ballesteros et al., 1964).

5.1.9.4

Innervation

Innervation of the trapezius muscle is by the spinal accessory nerve. In humans, and most

probably in apes, it may receive additional innervation by branches out of the cervical plexus (C3 and C4 in humans) (Gardner *et al.*, 1969).

5.1.10

The serratus anterior muscle

(*M. serratus anterior*; *M. serratus magnus*)

5.1.10.1

General

The serratus anterior muscle typically originates from the anterolateral part of the upper eight ribs. Its fibres pass dorsally and inferomedially to insert into the medial margin of the scapula.

5.1.10.2

Variation

In non-human hominoids the serratus anterior muscle is often found to be indistinguishable from the levator scapulae muscle. When these muscles

are found fused the combined muscle is often referred to as *M. serratus magnus*.

5.1.10.3

Actions

The serratus anterior muscle acts both to passively support and to actively protract the scapula holding it against the ribs. It assists in elevation of the scapula and acts as the upper component of a force couple that consists of the rhomboids and the trapezius muscle. This force couple acts to rotate the scapula (Inman *et al.*, 1944). It assists trapezius during flexion by pulling the scapula forward.

5.1.10.4

Innervation

Innervation of the serratus anterior muscle is from the long thoracic nerve.

5.1.11

The levator scapulae muscle (*M. levator scapulae*)

5.1.11.1

General

The levator scapulae muscle originates from the transverse processes of the first four cervical vertebrae. It inserts into the scapula between the superior angle and the root of the scapular spine.

5.1.11.2

Variation

The extent of origin from the cervical vertebrae varies considerably among hominoid species. In orang-utans the origin of levator scapulae is most commonly observed on the mastoid process although slips arise from the cervical vertebrae (Ashton and Oxnard, 1963).

5.1.11.3

Actions

Levator scapulae assists in elevation and medial rotation of the scapula.

5.1.11.4

Innervation

Innervation of levator scapulae is by the dorsal scapular and third and fourth cervical nerves.

5.1.12

The rhomboid muscles

(*M. rhombr.idei*)

5.1.12.1

General

In effect, the rhomboids constitute a single muscle which in action may be divided into major and minor parts. It exhibits considerable inter- and intra-generic variation in morphology.

Rhomboid minor is the upper slip. The rhomboids originate from the ligamentum nuchae, the spine of the seventh cervical vertebra, the first thoracic spines, the third and fourth cervical posterior tubercles, and the associated ligamenta supraspinalia. Their fibres pass caudolaterally to insert along the medial border of the scapula. The insertion extends from the triangular smooth surface at the medial end of the scapular spine (rhomboid minor) to the inferior angle. The insertion lies just dorsal to the insertion of the serratus anterior muscle. At its insertion it often presents a "double fold" or asymmetrical U-shaped attachment that has both dorsal and ventral layers. Above, these layers enclose the inferior border of the levator scapulae muscle in humans.

5.1.12.2

Variation

In humans the rhomboideus major and rhomboideus minor muscles are usually separate but the muscles may overlap and may be continuous.

In humans, rhomboid major occasionally inserts into a tendinous arch attached to the medial border of the scapula. It may also insert into the inferior angle of the scapula (Gardner *et al.*, 1969). With the exception of orang-utans, rhomboid minor is found in apes to originate from the middle of the ligamentum nuchae and often extends as an uninterrupted sheet to the fifth or sixth thoracic spines (Raven, 1950; Ashton and Oxnard, 1963; Swindler and Wood, 1973; present investigation). Variations observed in apes include division of the sheet into distinct cranial and caudal parts (Ashton and Oxnard 1963).

In orang-utans the cranial origin is usually at the ligamentum nuchae (Sarmiento, 1985). Numerous variations occur, including an occipital head taking origin from the external occipital protuberance and occasionally from the adjacent part of the superior nuchal line (Ashton and Oxnard, 1963). In gibbons the size of the muscle is much reduced and its parallel fibres run in a

generally transverse direction (Miller, 1932).

5.1.12.3

Actions

The rhomboids, acting with levator scapulae, assist in controlling the position and movements of the scapula. The rhomboids also assist in retraction of the scapula. In combination with teres minor and levator scapulae, they assist in rotation of the scapula. With the trapezius muscle, levator scapulae assists in elevation of the scapula and in the bearing of weight on the shoulder (Tobias *et al.*, 1988; Williams *et al.*, 1989).

5.1.12.4

Innervation

The rhomboids are innervated by the dorsal scapular nerve and in humans by both the dorsal scapular nerve and the fifth cervical nerve.

5.1.13

The latissimus dorsi muscle (*M. latissimus dorsi*)

5.1.13.1

General

The latissimus dorsi muscle arises from the spines and the supraspinous ligaments of the mid to lower thoracic vertebrae (T5 to T12), the iliac crest and indirectly from the upper lumbar and sacral vertebrae through the fascia thoracolumbalis. It lies superficially as it passes cranially and laterally, spiralling around the lower part of the teres major muscle, to converge into a tendon that inserts into the floor (and medial lip) of the intertubercular sulcus.

5.1.13.2

Variation

In the apes, save for the gibbon, fibres may separate from the main mass near the tendon of insertion to insert into the medial lip of the intertubercular sulcus with the teres major

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Variation

In the apes, save for the gibbon, fibres may separate from the main mass near the tendon of insertion to insert into the medial lip of the intertubercular sulcus with the teres major

muscle (Miller, 1932; Ashton and Oxnard, 1963; Swindler and Wood, 1973; present investigation). In humans a slip may arise from the lower three or four ribs and a few fibres from the inferior angle of the scapula (Ashton and Oxnard, 1963; Gardner *et al.*, 1969; Williams *et al.*, 1989). In gibbons the muscle does not arise from the ilium but interdigitates laterally with the serratus anterior muscle (Miller, 1932).

5.1.13.3

Actions

The latissimus dorsi muscle assists pectoralis major in humeral adduction. It is also a powerful extensor and assists in medial rotation of the shoulder as well as being a powerful retractor of the arm (de Soura *& Vitti.*, 1966; Tuttle and Basmajian, 1977). It is particularly important in activities that require extension of the forearm such as are performed during bipedal walking (Basmajian and de Luca, 1985) or swimming (Gardner *et al.*, 1969). It is active in assisting to elevate the trunk in

climbing and may play a role in deep inspiration. Its inconstant scapular relationship may assist in stabilising the inferior angle by holding it against the chest (Gardner *et al.*, 1969).

5.1.13.4

Innervation

The latissimus dorsi muscle is innervated by the thoracodorsal nerve.

5.1.14

The coracobrachialis muscle (*M. coracobrachialis*)

5.1.14.1

General

The coracobrachialis muscle originates as a tendon on the apex of the coracoid process, in common with the short head of the biceps muscle. It passes inferiorly to insert into the medial border of the mid-shaft of the humerus between the triceps and brachialis muscles. Its insertion on

the shaft is approximately opposite the deltoid tuberosity.

5.1.14.2

Variation

In humans, additional slips may arise from the lesser tubercle of the humerus. It may have fibres attached to the medial epicondyle of the distal humerus or to the intermuscular septum of the humerus (Williams *et al.*, 1989). In gibbons the muscle inserts as only a single short, heavy muscle into the medial crest of the intertubercular groove (Miller, 1932). No variation is reported for this muscle in the other ape species and the two chimpanzees dissected by the author showed no departure from the pattern described above.

5.1.14.3

Actions

The coracobrachialis flexes the arm at the shoulder. Its anterior fibres also assist the deltoid muscle during abduction by stabilising the arm.

5.1.14.4

Innervation

The coracobrachialis muscle is innervated by the musculocutaneous nerve (Gardner *et al.*, 1969).

5.1.15

The subclavius muscle (*M. subclavius*)

5.1.15.1

General

The subclavius muscle originates as a tendon attached to the cranial border of the first rib near its costochondral junction. It inserts into

the inferior surface of the clavicle near the middle of the body.

5.1.15.2

Variation

In the apes the insertion of the subclavius muscle on the clavicle is positioned more laterally than in humans, while some fibres also attach to the ligamentum costocoracoideum (Ashton and Oxnard, 1963; Swindler and Wood, 1973; present investigation). In gibbons the origin the muscle extends over the 1st three ribs (Miller, 1932). In humans the muscle infrequently has fibres that insert into the coracoid process.

5.1.15.3

Actions

There have been few successful EMG studies on the actions of the subclavius muscle. However, in humans it appears that the subclavius muscle is involved in pulling the clavicle inferiorly and anteriorly. During movements of the shoulder it

acts to steady the clavicle against the sternoclavicular articular disc.

5.1.15.4

Innervation

The subclavius muscle is innervated by the nerve to subclavius.

5.1.16

The atlanto-clavicularis muscle

(*M. atlanto-clavicularis*)

5.1.16.1

General

The atlanto-clavicularis, also called omocervicalis (Miller, 1932), muscle arises from the spinous process of the atlas. It travels distally, often blending with the medial part of

the trapezius muscle, inserting into the lateral end of the clavicle adjacent to trapezius.

5.1.16.2

Variation

Atlanto-clavicularis is absent in humans but present in all other hominoids. It blends with and is almost indistinguishable from the trapezius muscle in chimpanzees (Miller, 1932). In apes, the muscle is usually positioned deep to the trapezius muscle. However, Ashton and Oxnard have cited the description of a single chimpanzee specimen where the muscle lay superficial to the trapezius muscle. Whilst a single orang-utan specimen was found to exhibit cranial fibres of the atlantoscapularis anterior muscle attached to the occiput.

In humans, atlantoclavicularis is usually absent. However, as noted by Ashton and Oxnard (1963), several authors have described subjects where the muscle was present in this species.

When observed in humans, it may not be considered homologous to the levator scapulae muscle (Ashton and Oxnard, 1963).

5.1.16.3

Actions

The atlanto-clavicularis muscle assists the trapezius muscle in elevating the clavicle.

5.1.16.4

Innervation

Innervation of the atlantoclavicularis muscle is from the anterior primary rami of the third and fourth cervical nerves (Ashton and Oxnard, 1963).

5.1.17

The omohyoid muscle (*M. omohyoideus*)

5.1.17.1

General

The omohyoid muscle originates on the superior border of the scapula around the scapular notch. It passes mediolaterally to insert into the ventrolateral aspect of the body of the hyoid bone. The omohyoid possesses an intermediate tendon lying deep to sternocleidomastoid that attaches to the back of the clavicle.

5.1.17.2

Variation

In the hylobatids the muscle is strap-like (Ashton and Oxnard, 1963). In the great apes and humans the muscle is comprised of two bellies and an intermediate tendon. However, an intermediate tendon has been reported to be frequently absent in chimpanzees, orang-utans and humans (Sonntag, 1923, 1924; Ashton and Oxnard, 1963; present

investigation). In the hylobatids and chimpanzees the muscle inserts into the middle of the superior border of the scapula (Ashton and Oxnard, 1963; Swindler and Wood, 1973; present investigation). Ashton and Oxnard (1963) regard the variations in morphology that have been observed to have little relation to differences in the modes of locomotion observed between the anthropoid apes and humans.

5.1.17.3

Actions

Due to its position, electromyographical studies of the omohyoid muscle are difficult. The omohyoid muscle may tense the lower deep cervical fascia and probably assists in depression of the chest in prolonged inspiratory efforts (Williams *et al.*, 1989). Tobias et al. (1988) suggest that the omohyoid probably assists in relieving pressure on the apices of the lung in the area of the neck.

5.1.17.4

Innervation

The omohyoid muscle is innervated by either the superior ramus of the ansa cervicalis nerve only or the ansa cervicalis nerve.

5.1.18

The pectoralis minor muscle (*M. pectoralis minor*)

5.1.18.1

General

The pectoralis minor muscle lies deep to, and is completely obscured by, the pectoralis major muscle. It originates from the outer surfaces of the 1st to 5th ribs near their costochondral junctions. It passes craniolaterally to insert into the coracoid process of the scapula.

5.1.18.2

Variation

Very occasionally the origin of the pectoralis minor muscle is from the 4th and 5th rib in apes (Ashton and Oxnard, 1963; Swindler and Wood,

1973). In humans the muscle inserts only into the coracoid process of the scapula and not into the capsule of the shoulder joint as in most of the anthropoid apes. However, in some human specimens an infrequent slip from this muscle inserts into the rim of the glenoid cavity of the scapula (Macalister, 1867).

5.1.18.3

Actions

The pectoralis minor muscle helps the serratus anterior muscle to draw the scapula anterolaterally around the thorax thus depressing the superior part of the shoulder. Acting with the levator scapulae and rhomboid muscles it rotates the scapula inferolaterally. To this author's knowledge, no EMG studies have been performed on the actions of this muscle.

5.1.18.4

Innervation

The pectoralis minor muscle is innervated by the medial pectoral nerve and by fibres derived from the lateral pectoral nerves (Gardner *et al.*, 1969).

5.1.19

The pectoralis major muscle (M. pectoralis major)

5.1.19.1

General

A superficial muscle which is large, multilaminar and triangular in shape. It originates on the ventral aspect of the thoracic cage, specifically from the medial one-half of the clavicle, the sternoclavicular joint area, the manubrium sterni, the second to seventh costal cartilages and from the aponeurosis of the external oblique muscle of the abdomen. Pectoralis major inserts, by a bilaminar tendon, into the lateral lip of the intertubercular sulcus.

5.1.19.2

Variation

With the exception of orang-utans, all of the large bodied hominoids possess a significant clavicular origin of pectoralis major (*pars clavicularis*). In the orang-utan, the clavicular origin of this muscle is usually absent. In humans the tendon often has extensions to the capsule of the shoulder joint and the fascia of the arm (Gardner *et al.*, 1969). In all the hominoid groups the direction of the fibres of this muscle is predominantly lateral.

5.1.19.3

Actions

The pectoralis major muscle assists in humeral adduction and medial rotation. It also assists the latissimus dorsi, teres major and deltoid muscles in drawing the trunk upwards and forwards during climbing behaviour (Inman *et al.*, 1944; de Sousa & *Vitti*, 1966). The actions of the

pectoralis major muscle have been studied extensively in *Hylobates* by Stern *et al.* (1980). These authors have demonstrated that in this genus, the pectoralis major muscle can be divided functionally into a cranial and a caudal part. The caudal part is fundamental in assisting flexion, adduction and retraction at the shoulder during locomotion. It also acts as a propulsive muscle during the support phase of the climb and during the pull-up. The cranial part is also involved in adduction and retraction of the forelimb. However, its retractive abilities disappear as the forearm is raised. It may act also as a "shock absorber" during touchdown from brachiation (Stern and Susman, 1981).

5.1.19.4

Innervation

The pectoralis major muscle is innervated by the medial and lateral pectoral nerves.

5.1.20

The triceps muscle (*M. triceps brachii*)

5.1.20.1

General

This is a large muscle that may be divided into three heads: the long (*caput longum*), lateral (*caput lateriale*) and medial (*caput mediale*). The long head originates from the infraglenoid tubercle. The lateral head originates from the upper part of the posterior and lateral aspects of the humeral shaft and the capsule of the shoulder joint. The medial head originates from the distal one-third to one-half of the humeral shaft. All three heads pass inferiorly and converge to insert into the upper surface of the olecranon process of the ulna and, by means of the tricipital aponeurosis, into the fascia of the forearm.

5.1.20.2

Variation

In non-human hominoids the origin of the long head of the muscle is from the superolateral

one-half of the axillary margin of the scapula. In humans the long head originates from the infraglenoid tubercle only. In all hominoids the lateral head originates from the posterior and lateral surfaces of the superior one-half of the humeral shaft. However, in humans, the origin is typically found more superiorly than in apes. In non-human hominoids, the origin of the medial head is usually more distally placed on the posterior surface of the shaft of the humerus. There is little reported variation in the insertion of this muscle among the hominoid species.

5.1.20.3

Actions

The triceps muscle is the major extensor of the forearm. The medial head shows some degree of EMG activity in all forms of extension. However, the medial and lateral heads in combination show only minimal activity except when resisting extension. This indicates that the medial head is the more active of the two (Basmajian and de Luca, 1985). The long head

assists in adduction of the humerus and provides support to the shoulder joint from below. During forceful supination of the forearm, the triceps muscle contracts synergistically to maintain semiflexion.

5.1.20.4

Innervation

The heads of the triceps muscle are innervated separately by branches of the radial nerve.

5.1.21

The Sternocleidomastoid Muscle

(*M. sternocleidomastoideus*)

5.1.21.1

General

The sternocleidomastoid muscle originates from the superior surface of the clavicle and as a tendon from the front of the manubrium sterni lateral to the jugular notch. It inserts into the lateral part of the mastoid process, and the

superior nuchal line. When the clavicular attachment area is visible, the superior surface near the sternal articular surface is usually only slightly more rugose than the surrounding areas.

5.1.21.2

Variation

In non-human hominoids the area of attachment of this muscle is strong and localised on the superior surface of the clavicle, often encroaching onto the sternal articular surface (Ashton and Oxnard, 1963; Swindler and Wood, 1973; present investigation). In humans, the attachment area of the sternocleidomastoid muscle is rarely discernible on the surface of the clavicle.

5.1.21.3

Action:

The sternocleidomastoid muscle plays only a mildly active role in abduction of the arm (Basmajian and de Luca, 1985) and its function is not well understood. It has been suggested that the function of this muscle is fundamental in level rotation of the head and in tilting of the head cranially towards the ipsilateral shoulder. Tobias *et al.*, (1988) have suggested that the two heads, acting together, extend the skull on the atlas thus producing flexion at the atlanto-occipital joint. The more pronounced and localised area of origin of this muscle in the clavicles of apes suggests to this author greater development, or stronger action of this muscle in non-human hominoids than in humans.

5.1.21.4

Innervation

The sternocleidomastoid muscle is innervated by the spinal accessory nerve and fibres from the second and third cervical nerves.

5.1.22

Pectoralis abdominis

5.1.22.1

General

Pectoralis abdominis is not found in humans. In apes, the muscle arises from the sheath of the rectus abdominis on the front of the rib cage and inserts into the crest of the greater tubercle of the humerus.

5.1.22.2

Variation

There is no reported variation amongst apes in the origin or insertion of this muscle.

5.1.22.3

Actions

The muscle acts as a flexor of the arm (Aiello and Dean, 1990).

5.3

Summary

The major myological differences between the shoulders of apes and humans lie in differences observed in the origins, insertions and actions of certain muscles. Many of these differences may be related to differences in locomotor behaviour but such a relationship remains to be shown. In addition, several muscles or muscle groups are either absent in modern humans but present in extant hominoids, or are separated into individual components in humans but are fused into muscle groups in apes. To simplify the recognition of these differences amongst ape shoulders and between ape and human shoulders, tables have been constructed (Tables 4 and 5). These tables are syntheses of morphological and functional differences in the myology of the shoulder girdle of the apes and humans which are seen by this author as important in interpreting the musculature of the shoulder girdle of fossil hominids. When not specifically indicated, the attachments found in *Homo sapiens* do not

significantly differ from those observed in non-human hominoid species.

One may note that there are only two additional muscles in the shoulder girdles of apes that are not found in the shoulders of modern humans, atlanto-clavicularis and pectoralis abdominis. The absence of atlantoclavicularis in humans is most probably related to the lateral rotation of the scapula on the thorax and the habitual carriage of the forelimbs in the lowered position. In contrast, in humans, the lower fibres of pectoralis major act to assist in flexion of the arm and have replaced pectoralis abdominis.

Several of the muscles examined in this chapter exhibit differences in origins and insertions of muscles. These variations in origins of selected muscles are contrasted in Table 4. Variations in insertions of selected muscles are contrasted in Table 5. These tables thus allow an easy assessment of the myological

differences among the ape species and between apes and humans.

Chapter 6

The Skeletal Elements of the Hominoid Shoulder Girdle

6.1 General

The vertebrate skeleton serves both for protection and support whilst also providing a leverage platform for muscular actions. In addition, the bones of the skeleton act as a storehouse for minerals and fat as well as sites for blood cell formation. In the living animal the skeleton is a dynamic structure that is constantly changing and actively metabolising. The skeleton can be altered in shape, size and position by mechanical or biomechanical demands. Bones respond to changes in vitamin, mineral and hormone levels and inherent in these changes are changes in the construction and mechanical function of the body.

The mammalian skeleton is well studied (e.g. Webster and Webster, 1974 etc.). More specific information about the primate skeleton and the bones which comprise it may be found in texts such as Hill (1953), Swindler and Wood (1973) and Williams *et al.* (1989) amongst many others.

Bones are generally classified by shape. The terms long bones, short bones, flat bones, sesamoid bones and irregular bones are readily understandable. Long bones occur typically only in the extremities. Short bones are found in the carpal and tarsal regions. Flat bones are found in the proximal limb areas and in the head and thorax. Sesamoid bones are formed in tendons and are usually found near freely moving joints. Irregular bones are those of the vertebral column, parts of the skull and the three parts of the pelvis. The bones of the shoulder region comprise two categories: long bones (humeri and claviculae) and flat bones (scapulae).

6.2

The Hominoid Scapula

(Figure 29)

The scapula is the large flat bone of the shoulder. It is the most plastic of the bones of the shoulder girdle being readily altered by muscular stresses during growth (Roberts, 1974; Doyle *et al*, 1980; Kimes *et al*., 1979, 1980). The scapula is comprised of three main parts: the body, the spine and the head. It may also be considered to have three angles (articular, superior and inferior), three borders (lateral, medial and superior) and two surfaces (dorsal and costal).

The body of the scapula in hominoids is a kite or fan shaped, flat, or slightly concavoconvex plate, which has dorsal and ventral surfaces (*facies posterior* and *facies costalis* respectively). The dorsal surface is divided into the supraspinous fossa (*fossa supraspinata*) and the infraspinous fossa (*fossa infraspinata*) by the spine of the scapula (*spina scapulae*).

The spine of the scapula is the most prominent feature on the dorsal surface. The spine, in its simplest form, is a flat plate lying approximately perpendicular to the blade. It acts as a strut for support of the acromion process on its lateral end and as a structural support for the whole of the body of the scapula and as an apophysis for muscle attachments. In the scapulae of hominoids the spine begins in an area approximately three-quarters of the total length of the scapula up from the inferior angle, on the medial border. On the medial border it begins as a smooth area which gradually becomes wider, thinner and more elevated as it courses laterally. It thus presents superior and inferior surfaces throughout most of its length. The dorsal border, or crest of the spine, is slightly thickened and often rolled inferiorly in heavily muscled individuals. The perpendicular arrangement of the planes of the blade and the spine imparts considerable mechanical advantage and rigidity to the structure in resisting forces associated with muscle contractions and in

withstanding the stresses associated with transmitting the body's weight to the upper limbs (Roberts, 1974; Doyle et al., 1980). Laterally on the spine, there is a widened truncate process known as the acromion. This part of the bone lies subcutaneously and is easily palpable in the living animal. The acromion provides attachment for several muscles and it articulates with the clavicle.

The costal surface of the body of the scapula is comprised of a single, continuous subscapular fossa. On the dorsal surface it is comprised of the supraspinous and infraspinous fossae. The supraspinous fossa is bounded by the superior surface of the scapular spine and the adjacent dorsal surface of the scapula. The thin plate of bone is often sinuous and in many cases fenestrated. The superior or cranial margin (*margo superior*) is often thickened and in heavily muscled individuals, rolled dorsally.

Lateral and adjacent to the supraspinous fossa is the scapular notch (*incisura scapulae*) which marks the position of the constricted part of the bone. The supraspinous fossa and superior margin undulate as they reflect the concavity of the subscapular fossa.

The infraspinous fossa is roughly triangular in shape. Its longest border is the axillary, or lateral, margin (*margo lateralis*) and its acutest angle is the inferior angle. The axillary margin and medial margin (*margo medialis*) are thickened, while the floor of the fossa is extremely thin and may be fenestrated. The axillary margin is the thickest of the three borders of the scapula. Just inferior to the glenoid cavity it bears the infraglenoid tubercle (*tuberculum infraglenoidale*). This tubercle is usually located somewhat anteriorly on the lateral margin and , in most hominoid species, is the largest tubercle on the scapula. Its shape and form vary to a considerable degree both within and between species. The lateral edge of the axillary margin is often concave. In the inferior

third of the axillary border a flat, inferolateral expansion of the lip that is created by the attachment of the teres major muscle, usually occurs.

The head of the scapula is considered to include the glenoid cavity (*cavitas glenoidalis*), neck of the scapula and the coracoid process (*processus coracoideus*). The head area is referred to as the articular or lateral angle of the scapula. Functionally, this area is the most important part of the bone since it includes the glenoid cavity. The glenoid cavity is relatively shallow, roughly ovoid to pyriform in shape and extends cranially into the supraglenoid tubercle (*tuberculum supraglenoidale*) and the root of the coracoid process.

The supraglenoid tubercle usually projects cranially and dorsally. From this tubercle arises the single tendon of the long head of the biceps brachii muscle. The somewhat enlarged coracoid process may be found immediately superior to the supraglenoid tubercle. It crosses medially and

anteriorly over the superior part of the glenoid cavity. This process is homologous with the coracoid bone (*os coracoideus*) which may still be found as a distinct entity in some monotremes (Webster and Webster, 1974). To the coracoid process attaches the conoid and trapezoid ligaments, the pectoralis minor muscle, the tendon of coracobrachialis and the short head of biceps brachii.

6.4

The Clavicle

(Figure 30)

In hominoids, the clavicle (*clavicula*) is an irregular, sigmoid long bone that acts as a strut between the manubrium and scapula. The clavicle articulates medially with the manubrium's clavicular facet and the first costal cartilage (*facies articularis sternalis*) and laterally with the medial aspect of the acromion process of the scapula (*facies articularis acromialis*).

The clavicle may be divided into a lateral extremity (*extremitas acromialis*), a body (*corpus claviculae*) and a medial extremity (*extremitas sternalis*). It may be considered to possess superior and inferior surfaces throughout, anterior and posterior borders laterally. The clavicle is unique in being the only long bone to ossify in membrane and this occurs in humans around the fifth week of intra-uterine life (Tobias *et al*., 1988; Williams *et al*., 1989). Very little data are available on this bone's time of ossification in non-human hominoids. The clavicle's shape is highly dependent on the soft tissues which surround and attach to its surface and its morphology can be readily altered by the forces exerted by these soft tissues (Roberts, 1974).

The superior surface of the clavicle exhibits parts of the attachment areas of the trapezius and deltoid muscles laterally and of the sternocleidomastoid muscle medially.

On the inferior surface, laterally there are visible the conoid tubercle (*tuberculum conoideum*), trapezoid line (*linea trapezoidea*) and a small part of the attachment area of the inferior part of the deltoid muscle. On the inferior surface of the body, the groove for subclavius (*sulcus musculi subclavii*) and area of attachment of the clavipectoral fascia are usually visible. Inferomedially, the attachment areas of the pectoralis major muscle, sternohyoid muscle and the costoclavicular (rhomboid) ligament may be seen (*impressio ligamenti costoclavicularis*).

On the anterior surface are the attachment areas for the deltoid muscle laterally and the pectoralis major muscle medially.

The posterior surface exhibits the superior part of the attachment area of the trapezius muscle. In the middle is the attachment line for the clavipectoral fascia. The area of attachment for the costoclavicular ligament and sternohyoid muscle may be observed medially.

6.3

The Humerus

(Figure 31)

The humerus is the most proximal long bone of the upper limb (brachium) and is the largest bone in the hominoid arm. Proximally it articulates with the scapula and together with this bone forms the glenohumeral joint. Distally it articulates with the radius and ulna to form the elbow joint.

Anatomically, it may be divided into a body, a head and a distal extremity. In the present study the proximal humerus is considered to be comprised of the head, neck and the shaft superior to the deltoid tuberosity.

The proximal end of the humerus includes the rounded head of the humerus (*caput humeri*). This area usually approximates a hemisphere. The centre of the articular head faces mostly posteromedially and superiorly. Despite being hemispherical, the articular surface does not form a perfect arc in any one plane. The remainder of

the head is comprised of the greater and lesser tubercles (*tuberculum majus* and *tuberculum minus* respectively) and the superior part of the intertubercular groove (*sulcus intertubercularis*). The greater tubercle of the humerus is a large craniolaterally positioned projection of the proximal extremity of the humerus. It has a smooth summit that rarely extends higher than the head. It usually exhibits three facets (superior, posterosuperior and posterior) which serve for the insertions of the supraspinatus, infraspinatus and teres minor muscles respectively.

The lesser tubercle of the humerus, as its name implies, is smaller than the greater tubercle in humans and this is also true in the other large bodied hominoids. It lies on the anterior part of the head of the humerus and usually exhibits some flattening along its anterior face. The superior border of the lesser tubercle rarely extends as high as the head. The two tubercles are separated from the articular head by a shallow groove called the anatomical neck (*collum anatomicum*) and are united to the body (or shaft)

of the humerus by the surgical neck (*collum chirurgicum*).

The greater and lesser tubercles are separated by the intertubercular groove. The intertubercular groove provides space for the bicipital tendon and its accompanying lubricating sheath (Tobias *et al.*, 1988). The intertubercular groove continues inferiorly on the surgical neck and body of the humerus but typically ends within the superior one third of the shaft. In its proximal and middle parts it is bounded by the medial and lateral crests of the tubercles.

The body or shaft is the long, straight to slightly curved part of the humerus that unites the two extremities. It is typically compressed posterolaterally and possesses anterior (*facies anterior*), posterior (*facies posterior*), and medial surfaces (*facies medialis*). At a proximal point, beginning near the junction of the anterior and posterior surfaces, the crest of the greater tubercle continues inferiorly in an uneven arc to become continuous with the anterior limb of the

deltoid tuberosity (*tuberositas deltoidea*) at the insertion of the deltoid muscle. The deltoid tuberosity is usually positioned approximately 1/3 to 1/2 of the way down the shaft. Proximally, on the anterior surface, a crest for the insertion of the teres minor muscle forms an edge of the intertubercular groove.

Marking the slightly convex, and relatively smooth, dorsal surface along almost its entire length is the usually faint musculospiral groove (*sulcus radialis*) (Hughes, 1952). Along its length, the musculospiral groove exhibits a cranial convexity. The musculospiral groove marks the passage down the shaft of the radial nerve.

6.5

The Comparative Morphology of the Bones of the Extant Hominoid Shoulder Girdle

6.5.1

The Scapula

6.5.1.1

The Articular Areas

The most prominent articular feature of the scapula is the glenoid cavity. The glenoid cavity forms most of the socket of a ball and socket joint and its shape in part defines the potential range of movement at the glenohumeral joint. In addition, as the direct link between the pectoral girdle and brachium, this contact is associated with the strength, stability and movement of the upper limb and it even plays an important role in manipulative behaviour in humans (see Chapter 4). One of the most frequently discussed areas of scapular glenoid morphology is the variation in scapular glenoid cavity shape among various species of extant

Hominoidea (Vallois, 1928; Stewart, 1962; Corruccini and Ciochon, 1976; Vrba, 1979; Churchill and Trinkaus, 1990).

The glenoid cavities of hominoids are not perfect hemispherical concavities. Rather, in non-human hominoids the glenoid cavity tends to be more ovoid to pyriform in shape, whilst in humans the glenoid cavity is typically pyriform to inverted-keyhole in shape (Figure 32). In the more quadrupedal Old World monkeys, the glenoid cavity is narrower and more elongate. It is not presently understood how much glenoid cavity shape influences the degree of freedom allowed at the joint. However, most authors agree that differences in glenoid shape may offer advantages and disadvantages in stabilising and in resisting external forces, whilst restricting the glenohumeral joint's potential range of movement (e.g., Fahlstrom, 1981; Churchill and Trinkaus, 1990; Chapter 4, this volume). Jolly (1966) has pointed out that the narrow glenoid cavities of the more terrestrial quadrupeds limit / anteroposterior motion. This is in contrast to the

more rounded glenoid cavities of hominoids, which provide a greater degree of freedom of movement in almost every direction.

In order to compare the roundness of the glenoid cavities exhibited by the different hominoid species, indices which reveal the relative proportions of bone parts have been found to be more useful than absolute metrical values. One of the most commonly used indices of the scapular head that has been found to be reliable is the glenoid index (glenoid cavity maximum breadth (x 100) / glenoid cavity maximum length). When calculated, a high glenoid index score (one that approaches 100) indicates that the glenoid cavity breadth is large relative to its length and thus this score indicates a more spherical (or hemispherical) glenoid shape. Conversely, a low glenoid index score (usually one that approaches 50) indicates a glenoid cavity that is narrower in relation to its maximum length, as when the glenoid cavity is more ovoid or pyriform in shape. When combined with a rounded humeral head, one may surmise that the more circular a

glenoid cavity is, the greater degree of freedom of movement it will have (Jolly, 1966).

The small series of hylobatids possess the highest mean glenoid index values observed in any of the hominoid species (Table 6 and Figure 33). This indicates a relatively "round" glenoid cavity in these two species. Drawing on the conclusions of Jolly (1966), one may infer that the glenoid cavities of hylobatids are adapted to allow a high degree of freedom of movement in almost any direction. All the mean index values observed in the great apes are closely clustered (61.0 - 66.0) and do not differ significantly. The index values calculated for the human series are clearly higher than those calculated for the great apes but are still appreciably different from those of the hylobatids. It is important to emphasise that the pongids all exhibit a fairly restricted sample range of observed values for this index, with no observed values below 54.04 and no values above 77.41, thereby presenting a total sample range of only 23.37 amongst pongids. In contrast to the pongid series, the sample range of

the glenoid index in both gibbons and humans is observed to be very high. When the weighted means are calculated for each taxon (Table 6) the clustering of the great ape group is even more visible and th gap between the mean for Hylobates and this group is widened. In both this author's sample and the weighted means, the calculated glenoid index for humans clearly falls neatly between the mean values observed for the great apes and that observed for the lesser apes with limited overlap from either group.

Despite the reported usefulness of the glenoid index for the determining of glenoid cavity shape (Stewart, 1962; Jolly, 1966; Vrba, 1979; Churchill and Trinkaus, 1990), it is important to note that the glenoid index does not take into account irregularities outside the termini for the glenoid length and breadth measurements. One of the most common irregularities observed outside these termini is an indentation of the costal margin of the glenoid that affects the external shape outline and may give the glenoid cavity a pyriform

shape (see the human glenoid cavity outline in Figure 32).

Amongst hominoids, indentation, or notching, of the costal margin of the glenoid cavity is most commonly observed in the scapulae of humans and is rarely observed in the scapulae of apes. Fahlstrom (1981) has concluded that this notch acts as a locking position, or skeletal end-position, for the lesser tubercle of the humerus during flexion and medial rotation of the arm. This skeletal end-position, named the "sword draught position" by Fahlstrom, restricts further flexion, rotation and medial movement of the arm unless there is subsequent anterior and lateral movement of the whole shoulder girdle complex. The glenoid cavities of apes generally lack this indentation. This author believes that the lack of indentation in the glenoid cavities of apes may indicate that the morphology of the ape glenohumeral joint allows greater degrees of freedom of movement in forward and medial rotation of the arm. Brachiation and numerous modes of vertical climbing behaviour, performed efficiently by apes but less so by humans,

require extreme flexion and medial rotation of the arm (Hunt, 1990). Therefore, a strong skeletal end-position at the point at which the arm reaches Fahlstrom's sword draught position may be a disadvantage during these forms of locomotion. However, a locking position is inherently advantageous to a biped whose upper limb has been mostly freed from locomotor duties, since the lock position prevents over-extension of the joint reducing the likelihood of dislocation. One way of testing this hypothesis would be to compare the frequency of glenohumeral dislocation injuries in wild apes with that in humans. Such data are at present not available.

An additional skeletal feature that is directly related to freedom of movement at the glenohumeral joint is the lack of a strongly projecting supraglenoid tubercle in most extant hominoid species. This allows a greater degree of freedom of movement of the humerus, particularly when the arm is raised above the level of the shoulder. In monkeys, the supraglenoid tubercle is extremely well developed

and this morphology limits the degree to which the humerus can be moved upward in relation to the glenoid cavity, since the tubercle wedges, and locks into the intertubercular groove on the humerus (Ciochon and Corruccini, 1976). However, the small greater tubercle of the humerus of humans and apes has also been shown to brace against the glenoid cavity, particularly around 90 degrees of abduction (Fahlstrom, 1981).

Other skeletal end-positions where the head of the humerus and its tubercles brace against the edge of the glenoid cavity have been well documented (Henke, 1863; Ohnsorge, 1932; MacGregor, 1936; Martin, 1932; Saha, 1953). These locking positions may be related to glenoid cavity outline in specific instances. A detailed review of these positions is given by Fahlstrom (1981).

Hominoid species share very similar size relationships between the observed values for spinoglenoid notch depth and those for length and breadth of the glenoid cavity. These relationships are used by the present author to

express the relative "length" of the neck of the scapula. In Figures 34 and 35 it may be observed that the plotted values of these measurements in individual hominoid species indicate that all share remarkably similar regression slope values for glenoid cavity lengths/breadths against spinoglenoid notch depths. Furthermore, there is a high degree of interspecies homogeneity in these data and this may be observed in the restricted 95% confidence bands presented in Figure 35.

In contrast to that observed in hominoids, the cercopithecoids exhibit a significantly shallower regression slope and thus a different morphological trend (Figure 36). However, as was found for the ape data, cercopithecoids do exhibit a high degree of inter- and intraspecific homogeneity for these data. This indicates to this author that the differences observed between hominoids and cercopithecoids for these relationships are biologically significant and may be used as a separating factor between the ape and cercopithecid morphology. The functional

implications of the shortened scapular neck possessed by the more pronograde, quadrupedal monkeys is difficult to understand. However, it may be suggested that the shortened scapular neck observed in quadrupeds is related to the requirements of resisting forces that pass *through* the neck and blade of the scapula rather than resisting forces that pull *against* the neck and blade, a condition encountered by more arboreal forms (see Chapter 3). One might also consider that the scapular neck is "longer" in more arboreal forms so that the glenohumeral joint is positioned more laterally to increase the potential range of movement of the upper-limb.

Although it is difficult to express the size of the coracoid process relative to of the scapula, hominoids appear to possess relatively larger coracoid processes than monkeys. The coracoacromial index (coracoid length X 100 / acromion length) has been used to attempt to express the relative size of the coracoid process by relating its absolute size to that of the acromion (Ciochon and Corrucini, 1976).

According to the results of Ciochon and Corrucini, humans and orang-utans possess the smallest coracoid processes of the hominoid species, whilst hylobatids possess the largest coracoid processes (Table 7). Chimpanzees and gorillas possess coracoid processes that are approximately equal in size to each other. It is believed that these size differences are a result of differential lever advantages related to locomotion (Ciochon and Corruccini, 1977). However, the examination of coracoid size through the use of indices appears unsatisfactory due to the irregularities in shape presented by this process; the metrical examination of the coracoid is an area in need of further study.

In orientation, the coracoid processes of apes are directed more antero-inferiorly than those of humans (figures 32 and 37). The difference in orientation of the coracoid between human and ape scapulae allows humans to maintain a high degree of freedom of movement at the shoulder, even though the scapula is positioned more laterally on the thorax. This is because the position of

coracoid in humans move dorsaly and superiorly means that the coracoid removes itself from the path of the humeral head during rotational movements of the humerus.

6.5.1.2

The Body of the Scapula

Absolute measurements of the body of the scapula have been shown to be of little use in distinguishing between the scapulae of extant primate groups (Hrdlicka, 1942). Rather, the shape of the scapula, expressed as a series of angles and indices, exhibits striking modifications which are discernible among extant species of hominoids (Hrdlicka, 1942; Inman *et al.*, 1944; Oxnard, 1967a,b; Corruccini and Ciochon, 1976). These differences are directly related to differences in muscle size and shape and differences in performance demands placed on areas of the body of the scapula. Therefore, most of the discussion that follows examines variation in scapular body shape based primarily on the

analysis of indices and angles and discusses functional anatomy based on these observations.

The scapular index has been used to express the shape of the body of the scapula by indicating the relationship of length to breadth of the bone (Hrdlicka, 1942; Inman *et al.*, 1944; Oxnard, 1967a,b; Corruccini and Ciochon, 1976). Of all the hominoid species the hylobatids possess the highest individual values and the greatest mean values for the scapular index (Table 8). The high scapular index values observed in the hylobatids serve to illustrate the extremely long and narrow scapulae possessed by this group. Thus the scapulae of the hylobatids may be described as being as similar in shape to the scapulae of the monkeys as they are similar to those of the other hominoids. The values of around 120% that have been calculated for the mean of the scapular index of the hylobatids compare closely with values obtained for the most pronograde primates examined in the present study. The high mean index value indicates the extremely specialised adaptations of the scapular body in this, the only true

brachiating group within the Hominoidea (Oxnard, 1967a,b).

The scapular index values are substantially lower for the great apes and humans than for the hylobatids. The decreasing index values amongst humans and pongids serve to highlight the extremely "broad" scapulae of the large bodied hominoids, possibly reflecting differences in the size and shape of the muscles of the scapula (Inman *et al.*, 1944). Inman *et al.* (1944) have further surmised that the relative increase in breadth of the scapula in the great apes and humans is due to the increased freedom of movement which is present in the upper limbs of these forms. Theoretically the broader scapula of apes allows for a greater degree of freedom of movement at the scapular gliding mechanism. The true brachiation practised by the hylobatids restricts the potential freedom of movement in the glenohumeral joint by requiring adaptations to significant uni-directional stresses.

Among the large bodied hominoid species, gorillas and chimpanzees have the higher mean values for the scapular index (respectively 77.4% and 75.8%) and thus the more restrictive mechanism amongst the hominoids. These restrictions are most probably a result of the more quadrupedal locomotor habits of these two species, a proposition also set forward by Inman *et al.* (1944). Orang-utans have mean scapular index values (69.5%) between those of the two African apes and those of humans (63.7%), probably indicative of the high degree of mobility present in the shoulder girdle of the orang-utan. Humans, being bipeds but also the most orthograde of the extant hominoid species, have upper limbs that are freed from the requirements of locomotion. These behaviours have influenced adaptation in scapular body morphology for an almost three dimensional field of movement at the shoulder. In addition, human scapulae have few requirements for extreme resistance of external stresses.

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While the above-mentioned scapular index expresses both shape and the total length to breadth relationship of the body of the scapula, it does not reveal the region(s) of the scapular body that most affect shape. Inman *et al.* (1944) indicate that most of the shape differences that may be observed in the scapulae of higher primates are in the infraspinous fossa. Traditionally two indices have been used to reflect the differences in the relative sizes of each of the fossae of the scapula, namely the infraspinous and supraspinous indices (Hrdlicka, 1942; Inman *et al.*,1944; Oxnard, 1967; Roberts, 1974; Larson and Stern, 1986).

By the use of linear measurements of the scapular fossae, many studies have indicated that the human scapula possesses a small supraspinous fossa relative to its infraspinous fossa (Figure 39) (e.g. Inman *et al.*, 1944; Roberts, 1974; Larson and Stern, 1986). In contrast , the scapulae of African apes have larger supraspinous fossae relative to their infraspinous fossae. These differences in relative sizes have been

interpreted as indicating that African apes possess relatively larger rotator cuff muscles. The enlarged musculatures are theoretically required to stabilise the shoulder joint during suspensory locomotion (Larson and Stern, 1986). However, these two fossorial indices only relate the breadth of each fossa to the total scapular length and thus do not reflect the actual muscle attachment areas. Obviously, the comparison of linear measurements is not the preferred method of contrasting the size of two regions which form planes rather than lines.

To test the validity of the hypotheses developed by Inman *et al.* (1944), Roberts (1974) and Larson and Stern (1986) from the above indices, the areas of the infraspinous and supraspinous fossae of selected scapulae were calculated as described in the Methods chapter (Chapter 3). The results of this analysis are given in Figure 40, where the data have been plotted as a bivariate plot regression. A "fossorial index" (area of supraspinous fossa x 100/area of infraspinous fossa) is used to

compare the relative sizes of the two fossae (Figure 40 and Table 10). The results obtained using these methods do differ from those obtained using linear indices but not substantially. It may be seen from Figure 41 that whilst gorillas, and in particular male gorillas, have relatively the largest infraspinous fossae of any of the hominoid groups, humans do not possess relatively smaller infraspinous fossae than orang-utans but do possess relatively smaller infraspinous fossae than both African apes and this is corroborated by the results calculated for the fossorial index (Table 10).

Several morphological features of the scapula show few differences between the hominoid species but do separate the scapulae of hominoids from those of cercopithecoids. The size and projection over the glenoid cavity of the acromion process of the hominoid scapula is such a feature. Acting as a lever, it is fundamental in increasing the mechanical advantage of the deltoid muscle during abduction of the arm. In hominoid species, the acromion process positions the origin of deltoid

more laterally over the shoulder joint thereby giving deltoid a lever advantage over its insertion on the mid-shaft of the humerus (Inman *et al.*, 1944; Ciochon and Corruccini, 1977). Hominoids thus have a leverage advantage in abduction over cercopithecoids, in which the acromion process does not extend substantially over the glenoid cavity. The major differences between hominoids and cercopithecoids may be expressed as an acromion projection index (acromion projection - spinoglenoid notch depth x100 / anatomical length of the scapula) (Table 11). It may be seen from this table that the extension of the acromion process in hominoids far exceeds that observed in cercopithecoids.

Oxnard (1968b,c) has noted that in humans the insertions of the major upward rotators of the scapula resemble those insertions observed in the scapulae of pronograde primates more closely than they resemble those insertions in non-human hominoids. To illustrate these differences, the upward angulation of the crest of the spine may be used to indicate the angle of insertion of the

trapezius muscle (Oxnard, 1968b,c) (Figure 42). In humans, this angle is small and corresponds most closely with the angle in quadrupeds (Figure 43) (Oxnard, 1968b,c). In contrast, in the scapulae of apes, the angle is appreciably wider but the absolute values are still quite small. This feature, it has been suggested (Oxnard, 1968b,c), indicates that the human arm lacks power in elevation and is a result of the arm being habitually used in the lowered position.

Another angle may be used to represent the force couple created by the relationship between the medial end of the insertion of trapezius on the spine of the scapula and both the insertions of the trapezius and the serratus magnus muscles (Figure 44, see also Chapter 3 for more details on the measurment of this angle) (Oxnard, 1963). Oxnard has reported that in human scapulae, the orientation of this trapezius/serratus magnus force couple more closely resembles the condition in quadrupedal monkeys. In addition, Oxnard's results indicate that there is clear

differentiation between the angle values observed in apes and those observed in humans (Figure 45). However, the results of the present study suggest that Oxnard's data for apes are too heavily weighted with chimpanzee and hylobatid values and that the grouping "apes" may be too broad a category (Figure 45). This author's data for humans confirm Oxnard's values but indicate that the human sample range overlaps with those of gorillas and orang-utans. Thus, gorillas and orang-utans form an intermediate group between the chimpanzee/hylobatid cluster and the human/quadruped cluster. Therefore, the mean values may still be used to distinguish between samples of apes and humans, but the human overlap with gorillas and orang-utans militates against this feature being used to determine the affinities of individual specimens with uncertain taxonomic status. Nevertheless, in broad terms, humans may be considered more similar to quadrupedal primates in their trapezius/serratus magnus force couple than they are to the living apes. The reason for this similarity is the more lateral facing glenoid cavity in quadrupeds and

bipedal humans and, as Oxnard (1963) has suggested, the human arm may lack power in elevation as a result of its being used habitually in the lowered position.

In humans and monkeys, the glenoid cavity faces more laterally, whilst in apes the glenoid cavity faces more cranially (Inman et al., 1944; Ashton and Oxnard, 1963; Oxnard, 1963, 1968c, 1969; Ciochon and Corruccini, 1976; Senut, 1978; Vrba, 1979). These differences in orientation of the glenoid cavities between primates may be metrically expressed by the axilloglenoid angle. The axilloglenoid angle is defined as the angle between the craniocaudal axis of the glenoid cavity and a line parallel to the axis of the axillary margin that passes through the inferior angle. Human scapulae exhibit much higher values of this angle than are observed in the apes and are most similar to those of quadrupedal monkeys (Table 12). High axilloglenoid angles have been correlated with more laterally facing glenoid cavities and more medially positioned scapulae on the thorax (Inman et al., 1944; Oxnard, 1963,

1968c). In contrast, the apes possess relatively low axilloglenoid angle values which indicates that their scapular glenoid cavities are orientated more cranially and their scapulae positioned more laterally on the thorax (Inman et al., 1944; Ashton and Oxnard, 1963; Oxnard, 1963, 1968a,b, 1969; Ciochon and Corruccini, 1976; Vrba, 1979). This feature in apes has been suggested to be directly related to the need for this group to use their upper limbs above their heads during upper-limb dependent arboreal activities (Oxnard, 1963, 1968c). The more lateral positioning of the glenoid cavity combined with a more medially positioned scapular body that is observed in the scapulae of humans, has been associated with the brachium hanging free alongside the thorax, a position that allows the human arm a wide field of movement in front of the body but correspondingly restricts activities which require extension of the limb above the head (Oxnard, 1963). However, Oxnard (1963) has also noted that the more laterally orientated glenoid cavity in humans most probably indicates that the human arm lacks power in elevation at the shoulder joint since the

trapezius and serratus magnus muscle force couple, which has been discussed above, has a reduced lever advantage in the human arm when raised.

As briefly mentioned above, the cranial orientation of the glenoid cavity has been associated with adaptation to frequent use of the forelimb in a raised position (Oxnard, 1963, 1968c). Thus hylobatids, which amongst all apes most frequently use their arms in the raised position since they are dependent on brachiation as a principal mode of locomotion, exhibit the lowest mean axilloglenoid index value amongst apes. The mean values observed for the axilloglenoid angle values amongst large bodied apes cluster closely and are less diagnostic. However, the sample range of index values for the great apes and humans is extensive with major overlapping between the human range and the apes' ranges (Figure 68). Thus, this author's data indicate that the axilloglenoid angle may not be as useful a taxonomic or functional indicator amongst living hominoids as some have claimed

(Ashton and Oxnard, 1963; Oxnard, 1963, 1968a,c, 1969; Ciochon and Corruccini, 1976; Vrba, 1979).

The origin of the teres major muscle on the axillary margin is more pronounced in the scapulae of the large bodied apes than it is in most human scapulae. Often the superior part of the attachment area of this muscle forms a lateral pronouncement of the margin near the superior part of its attachment area, especially in the scapulae of some large bodied non-human hominoids. This greater pronouncement in the scapulae of some great apes may be due to the more localised area of attachment of teres major in the apes than in humans. In an examination of ape scapulae, it was noted by the author that among the apes, male gorillas exhibit the highest frequency and greatest degree of lateral margin pronouncement, but such pronouncement is not uncommon in the scapulae of orang-utans and male chimpanzees. Lateral margin pronouncement is less frequently observed in the scapulae of hylobatids and female chimpanzees. However, when present, the scapulae of these two forms exhibit

the slightest degree of lateral margin pronouncement amongst apes. In contrast, humans less frequently exhibit the degree of pronouncement observed in the apes. However, it is not uncommon to find that the scapulae of heavily muscled human males possess some expansion of the lateral margin at the superior end of the teres major muscle's attachment. Nevertheless, in these indviduals, the whole area of attachment of the muscle is also expanded into the inferior angle thereby adhering to the general human pattern of possessing an expanded inferior area for the attachment of teres major.

6.5.2

The Proximal Humerus

As with the g.enoid cavity, the proximal end of the humerus possesses several morphological features that assist in creating an extremely mobile joint. The most prominent features of the proximal humerus are the two tubercles, the intertubercular sulcus and the articular part of the head. In this section, indices will be used

to discuss variations in the morphological features of the humeri amongst the hominoid groups.

Just as the supraglenoid tubercle of the hominoid scapula has become reduced, thus allowing a greater degree of upward movement of the humeral head within the glenoid cavity, correspondingly both the greater and lesser tubercles are reduced over those observed in more quadrupedal primates. The greater and lesser tubercles of ape and human humeri are typically positioned well below the humeral head (Table 14). This has been suggested as an adaptation towards allowing the humeral head greater freedom of movement within the glenoid cavity (Larson and Stern, 1989). The relatively small size of the greater and lesser tubercles in apes and humans is in contrast to the pattern observed in the humeri of more terrestrial mammals as well as with the pattern exhibited by monkeys. In both of these groups, the greater tubercle projects well over the humeral head. This restricts cranial movements of the humeral head articular surface

within the glenoid cavity and thus restricts freedom of movement in the whole glenohumeral joint (Zapfe, 1960).

The inferiorly positioned tubercles of the hominoid humeral head allow for a high degree of upward movement of the humeral head in the glenoid cavity without interference with the passage of the supraglenoid tubercle into the intertubercular groove (Larson and Stern, 1989). Theoretically, there is also an increase in the leverage advantage of the the rotator cuff muscles that insert into the tubercles. In particular a leverage advantage is provided for movements which involve rotation, abduction and adduction (Aiello and Dean, 1990).

The articular part of the head of the humerus may be considered almost completely hemispherical in apes. In humans, the head tends to possess a slightly greater length diameter in relation to breadth (Table 15) (Knussman, 1967; Ciochon and Corruccini, 1976; Senut, 1978). Thus the whole articular surface presents more of an ellipsoid in

shape in humans. The humeral head index (humeral head breadth /humeral head length x100) has been used to express these shape differences (Senut, 1978). While the values calculated for the humeral head index overlap to some degree in all the primate species observed by this author, humans exhibit the lowest mean values. These results are somewhat in contradiction with the findings of Knussman (1967), who reported that the relationship of length to breadth of the humeral head in humans is mid-way between the "round" humeral head possessed by apes and the "elongated" head possessed by monkeys. The present author found that the series of *Papio ursinus* have relatively broad humeral heads in relation to head length. In addition, the *Cercopithecus aethiops* series possess both the lowest recorded mean value and the greatest range of values for this index for any of the primate groups examined by this author. This author's results, which contradict the statements of Knussman (1967), may be due to the presence of a large percentage of captive animals in the monkey series examined in

the present study or that this author examined more animalsor different species than Knussman.

The relative width of the intertubercular sulcus, and by inference the size of the biceps brachii tendon and its investing sheath, are expressed by the intertubercular index (intertubercular sulcus width x100/mediolateral diameter of the humeral head). Hominoids possess considerably smaller intertubercular grooves than the pronograde Old World monkeys (Table 16). Among the hominoid species, the mean index values do not significantly differ.

There is a great deal of variation amongst hominoids in the position of the intertubercular sulcus in relation to the greater and lesser tubercles. The greatest degree of difference is observed between the arbitrary hylobatid grouping and the human/pongid grouping (Figure 46) (Inman *et al.*, 1944; Zapfe, 1960). Hylobatids have intertubercular sulci which are approximately centrally located between almost equal sized greater and lesser tubercles, a condition most

similar to that observed in cercopithecoids and other old world monkeys (Inman *et al*., 1944). In contrast, the large bodied hominoids possess intertubercular sulci which are more medially positioned between tubercles that are unequal in size. Amongst large bodied hominoids the lesser tubercle attains its greatest relative size in humans.

The abovementioned medial displacement of the intertubercular sulcus has been linked by several authors to the degree of humeral torsion (Inman *et al*., 1944; Zapfe, 1960). It has been noted, that in any animal which has reduced, or absent, humeral torsion, the intertubercular groove is centrally located between the two tubercles (Zapfe, 1960). As humeral torsion increases, the position of the intertubercular groove is shifted medially (Inman *et al*., 1944). Thus hylobatids, which exhibit the lowest degree of humeral torsion amongst hominoids, have the most centrally positioned intertubercular sulci. In addition, Zapfe (1960) has reported that the higher the humeral torsion, the narrower and

deeper the intertubercular groove. In support of Zapfe's conclusion, it was observed by the author that in the chimpanzee and gorilla, the two species which possess the highest degree of humeral torsion amongst the apes (Table 17), the humeri possess the narrowest and deepest intertubercular sulci. In both hylobatid species, which were observed to possess the lowest degree of humeral torsion, the intertubercular groove was found to be wide and shallow. Orang-utans and humans appear to be the exception to Zapfe's observation. Orang utans possess relatively low degrees of humeral torsion but also have narrow and deep intertubercular grooves. Humans, who possess the highest degree of humeral torsion of any hominoid species, have relatively shallow and wide intertubercular grooves. The functional implications of the relationship between intertubercular sulcus dimensions and humeral torsion are not clear and deserve further study.

The evolution of humeral torsion and its function have been debated at considerable length

(Miller, 1932; LeGros Clark, 1971; Larson, 1988). It suffices to say that the most recent studies suggest that humeral torsion in the apes and humans is most probably not a plesiomorphy, but is more likely the result of parallel evolution in response to selection pressures (Larson, 1988). Larson has suggested that for humans, the selection pressure for humeral torsion was provided by an adaptation to manipulative behaviour. The increased torsion of the humerus in humans would thus be in keeping with the more laterally positioned shoulder joint. Torsion of the humerus orientates the elbow anteriorly, thus placing the hands in front of the body. Conversely, Larson (1988) suggests that apes evolved either humeral torsion, or lack of humeral torsion, in response to a variety of differing upper limb dependent locomotor needs. For example, gibbons possess very low humeral torsion values in keeping with the need to laterally rotate the arm at the shoulder joint, whilst the arm is hypersupinated at the elbow. This position is maintained in preparation for grasping a new support in advance of the body during the final

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swing phase of brachiation (Sarmiento, 1985; Larson, 1988).

6.5.3

The Clavicle

Several morphological features on the clavicle may be used to distinguish between the various species of hominoids and in particular, between humans and apes. Most prominent among these features is the cranial twisting of the clavicular body. This feature allows the clavicles of apes to reach their more cranially positioned acromion. Thus, the lateral ends of the clavicle in apes exhibit a pronounced cranial twist (Figure 47) (Oxnard, 1984). This cranial twisting is generally absent in human clavicles, although there are instances of deviation from this rule.

Several features associated with muscular attachment areas exhibit extensive intra- and interspecific variation amongst primates. The morphology of the area of origin of the sternohyoid muscle on the medial part of the

clavicle is one such feature that, although localised in position, is variable in appearance amongst hominoids. A visible attachment area for sternohyoid is almost universally present in human clavicles and the clavicles of orang-utans, but it is not always detectable in the clavicles of chimpanzees and gorillas. The origin of sternohyoid in human clavicles is observable as a rugose or depressed area situated just medial to the rhomboid fossa. In non-human hominoids, it is typically observed as a large area of slightly rugose bone located in the same position as those of humans.

Concerning ligamentous structures, in most African apes the area of attachment of the costoclavicular ligament is not pronounced since the costoclavicular ligament spreads its attachment over a much lerger region of the inferomedial surface of the clavicle than in humans. In modern human clavicles the area of attachment of the costoclavicular ligament tends to be more localised and to form what is known as the rhomboid fossa. The presence or absence of a

rhomboid fossa has been extensively studied in medical research (Parsons, 1916; Longia *et al.*, 1982; Jit and Kaur, 1986). These studies have indicated that in modern human populations as many as 95.7 % of clavicles exhibit a rhomboid fossa (Srivastava *et al*, 1977), but frequencies vary widely amongst populations. Human populations have been known to record frequencies as low as 10% (Parsons, 1916; Longia *et al.*, 1982; Jit and Kaur, 1986) and one would expect that such variability would also be present in ape populations.

Whereas it is well recognised that both the relative curvature and the relative torsion of the hominoid clavicle exhibit considerable intraspecific variability (Schultz, 1930, 1937; Slowik, 1945; Ashton and Oxnard, 1964; Oxnard, 1969; Sarmiento, 1985), the functional significance of such variation is not well understood (Ashton and Oxnard, 1964; Oxnard, 1968a; Frost, 1973; Boaz, 1980). It is recognised that apes possess generally straighter clavicle shafts, whilst humans possess a considerably

greater degree of sigmoid curvature. In contrast, human clavicles exhibit a relatively low degree of clavicular torsion, whilst those of apes exhibit relatively high degrees of clavicular torsion. Figure 48 shows that, amongst extant hominoids, the degree of torsion is greatest in the clavicles of gorillas and lowest in human clavicles. Both chimpanzees, hylobatids and orang-utans exhibit clavicular torsion values intermediate between these extremes although all the apes cluster closely together.

In their landmark study of clavicular torsion , Ashton and Oxnard (1964, p. 429) concluded that the degree of clavicular torsion reflects "the extent to which the shoulder girdle is twisted cranially and positioned rather more superiorly on the thorax" in hominoids. As the mean value of clavicular torsion rises from one group to another, we may observe an apparent rise in the frequency of upper limb dependent behaviour associated with suspension of the body (e.g. brachiation in the hylobatids).

Possibly related to clavicular torsion is the degree of sigmoid curvature observable in clavicles of apes. Certainly, sigmoid curvature may be used to separate the clavicles of hominoids from those of monkeys (Boaz, 1980). However, although examined by numerous authors (Schultz , 1930; Inman *et al.*, 1944; Lockhart *et al.*, 1959; Oxnard, 1968a, 1969; Frost, 1973; Boaz, 1980; Sarmiento, 1985), the degree of sigmoid curvature of the clavicle and the consequent variation among hominoid species, is not generally quantified. Figure 49 presents a scoring method of sigmoid curvature devised by this author that is based on standards for five degrees of curvature . In this system, the absence of observable curvature in the shaft of the clavicle is scored as 0 whilst strong sigmoid curvature is scored as 5. Thus orang-utan modal clavicles score 0 to 1 on sigmoid curvature; gorilla modal clavicles score 1 to 2; hylobatids 2 to 3; whilst humans and chimpanzees typically score 3 , 4 or 5. Most monkey clavicles would score 0 for sigmoid curvature.

As Oxnard (1969) has noted, the exact nature of the relationship of the degree of sigmoid curvature to mechanical function is not known. However, several authors have suggested explanations for the increased sigmoid curvature in modern hominid clavicles.

Inman *et al.* (1944) have suggested that the high degree of sigmoid curvature present in human clavicles allows them to act as a crankshaft during elevation of the arm. Lockhart *et al.* (1959) hypothesise that the sigmoid curvature in human clavicles acts as a more powerful bracing mechanism for the shoulder girdle. Frost (1973) suggests that the degree of sigmoid curvature is related to differential bone deposition in response to forces exerted by differentially placed muscle attachment areas in the clavicles of humans. Alternatively, Boaz (1980) and Sarmiento (1985) suggest that the sigmoid curvature in the clavicles of hominids is due to the more posterior position of the shoulder girdle with respect to the centre of gravity of the body and to thoracic shape (e.g. the barrel shaped chests of hominids

as opposed to the more fusilined shaped chests seen in apes). Regardless of the specific function of clavicular sigmoid curvature, the interspecific differences in the degree of sigmoid curvature make it possible to determine the morphological affinities of early hominid clavicles.

As a rule of thumb, in African apes the body of the clavicle is not heavily marked by soft tissue attachment areas, whilst in human clavicles and to a lesser extent in the clavicles of Asian apes, there is a tendency for areas of muscular attachment to be more pronounced. The most striking attachment area in the human clavicle is usually the raised ridge on the antero-inferior surface that is created by the lateral continuation of the origin of the pectoralis major muscle and by the medial half of the insertion area of the subclavius muscle. These two areas of muscular attachment meet just medial to the middle of the human clavicular body creating the raised ridge. This ridge runs diagonally across the inferior surface of the

clavicular body. Often, on the sternal part of the anterosuperior surface of the body of human clavicles, the rugose area of origin of the pectoralis major muscle is visible as an elongated island of raised bone.

In the clavicles of humans the attachment area of the costoclavicular ligament is more laterally and posterosuperiorly positioned than in the clavicles of non-human hominoids and is almost always more localised. The position of the attachment area becomes progressively more inferiorly and anteriorly positioned from the condition observed in the African apes to that observed in the Asian apes. In the African apes the attachment area of the costoclavicular ligament is typically observed as a small bulb or depression that is similar in shape and form to that observed in human clavicles. The exact point of attachment of this ligament is usually situated just lateral to, and often encroaches onto, the sternal articular surface. In the clavicles of the Asian apes, the attachment area of the costoclavicular ligament often forms a

distinct blade, or ridge along the length of the inferior surface. The ridge most often has a strong anterior orientation. On the whole, the area of attachment of the costoclavicular ligament in the clavicles of chimpanzees, gorillas and orang-utans is more medially positioned than in human clavicles.

The function of the costoclavicular ligament is not completely understood. Most studies suggest that besides offering a structural attachment between the clavicle, first rib and costal cartilage, the costoclavicular ligament acts as a restraint against extreme clavicular axial rotation (Cave, 1961a,b; Williams and Warwick, 1980; Williams *et al.*, 1989). A stronger, more medially positioned costoclavicular ligament attachment, as is observed in the clavicles of apes, suggests that a wider range of movement is allowed during lateral axial rotation. Since greater lateral axial rotation would give a lever advantage to the lateral part of the clavicle, thereby increasing the likelihood of dislocation of the lateral end, the strong area

of attachment may indicate compensation for the added stresses placed on the medially positioned ligament in apes.

The pectoralis major muscle presents a large area of origin on the medial end of the clavicle. In human clavicles the most visible area of attachment of pectoralis major is on the posterosuperior part of the medial end. In this species the attachment area of pectoralis major is typically observed as a large, rugose area of bone. The area of attachment curves from the extreme superomedial edge of the sternal end of the clavicle laterally and anteriorly until it blends with the rather featureless anterosuperior surface of the middle part of the clavicle.

In the clavicles of apes, the area of attachment of pectoralis major is almost always more localised and more strongly developed than in the clavicles of humans. The localisation of the muscle greatly affects the shape of the medial end. In all non-human hominoid groups the origin of the pectoralis major muscle usually

occupies most of the anterior face of the sternal end. In this region it generally attaches to a triangular area of flattened bone. The triangular area of attachment usually continues laterally and ends in a ridge that may be observed on the anterior surface, near the middle of the body. In combination with the large muscles of the shoulder girdle, pectoralis major assists in drawing the thorax up and forward (see Chapter 5), thus the strong alteration of the medial morphology of the clavicle observed in the apes most probably is a result of the localization of the area of attachment in these forms.

The author observed that there is extensive variation amongst hominoid species in the cross-sectional shape of the body of the clavicle and it was decided to examine the shape differences to see if any useful taxonomic indicators might be observed. Therefore the cross-sectional shape of the body of the clavicle was taken at the approximate mid-point of the greatest length, which in humans usually lies at or around the point where the anterior

curvature of the body of the clavicle gives way to the posterior curvature. Variation in cross-sectional shape of the body of the clavicle was observed to be high between hominoid species (Figure 50). Humans were found to generally exhibit a lunate shape that has rounded borders, although the presence of an angular, flattened slope on the anterior surface is not uncommon (Figure 50). In contrast the clavicles of orang-utans and hylobatids typically present a more angular and almost triangular cross-sectional outline of the body. The clavicles of chimpanzees and gorillas are more flattened and, in cross-sectional shape, resemble a reversed airfoil, being somewhat flattened on the inferior surface and usually exhibit a long, anterior facing slope on the superior surface.

No previous in-depth studies have been conducted on the functional significance of these varieties of clavicular body shape. However, it may be surmised that the lunate shape observed in the clavicles of humans may be associated with increased sigmoid curvature. This correlation

has also been observed by the present author in chimpanzee clavicles that exhibit increased sigmoid curvature (3 and above on this author's sigmoid curvature scale). In these specimens, it has been noted that the more pronounced the sigmoid curvature, the more lunate the cross-sectional shape. Conversely, in human clavicles that exhibit less sigmoid curvature, the cross sectional shape of the body is more flattened.

As was noted for the cross-sectional body shape, the cross-sectional shape of the medial, or sternal, end of the clavicle varies dramatically among the hominoid groups. Human clavicles tend towards a more rounded or ovoid cross-sectional shape (Figure 51). The outline is usually interrupted by rugose ligament attachment impressions in clavicles of male individuals, while these markings are less obvious in clavicles of female individuals. The cross-sectional shapes of the sternal ends of non-human hominoid clavicles are usually less rounded than those of human clavicles. However,

those of African apes are more similar to the clavicles of humans. The clavicles of orang-utans and hylobatids are more flattened and less similar to those of human clavicles.

6.6

Summary

The skeletal elements of the shoulder girdle of extant hominoids comprise a complex that is very mobile, offering a high degree of freedom of movement to the upper-limb. However, amongst hominoids there are varying skeletal features that may be related to locomotor behaviour. This chapter has highlighted numerous morphological features of the shoulder girdle which enable the author to distinguish between the functional morphologies of extant taxa. What is most readily evident is that single features are, for the most part, unreliable for systematic or functional interpretations, since there is a high degree of overlap between the observed morphology of individual features amongst extant hominoids. Rather, "packages" of traits are more useful in

distinguishing between species. Nevertheless, modern hominoid morphology is remarkably homogeneous between species, and only with careful assessment may the different locomotor behaviour be distinguished.

In chapter 7, the knowledge gained in this study of the extant hominoid shoulder girdle will be applied to the fossil hominid record.

Chapter 7

The Anatomy of the Early Hominid Shoulder Girdle

7.1 Introduction

Recent discoveries of numerous fossil hominid shoulder girdle elements from Sterkfontein allow the first comparisons between shoulder girdle elements of two well represented species of Plio-Pleistocene hominid. This chapter is an attempt to apply the functional and morphological knowledge gained from the study and analysis of the modern hominoid shoulder girdle (Inman *et al.*, 1944; Ashton and Oxnard, 1963; Oxnard, 1968c, 1969, 1990; Senut, 1978; Larson and Stern, 1986, 1989 etc.; this study) to the fossil hominid material. The goal is to explore what functional adaptations may be shown by the fossil forms and to make observations on possible phylogenetic relationships. Therefore, this chapter not only compares the fossils with extant forms, but also compares intra- and interspecific adaptations and

relationships where fossil preservation and numbers allow.

This chapter begins with descriptions and discussions of the fossil shoulder girdle material referred to the early hominid species. The statistical data presented in this chapter are primarily presented as means, standard deviations and observed ranges.

Illustrations of fossil hominid specimens that have previously been described are included as guides to assist the reader in identifying and visualizing important morphological features of the bones. The Plates and Figures of the previously undescribed fossils from Sterkfontein are anatomically accurate and may be considered as reasonable facsimiles of the original specimens.

7.2

Specimens Referred to, or Associated With, *Australopithecus africanus*

7.2.1

Descriptions

7.2.1.1

The Scapulae

7.2.1.1.1

Sts 7

(right scapular fragment (Figure 52)

(Broom *et al.*, 1950)

This specimen comprises the glenoid area, the lateral one-half of the spine, part of the acromion, the coracoid process, the infraglenoid tubercle, supraglenoid tubercle, and the superior half to three fifths of the axillary margin of a right scapula. Most of the glenoid cavity is preserved, but there is superficial scoring of most of the articular surface.

The glenoid cavity of Sts 7 may be described as pyriform in shape. This shape is emphasised by the strong mid-costal margin notching. There have been numerous estimates of the dimensions of the glenoid cavity but due to damage to the area, estimates vary greatly (Broom *et al.*, 1950; Robinson, 1978; Senut, 1978; Vrba, 1979) (Table 18). This author's estimate of the glenoid cavity greatest length (GL) is c38.0 mm. This estimate is based on the assumption that the superior part of the supraglenoid tubercle is complete, or nearly complete, and that there is minimal anteroposterior distortion along the length of the glenoid cavity. On the basis of her reconstruction, Vrba (1979) has also reported a glenoid cavity length of c38.0 mm.

The breadth dimensions of the glenoid cavity are more difficult to assess due to significant damage to the dorsal glenoid margin and minor damage to the lower part of the costal glenoid margin. Nevertheless, there have been several estimates for glenoid cavity breadth in this specimen (Broom *et al.*, 1950; Robinson, 1972;

Senut, 1978; Vrba, 1979). However, all estimates of breadth that were made before Vrba's cleaning of the specimen in the late 1970's (Vrba, 1979) may be considered invalid, since her removal of the attached breccia has revealed considerably more bone than had previously been surmised. After her reconstruction of the specimen, Vrba estimates an articular surface breadth (AB) of 19.5 mm and a glenoid cavity greatest breadth (GB) of 22.0 mm. This author estimates articular breadth at c19.0 mm and greatest breadth at c23.0 mm. This author's estimate is based on the belief that the raised ridge that is visible along the costal margin near the point of greatest breadth, is the line of attachment for the glenoid labrum. This indicates to this author that the articular surface is complete at this point. This author's reconstruction of original greatest breadth is slightly higher than Vrba's because allowance has been made for some bone loss on both the lower dorsal and costal margins, a situation not taken into account by Vrba. Nevertheless, the resulting glenoid index value (GI) of around 60% is comparable with previous glenoid index

estimates save for that of Robinson (1972), whose estimated index value of 51.4% clearly results from his underestimate of the glenoid cavity breadth in the unprepared specimen. Glenoid cavity articular depth is estimated by this author as 1.5 mm.

The supraglenoid tubercle is pronounced, and is costolaterally orientated. The infraglenoid tubercle is narrow (c3.0 mm) and long (c17.0 mm). In its superior part there is a well-defined tubercle-like projection which Vrba (1979) thought might represent a "postmortem deformation".

The axillary margin is thin. It has a slight costal curvature along its entire length. Total length of the preserved axillary margin is 71.0 mm.

The acromion of the specimen has been lost during the past half-century but fortunately it is illustrated in Broom *et al.* (1950, Plate 2: Figure 9). From this plate it may be seen that

the acromion extends medially for some distance over the glenoid cavity. However, it is also evident from this plate that the acromion fragment was not complete. The spine of the scapula is slightly thickened at the base. Spinoglenoid notch depth (SGD) is c12.0 mm.

The coracoid process of STS 7 is mostly complete. Authors vary in their estimates of the original extent of the lateral projection of the coracoid process of Sts 7. Vrba (1979) estimates as much as c10.0, whilst Ciochon and Corruccini (1976) feel that the coracoid was mostly complete. The remainder of the coracoid is fairly robust, but the neck of the coracoid is quite slender. Sts 7 has what appears to be a strongly developed dorsolateral tubercle on the coracoid which Vrba (1979) believes is the homologue of the attachment area of the conoid part of the coracoclavicular ligament. The scapular neck has an estimated width of c50.0 mm.

7.2.1.1.2

Stw 162

(left scapula (Plate 1))

(new specimen)

This specimen includes the well-preserved glenoid cavity, lateral part of the base of the spine, infraglenoid tubercle and part of the axillary border of a left scapula. The articular surface is in good condition, but some slight damage has occurred over the inferior and dorsal parts of the glenoid cavity rim. The glenoid cavity is shallow (c 1.0 mm), slightly concave across its breadth, but more noticeably concave along its length. The concavity is a result of a superolateral inclination of the cranial one-third of the glenoid cavity.

The inferior two-thirds of the articular surface is expanded anteroinferiorly. Maximum breadth is 25.8 mm, estimated length is c37.0 mm; actual length is 34.8 mm. The resulting glenoid index is 70%. The costal notching of the glenoid rim is extreme and this gives the glenoid cavity

a distinctively "inverted keyhole" shape. In all places where preserved, the attachment area for the glenoid labrum is wide and pronounced, encroaching some 4.0 - 4.5 mm inside the actual glenoid rim. This gives a greatest articular surface breadth of around 20.0 mm. The supraglenoid tubercle is identifiable as a roughened area of the superior articular surface. The roughened area extends superiorly into the damaged area where the base of the coracoid would have been.

The infraglenoid tubercle is large and anteriorly expanded. Its form is bulbous and the surface is rugose. Anterolateral to this tubercle is a large depression that may mark the supero-anterior limits of the origin of the long head of the triceps brachii muscle and possibly the attachment of the coracohumeral ligament. On the costal surface, the axillary margin is broad and well defined. A small boss of bone, located near the inferior extent of the axillary margin, is probably a postmortem defect. On the dorsal surface the base of the spine is

robust. Laterally it rises away from the dorsal surface at around 80°.

The spinoglenoid notch depth may be estimated at 13.7 mm. Just inferior to the base of the spine is a large concavity that is probably the craniolateral end of the attachment area of the infraspinatus muscle. Just superior to the spine is a large vascular foramen passing into the neck and superior angle.

All the superior part of the specimen is missing, having been broken from the base of the coracoid medially across the supraspinous fossa. The edge of the axillary margin is missing from the inferior part of the infraglenoid tubercle. There are numerous flakes of bone missing from all surfaces of the specimen. A large fossilization crack runs diagonally across the inferior face of the base of the spine. Apart from the positions mentioned, none of the damage has caused any manifest distortion or metric change.

7.2.1.1.3.

Stw 431

(right scapula (Plate 2)

(new specimen)

This scapula fragment forms an element of the partial skeleton Stw 431. It consists of four pieces that, when joined, fit in perfect alignment. When reconstructed, it comprises approximately 140.0 mm of the axillary margin of a right scapula with both the inferior angle and part of the infraglenoid tubercle intact. The estimated original length of the axillary margin is 143.0 mm. This estimate is based on the assumption that the specimen is broken just below the lowest point of the glenoid cavity, as suggested by a small amount of anterior curvature to the inferomedial half of the axillary margin. At the superolateral point of breakage c8.0 mm of the infraglenoid tubercle is intact. Anatomically, the tubercle is costolaterally rotated.

On the dorsal surface of the blade of the scapula the attachment of the teres minor muscle is slightly rugose. Along the length of the axillary margin this muscle is attached mostly along the extreme lateral edge of the blade. About 40.0 mm down from the uppermost point of breakage is a slight depression which may mark the point of passage of the dorsal scapular artery. Approximately two-thirds down the length of the axillary margin, the inferior attachment of teres minor and the superior attachment of teres major are separated by a prominent ridge. At the point of juncture of these two muscle areas is a slight depression that crosses the ridge at an oblique angle; it is most likely the homologue of the oblique line. The ridge continues inferomedially to end near the axis of the inferior angle. Blending inferiorly with this ridge is what appears to be an overlapped part of a prominent attachment area for the serratus magnus muscle and a small part of the inferior continuation of the rhomboid major muscle. This author is unable to discern whether the small, tubercle-like ridge near the attachment of

the serratus magnus muscle is an attachment area for lattisimus dorsi. Alternatively, the tubercle-like area may simply be a rugosity created by the meeting of teres major and serratus magnus.

At the superior point of attachment of the teres major muscle, a protuberance projects laterally from the axillary margin; it possesses a distinct tubercle at its superolateral tip. The attachment area of teres major continues inferiorly until it contacts the superomedial continuation of serratus magnus.

On the anterior surface the specimen's ventral bar is straight in the inferosuperior axis. However, the ventral bar exhibits a slight costal curvature along the length of the margin. There is a laterally expanded, but transversely thin, axillary sulcus just inferior and medial to the most distal part of the infraglenoid tubercle. This feature most likely accommodates an enlarged, overlapped attachment for the long head of triceps brachii. At the inferior angle, the

distal insertion of the serratus magnus muscle is rugose and continues medially until meeting an area of damage. In the middle of the rugose area is a distinctive ovoid impression. Just superior to the rugose area created by serratus magnus is the inferior part of a pronounced subscapular fossa muscular line.

The head of the scapula, the supraspinous and infraspinous fossae are missing, save for a small area of the infraspinous fossa within the inferior angle. There is no visible distortion of the specimen.

7.2.1.2

The Clavicle

7.2.1.2.1

Stw 431

(right clavicle (Plate 3))

(new specimen)

This right clavicular fragment, associated with the **Stw 431** partial skeleton, is 71.5 mm in length but is missing both articular ends. It

appears to possess a low degree of sigmoid curvature and if the line of curvature continues, would score approximately a 2 on the sigmoid curvature scale used in this tnesis. The specimen possesses an enlarged deltoid crest. The crest is seen as a sharp ridge on the anterior part of the inferior surface c23.5 mm from the lateral point of breakage. It continues medially for c20.0 until it meets the medial breakage point. On the posterior margin of the inferior surface near the lateral point of breakage there is the beginnings of a roughened ridge that is probably a medial continuation of a pronounced conoid tubercle.

On the superior surface, at the mediolateral point of breakage, the only distinctive morphology is a roughened, raised area (c13.0 mm in length) that is an extension of the deltoid tuberosity. The area of attachment of deltoid continues medially from the tubercle, across the superior surface, then inferiorly onto the anterior and inferior surfaces and forms, along the route of its passage, a pronounced deltoid crest. The

remainder of the specimen is relatively smooth and devoid of visible muscle and ligamentous attachment areas. No apparent distortion is observable. Dimensions of the shaft at the most medial point of breakage are 8.7 mm supero-inferiorly, and 13.1 mm anteroposteriorly. Cortical bone thickness averages 3.0 mm at the most medial point of breakage and 1.5 mm at the most lateral point of breakage.

In cross section the inferior surface is flattened whilst the superior surface is rounded. Whilst one can see that the complete specimen would have possessed some degree of torsion by the differences in angulation of the bone from lateral to medial, it is impossible to assess acurately the exact degree of torsion.

7.2.1.3

The Humeri

7.2.1.3.1

Sts 7

(right humerus (Figure 53)

(Broom *et al.*, 1950)

The **Sts 7** right humerus comprises a nearly perfect articular surface, slightly damaged greater and lesser tubercles and a badly crushed shaft. The articular surface is rounded with a mediolateral diameter (MHD) of 39.9 mm and an anteroposterior diameter (AHD) of 35.1 mm. The humeral head index (HHI) is thus 88.0%. The lesser tubercle is well developed and leads down to a strong ridge, the crest of the lesser tubercle, that bounds the intertubercular groove. There is very little anterior or posterior curvature of this ridge. The greater tubercle is not large and does not extend above the head of the humerus, its most proximal point lying approximately 3.5 mm below the articular surface. There is a ridge near the superior point of the tubercle and

according to Robinson (1972) the ridge separates the attachment areas of infraspinatus and supraspinatus. The attachment area of the teres minor muscle on the posterosuperior part of this tubercle is visible as a distinct concavity. The greatest intertubercular groove width is c6.0 mm. Where the intracapsular non-articular area meets the inferior part of the articular surface there is a prominent ridge that may in part be due to the distortion caused by crushing of the shaft. The remainder of the specimen is too badly damaged to identify any morphological features. However, from the surviving length of shaft Broom *et al.* (1950) have estimated the reconstructed length of the complete humerus to be 290.0 - 310.0 mm.

7.2.1.3.2

Stw 328

(right proximal humeral fragment (Plate 4))

(new specimen)

This humeral fragment comprises approximately three-quarters of the head, part of the greater tubercle, most of the lesser tubercle

and a small amount of the shaft of a right humerus (c30.0 mm). Probable carnivore damage and some exfoliation of the bone surface due to weathering are present on the anterior and posterior surfaces of the articular head, as well as on the lateral part of the anatomical neck.

The mediolateral head diameter of the specimen is estimated at 34.0 mm (Table 21). The supero-inferior head diameter cannot be estimated due to damage. At the most distal point of the articular surface of the head, the surface forms a ledge over the intracapsular non-articular area. The intracapsular non-articular area is slightly concave, with some anterior flaring below the lesser tubercle.

The greater tubercle is large and bulbous, but its cranial extent cannot be established due to surface damage. The lesser tubercle is rugose and projects strongly anteriorly. On the lower part of the lesser tubercle, there is a large, rugose area, which is most probably the insertion area of the subscapularis muscle. The

intertubercular groove is badly weathered, but a minimum greatest breadth can be estimated at c5.0 mm. The medial lip of the groove is pronounced, becoming less so distally as it blends with the insertion area of teres major. Dorsally, within the interior of the groove, a slight roughened area of the bone surface most likely marks the insertion area of latissimus dorsi. Cortical bone thickness of the shaft varies, wherever measurable, from c3.0 to c3.5 mm.

Damage to the specimen has removed most of the anterior, posterior, and superior parts of the surface of the head. This damage has exposed large areas of underlying cancellous bone. Most of the posterior part of the shaft has been lost, leaving only about 21.0 mm of the greater tubercle intact. Some distortion has occurred to the specimen due to the fossilization cracks within the intertubercular sulcus.

7.2.1.3.3

Stw 517

(left proximal humeral fragment (Plate 5))

(new specimen)

This specimen is a left proximal humerus with most of the articular surface, lesser tubercle, and anatomical neck intact. The head of the humerus is slightly elliptical in shape, the inferior margin forming a slight lip over the intracapsular non-articular area. Apparent carnivore gnawing has damaged the superior parts of the lesser and greater tubercles and the inferolateral part of the neck. Despite being recognisable as a humeral head of a hominoid, **Stw 517** possesses little preserved morphology that assists in further taxonomic comparison.

The mediolateral head diameter of **Stw 517** is c36.3 mm and anteroposterior head diameter is 34.0 mm (Table 21). The humeral head index is 93.7 mm. The lesser tubercle is well preserved. Along its anterolateral surface the area of insertion for the subscapularis muscle is visible.

The greater tubercle is poorly preserved. There is a slight amount of posterior orientation to the whole of this tubercle. Lying between the two tubercles is the badly damaged intertubercular groove for which a maximum width of c6.0 mm has been determined.

The intracapsular non-articular area is wide and flaring. Dotting the anterior part of this area are numerous large foramina. Cortical bone thickness along the distal part of the shaft averages 3.0 mm. Superior to inferior length of the whole specimen is c58.0 mm.

Scarification has occurred to most of the articular surface whilst a majority of the cranial and posterior parts of this surface have been lost. Several small areas of damage that expose underlying cancellous bone occur across the remainder of the articular surface. The superior part of the greater tubercle is missing. A large fossilization crack runs supero-inferiorly through the intertubercular groove. This crack has distorted much of the posterior part of the

specimen. The distal continuation of the lesser tubercle is damaged. The specimen is broken diagonally across the surgical neck. A considerable amount of mediolateral compression has distorted the shaft of the specimen.

7.3

Specimens Referred to, or Associated With, *Australopithecus afarensis*

7.3.1

Descriptions

7.3.1.1

The Scapula

7.3.1.1.1

A.L. 288-1L

(right scapula fragment (Figure 59))

(Johanson *et al.*, 1982)

The **A.L. 288-1l** scapula fragment comprises the glenoid cavity, parts of the base of the spine, the base of the coracoid process and c49.0 mm of the axillary margin of a right scapula.

The scapular glenoid cavity is in near perfect condition. The specimen comprises three major pieces which when reconstructed fit in nearly perfect alignment. Several cracks are found in the specimen but appear to have caused no distortion or metrical change. A small subchondral defect, which Johanson *et al.* (1982) have described as premortem, is observable on the articular surface of the glenoid cavity, near the junction of the superior two-thirds and inferior one-third. The superior angle has been sheared away. All the specimen medial to c20.0 mm from the base of the spine has been lost.

The raised ridge that marks the attachment of the glenoid labrum is prominent dorsally, and in particular, in the superior one-half of the cavity. The supraglenoid tubercle is distinguishable as a prominent, superolaterally extending protuberance, which is part of the raised, rugose area of the attachment of the long head of biceps and the coracohumeral ligament. The infraglenoid tubercle is visible as a

flattened bulb that forms a part of the rim of the glenoid cavity. There are slight discrepancies concerning the actual metrics of the dimensions of **A.L. 288-11**. Senut (1978) has published values for glenoid cavity length as 26.8 mm and glenoid cavity breadth as 18.1 mm. Johanson *et al.* (1982) give values of 25.7 mm and breadth as 18.2 mm respectively. Since this author has not personally examined the original Hadar material both values for the glenoid index have been used in the present investigation (67.5% - 70.8%). Spinoglenoid notch depth is estimated from a cast at c10.0 mm.

The axillary margin is anteroposteriorly narrow. Costally it exhibits a deep ventral sulcus that has been described as "triangular ovoid" form (Johanson *et al.*, 1982). On the dorsal surface of the axillary margin a groove, which lies c16.0 mm down from the glenoid margin, has been interpreted as either the inferior limit of the attachment of triceps muscle and superior end of the attachment of teres minor, or a superiorly positioned groove for the circumflex scapular

artery (Johanson et. al, 1982). An estimate of the axilloglenoid angle has been made by Stern and Susman (1983, pp. 284-285) using their "bar glenoid" angle. This estimate results in a best guess of c130° for the bar glenoid angle, a figure that converts to around 122° for the axilloglenoid angle (Stern and Susman, 1983). Senut (1978) has estimated an axilloglenoid angle for this specimen of around 115°. This author's estimates of the range of possible axilloglenoid angle values (based on a study of the cast) are 115°- 125° with a "best guess" of around ?120°.

7.3.1.2

The Claviculae

7.3.1.2.1

A.L. 288-1bz

(right clavicular fragment (Figure 60))

(Johanson *et al.*, 1982)

This specimen is the lateral one-third of a right clavicle that is missing the acromial articular end. The specimen presents a concave anterior border and a convex posterior border.

The superior surface possesses the only major muscular marking observable and this has been interpreted as the area for attachment of deltoid. The inferior surface is separated from the posterior border by a sharp ridge that represents the continuation of the small conoid tubercle. The area surrounding the conoid tubercle is roughened for ligamentous attachments. The medial part of the inferior surface shows evidence of the subclavian groove.

Viewed laterally the specimen is rounded superiorly and flattened inferiorly. Its dimensions are 7.4 mm superoinferiorly and 11.9 mm anteroposteriorly. The medial cross-section is ovoid and measures 8.4 mm supero-inferiorly and 10.5 mm anteroposteriorly. The total length of the fragment is 34.7 mm.

7.3.1.2.2

A.L. 333-6/9

(right clavicular fragment (Figure 61))

(Lovejoy *et al.*, 1982b)

This specimen is a right clavicular shaft missing both articular ends. It was recovered in two separate pieces that, when aligned, unite perfectly.

The clavicle is described as being "moderately robust". However, the shaft has a "particularly undifferentiated surface with respect to muscle and ligament insertions" (Lovejoy *et al.*, 1982b, p. 638). The most prominent feature on the superior surface is the ridge for the origin of the deltoid muscle. On the inferior surface the conoid tubercle is absent, being apparently replaced by an angular margin that separates the inferior surface from the posterior surface. The posterior surface shows a slight roughened area at the attachment of the coracoclavicular ligament. The lateral aspect of the specimen has a distinctly rhomboid shape. Measurements at the most medial point of breakage are: 15.0 mm (anteroposterior height), 12.5 mm (supero-inferior breadth). Measurements taken at the conoid tubercle are 12.4 mm (anteroposterior), 9.3 mm (supero-inferior). Measurements taken at