



The Krapina Scapulae

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Abstract

The early Neandertal sample from Krapina preserves twenty partial scapulae, from immature and mature individuals, males and females. Their relatively broad scapulae and narrow glenoid fossae, similar to those of most Neandertals and contrasting with those of most early and recent modern humans, appear to be characteristic of archaic Homo generally, and they are therefore a retained ancestral configuration that persists through the terminal Middle Pleistocene time of the Krapina sample. Their axillary borders, with a considerable range of variation but showing a slight predominance of the dorsal sulcus pattern, are similar to Middle and Late Pleistocene archaic Homo, but they contrast with those of Early Pleistocene Homo and most recent humans, suggesting that the dorsal sulcus pattern and the less pronounced bisulcate arrangement are derived among at least western Old World late archaic humans. The functional significances of these variations remain unclear, although it is unlikely that the axillary border pattern reflects muscular hypertrophy.

INTRODUCTION

The human paleontological sample from the Hušjakova Rockshelter at Krapina preserves an exceptional number of scapulae, which exhibit considerable morphological variation. The large size and morphological attributes of this sample led D. Gorjanović-Kramberger (1, 2) to devote considerable effort to the Krapina scapular sample, following on earlier comments on Neandertal scapular morphology (3) and foreshadowing subsequent efforts during the twentieth century to document, analyze and account for the morphology of Neandertal scapulae (e.g., 6–18). However, although there are currently a number of Neandertal scapulae known from time periods subsequent to the Krapina sample, penecontemporaneous archaic *Homo* scapulae from OIS 6 or 5e are limited to the Tabun 1 partial skeleton and the fragmentary Bourgeois-Delaunay 2 scapula (9, 19). The early modern human ones from Qafzeh and Skhul (9, 20, 21) are slight younger, within OIS 5. Geologically older *Homo* scapulae are known from the Middle Pleistocene Atapuerca-SH sample (22) and the Early Pleistocene KNM-WT 15000 partial skeleton (23), plus the Early Pleistocene Dmanisi 4166 scapula (24). As a result, the Krapina scapulae provides a paleontological window on both the early Neandertal pattern and some indication of the expected degree of variability within one archaic *Homo* sample.

Given the degree of fragmentation of the Krapina scapulae, and Pleistocene *Homo* scapulae in general, this presentation will consider three aspects of their morphological variation: morphological (medio-lateral) length, glenoid fossa proportions, and axillary border morphol-

ogy. Angles between the glenoid plane, the spine and the axillary border are available for a number of scapulae, but fragmentation and variance in measurement technique make comparisons difficult; for completeness, the available Krapina angles are provided but only generally assessed. Other details are either too poorly preserved or present little variation of note (as with their coracoid processes).

THE KRAPINA SCAPULAE

The Krapina scapular sample has been inventoried in detail in Radovčić *et al.* (25: 81–84). It consists of twenty partial scapulae, Krapina 121 to Krapina 139. Two scapular spines originally separate (Krapina 140 and 141) have been attached along clean breaks to Krapina 124 and 129 respectively. Of these scapulae, seven are immature and eleven are right (Table 1). Ten of the mature scapulae provide partial or complete glenoid fossae, and all except four scapulae provide information on axillary border morphology. The scapular spines and coracoid processes are variably complete, but four of the scapulae (Krapina 125, 127, 130 and 132) have sufficiently complete glenoid fossae and spines to permit estimation of their mediolateral morphological lengths (none actually retains the vertebral border) (Figure 1).

Among the immature scapulae, it is not possible to assign developmental ages. However, from size and morphology they can be age sequenced, from youngest to oldest, from Krapina 122, to Krapina 121 and 137, to Krapina 123, 124 and 136.

TABLE 1

The Krapina scapulae. *provides data on the glenoid fossa. †provides data on the axillary border.

	Right	Left
Immature	121†	124†
	122†	136
	123†	137†
		137.1
Mature	126*†	125*†
	127*†	130*†
	128†	131*†
	129*†	138
	132*†	139*
	133*	
	134*†	
	135†	

Among the mature scapulae, most of the specimens can be assigned to »small« versus »large« morphs, something which is possible for most of the postcranial bones for which adequate samples are preserved. It is tempting to infer that the »small« morphs represent females and the »large« morphs males, but this cannot be confirmed (in the full Krapina sample, only the Krapina 207 and 209 pelvic remains are reliably sexable). Moreover, the level of sexual dimorphism of the Neandertals was not significantly different from that of recent human populations (26), indicating significant overlap in body size of the two sexes.

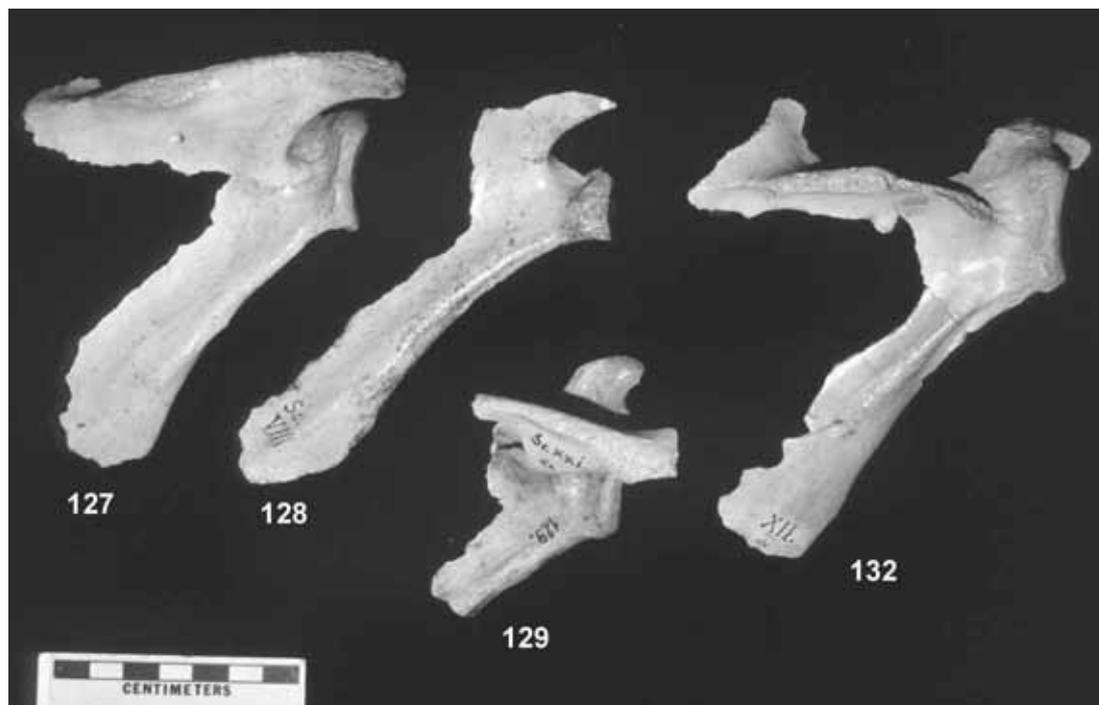


Figure 1. Dorsal views of four of the Krapina right scapulae, Krapina, 127, 128, 129 and 132. Krapina 127 and 132 provide estimates of their morphological lengths.

The resultant »small« morphs are Krapina 126, 127, 129, 131 and 132, and the »large« ones are Krapina 125, 128, 130, 133, 134 and 139. In addition, despite the normal levels of asymmetry in human scapulae (12, 27, Churchill pers. comm.), three sets of Krapina scapulae appear remarkably as though they are right-left pairs of the same individuals. They are the Krapina 121 and 137 immature scapulae, the Krapina 129 and 131 scapulae, and the Krapina 130 and 133 scapulae. These pairs are based on both qualitative assessments of morphology and, to the extent possible given the immaturity of the first pair and the pathological glenoid fossa of Krapina 130, on their glenoid fossa dimensions (Table 2).

Given the generally young age of the Krapina sample (28), it is not surprising that there is little pathological degeneration of the scapulae. The only cases involve osteoarthritis of right glenoid fossae. The central depression of the Krapina 125 slightly irregular glenoid fossa surface leads onto two vascular sulci, one 1.8 mm wide going ventrally and one 1.4 mm wide extending caudally. The subchondral bone of the Krapina 130 glenoid fossa is largely smooth with irregularities up to 8.5 mm wide ventrocaudally, and the margins on the ventrocaudal two-thirds have osteophytic growths. Neither seems to have affected function or other aspects of their morphology.

COMPARATIVE SAMPLES

The morphological assessment of the Krapina scapulae requires their placement in a comparative framework, which consists largely of the penecontemporaneous (late OIS 6 and OIS 5e) Bourgeois-Delaunay 2 and Tabun 1 scapulae, the early last glacial (late OIS 5 to mid OIS 3) western Eurasian Neandertals, the extreme southwest Asian Middle Paleolithic early (OIS 5) modern humans (from Qafzeh and Skhul), and the earlier Upper Paleolithic (OIS 3) early modern humans. In addition, as preserved, data are included from the earlier Atapuerca-SH, KNM-WT 15000 and Dmanisi *Homo* scapulae and for samples of recent human scapulae. As appropriate, reference is made to morphological patterns evident in earlier *Australopithecus*.

MORPHOLOGICAL LENGTH

Gorjanović-Kramberger (1) noted that the Krapina scapulae appeared relatively broad, but he did not provide a detailed assessment of their size. Since then, it has been documented that Neandertal scapulae are relatively broad compared to their humeral lengths (13) and even relative to their long clavicles (27). Since the breadth of the scapula reflects in part the development of rotator cuff muscles on its supraspinatus and infraspinatus surfaces, as well as the moment arms for the thoracoscapular muscles which produce scapular rotation (especially trapezius and serratus anterior) (29, 30), its dimensions are of relevance for scapular function. Scapular height, or even full axillary border length, is rarely preserved on Pleistocene *Homo*, but the relative durability of the spine provides a measurement or an approximation of mor-

phological (mediolateral) length [M-2 (31)] on a number of Late Pleistocene specimens (Table 2).

None of the Krapina scapulae is complete to the vertebral border, but four of them are sufficiently close to provide reasonable ($\pm 1-2$ mm) estimates of their morphological lengths (Table 2). Their values are relatively high, as are those of other Neandertals, but they fall well within the range of variation of the early modern human sample. In order to scale the morphological length to an indicator of body size on an isolated scapula, it was first assessed whether glenoid height could provide a surrogate measure of body size, given its general correlation with humeral articular dimensions (15). Using the side available (or right-left averaged) measurements for gle-

TABLE 2

Morphological lengths of the Krapina and comparative Late Pleistocene scapulae. Measurements in millimeters, and estimated values are in parentheses. Krapina, Neandertal and Qafzeh-Skhul data from personal measurement and Mc Cown & Keith (9). Upper Paleolithic data from Churchill (17), Kozlovskaya & Mednikova (43) and Trinkaus (27); Mean \pm standard deviation (N) provided for the recent human samples; data from Churchill (pers. comm.).

	Left	Right
Krapina 125	(115)	–
Krapina 127	–	(100)
Krapina 130	(107)	–
Krapina 132	–	(107)
<i>Neandertals</i>		
La Ferrassie 1	–	121.5
Kebara 2	107	(115)
Shanidar 1	–	110
Shanidar 2	–	(116)
Shanidar 3	(115)	–
Shanidar 4	(115)	–
<i>Qafzeh–Skhul</i>		
Qafzeh 9	–	(94)
Skhul 4	–	(95)
Skhul 5	–	102.5
<i>Early Upper Paleolithic</i>		
Arene Candide IP	(90)	–
Baouso da Torre 2	(96)	–
Dolní Věstonice 13	102.5	102
Dolní Věstonice 14	(108)	–
Dolní Věstonice 15	(92)	–
Dolní Věstonice 16	(108)	–
Pataud 5	–	(92)
Sunghir 1	(120)	–
<i>Recent Humans</i>		
Euroamericans	103.9 \pm 8.1 (30)	
Amerindians – Pueblo	98.1 \pm 4.3 (35)	
Aleuts	96.8 \pm 5.7 (46)	
Afroamericans	102.7 \pm 8.2 (50)	

noid height, humerus maximum length (M-1) and humerus distal articular breadth (M-12a), there are moderately strong correlations between glenoid height and the other two dimensions (Figure 2; $r = 0.758$ and 0.760 respectively). The Neandertals have slightly higher values on average relative to humerus length and slightly lower ones relative to distal articular breadth. The former reflects the moderately abbreviated proximal limbs of the cold-adapted Neandertals (32), and the latter reflects their upper limb articular hypertrophy (13). Glenoid height should therefore provide a reasonable average indicator of humeral, and therefore body, size.

In the resultant comparison of scapular morphological length to glenoid height (Figure 3), there is considerable scatter of the recent humans, but the majority of them fall within a relatively narrow distribution. The Krapina specimens and the early modern humans are completely separate, with the Krapina specimens having broader scapulae than any of the early modern humans and almost all of the recent humans. The OIS 3 Neandertals are more variable, with La Ferrassie 1 and Kebara 2, despite their broad scapulae relative to both

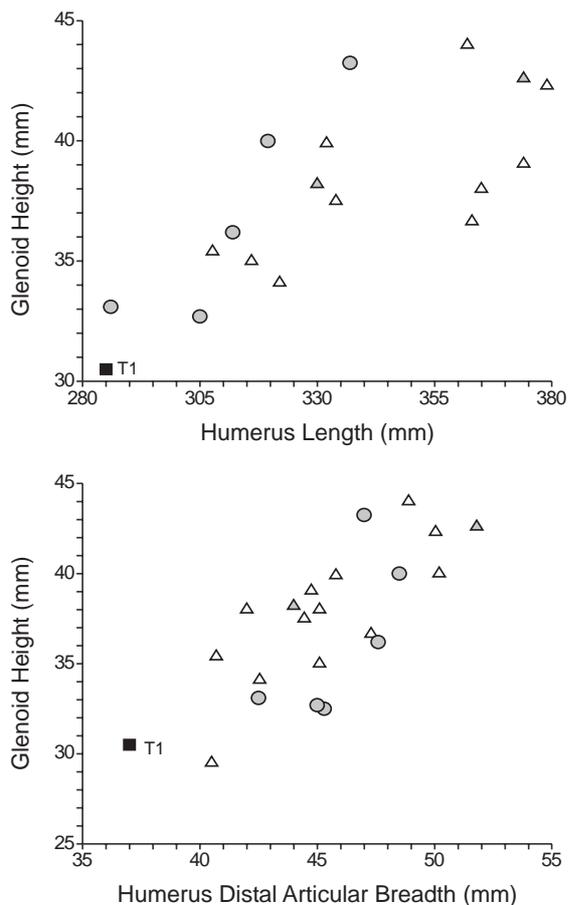


Figure 2. Bivariate plots of glenoid articular height versus associated humerus maximum length (above) and humerus distal articular breadth (below). Black square (T1): Tabun 1; gray circles: Neandertals; gray triangles: Qafzeh 8 and 9; open triangles; earlier Upper Paleolithic specimens.

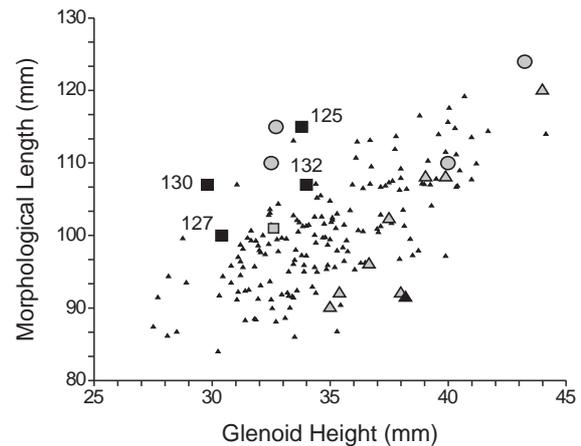


Figure 3. Bivariate plot of scapular morphological (mediolateral) length versus glenoid articular height. Black squares: Krapina scapulae (with specimen numbers indicated); gray square: KNM-WT 15000; gray circles: Neandertals; black triangle: Qafzeh 9; gray triangles: earlier Upper Paleolithic scapulae; small triangles: pooled recent humans (see Table 2 for samples)

humeral and clavicular length (13, 27), falling with the early modern humans. Shanidar 1 and 4 cluster with the relatively broad Krapina specimens.

The one earlier *Homo* scapula preserving both dimensions is from KNM-WT 15000 (23); the specimen is of an early adolescent (33), and it is not clear how differential development of morphological length and glenoid height might have affected its scapular proportions. Yet, its linear body proportions (34) imply that its scapulae should have been relatively narrow (35). Its position (based on its preserved breadth, which should be slightly larger given its still cartilagenous vertebral border) is along the broader margin of the recent human distribution, adjacent to the Krapina 127 and 132 specimens, and distinct from the early modern humans. Qafzeh 9 falls at the narrow margin of the entire distribution. These data suggest that a relatively broad scapula is the archaic *Homo* pattern, and that the Krapina specimens are following that ancestral pattern.

GLENOID FOSSA PROPORTIONS

Since at least the studies of Vallois (8), the relative narrowness of the Neandertal scapular glenoid fossa has been noted, usually expressed as a glenoid (breadth / height) index. Subsequent analyses and descriptions of their scapulae have reinforced this pattern, albeit noting some variation (e.g., 15, 22). In particular, Churchill & Trinkaus (15) documented that it was principally variation in glenoid breadth that produced the variation in indices, and they proposed that it is related to habitual degrees of loading in medial and lateral hyperrotation of the glenohumeral articulation.

As recently noted (27), if the upper limb asymmetry and right-handedness of almost all Pleistocene *Homo* (36) is taken into account, right and left glenoid fossa

TABLE 3

Diameters of the Krapina glenoid fossae. Maximum diameters include the glenoid labrum attachment areas, whereas articular diameters include only the subchondral bone within the glenoid labrum attachment (15, 17). Measurements in millimeters; measurements in parentheses are estimated. (P) indicates pathological alteration of the external margins.

	Side	Maximum height	Maximum breadth	Articular height	Articular breadth
125	Left	(36.6)	24.6	33.8	23.0
126	Right	—	—	—	21.0
127	Right	34.6	20.8	30.4	19.9
129	Right	32.4	19.8	30.4	18.7
130	Left	43.0(P)	28.4(P)	34.0	—
131	Left	33.5	20.0	30.0	19.0
132	Right	32.8	21.3	29.8	20.0
133	Right	37.2	24.5	34.0	23.5
134	Right	—	—	(33.5)	—
139	Left	—	—	36.5	—

provide slightly different distributions. The dimensions of the Krapina glenoid fossae (Table 3; Figure 4), using the articular height and breadth, are compared to other Pleistocene *Homo* scapulae using bivariate plots (Figure 5) and glenoid indices (Table 4). The latter are not significantly correlated with glenoid height (r^2 values of <0.001 and 0.059 for the Pleistocene sample, 0.013 and 0.009 for the pooled recent human sample), indicating that they should be a good reflection of the articular proportions.

The left glenoid fossae of the Krapina 131 and the Atapuerca-SH scapulae are relatively narrow, but Krapina 125, Tabun 1 and three of the Neandertals fall within the recent and early modern human distributions. The

TABLE 4

Comparative right and left glenoid indices (breadth / height x 100) for the Krapina, other Pleistocene and recent human samples. For sufficiently large samples, mean \pm standard deviation (N) are provided. Recent human data from Churchill (pers. comm.) except for the pooled right and left sample from Coimbra (22).

	Right Glenoid Index	Left Glenoid Index
Krapina (Tabun 1)	61.5, 65.4, 67.1, 69.1	63.3, 68.0 (63.9)
Atapuerca-SH	67.0, 62.5	62.2, 63.9
KNM-WT 15000, Dmanisi 4166	66.9, 67.6	—
Neandertals	66.8 \pm 6.9 (4)	69.1 \pm 2.9 (5)
Earlier Upper Paleolithic	72.5 \pm 5.7 (17)	71.7 \pm 3.8 (14)
Recent Euroamericans	72.7 \pm 4.4 (79)	72.0 \pm 4.0 (83)
Recent Europeans – Coimbra	72.6 \pm 4.2 (158)	
Recent Amerindians – Pueblo	72.5 \pm 3.7 (57)	73.0 \pm 3.7 (51)
Recent Inuits – Koniag	72.4 \pm 3.0 (74)	70.0 \pm 3.3 (73)
Recent Aleuts	70.4 \pm 4.6 (43)	70.0 \pm 6.2 (39)
Recent Afroamericans	72.5 \pm 3.1 (50)	71.9 \pm 2.5 (50)
Recent Amerindians – Peru	72.6 \pm 3.9 (17)	70.9 \pm 2.3 (16)

other two Neandertals (La Ferrassie 1 and Kebara 2), along with two earlier Upper Paleolithic specimens (Barma Grande 2 and Sungir 1), also have moderately narrow left glenoid fossae.



Figure 4. Lateral views of the Krapina 129 («small» morph) and 133 («large» morph) glenoid fossae. Scale in centimeters.

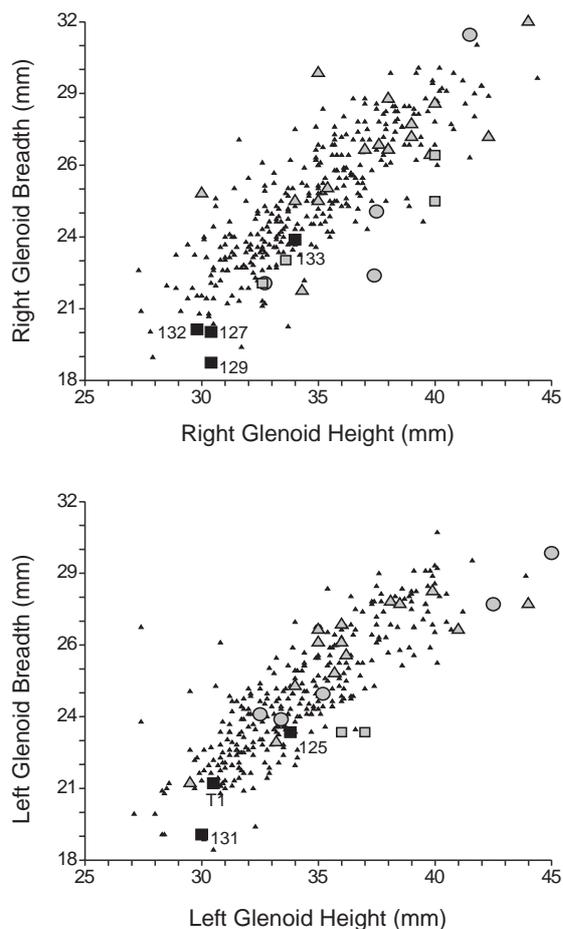


Figure 5. Glenoid articular breadth versus glenoid articular height for right (above) and left (below) scapulae. Black squares: Krapina (with specimen numbers indicated) and Tabun 1 (T1); gray squares: KNM-WT 15000, Dmanisi 4166 and Atapuerca-SH; gray circles: Neandertals; gray triangles: earlier Upper Paleolithic; small triangles: recent humans (see Table 4 for samples).

In the right glenoid fossa, however, the archaic *Homo* specimens, whether Early, Middle or Late Pleistocene in age, are largely below the core of the earlier Upper Paleolithic modern human distribution and, at most, along the narrow margin of the recent human scatter. There is some overlap in the early modern human and archaic human distributions, with the La Ferrassie 1 Neandertal having a relatively high position and two early modern humans, Barma Grande 2 and Muierii 3, falling with the archaic *Homo* specimens (Figure 5). None of the three adult Qafzeh-Skhul specimens with glenoid fossae (Qafzeh 8 and 9 and Skhul 5) is sufficiently complete to provide both measurements reliably (Trinkaus pers observ.), but the preserved portions [and published measurements (19, 20)] suggest that they may also have had moderately narrow glenoid fossae. The Atapuerca-SH, KNM-WT 15000 and Dmanisi 4166 glenoid fossa dimensions distribute with the Krapina and Neandertal scapulae, narrower than most of the earlier Upper Paleolithic modern human distribution. Most of the recent humans have

broader glenoid fossae on average, even though there are a few narrow ones in these samples and recent human samples are known (e.g., 37) with relatively narrow glenoid fossae.

From these data, it appears likely that a relatively narrow glenoid fossa, on average, is the ancestral pattern [it is also present in *Australopithecus* (22, 38, 39)], which was maintained in later Pleistocene archaic *Homo*. It could be argued that the differences in the right versus left distributions and the dorsoventral expansion of the fossa in Upper Paleolithic and subsequent modern humans may primarily reflect differential loading patterns with the emergence of Upper Paleolithic technologies [as previously suggested (15)]. In this case, the suggestion of relatively narrow fossae in the Middle Paleolithic Qafzeh-Skhul sample, despite their relatively gracile upper limbs (40, 41), may not be anomalous. However, the persistence of relatively broader glenoid fossae in most recent human samples, including modern industrial populations (Table 4; Figure 5), might argue against a strictly functional interpretation of fossa proportions. Regardless of the ultimate cause of these variations, the Krapina sample conforms to the pattern evident in other archaic *Homo*.

AXILLARY BORDER MORPHOLOGY

Variation in the form of the scapular axillary border has been central to assessments of Neandertal shoulder remains. In particular, it has been repeatedly noted that they frequently exhibit a pronounced dorsal axillary ridge, bordered dorsolaterally by a clear sulcus, and adjacent to a lateral crest which is displaced ventrally (the dorsal pattern). Such a pattern is present in recent human samples but exceedingly rare. Approximately two-thirds of recent humans have a flat dorsal surface, a dorsally located lateral margin, and a variably pronounced ventral sulcus (the ventral pattern) (Table 6). The remaining third of recent humans have a lateral crest in the middle of the axillary lateral border, small sulci adjacent to the crest, and evenly convex dorsal and ventral surfaces (the bisulcate pattern).

The Krapina sample (Table 5; Figures 6–8) shows considerable variability. None of the scapulae exhibits a clear ventral pattern, although the Krapina 127 exhibits the lateral margin displaced to the dorsal side but the lateral crest closer to the middle of the lateral margin; its overall form therefore approaches the ventral sulcus pattern, but its crest position suggests the bisulcate configuration. At the other extreme, the adult Krapina 132 and the immature Krapina 122 scapulae have the lateral crest fully ventral and a concave (or sulcal) dorsal margin, exhibiting the full dorsal pattern. The remainder of the scapulae, both immature and mature, vary between these extremes in the sample, with six of them being intermediate between strict dorsal and bisulcate designations, two having the usual bisulcate pattern, and six being strictly dorsal. The variation is principally within the

TABLE 5

Axillary border morphology of the Krapina scapulae. Ventral: mediolateral contour from the subscapularis surface to the lateral muscular crest. Dorsal: mediolateral contour from the infraspinatus surface to the lateral muscular crest; »ridge« refers to a prominent dorsal ridge parallel to the axillary border. Crest: approximate dorsoventral position of the lateral muscular crest. Diagnosis: axillary border category following Eickstedt (6).

	Side	Maturity	Ventral	Dorsal	Crest	Diagnosis
121	right	immature	convex	flat	mid lateral	dorsal to bisulcate
122	right	immature	flat	concave	ventral	dorsal
123	right	immature	convex	concave	ventral third	dorsal
124	left	immature	convex	flat	mid lateral	dorsal to bisulcate
125	left	adult	convex	flat	dorsal third	bisulcate
126	right	adult	convex	convex	mid lateral	bisulcate
127	right	adult	convex	convex	dorsal third	bisulcate to ventral
128	right	adult	convex	concave with ridge	ventral third	dorsal to bisulcate
129	right	adult	convex	concave with ridge	ventral third	dorsal
130	left	adult	convex	concave with ridge	mid lateral	dorsal to bisulcate
131	left	adult	convex	concave with ridge	ventral third	dorsal
132	right	adult	convex	deep sulcus with prominent ridge	ventral	dorsal
134	right	adult	convex	flat with ridge	mid lateral	dorsal to bisulcate
135	right	adult	convex	concave with prominent ridge	mid lateral	dorsal
137	left	immature	convex	flat	mid lateral	dorsal to bisulcate

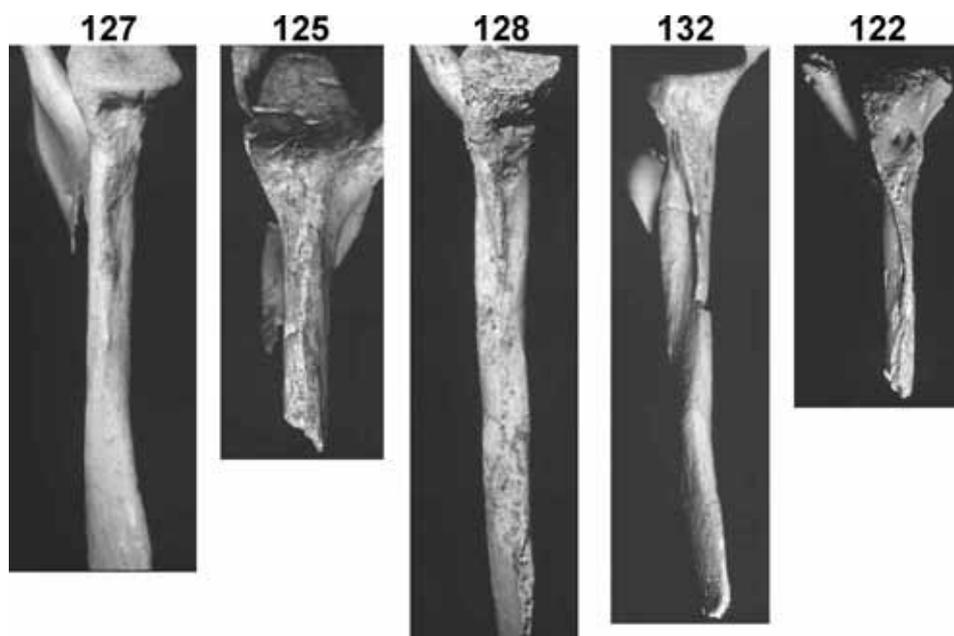


Figure 6. Laterocaudal views of Krapina scapulae axillary borders. From left to right, Krapina 127 (ventral/bisulcate), 125 (bisulcate), 128 (dorsal/bisulcate), 132 (dorsal), and 122 (immature dorsal). Scapulae not to scale.

dorsal surface and involving the dorsoventral position of the lateral crest.

Pooling together the probable pairs of Krapina 121 and 137 and Krapina 129 and 131, and then counting each scapula split between two categories as one-half for each category, a little more than half of the Krapina scapula exhibit the dorsal pattern, with the remainder largely presenting a bisulcate one (Table 6). The addition of the penecontemporaneous Bourgeois-Delaunay 2 and Ta-

bun 1 scapulae, both of which exhibit the dorsal pattern, raises the dorsal pattern frequency for the OIS 6/5e sample close to two-thirds and the bisulcate one to one-third. These figures are slightly below those of the later Neandertal sample, but generally similar to them.

Both of these late archaic samples contrast with the early modern human samples. In the latter samples, the bisulcate pattern is dominant, even though the dorsal pattern is present in the Upper Paleolithic sample. Among

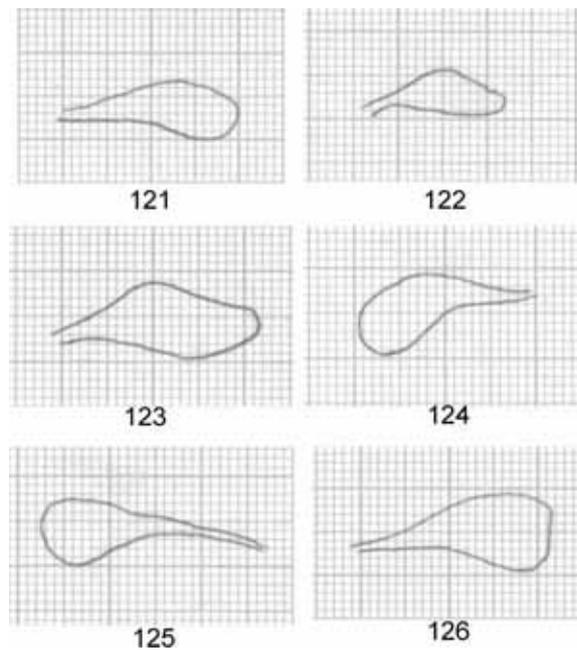


Figure 7. Subperiosteal contours of the Krapina 121 to 126 axillary borders, at the approximate midpoints of the axillary borders. The sections are oriented approximately mediolaterally, with the dorsal sides above. Grids in millimeters. Krapina 121 to 124 are immature.

earlier *Homo*, the three incomplete Atapuerca-SH scapulae appear to have the dorsal pattern (22), but the Early Pleistocene Dmanisi 4166 and KNM-WT 15000 scapulae (23, 24), as well as *Australopithecus* scapulae (38, 39), exhibit the ventral sulcus pattern. As noted by Boule (4;

see also 7, 22), the ventral pattern is the ancestral (and general Anthropoid primate) pattern, with the dorsal (and perhaps bisulcate) pattern being derived. If this is the case, the derived pattern had emerged at least in Europe by the middle Middle Pleistocene, and then it shifted back to the more ancestral pattern only well after the emergence of modern humans. Whatever the polarities are of the character states, it is apparent that the border morphology remained variable within the Krapina sample and within the more diverse Neandertal sample.

As previously noted (15), the functional interpretation of the axillary border variation as reflecting differential hypertrophy of the rotator cuff muscles (12; see also 7) is no longer considered as valid. Even though the more »dorsal« patterns occur differentially on the right side in asymmetrical recent humans (12, 42), possibly reflecting dominant arm hypertrophy, there is little correlation between the axillary border morphology and indicators of upper limb hypertrophy in samples of Late Pleistocene and recent humans (18).

The presence of the clear dorsal pattern in two of the immature scapulae, and the dorsal to bisulcate pattern in the other two, indicates that this morphological pattern emerges relatively early during scapular development. This both justifies the pooling together of mature and immature scapulae in the frequency assessment of axillary border patterns and reinforces the interpretation that the morphology is principally epigenetic.

THE SCAPULAR ANGLES

For angular variations of the Krapina scapulae, Table 7 provides their spinoglenoid angles and two variants of

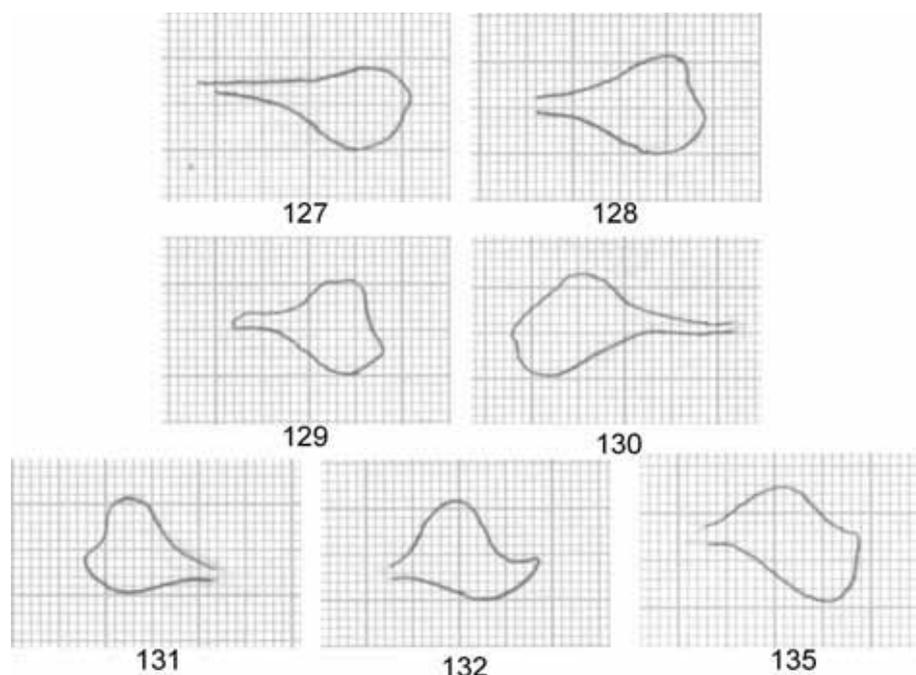


Figure 8. Subperiosteal contours of the Krapina 127 to 132 and 135 axillary borders, at the approximate midpoints of the axillary borders. The sections are oriented approximately mediolaterally, with the dorsal sides above. Grids in millimeters.

TABLE 6

Comparative frequencies of axillary border morphology for Late Pleistocene western Eurasian samples and recent human samples. Recent human data from Trinkaus (12)*, Chambers (42)†, Carretero *et al.* (22)‡ and Dittner (44)§.

	Ventral Sulcus	Bisulcate	Dorsal Sulcus	N
Krapina	3.3%	36.7%	60.0%	15
Krapina + Bourgeois-Delaunay 2 & Tabun 1	2.9%	32.4%	64.7%	17
Neandertals	0.0%	25.0%	75.0%	10
Qafzeh-Skhul	20.0%	80.0%	0.0%	5
Earlier Upper Paleolithic	12.5%	73.9%	13.6%	22
Recent Europeans – Serbia*	75.8%	23.8%	0.4%	120
Recent Europeans – Germany†	65.3%	21.9%	6.4%	171
Recent Europeans – Portugal‡	67.3%	32.7%	0.0%	124
Recent Amerindians – Pecos*	86.6%	13.4%	0.0%	119
Recent Amerindians – Arikara§	62.6%	36.7%	0.6%	198

TABLE 7

Krapina scapular angles for sufficiently complete bones. The glenoaxillary angle was taken using the lateral edge of the axillary border (or an approximation of it) (M-17) and using the dorsal bar of the axillary margin (45) (the glenoaxillary lateral angle and the glenoaxillary bar angle respectively). Estimated angles are in parentheses, due to the incompleteness of the axillary border and/or the scapular spine. The Krapina 126 glenoid fossa is incomplete, resulting in the provided range of values.

	Side	Maturity	Spinoglenoid Angle	Glenoaxillary Lateral Angle	Glenoaxillary Bar Angle
121	right	immature	–	138°	135°
123	right	immature	–	153°	152°
125	left	adult	(81°)	–	146°
126	right	adult	–	138°–141°	134°–137°
127	right	adult	(83°)	124°	138°
128	right	adult	–	(133°)	(130°)
129	right	adult	–	–	141°
130	left	adult	(75°)	134°	127°
131	left	adult	–	–	138°
132	right	adult	(83°)	139°	136°

the glenoaxillary angle. These angles show considerable variation within and among recent human populations (8).

The limited comparative spinoglenoid angle data for earlier *Homo* scapulae, 89° and 87° for two Atapuerca-SH scapulae and an angle was close to 90° for KNM-WT 15000 (22, 23), cluster around a right angle. The Krapina values are all relatively low, similar to those of other Neandertals (13), and close to the lower ends of recent human ranges of variation (8).

The Krapina scapulae have glenoaxillary lateral angles (Table 7) close to the middle of recent human values, and they are moderately lower than the values for most Neandertals (138.9° ± 7.3°, N=7) and the earlier Atapuerca-SH scapulae (140° & 144°). KNM-WT 15000 (127°) and Dmanisi 4166 (129°) have angles close to the lower end of the later Pleistocene archaic *Homo* scapular

variation (24). However, all of these archaic *Homo* angles fall within recent human ranges of variation, including those of early modern humans, and above those of most large bodied apes. It is unclear to what extent they are measuring minor variations in the lateral deviation of the axillary border versus the cranial deviation of the glenoid fossa. Moreover, all of them are independent of *in vivo* anatomical orientations of the scapula on the thorax (probably best indicated by the vertebral border) and therefore of uncertain functional significance.

CONCLUSIONS

These brief morphological and morphometric considerations of the Krapina scapular sample reinforce their general affinities to other archaic *Homo* samples, especially those of the Middle and Late Pleistocene of the northwestern Old World. The Krapina specimens ex-

hibit the relatively large mediolateral dimensions and narrow glenoid fossae that characterize most archaic *Homo*. At the same time, they show a distinct sample distribution towards the dorsal axillary border morphology, in contrast with Early Pleistocene *Homo*, *Australopithecus* and large-bodied apes. In this distribution, they are similar to earlier Atapuerca-SH and more recent Neandertal scapulae. In terms of the polarities of these traits, the Krapina scapulae show the combination of ancestral and derived features, some of the latter shared with early and recent modern humans, that characterize the later Neandertals. It remains to be assessed whether these features, from scapular length, to glenoid fossa breadth, to axillary border morphology, principally reflect changing technology and arm loading levels and patterns, or are more indicative of inter- and intra-populations patterns of epigenetic variation.

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