Scapular Axillary Border Morphology in Modern Humans and Neandertals

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Abstract

It has been nearly 100 years since Gorjanović-Kramberger published his seminal Krapina scapular axillary border study. The current study attempts to build on Gorjanović-Kramberger's work and that of the many researchers who have attempted to unlock the significance of axillary border variation before and since. The high frequency of dorsal sulci on Neandertal axillary borders and their relatively low frequency among recent humans has more recently been interpreted as indicative of overall greater Neandertal robusticity and reflective of a steady decrease in the levels of biomechanical stress across the shoulder, corresponding to increases in the level of cultural efficiency during the Upper Pleistocene. This study examines (1) the robusticity of axillary border shape and (2) the relationship between axillary border length and thickness to overall scapular, infraspinous, and scapular spine size in modern humans and two Neandertals (Kebara 2 and Tabun C1). The results suggest that the bisulcate axillary border condition, present in high frequency among modern humans, appears to represent greater robusticity (i.e, able to resist greater biomechanical forces) than either the dorsal or ventral types. Additionally, the results confirm the hypothesis that axillary border length and thickness correlate highly to scapular size and scapular spine measures. These results do not challenge the notion that Neandertal post-crania are characteristically robust. Rather, the potential plasticity of the scapula suggests that caution should be implemented when utilising it in phylogenetic interpretations.

> *I do not know what range of variation a great series of the scapulae of the larger felidae might present, but a small one shows nothing like that of the human race...* (2: p. 23)

INTRODUCTION

Neandertal scapulae are notable in many regards (*i.e.* relatively narrow glenoid fossae, tall acromial spines, wide scapular breadths, *etc.*, compared to modern humans). By far the one scapular feature which has received the greatest amount of discussion is the morphology of their axillary borders, establishing this region of their scapulae as the most peculiar compared to more recent humans. Specifically, the majority of Neandertals, including those scapulae from Krapina, show a marked sulcus on the dorsal side of the border, whereas the majority of modern humans have a sulcus on the ventral side. The intermediate condition, a bisulcated axillary border, is present in some Neandertal and modern human individuals (*e.g. 1–10*).

While previous interpretations and explanations of Neandertal and modern human axillary border shape are not lacking (see discussion below), the approach here differs. The hypothesis of this study is that axillary border morphology correlates and responds in large part to overall increases in the size of the scapula, and in particular to the size of the infraspinous region.

BACKGROUND

The axillary border is the thickest section of bone on the inferior body of the scapula, running inferomedially between the infraglenoid tubercle and the *protuberantia marginis axillaris*. Amongst paleoanthropologists axillary borders are most commonly described as exhibiting one of three axillary sulcus (*sulcus axillaris*) patterns which grade into one another: a single ventral sulcus, a single dorsal sulcus, or a bisulcated border (ventral and dorsal sulci) (Figure 1). Both ventral and dorsal sulci have a labium on either side of the sulcus, one dorsal and the other ventral. In either case the labia running lateral to the sulcus is usually crest- or margin-like (similar to the interosseous crest of the radius) in morphology, whereas the medial labia is torus-like in shape. For example, a dorsal sulcus usually displays a marked oblique cranio-caudal thickening on the dorsal side of the scapula, medial to and adjacent to the sulcus, with a thinner crest positioned more ventrally along the axillary border. Thus, the sulcus is located between the two labia. In the case of a bisulcate form there is a central crest dividing the two sulci along the axillary border, and generally a torus-like ridge on the other side of each, one ventral and the other dorsal.

Testut *(11)* was among the first to comment on the structure of the axillary border, describing in detail the first bisulcate, represented by the Chancelade skeleton. In contrast to the case of most modern humans whom he stated have a deep longitudinal sulcus on the ventral side of the axillary border, the Chancelade male has two shal-
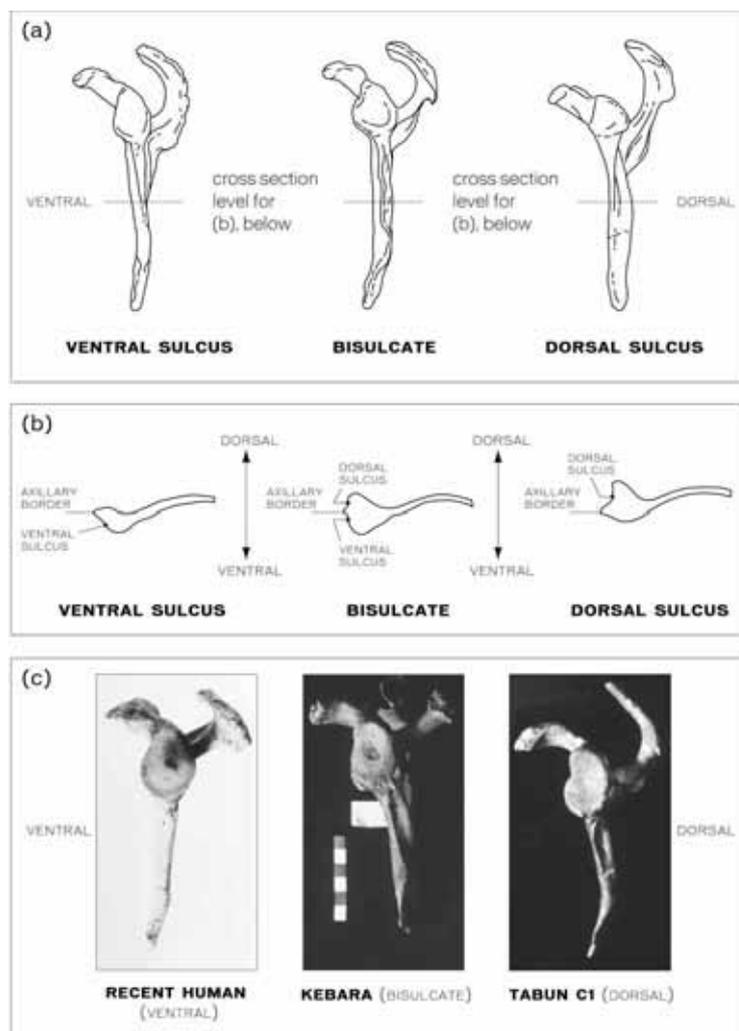

Figure 1. *Scapular Axillary Border Types: (a) lateral view of left scapulae showing dorsal sulcus, bisulcate, and ventral sulcus patterns; (b) Cross-sections through the mid-axillary region showing outlines of each sulcus pattern, and (c) photographs (lateral view) of examples of each type. Tabun C1 right scapula show reversed for ease of comparison. All photographs by the author, except recent human (by Chris Knüsel).*

low longitudinal sulci, one on each side of the border and facing laterally. Testut, however, did not introduce any names to the sulci *(11)*. Thus, the bisulcate condition is sometimes referred to as the Chancelade type of axillary border. Marcellin Boule *(3)* brought attention to the dorsal type of sulcus, using the scapulae of La Ferrassie I and the Neandertal skeleton as examples. He referred to the pattern as the Neandertal-type. Two years later Schwalbe *(7)* introduced the term *sulcus axillaris*, but did not discriminate between types.

In describing several of the scapulae from Krapina Gorjanović-Kramberger in 1925 *(1)* introduced the terms *sulcus dorso-axillaris* and *sulcus ventro-axillaris* and concluded that Neandertals and modern humans have distinctive types of axillary borders.

Von Eickstedt *(12)* significantly revised axillary border terminology from observations he made on a variety of modern human scapulae. He was the first to look at a significantly large sample (409 individuals), as well as place the Chancelade type in the intermediate position between Neandertals and modern humans. He substituted *sulcus axillaris teretis* for *sulcus dorso-axillaris*, *sulcus axillaris subscapularis* for *sulcus ventro-axillaris*, and *facies axillaris bisulcata* for the Chancelade type. He noted variation within each type, and provided a more detailed classification system. Von Eickstedt was able to identify dorsal sulci in a small percentage of his sample (6.4% were clearly dorsal and 15.6% were suggestive of a dorsal sulcus), with the majority ventral (44.7%) as well as a large number of bisulcates (31.4%). Fifteen years later, in their classic description of the Mount Carmel scapulae from Tabun and Skhul, McCown and Keith *(6)* were somehow unaware of the extent of literature on axillary borders, including the Latin names proposed for Ne-

andertal and other scapulae. Instead, they referred to the dorsal sulcus as »Boule's sulcus« or »marginal sulcus«.

In describing the Shanidar scapulae Stewart *(8)* chose Gorjanović-Kramberger's terminology (*sulcus dorso-axillaris*, *sulcus ventro-axillaris)* except for retaining use of the Chancelade category for bisulcates. At the time of Stewart's publication the Skhul hominids were considered to be Neandertals and from the same population as those from Krapina, Neandertal, La Ferrassie, Shanidar, and Tabun. Stewart divided the axillary borders of the known Neandertals at the time into two groups: (1) Dorsal – La Ferrassie I and II, Neandertal, Shanidar I, and Tabun; (2) Bisulcates – Skhul IV, V, and Shanidar III. Most current researchers do not consider the Skhul (and Qafzeh) individuals to be Neandertals.

MUSCULATURE OF THE AXILLARY BORDER

An understanding of the musculature along and adjacent the axillary border is requisite to morphology interpretation of this region. The principal muscles originating in this region are t. minor, the lateral portions of infraspinatus and subscapularus, t. major, and triceps brachii (Figure 3).

T. minor and infraspinatus both originate on the dorsal scapular surface and work in close association as primary lateral humeral rotators (the other primary humeral rotator, the posterior fibres of deltoid, originates on the acromion). T. minor is a narrow band of muscle situated along the proximal two-thirds of the axillary border lateral to infraspinatus. It follows the same path as infraspinatus and inserts on the lowest of three attachments of the greater tuberosity of the humerus. Infraspinatus is a

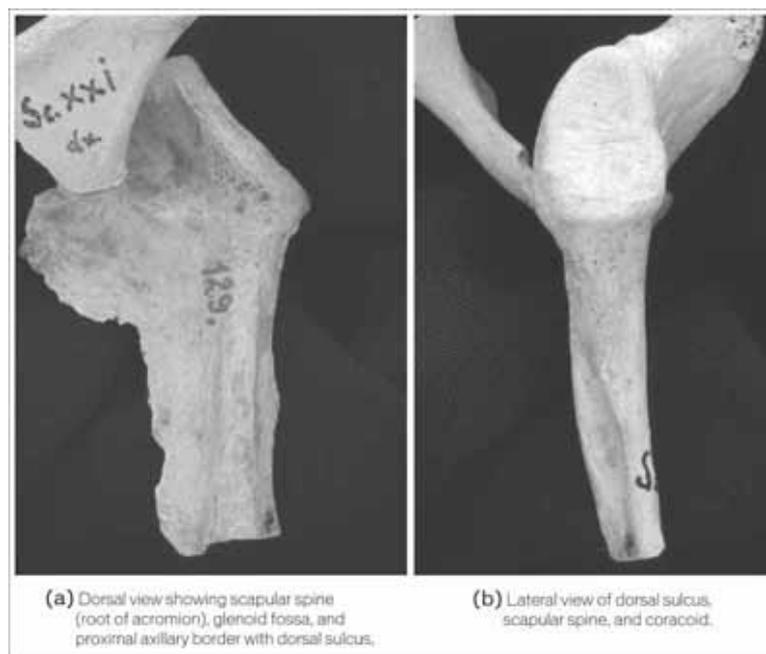(a) Dorsal view showing scapular spine (root of acromion), glenoid fossa, and proximal axillary border with dorsal sulcus.

(b) Lateral view of dorsal sulcus, scapular spine, and coracoid.

Figure 2. *Krapina 129 right scapula. Photo by David Frayer.*

Frequency of axillary border types in samples of fossil and recent humans. Table compiled from Trinkaus (*9–10*).

Group		Dorsal		Bisulcate		Ventral	
	N	%	n	%	n	%	n
Neandertals	22	59.10	13	36.40	8	4.50	1
Skhul & Qafzeh Hominids	3	0.00	0		4	0.00	0
European U. Paleolithic	7	4.30	0	85.70	6	0.00	0
Recent Europeans	##	0.80	1	23.30	28	75.80	91
Recent Amerindians	##	0,00	0	13.40	16	86.60	##

thick muscle occupying most of the infraspinous fossa. It originates on the medial three-quarters of the fossa and then continues superolaterally across the posterior surface of the glenohumeral joint and inserts on the middle of three attachments on the greater tuberosity (*13, 14*).

Subscapularis is a flat fleshy band of muscle which originates on the medial two-thirds of the subscapular fossa, then passes laterally in front of the capsule of the shoulder joint and inserts on the lesser tuberosity of the humerus. In contrast to the actions of infraspinatus and t. minor (lateral humerus rotators), subscapularis is the primary medial rotator of the upper arm (*14*).

Subscapularis, infraspinatus, and t. minor also form a functional group which act as a second or inferior group of the force couple during humeral abduction. They are continuously active during both flexion and abduction. In abduction, activity in infraspinatus and t. minor rise linearly while in subscapularis reaches a zenith beyond ninety degrees and then falls off (*15*).

T. major is a thick muscle originating on the distal third of dorsal scapular surface immediately distal to t. minor along and adjacent the axillary border. It occupies an oval to diamond shaped area immediately superior to the inferior angle and passes laterally across the axillary border inserting onto the crest of the lesser tuberosity of the humerus. T. major is a secondary humeral extensor, and contributes as well to both medial rotation and minorly to adduction (*14*). T. major is not considered a true rotator cuff muscle because it does not fuse with the capsule of the shoulder joint (*16*). Broome and Basmajian (*17*) have demonstrated that t. major is not recruited in free movements of the shoulder unless resistance to these movements (medial rotation, adduction, and extension) is added.

The long head of triceps brachii originates on the scapular infraglenoid tubercle (the lateral and medial heads originate on the posterior surface of the humerus above and below the radial groove, respectively). All three heads of t. brachii travel distally on the posterior humerus and unite midway along the humerus and insert on the upper part of the posterior surface of the olecranon process of the ulna. Triceps brachii is the primary extensor of the forearm (*14*).

T. minor, infraspinatus, subscapularus, and t. major (all of which insert on the proximal humerus) are individually capable of producing more than a single movement of the scapulohumeral joint and collectively are involved in many coordinated movements. It can be seen, however, that there are no prime humeral adductors originating on the scapula. T. major and t. brachii play minor roles in comparison to pectoralis major and latissimus dorsi, the prime of humeral adductors (Gardner & Osburn, 1973). The posterior fibres of deltoid are quite active during humeral adduction, however only to resist the medial rotation that the main adductors would produce if unresisted (*15*).

INTERPRETATION OF AXILLARY BORDER MORPHOLOGY

While the studies outline above were, for the most part, concerned with axillary border variation and its phylogenetic implications, the first comprehensive functional analyses of Neandertal axillary border morphology were those of Trinkaus (*9, 10*). By tabulating the frequency and distribution of axillary types among Neandertals, the Skhul hominids, European Upper Paleolithic hominids, and recent *Homo sapiens* (Europeans and Amerindians) he demonstrated that the frequency distribution of sulcus types from the Middle Paleolithic to present follows a consistent pattern: a decrease in the dorsal type and an increase in the ventral type (Table 1; combination of Trinkaus' data from *9–10*). The Neandertals in Trinkaus' samples exhibit all three axillary types in varying percentages, with the ventral type rare at 4.5%, the dorsal type predominant at 59.1%, and the bisulcate condition common, present in 36.4% of the sample. A temporal anomaly is presented by the Skhul hominids who, in contrast to their Middle Paleoloithic contemporaries, do not display dorsal sulci. Rather, they all have bisulcated axillary borders (n=4). The Upper Paleolithic sample (n=7) is comprised of one dorsal (Predmosti 14) and six bisulcate scapulae. Among Trinkaus' two recent human samples only one individual displayed a dorsal sulcus, with the remainder comprised of 44 bilsulcate and 194 ventral.

Trinkaus' (*9*) analysis of the functional significance of each axillary border type is based on his interpretation of the surrounding musculature. Assuming that the lateral
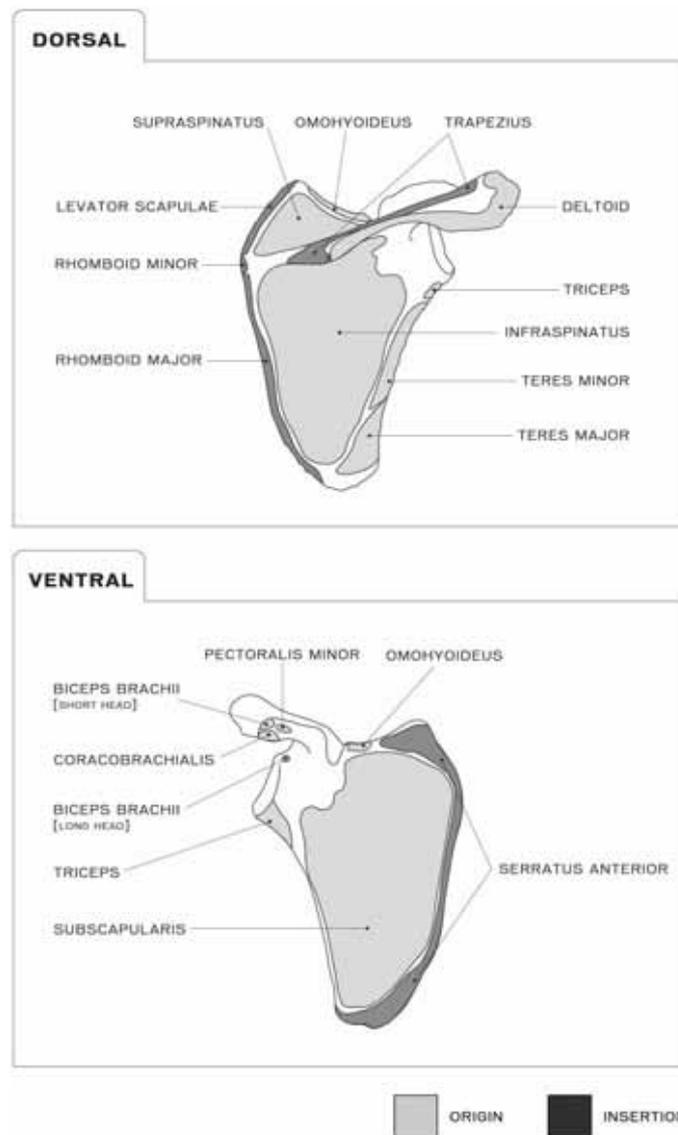
Figure 3. *Muscular origins and insertions on the scapula. Right scapula shown.*

fibres of subscapularis and teres minor attach along the mid-axillary border (Figure 3), Trinkaus proposes that for modern humans exhibiting the ventral type of border most of the axillary border is occupied by subscapularis, whereas t.minor is limited to the dorsal surface with a clear crest separating the extent of t.minor along the dorsally placed axillary margin. In contract, Trinkaus suggests that when the axillary margin is more ventrally placed, as in the dorsal type, the lateral extent of t.minor has increased. In this interpretation the dorsal type sees most of the axillary border occupied by t.minor. Trinkaus proposes that the relative increase in the attachment area for t.minor with the bisulcate pattern and the full dorsal sulcus strongly implies a larger, more powerful t.minor. He adds that it does not imply a concomitant relative decrease in the development of subscapularis, since its dimensions are related to factors other than the configuration of the axillary border *(9)*.

As discussed above, t.minor, along with infraspinatus, is a primary lateral rotator of the humerus (besides serving this function, during abduction of the humerus (by deltoid and supraspinatus) it aids in retaining the humeral head in the glenoid fossa). However, Trinkaus *(9)* suggests that this alone cannot account for the pronounced development of t. minor in the dorsal border type. Rather, he proposes that the hypertrophy of t.minor is due to stabilisation of the arm during adduction. The primary adductors, latissimus dorsi, pectoralis major, and teres major are also strong medial rotators of the humerus. Thus, if the humerus is powerfully adducted, the medial rotation caused by these muscles must be counterbalanced, and this is precisely what Trinkaus suggests t.minor does, explaining its strong development in the shape of a dorsal sulcus *(9)*. Additionally, as the humeral adductors in Neandertals were quite powerful (as suggested by their strong humeral attachments), hypertrophy of t.minor (as

well as infraspinatus and the posterior fibres of deltoid) may have been necessary facilitate precise manual dexterity.

Trinkaus has more recently developed this interpretation further effectively relating the axillary border to robusticity, whereby the dorsal type is seen as the most robust axillary border type, followed by the bisulcate and the ventral types *(10, 18–20)*. In this revised interpretation Trinkaus *(19, 20)* states that the dorsal sulcus axillary border »probably reflects a structural reinforcement of the axillary border in response to dorso-ventral oriented bending stress, particularly when the humerus was in an abducted position« *(20*: p.334*)*. He adds that this stress was created by the apparently hypertrophied rotator cuff musculature (discussed previously), as well as t. major, and again notes that the transition to early modern humans involved a decrease in the frequency of the dorsal sulcus *(19, 20)*.

At the cultural level, Trinkaus *(9, 10)* asserts that the evolution of the border to the bisulcate pattern of the Skhul and Upper Paleolithic hominids *(9)* and the ventral sulcus pattern characteristic of recent humans indicates a steady decrease in the levels of biomechanical stress of the shoulder in accordance with the corresponding increases in the level of cultural efficiency during the Upper Pleistocene.

MATERIALS AND METHODS

Two recent human populations and two Levantine Neandertal individuals are examined and compared. The recent human samples comprise Pacific Northwest Coast natives (NWC; n=51) and North American Pioneers (NAP; n=10). The Neandertal axillary border data is from Kebara 2 (male; right scapula) and Tabun C1 (female; left scapula). All measurements were recorded from the original fossils and collections by the author (both recent humans samples were examined in the Department of Archaeology, Simon Fraser University, Burnaby, BC, Canada; Tabun C1 at the Department of Palaeontology at the British Museum of Natural History; Kebara 2 at the Sackler School of Medicine, Tel Aviv University). Care was taken to include only those individuals who were unaffected by pathological changes or degenerative joint disease in the shoulder. Individuals showing compensatory (*i.e.* pathology-induced) use of one arm, and thus a high degree of asymmetry, were excluded. The measurement most central to this study – axillary border thickness (AXTK) – is not currently reported in published sources for either Neandertals or modern humans, and as such restricted the amount of data available to this study.

Ten adults from the Golden Pioneer cemetery in British Columbia, Canada, were analysed. The Golden cemetery was used from 1882 to 1894. Only two individuals are identified as female, and the sex of one is equivocal *(21)*. The remainder are designated male with a high degree of confidence. The majority (eight) are described as caucasoid, while two (one of each sex) show caucasoid/mongoloid admixture. Golden came into existence in the

late 1800s as a railway community, situated along the Canadian Pacific Railway. Many of the early settlers, primarily of European descent, came to Golden as railway workers, miners, and construction tradesman. The occupations of the recovered individuals appear to have been physically demanding, as attested to by their skeletal morphology, muscular hypertrophy, and degenerative changes, suggesting that several of the individuals were labourers *(21)*.

The Northwest Coast native sample (n=51) originates from six coastal archaeological sites dating to between 6170 yBP and 1000 yBP within the Gulf of Georgia and Fitz Hugh Sound regions of British Columbia, Canada. The prehistoric period of this region displays cultural, physical, linguistic, and mythological continuity *(22)*. The economy of prehistoric NW Coast peoples was based heavily upon fish, mollusca, and wood procurement and processing and is visible both archaeologically, osteologicallly, and ethnographically *(23)*.

Kebara 2, a 25–35 year old adult male Neandertal, dates by ESR to between 64,000 and 60,000 yBP, and by TL to between 61,000 and 59,000 yBP *(24–26)*. Tabun C1 is an adult female Neandertal who was approximately 30 years old at death *(6, 26)*. Until very recently Tabun C1 was believed to date to 50,000 yBP *(28, 29)*. More recent ESR dates from layer C at Tabun have provided significantly older dates, ranging between 102,00 (±17,000) and 119,000 (±11,000) yBP *(30, 31)*. There is some concern, however, that the skeleton may actually have been positioned in the more recent layer B and was intrusive to layer C *(32)*.

Scapulae are among the more poorly preserved elements archaeologically, even in cases where a skeleton is fairly well preserved *(2)*. This is to be expected given the thinness and fragility of the scapular body on either side of the spine. Among the comparative samples, most of the NW Coast scapulae, and many of the humeri, were fragmented, incomplete, and required refitting. Refitting was only performed between clean breaks. The most common preservational state of the scapulae from the NW Coast collection mirrors that of Krapina scapulae and most others from archaeological contexts, consisting of the glenoid fossa with the acromion and coracoid roots and the proximal 60% of the axillary border attached. Among the NW Coast sample the spine and medial angle were the next most commonly preserved portions. Recovery of the superior angle was rare, and inferior angle exceedingly rare. The NA Pioneer sample was remarkably well preserved, not surprising given their relatively recent date of burial. Among the fossil sample, Kebara 2's right scapula is lacking only a fraction of the superior angle, which can be confidently estimated, and Tabun C1 contained all of the required landmarks for this study.

Figure 4 shows the measurements used in this study. All measurements were recorded with sliding calipers to an accuracy of one-tenth of a millimetre, with the exception of humeral length which was measured on an
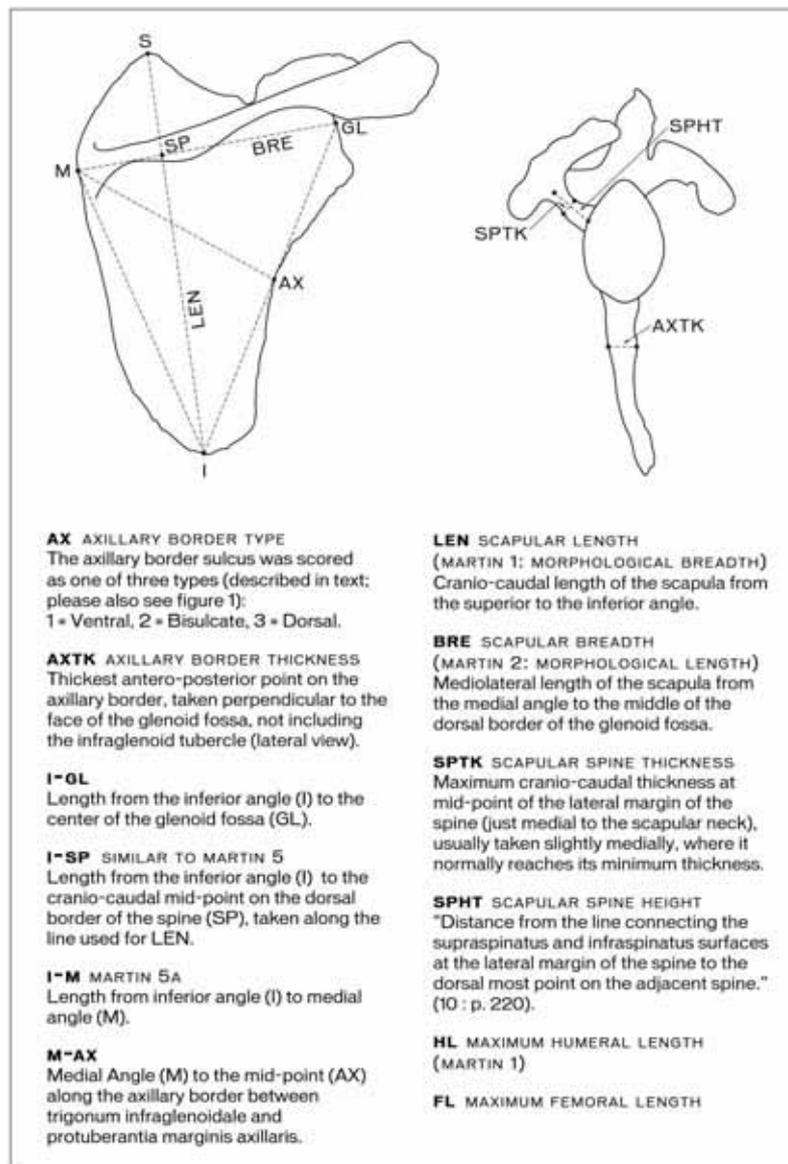
AX AXILLARY BORDER TYPE
The axillary border sulcus was scored as one of three types (described in text; please also see figure 1):
1 = Ventral, 2 = Bisulcate, 3 = Dorsal.

AXTK AXILLARY BORDER THICKNESS
Thickest antero-posterior point on the axillary border, taken perpendicular to the face of the glenoid fossa, not including the infraglenoid tubercle (lateral view).

I-GL
Length from the inferior angle (I) to the center of the glenoid fossa (GL).

I-SP SIMILAR TO MARTIN 5
Length from the inferior angle (I) to the cranio-caudal mid-point on the dorsal border of the spine (SP), taken along the line used for LEN.

I-M MARTIN 5A
Length from inferior angle (I) to medial angle (M).

M-AX
Medial Angle (M) to the mid-point (AX) along the axillary border between trigonum infraglenoidale and protuberantia marginis axillaris.

LEN SCAPULAR LENGTH
(MARTIN 1: MORPHOLOGICAL BREADTH)
Cranio-caudal length of the scapula from the superior to the inferior angle.

BRE SCAPULAR BREADTH
(MARTIN 2: MORPHOLOGICAL LENGTH)
Mediolateral length of the scapula from the medial angle to the middle of the dorsal border of the glenoid fossa.

SPTK SCAPULAR SPINE THICKNESS
Maximum cranio-caudal thickness at mid-point of the lateral margin of the spine (just medial to the scapular neck), usually taken slightly medially, where it normally reaches its minimum thickness.

SPHT SCAPULAR SPINE HEIGHT
"Distance from the line connecting the supraspinatus and infraspinatus surfaces at the lateral margin of the spine to the dorsal most point on the adjacent spine."
(10 : p. 220).

HL MAXIMUM HUMERAL LENGTH
(MARTIN 1)

FL MAXIMUM FEMORAL LENGTH

Figure 4. *Metrics and landmarks utilised in this study.*

osteometric board to an accuracy of one millimeter. Very few of the values in the dataset are estimates. Estimates were included only in cases where a small fragment or margin of bone was missing, and are considered reliable.

DATA PREPARATION

The first stage of data preparation was reduction of measurements taken from both sides of an individual to a single, usable measurement per individual (side-selection). After considering the possible methods utilized in studies such as this (*i.e.* averaging sides, choosing all variables from the same side of an individual, mixing sides based on preservation *etc.*) the method applied to the scapulae in this study is as follows: (1) The best preserved side was chosen. If the sides were equally preserved then one side was randomly picked. (2) Mis-

sing values were plugged in from the opposite side if asymmetery was lower than 3.0% for a respective measurement (which it was for all but one measurement, described below).

Asymmetry was assessed in the sample by averaging Right minus Left scores (for each sex) for each measurement. As a result it was determined that asymmetry was very low for most of the variables, with most values lying between +0.1% to +3.0% (+ = right side asymmetry, – = left side asymmetry). Some variables displayed very low left side (–) asymmetry. Spine Thickness (SPTK) was the only variable to displayed asymmetry over 3.0%, measuring +6.6% for males and +3.0% for females. Prediction equations were calculated and used for SPTK for those individuals whose non-chosen side preserved the missing measurement. Humeral side selection in-

Frequency of axillary border types in the modern human samples examined in this study (Males and Females).

Group		Dorsal			Bisulcate		Ventral	
	N	%	n		%	n	%	n
NW Coast	41	0.00	0		31.70	13	68.30	28
NA Pioneer	10	0.00	0		40.00	4	60.00	6
Totals	51		0			17		34

volved the same criterion as for the scapulae, but priority was given to choosing the same side as that for the scapula. On the occasion that sides could not be matched, the opposite side humerus was chosen. Asymmetry was low for humeral length (males = +0.2% males, females = +0.3%). Side-selection for the femora involved matching to the chosen humeral side if possible, or using the opposite side if necessary. Femoral length showed minimal asymmetry (–0.1% in males, –0.3 in females). As the femur does not share a direct mechanical relationship with the scapula or humerus there was no concern about its influence on the scapular data if the opposite side femur had to be utilised.

SIZE STANDARDISATION

Both non-scaled and scaled data were analysed. In anticipation of size standardization (for the scaled analysis), which arguably provides a more realistic measure of shape differences, humeral and femoral lengths were measured in individuals preserving these elements. As the humerus is not weight-bearing *(33)*, and thus less suspect to curvature, it was chosen as the better element of the two for standardisation. In a study of paired male humeri from crew of the *Mary Rose*, Stirland *(34)* observed a number of ride-side asymmetries, and that of these only maximum humeral length appears to be congenital in origin. She concluded that humeral length appears to be unaffected by activity, but adds that »congenital asymmetry in humeral length may be enhanced by preferential use of the right arm« *(34*: p. 109*)*. For individuals lacking humeri, humeral length was predicted from femoral length, as the two values correlate highly. As well, plotted residuals displayed a constant width (random) pattern and attest to the linearity of humeral and femoral lengths. In cases where humeral and femoral lengths were unavailable, scapular values were still included in the non-scaled tests.

RESULTS

Border Type Frequencies

Table 2 lists the frequencies of sulcus types in the sample of recent humans (sexes combined). The majority of the scapulae in both populations possess ventral sulci. However, the bisulcates constitute a notably high percentage of each (NW Coast 31.7%, NA Pioneer 40.0%), in greater percentages than Trinkaus' *(9, 10)* recent Europeans (23.3%) and Amerindians (13.4%). Both Kebara 2

scapulae possess bisulcate axillary borders (corroborated by Vandermeersch *(35)*), while that of Tabun C1 is clearly dorsal (Figure 1).

Table 3 presents a comparison of axillary border thickness by sulcus type. Sexes were split because there was a significant difference (p<0.0001) between males and females in axillary border thickness. Despite the limited sample size there is an apparent correlation between border thickness and type. In both the females (p= 0.0178) and male (p=0.0388) the axillary borders of bisulcated scapulae are significantly thicker than the ventral type's. Of significance, as well, is that Kebara 2's axillary border is appreciably thicker than those of the modern human bisulcates.

The thickening of the axillary border may reflect robusticity (with robusticity here defined as per Ruff *et. al. (33)*, as bone strength relative to an appropriate measure of size) and as such should arguably be scaled for size *(36)*. Table 4 presents axillary border thickness scaled against humeral length. Once again, as in the unscaled comparison above, there is an observable difference between the border thickness across the axillary types. Among the female recent humans the bisulcates are significantly thicker (p=0.0279). It is likely that the male recent human bisulcates, while not significantly different from the ventral males at p<0.05 (p=0.0799), were appreciably thicker. As in the unscaled analysis, Kebara 2 clearly lies well above the recent human mean, and has a very thick axillary border relative to its humeral length. Among the females, Tabun C1, a dorsal type, would fit in the lower range of the female recent human bisulcates and at the upper of the female ventral types.

The results thus far are indicative of a relationship between axillary border type and the dorso-ventral thickness of the border itself. With the exception of the scaled male sample, the scapulae with bisulcated borders among the samples and individuals in this study, on average, exhibit thicker axillary borders than either the ventral and dorsal types (although it is important to note that the dorsal example comprises only one individual, Tabun C1). Trinkaus *(20)* has suggested that the dorsal sulcus morphology »*More appropriately… probably reflects a structural reinforcement of the axillary border in response to dorso-ventral bending stress, particularly when the humerus was in an abducted position* (20*: p. 334). Although Trinkaus *(20)* did not quantify the thickness of the border in his study, the results here support the notion that the

TABLE 3

Axillary Border Thickness (AXTK) among males and females of recent humans and a fossil sample, by axillary border type (Mean, one standard-deviation of the mean (bracketed), standard error, and 95% confidence interval). Italicised values represent single individuals. All values in millimeters.

Group		Dorsal		Bisulcate		Ventral		p-value
Males	N	AXTK	n	AXTK	n	AXTK	n	(Bi vs. Ventral)
Recent Humans	32	–		14.1 (1.6)	11	12.6 (1.7)	21	0.0388 *
				se=0.46		se=0.37		
95% Mean (Upper-Lower)				13.1–15.1		11.8–13.4		
Kebara 2	1	–		15.6		–		
Females	N	AXTK	n	AXTK	n	AXTK	n	
Recent Humans	32	–		12.4 (1.4)	6	10.7 (1.3)	13	0.0178 *
				se=0.55		se=0.36		
95% Mean (Upper-Lower)				11.0–13.8		9.9–11.5		
Tabun C1	1	11,0		–		–		

* differences at P<0.05

TABLE 4

Size Scaled Axillary Border Thickness (AXTK/HL x 100) among males and females of recent humans and a fossil sample, by axillary border type (Mean, one standard-deviation of the mean (bracketed), standard error, and 95% confidence interval). Italicised values represent single individuals. All values in millimeters.

Group		Dorsal		Bisulcate		Ventral		p-value
Males	N	AXTK	n	AXTK	n	AXTK	n	(Bi vs. Ventral)
Recent Humans	28	–		4.3 (0.5)	9	4.0 (0.4)	19	0,0799
				se=0.17		se=0.08		
95% Mean (Upper-Lower)				3.9–4.7		3.8–4.2		
Kebara 2	1	–		4.9		–		
Females	N	AXTK	n	AXTK	n	AXTK	n	
Recent Humans	16	–		4.2 (0.4)	5	3.7 (0.4)	11	0.0279 *
				se=0.16		se=0.12		
95% Mean (Upper-Lower)				3.7–4.6		3.4–3.9		
Tabun C1	1	3,8		–		–		

* differences at P<0.05

axillary border is a structure which provides increased resistance to dorso-ventral bending stress

In this model, the buttressing of the axillary border is a response to biomechanical forces and therefore constitutes an expression of robusticity. As such, the bisulcate condition may, in fact, be more *robust* than the dorsal type. What can be concluded from this portion of this study is that the axillary borders of bisulcates are thicker, and theoretically provide more resistance to dorso-ventral bending stress than do the ventral type. If, as Trinkaus *(20)* has claimed, this is the main function of the thickened Neandertal dorsal sulcus, Neandertals are not the only populations to respond in this way to these stresses. Clearly the NW Coast and NA Pioneer groups (which constitute the *recent human* sample here) contain many individuals whose axillary borders withstood biomechanical stresses in excess of those met by Neandertals.

AXILLARY BORDER THICKNESS AND SCAPULAR SIZE

As a structural component of the infraspinous fossa – essentially the main body of the scapula – the axillary border (length and thickness) should logically bear an architectural relationship to other metrics in this region. To examine how axillary border length and thickness correlates with infraspinous fossa and scapular size (a) six variables which describe the size of the infraspinous region (I-GL, I-SP, I-M, M-AX) and scapular size in general (LEN, and BRE) and (b) two variables which measure the height and thickness of the scapular spine at the proximal subscapular border (SPTK and SPHT) were examined. The results of these analyses are shown in Table 5, in which a clear and statistically significant relationship is seen between the axillary border and infraspinous size, scapular size, and spine height and thickness.

TABLE 5

(A) Axillary Border Thickness (AXTK) and (B) Axillary Border Length (I-GL) regressed on metrics describing infraspinous size, scapular size, scapular spine thickness and height. Data represents grouped study sample.

(A)			
Axillary Border Thickness (AXTK) vs.	n	R squared	P-value
I-GL	25	0.479	<0.0001 *
I-SP	20	0.451	0.0012 *
I-M	17	0.390	0.0073*
M-AX	23	0.219	0.0242*
LEN	17	0.281	0.0285*
BRE	25	0.150	0,0557
SPTK	51	0.277	<0.0001 *
SPHT	48	0.379	<0.0001 *
(B)			
Axillary Border Length (I-GL) vs.	n	R squared	P-value
I-SP	20	0.599	<0.0001 *
I-M	17	0.456	0.0029*
M-AX	17	0.671	<0.0001 *
LEN	17	0.665	<0.0001 *
BRE	17	0.783	<0.0001 *
SPTK	24	0.354	0.0021*
SPHT	25	0.312	0.0037*

* differences at $p < 0.05$

The analyses (Table 5a) indicate that axillary border thickness bears a significant relationship ($p < 0.05$) to the cranio-caudal length of the scapula (LEN), to two measures of the cranio-caudal length of the infraspinous fossa (I-SP and I-M), as well as to the cranio-lateral length of the fossa (M-AX). The only infraspinous value which does not correlate significantly with axillary border thickness is scapular medio-lateral breadth (BRE; ($p=0.0557$)). Both scapular spine measures, spine height (SPHT) and spine thickness (SPTK), correlate significantly ($p < 0.0001$) with axillary border thickness. And finally, axillary border length (I-GL) correlates highly ($p < 0.0001$) with border thickness (Table 5a). Overall, axillary border length (I-GL) correlates with even greater overall significance to the same scapular metrics (Table 5b). Border length correlates with scapular length, breadth, and cranio-lateral and cranio-caudal infraspinous fossa lengths (LEN, BRE, M-AX, and I-SP) at $p < 0.0001$ and with the remain metrics (I-M, SPTK, SPHT) at $p < 0.05$.

DISCUSSION

When axillary border morphology is analysed in the context of the entire scapular body and infraspinous region, and by axillary border type, a more informative and complex picture emerges. The results of this study suggest that axillary border thickness differs by axillary border type (ventral, bisulcate, dorsal) with the bisulcate condition being the thickest and arguably most robust. It should be noted that the only dorsal scapula available to this study was that of Tabun C1 (11.0 mm thick), which falls well outside the 95% range of variation of the modern human males and at the cusp of variation of the modern human females. Axillary border thickness data from other Neandertals will clearly assist in providing greater perspective on the significance of this observation. Data from other modern human samples would be invaluable, as well. In this regard, it should be noted that in their study of the scapulae of recent British Bainbridge & Tarazaga (31) described one 65 year old male's axillary border as »*strikingly recalling the Neandertal type, having a strongly developed dorso-axillary [dorsal] crest transgressing onto the infraspinous fossa and a very light ventro-axillary [ventral] crest disappeared below the middle third of the border*«.

The dorsal type of axillary border has previously been interpreted as the most robust, said to reflect a structural reinforcement of the border to dorso-ventral bending stress (20). If the notion that increased buttressing of the axillary border reflects stress response, then the results here indicate, to the contrary, that the bisulcate condition, not the dorsal, is the more robust and therefore anatomically better suited to resisting biomechanical stresses. Further, it cannot be generalized from axillary border morphology alone, as has been stated, that the ventral sulcus is indicative of a steady decrease in the levels of biomechanical stress of the shoulder in accordance with

the corresponding increases in the level of cultural efficiency during the Upper Pleistocene *(10, 18–20)*.

That there were increases in cultural efficiency during the Upper Pleistocene which lessened overall biomechanical loads is clear. However, axillary border morphology is not a testament to this, as the most robust type of axillary border (with robusticity here assumed to be a measure of biomechanical stress) is the bisulcate condition, which still occurs in high frequencies in modern human groups – both hunter-gatherer level (NW Coast) and industrial populations (NA Pioneers).

The question still remains as to the origin of the axillary border morphology – i.e. what is the ultimate, or specific anatomical and muscular, origin of sulcus morphology? It is unlikely that axillary border morphology can be explained simply by the hypertrophy or re-positioning of a single muscle alone (as with teres minor, suggested in the past). The morphology more likely reflects overall osseous changes related to (a) muscular hypertrophy and re-orientation and (b) robusticity (buttressing, thickening) of the actual axillary border itself. In this scenario, the thickening of the border allows for greater surface area for muscular attachment, and the increased area may therefore be a by-product of biomechanical forces rather than muscular hypertrophy. An examination of the internal structure of the axillary border, through bi-planar radiographic reconstruction, observation of natural breaks, and/or the use of computed tomography would add invaluable data to understanding this issue.

Considering that dorsal sulci can be found among modern humans, and that all three types are seen within single Neandertal sites (*i.e.* Krapina: Gorjanović-Kramberger *(1)*), axillary border shape in this regard is most likely acquired by an individual, rather then being congenital in nature. This notion is also supported by the fact that among this study's comparative samples three individuals possessed asymmetrical scapula, whereby one side was bisulcate and the other ventral. The axillary border most likely gains its shape through biomechanically- and muscular-influenced remodeling, owing to the complex array of muscles in the shoulder girdle and through its role in overall thoracic architecture. In light the wide range of movement and manipulation possible with the head, hand, arm, shoulder, and thoracic cavity it should not be surprising that the morphology of the scapula – essentially a floating bone – and its axillary border are highly variable.

The examination of the relationship between the axillary border and scapular shape indicates that axillary border length and thickness correlate significantly to changes in infraspinous, overall scapular, and scapular spine size. In general, the axillary border lengthens and thickens as the subscapular region and scapular spine enlarge. These results, therefore, support the stated hypothesis that axillary border morphology responds to overall increases in the size of the scapula, and in particular to the size of the infraspinous region. Trinkaus has previously suggested that the long scapular spine heights seen in Neandertals is indicative of overall musculature hypertrophy of this region *(10)*, specifically of the rotator cuff muscles on the dorsal scapular surface (supraspinatus and infraspinatus) *(20)*. The findings in this study of strong correlations between axillary border thickness, spine height, and spine thickness is in agreement with this notion of muscular hypertrophy and general scapular robusticity.

CONCLUSIONS

A reexamination of axillary border morphology in modern humans and two Neandertals reveals that the bisulcate condition, present in large quantities among modern humans, is more robust than the dorsal type among those samples and individuals observed in this study. As the bisulcate condition is common in modern hunter-gatherer and industrial populations, it is clear that scapular robusticity is not exclusive to Neandertals. Further data from dorsal axillary borders will aid in assessing the strength and meaningfulness of this result. Further, the results support the hypothesis that axillary border length and thickness correlate to measures of scapular size and scapular spine height. Future analyses of axillary border shape, particularly among the dorsal type, should aid in resolving these issues further. In particular, future analyses should aim to interpret the anatomical significance of axillary border shape, and how muscular hypertrophy affect sulcus shape and thickness.

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