

Original scientific paper

Krapina and Other Neanderthal Clavicles: A Peculiar Morphology?

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Abstract

The clavicle is the less studied element of the shoulder girdle, even if it is a very important bone for human evolution because it permits all movements outside the parasagittal plan. In this work, clavicle curvatures are studied by projecting them on a cranial and a dorsal plan, which are perpendicular. In cranial view, there is no difference within the genus Homo, and Neanderthal clavicles are not more S-shaped than modern human ones. On the contrary, the dorsal view allows to distinguish two human groups. The first includes Homo habilis, Homo ergaster and Neanderthal. Their clavicles are characterized by two curvatures, an inferior one at the acromial end and a superior one at the sternal end. The second group includes only modern human, whose clavicles are characterized by the presence of the inferior curvature only. The shape of the clavicle in dorsal view is associated to the position of the scapula in regard to the thorax. Two curvatures are associated to a high scapula, and, on the contrary, a unique curvature is associated to a scapula in a low position in regard to the thorax. Moreover, the two curvatures of the modern human clavicle in dorsal view constitute an apomorphic character in regard to the other human species.

INTRODUCTION

E ven if the clavicle is less studied than the other two bones of the shoulder complex, it is not out of interest because it allows all movements of the upper limbs outside the parasagittal plane. Most works on this bone are strictly anthropological and give a good overview of its morphological variations (1-15). On the contrary, just a very few studies compare Primate clavicles from the point of view of comparative anatomy or functional morphology (16-26). This latter remark explains in part why fossil clavicles are so neglected and limited to descriptions although some authors have tried to go further (25, 27-30).

In this work we describe clavicle morphology within the genus *Homo*, from *Homo habilis* to modern human, and try to interpret differences and similarities in adaptive and evolutionary ways.

MATERIALS AND METHODS

Materials

Our samples include the following fossils: *Homo habilis*, *Homo ergaster*, *Homo antecessor*, Neanderthal and Upper Palaeolithic remains (Table 1) and modern human (MH) or *Homo sapiens sapiens* from sev-

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 TABLE 1

 Fossil clavicles studied; * Original remains; R: right and L: left; Upper Palaeolithic humans include Abri Pataud, Omo I KSH

Middle Palaeolithic Neanderthal (Nd)	Upper Palaeo	olithic humans (UP)	
Régourdou (R)	Abri Pataud (R)* Omo I KSH (L) Qafzeh 9 (L)		
Régourdou (L)	Tafe	oralt (Taf)	
Kebara 2 (R)	Taf V-6* (<i>R</i>)	Taf XIIIa* (L)	
ebara 2 (L)	Taf XXIII* (L)	Taf VIII-3bis* (L)	
a Ferrassie I (R)*		` '	
a Ferrassie I (L)*	Taf XIX-3a* (L)	$\operatorname{Taf} XXVa^*(R)$	
Teanderthal (R)	Taf V-24* (<i>L</i>)	Taf IX-39* (<i>L</i>)	
rapina 153 (L)*	Taf XI-AR* (R)	Taf XIIIb* (R)	
Krapina 142 (R)*	$\operatorname{Taf} XVa^*(L)$	Taf XVIIa* (R)	
Krapina 143 (R)*	Taf XVc* (L)	Taf XVI-15* (R)	
Krapina 154 (L)*	Taf XVII-26* (<i>R</i>)	Taf XVI* (R)	
Krapina 145 (R)*	Taf XVIII-6* (R)	Taf XIV * (L)	
Grapina 145 (R)*	Taf 24-5* (R)	Taf XIX-3* (R)	
Krapina 155 (L)*	Taf XXVc* (L)		
Krapina 149 (R)*	` '		
Krapina 144 (R)*	Lower Palaeolithic		
Krapina 156 (L)*	Homo antecessor	Homo ergaster	
a Chapelle-aux-Saints (L)*	Gran Dolina ATD6-50	KNM-WT 15000	
	Homo habilis		

and all Taforalt remains.

eral parts of the world (33 clavicles). This material belongs to the *Laboratoire d'Anthropologie Biologique du Musée de l'Homme*, Paris (France), the *Institut de Paléontologie Humaine*, Paris (France) and the Croatian Natural History Museum, Zagreb (Croatia).

Most fossil clavicles used in this study are well preserved even if some are eroded at their extremities, and only La Chapelle-aux-Saints, Krapina 149 right, 145 right, 144 right, 155 left, 156 left and Qafzeh 9 left are not complete (31–33).

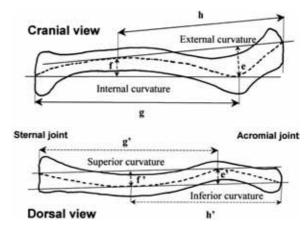
Methods

Due to its complexity, the morphology of the clavicle will be approached in regard to its curvatures. When projected on two perpendicular plane, one cranial and one dorsal, the clavicle morphology can be decomposed in elementary curvatures, as shown on Figure 1.

The middle arc of curvature is estimated according to Olivier's method (*34*) as the proportion between the length of the chord and the height of the curvature (Figure. 1):

Cranial plane:

- The acromial curvature (external one): e / h.100
- The sternal curvature (internal one): f/g.100



OH 48

Figure 1. Masurements of clavicle curvatures (34). Example on a right clavicle of Pan troglodytes.

Dorsal plane:

- The acromial curvature (inferior one): e' / h'.100
- The sternal curvature (superior one): f'/g'.100

The total length of the clavicle is measured with a calliper square as the greatest length of the bone.

The measurements and distribution of the variables have been computed with ViStat 6.4° (35). Graphics showing the range of variation of each variable are represented by the mean and \pm 1 two times standard deviation.

RESULTS

Curvatures in cranial view

In superior view, all fossil clavicles studied here are distributed within the range of variation of modern human ones (Figure 2, Table 2). This result means that Neanderthal clavicles, in superior view are less S-shaped than classically described (27, 29, 31, 36, 37) and show no differences with modern human ones in cranial view (Table 3). This result is confirmed by other recent works (24–26).

Some of the older remains display nevertheless some features of their own, even if their range of variation stays within that of modern human clavicles. In KNNM-WT 15000 (left and right) and OH 48 clavicles the internal curvature is more pronounced than the external one (Table 2). In the case of OH48, this morphology may be due to its state of conservation, because, as Napier (38) showed it, this clavicle lack a great part of is acromial extremity and thus its external curvature is underestimated. On the contrary, the KNM-WT 15000 clavicles is nearly complete (39).

Curvatures in dorsal view

In dorsal view, modern human clavicles can be classified into three morphological groups, or types (Figure 3

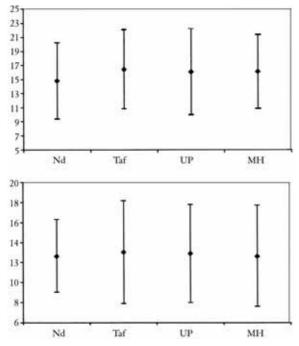


Figure 2. Mean and range of variation of clavicle curvatures in superior view in Neanderthal, Taforalt, Upper Palaeolithic remains and Modern Human. Above: external curvature; Beneath: internal curvature.

TABLE 2

Values of the external and internal curvatures in Upper Palaeolithic remains, Neanderthal, *Homo antecessor, Homo ergaster* and *Homo habilis. #*: The incompleteness of the bone make impossible to know if a curvature exist or not.

	Individual	Internal	External
Linner	Abri Pataud	curvature 9.7	12.1
Upper Palaeolithic	Omo I KSH (L)	13.1	14.56
T dideontine	Qafzeh 9 (L)	10.7	/
	Taf V-6 (R)	19.1	16.3
	Taf XXIII (L)	10.9	9.9
	Taf XIX-3a (L)	14.0	10.6
	Taf V-24 (L)	16.3	13.2
	Taf XI-AR (R)	13.4	11.2
	Taf XVa (L)	18.0	13.8
	Taf XVc (L)	18.9	16.5
	Taf XVII-26 (R)	19.3	12.7
	Taf XVIII-6 (R)	16.3	15.0
	Taf XIIIa (L)	11.9	11.4
	Taf VIII-3bis (L)	16.5	13.2
	Taf XXVa (R)	17.1	10.5
	Taf IX-39 (L)	17	10.5
	Taf XIIIb (R)	16.5	12.8
	Taf XVIIa (R)	14.3	14.4
	Taf XVI-15 (R)	13.1	8.2
	Taf XVI (R)	20.8	16.8
	Taf XIV (L)	16.2	12.2
	Taf 24-5 (R)	14.7	11.6
	Taf XIX-3 (R)	20.5	18.2
	Taf XXVc (L)	20.2	14.0
Neanderthal	Régourdou (R)	10.0	14.5
	Régourdou (L)	11.9	13.2
	Kebara (L)	11.1	16.5
	Kebara (R)	11.3	9.5
	La Ferrassie 1 (R)	13.2	14.2
	La Ferrassie 1 (L)	12.3	17.7
	Neanderthal (R)	13.2	16.7
	Krapina 153 (L)	10.8	10.3
	Krapina 142 (R)	17.4	16.7
	Krapina 143 (R)	13.9	12.1
	Krapina 154 (L).	14.1	11.4
	Krapina 149 (R)	20.0	/
	Krapina 145 (R)	/	11.3
	Krapina 144 (R)	12.0	/
	Krapina 155 (L)	18.1	/
	Krapina 156 (L)	/	14.7
	La Chapelle-aux-Saints (L)	/	12.2
	Mean	13.5	13.6
	Standard deviation	3.0	2.6
Ното	KNM-ER15 000 (R)	13.1	14.6
ergaster	KNM-ER15 000 (L)	15.3	14.7
Homo antecessor	ATD-6 50 (R)	12.4	18.7
Homo habilis	OH48 (L)	14.3	13.8

TABLE 3

T-test comparing the external and internal curvatures between Neanderthal, modern human, Upper Palaeolithic and Taforalt remains for a confidence interval level of 95%.

EXTERNAL CURVATURE					INTERNA	L CURVATUR	E		
Sample stati	istics				Sample statistics				
	N	Mean	StDev	Var		N	Mean	StDev	Var
MH	33	16.115	2.645	6.995	MH	33	12.616	2.522	6.362
UP	23	16.055	3.053	9.320	UP	24	12.866	2.446	5.985
1 33	Sample Differences DiffMean = 0.060 StErr = 0.765 Var = 7.942 (Pooled)				Sample Differences DiffMean = -0.25		= 0.668 Var	= 6.205 (I	Pooled)
Significance Test Result		078 df = 5	4.0	P = 0.9381	Significance test Test Result T	= -0.374	Df = 55.0	P = 0	.7097
Sample stati	istics				Sample statistics				
1	N	Mean	StDev	Var		N	Mean	StDev	Var
MH	33	16.115	2.645	6.995	MH	33	12.616	2.522	6.362
Taf	21	16.429	2.824	7.974	Taf	21	13.000	2.567	6.587
Sample Diffe DiffMean =		StErr = 0.758	Var =	7.372 (Pooled)	Sample Differences $DiffMean = -0.38$		= 0.709 Var	= 6.449 (I	Pooled)
Significance Test Result		Df = 5	52.0	P = 0.6803	Significance test Test Result T	= -0.542	Df = 52.0	P = 0	.5901
Sample stati	istics				Sample statistics				
F	N	Mean	StDev	Var		N	Mean	StDev	Var
Nd	17	14.798	2.698	7.281	Nd	17	12.614	1.812	3.282
MH	33	16.115	2.645	6.995	MH	33	12.616	2.522	6.362
Sample Diffe DiffMean =		StErr = 0.795	Var =	7.091 (Pooled)	Sample Differences. DiffMean $= -0.00$		= 0.690 Var	= 5.335 (I	Pooled)
Significance Test Result		1.657 Df = 4	18.0	P = 0.1041	Significance test Test Result T	= -0.002	Df = 48.0	P = 0	.9981

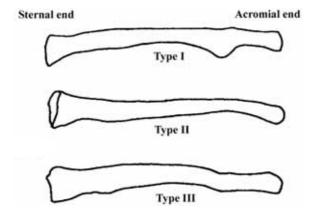


Figure 3. The three type of modern human clavicle (for a definition see text).

and Table 4). The most frequent one is type I (34), with possesses only the inferior curvature. Type II clavicles are far less common, and display two curvatures in dorsal view, a superior one at the sternal end and an inferior one

TABLE 4
Clavicle type proportions. Some clavicles show both type II and III morphologies, and thus the sum can be higher than 100%.

	Type I	Type II	Type III
Taforalt	61.9%	38.1%	33.3%
Upper Palaeolithic	60.9%	39.1%	30.4%
Modern human	84.9%	15.1%	24.2%
Neanderthal	21.4%	78.6%	0.0%

at the acromial end (34). Type III clavicles show also two curvatures, but the superior one is at the acromial end, and not at the sternal part (34). Type III is by far the less frequent one.

Upper Palaeolithic clavicles are very similar in shape to modern human ones (Table 6), but three clavicles in the Taforalt population display a peculiar type II morphology. Clavicles Taf VIIa and Taf XXVc possess only a

TABLE 5

Values of the internal and external curvatures in Upper Palaeolithic remains, Neanderthal, *Homo antecessor, Homo ergaster* and *Homo habilis*. Present: curvature extant but impossible to assess because of the incompleteness of the fossil.; /: The incompleteness of the bone make impossible to know if a curvature exist or not.

Upper		Individual	Inferior curvature	Superior curvature
Qafzeh 9 (L) 8.6 / Taf V-6 (R) 5.8 0 Taf XXIII (L) 5.1 0 Taf XIX-3a (L) 3.7 3.5 Taf V-24 (L) 3.4 0 Taf XV-24 (L) 5.3 0 Taf XV-1-26 (R) 6 0 Taf XVIII-6 (R) 4.6 0 Taf XVIII-6 (R) 4.6 0 Taf XVIII-5 (R) 4.6 0 Taf XVIII-7 (R) 4.5 3.1 Taf XVIII (R) 0 2.5 Taf XVIII (R) 0 2.5 Taf XVIII (R) 6.3 3.3 Taf XVI (L) 0 0 Taf XXIV (L) 0 0 Taf XXIV (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (R) 7.4 8.0 Régourdou (R) 7.4 8.0 Résourdou (R) 7.4 6.2 Responsable 1 (R) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (R) 5.4 6.2 Krapina 143 (R) 6.3 0 Krapina 144 (R) 7.4 6.2 Krapina 145 (L) 6.3 6.6 Krapina 145 (L) 6.3 6.6 Krapina 145 (R) 7.2 Krapina 145 (R) 7.2 Krapina 145 (R) 7.2 Krapina 145 (R) 7.2 Krapina 146 (R) 7.2 Krapina 147 (R) 7.2 Krapina 148 (R) 7.2 Krapina 149 (R) 13.3 7 Krapina 149 (R) 13.3 8 Krapina 150 (L) 5.3 8.1	Upper	Abri Pataud	6.9	0
Taf V-6 (R) 5.8 0 Taf XXIII (L) 5.1 0 Taf XXIII (L) 5.1 0 Taf XIX-3a (L) 3.7 3.5 Taf V-24 (L) 3.4 0 Taf XI-AR (R) 5.7 0 Taf XVa (L) 5.3 0 Taf XVe (L) 0 0 Taf XVII-26 (R) 6 0 Taf XVIII-26 (R) 4.6 0 Taf XVIII-3bis (L) 10.7 0 Taf XIIIa (L) 3.9 0 Taf VIII-3bis (L) 10.7 0 Taf XXIII (R) 3.3 3.6 Taf XIIIb (R) 3.3 3.6 Taf XVII (R) 0 2.5 Taf XIII (R) 0 2.5 Taf XVI (R) 6.3 3.1 Taf XVI (R) 6.3 3.3 Taf XIV (L) 0 0 Taf 24-5 (R) 3.1 0 Taf XXVa (R) 3.5 Taf XIX-3 (R) 3.4 5.97 Taf XXVe (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 Krapina 153 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 144 (R) 6.3 0 Krapina 145 (R) 6.3 0 Krapina 145 (R) 7.2 Krapina 145 (R) 7.3 Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1	Palaeolithic	Omo I KSH (L)	4.3	3.6
Taf XXIII (L) 5.1 0 Taf XIX-3a (L) 3.7 3.5 Taf V-24 (L) 3.4 0 Taf XI-AR (R) 5.7 0 Taf XVa (L) 5.3 0 Taf XVc (L) 0 0 0 Taf XVII-26 (R) 6 0 Taf XVIII-6 (R) 4.6 0 Taf XVIII-8 (R) 3.5 2.7 Taf IX-39 (L) 6.6 0 Taf XIIIb (R) 3.3 3.6 Taf XVII (R) 0 2.5 Taf XVII-15 (R) 4.5 3.1 Taf XVII (R) 0 2.5 Taf XVII-15 (R) 4.5 3.1 Taf XVI (R) 6.3 3.3 Taf XIV (L) 0 0 Taf XIX-3 (R) 3.5 2.7 Taf XXV-3 (R) 3.5 2.7 Taf XVI (R) 5.3 3.1 Taf XIV (L) 5.3 Taf XIX-3 (R) 5.9 Taf XXV-3 (R) 5.9 Taf XXV-4 (R) 5.9 Taf XXV-5 (R) 5.9 Taf XXV-6 (R) 5.9 Taf XXV-6 (R) 5.9 Taf XXV-6 (R) 5.4 5.8 La Ferrassie 1 (R) 5.4 5		Qafzeh 9 (L)	8.6	/
Taf XIX-3a (L) 3.7 3.5 Taf V-24 (L) 3.4 0 Taf XI-AR (R) 5.7 0 Taf XVa (L) 5.3 0 Taf XVIII (L) 0 0 0 Taf XVIII-26 (R) 6 0 Taf XVIII (L) 3.9 0 Taf XIII (L) 3.9 0 Taf XIII (L) 3.5 2.7 Taf IX-39 (L) 6.6 0 Taf XVIII (R) 0 2.5 Taf XVII (R) 3.3 3.6 Taf XVII (R) 0 2.5 Taf XIV (L) 0 0 Taf XVII (R) 0 1.5 Taf XVX (R) 3.5 2.7 Taf IX-39 (L) 6.6 0 0 Taf XIII (R) 0 1.5 Taf XVI (R) 6.3 3.3 Taf XIV (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 Krapina 153 (L) 3.8 3.9 Krapina 144 (R) 6.9 5.9 Krapina 145 (R) 6.3 6.6 Krapina 145 (R) 7.2 Krapina 146 (R) 7.4 Krapina 147 (R) 6.3 6.6 Krapina 149 (R) 13.3 / Krapina 144 (R) 9.3 / Krapina 145 (L) 6.3 6.6 Krapina 145 (L) 2.2 / La Chapelle-aux-Saints (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1		Taf V-6 (R)	5.8	0
Taf V-24 (L) 3.4 0 Taf XI-AR (R) 5.7 0 Taf XVa (L) 5.3 0 Taf XVc (L) 0 0 Taf XVIII-26 (R) 6 0 Taf XVIII-6 (R) 4.6 0 Taf XIIIa (L) 3.9 0 Taf VIII-3bis (L) 10.7 0 Taf XXVa (R) 3.5 2.7 Taf IX-39 (L) 6.6 0 Taf XVIII (R) 0 2.5 Taf XVII (R) 0 2.5 Taf XVI (R) 6.3 3.3 Taf XVI (R) 6.3 3.3 Taf XVI (R) 6.3 3.3 Taf XIV (L) 0 0 Taf XIX-3 (R) 3.1 0 Taf XIX-3 (R) 3.4 5.97 Taf XXVc (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 144 (R) 6.3 6.6 Krapina 149 (R) 13.3 / Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 Standard deviation 2.8 Homo articles of the decision of the contents of the conte		Taf XXIII (L)	5.1	0
Taf XI-AR (R) 5.7 0 Taf XVa (L) 5.3 0 Taf XVc (L) 0 0 Taf XVIII-26 (R) 6 Taf XVIII-26 (R) 4.6 Taf XIIIa (L) 3.9 0 Taf VIII-3bis (L) 10.7 0 Taf XXVa (R) 3.5 2.7 Taf IX-39 (L) 6.6 0 Taf XVIII (R) 3.3 3.6 Taf XVII (R) 0 2.5 Taf XVI-15 (R) 4.5 3.1 Taf XVI (R) 6.3 3.3 Taf XVI (R) 6.3 3.3 Taf XVI (R) 6.3 3.1 Taf XIX-3 (R) 3.4 5.97 Taf XXVc (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 154 (L) 6.3 6.6 Krapina 155 (L) 6.8 Present Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 La Chapelle-aux-Saints (L) 4.9 Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4		Taf XIX-3a (L)	3.7	3.5
Taf XVa (L) 5.3 0 Taf XVc (L) 0 0 Taf XVIII-26 (R) 6 Taf XVIII-6 (R) 4.6 Taf XIIIa (L) 3.9 0 Taf VIII-3bis (L) 10.7 0 Taf XXVa (R) 3.5 2.7 Taf IX-39 (L) 6.6 0 Taf XVIIIb (R) 3.3 3.6 Taf XVII (R) 0 2.5 Taf XVI-15 (R) 4.5 3.1 Taf XVI (R) 6.3 3.3 Taf XVI (R) 6.3 3.3 Taf XIV (L) 0 0 Taf XIX-3 (R) 3.1 0 Taf XIX-3 (R) 3.4 5.97 Taf XXVc (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 145 (R) 6.3 0 Krapina 145 (R) 6.3 6.6 Krapina 146 (R) 7.4 Krapina 147 (R) 6.3 6.6 Krapina 148 (R) 6.3 0 Krapina 149 (R) 13.3 / Krapina 145 (R) 7.2 Krapina 146 (R) 9.3 / Krapina 147 (R) 9.3 / Krapina 148 (R) 6.3 0 Krapina 149 (R) 13.3 / Krapina 149 (R) 13.3 / Krapina 149 (R) 13.3 / Krapina 145 (L) 2.2 / La Chapelle-aux-Saints (L) 2.2 / La Chapelle-aux-Saints (L) 3.8 Standard deviation 2.8 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4		Taf V-24 (L)	3.4	0
Taf XVc (L) 0 0 0 Taf XVIII-26 (R) 6 0 Taf XVIII-6 (R) 4.6 0 Taf XIIIa (L) 3.9 0 Taf VIII-3bis (L) 10.7 0 Taf XXVa (R) 3.5 2.7 Taf IX-39 (L) 6.6 0 Taf XIIIb (R) 3.3 3.6 Taf XVIIa (R) 0 2.5 Taf XVI-15 (R) 4.5 3.1 Taf XVI (R) 6.3 3.3 Taf XIV (L) 0 0 Taf 24-5 (R) 3.1 0 Taf XXVc (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 144 (R) 6.3 Krapina 145 (L) 6.3 Krapina 146 (R) 7.2 Krapina 155 (L) 6.8 Krapina 147 (R) 7.2 Krapina 148 (R) 9.3 Krapina 149 (R) 13.3 Krapina 140 (R) 7.2 Krapina 140 (R) 7.3 Krapina 150 (L) 7		Taf XI-AR (R)	5.7	0
Taf XVII-26 (R) 4.6 0 Taf XVIII-6 (R) 4.6 0 Taf XVIII-6 (R) 4.6 0 Taf XIIIa (L) 3.9 0 Taf VIII-3bis (L) 10.7 0 Taf XXVa (R) 3.5 2.7 Taf IX-39 (L) 6.6 0 Taf XIIIb (R) 3.3 3.6 Taf XVIIa (R) 0 2.5 Taf XVI-15 (R) 4.5 3.1 Taf XVI (R) 6.3 3.3 Taf XIV (L) 0 0 Taf XIX-3 (R) 3.4 5.97 Taf XXVc (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (R) 5.4 5.8 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 143 (R) 6.3 0 Krapina 144 (R) 9.3 Krapina 145 (R) 7.2 Krapina 146 (R) 7.2 Krapina 156 (L) 2.2 / La Chapelle-aux-Saints (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4 antecessor		Taf XVa (L)	5.3	0
Taf XVIII-6 (R) 4.6 0 Taf XIIIa (L) 3.9 0 Taf VIII-3bis (L) 10.7 0 Taf XXVa (R) 3.5 2.7 Taf IX-39 (L) 6.6 0 Taf XIIIb (R) 3.3 3.6 Taf XVIIa (R) 0 2.5 Taf XVI-15 (R) 4.5 3.1 Taf XVI (R) 6.3 3.3 Taf XIV (L) 0 0 Taf XIX-3 (R) 3.4 5.97 Taf XXVc (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 144 (R) 6.3 Krapina 145 (R) 7.2 Krapina 145 (R) 7.2 Krapina 156 (L) 2.2 / La Chapelle-aux-Saints / (L) Mean 6.3 4.4 Homo ergaster KNM-ER15 000 (R) 5.0 Antecessor		Taf XVc (L)	0	0
Taf XIIIa (L) 3.9 0 Taf VIII-3bis (L) 10.7 0 Taf XXVa (R) 3.5 2.7 Taf IX-39 (L) 6.6 0 Taf XIIIb (R) 3.3 3.6 Taf XVIIa (R) 0 2.5 Taf XVI-15 (R) 4.5 3.1 Taf XVI (R) 6.3 3.3 Taf XIV (L) 0 0 Taf 24-5 (R) 3.1 0 Taf XXVc (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 144 (R) 6.3 Krapina 145 (R) 7.2 Krapina 144 (R) 9.3 Krapina 145 (R) 7.2 Krapina 144 (R) 9.3 Krapina 145 (L) 2.2 La Chapelle-aux-Saints (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4 antecessor		Taf XVII-26 (R)	6	0
Taf VIII-3bis (L) 10.7 0 Taf XXVa (R) 3.5 2.7 Taf IX-39 (L) 6.6 0 Taf XIIIb (R) 3.3 3.6 Taf XVIIa (R) 0 2.5 Taf XVI-15 (R) 4.5 3.1 Taf XVI (R) 6.3 3.3 Taf XIV (L) 0 0 Taf 24-5 (R) 3.1 0 Taf XXVc (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 143 (R) 6.3 0 Krapina 144 (R) 6.3 Krapina 145 (R) 7.2 Krapina 145 (R) 7.2 Krapina 146 (R) 7.2 Krapina 147 (R) 9.3 / Krapina 148 (R) 9.3 / Krapina 149 (R) 13.3 / Krapina 140 (R) 7.2 Krapina 140 (R) 7.2 Krapina 150 (L) 2.2 / La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 KnM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4		Taf XVIII-6 (R)	4.6	0
Taf XXVa (R) 3.5 2.7 Taf IX-39 (L) 6.6 0 Taf XIIIb (R) 3.3 3.6 Taf XVIIa (R) 0 2.5 Taf XVI-15 (R) 4.5 3.1 Taf XVI (R) 6.3 3.3 Taf XIV (L) 0 0 Taf 24-5 (R) 3.1 0 Taf XIX-3 (R) 3.4 5.97 Taf XXVc (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 143 (R) 6.3 0 Krapina 149 (R) 13.3 / Krapina 149 (R) 13.3 / Krapina 144 (R) 9.3 / Krapina 145 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 Antecessor		Taf XIIIa (L)	3.9	0
Taf IX-39 (L) 6.6 0 Taf XIIIb (R) 3.3 3.6 Taf XVIIa (R) 0 2.5 Taf XVII-15 (R) 4.5 3.1 Taf XVI (R) 6.3 3.3 Taf XIV (L) 0 0 Taf 24-5 (R) 3.1 0 Taf XIX-3 (R) 3.4 5.97 Taf XXV-6 (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 143 (R) 6.3 0 Krapina 144 (R) 9.3 Krapina 145 (R) 7.2 Krapina 146 (R) 9.3 / Krapina 156 (L) 2.2 / La Chapelle-aux-Saints (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 ATD6-50 (R) 8.8 5.4 ATD6-50 (R) 8.8 5.4		Taf VIII-3bis (L)	10.7	0
Taf XIIIb (R) 3.3 3.6 Taf XVIIa (R) 0 2.5 Taf XVI-15 (R) 4.5 3.1 Taf XVI (R) 6.3 3.3 Taf XIV (L) 0 0 0 Taf 24-5 (R) 3.1 0 Taf XIX-3 (R) 3.4 5.97 Taf XXVc (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 143 (R) 6.3 0 Krapina 144 (R) 6.3 6.6 Krapina 145 (R) 7.2 Krapina 144 (R) 9.3 / Krapina 144 (R) 9.3 / Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4 antecessor		Taf XXVa (R)	3.5	2.7
Taf XVIIa (R) 0 2.5 Taf XVI-15 (R) 4.5 3.1 Taf XVI (R) 6.3 3.3 Taf XIV (L) 0 0 Taf 24-5 (R) 3.1 0 Taf XXVc (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 144 (R) 6.3 0 Krapina 145 (R) 7.2 Krapina 146 (R) 7.2 Krapina 147 (R) 9.3 / Krapina 148 (R) 9.3 / Krapina 149 (R) 13.3 / Krapina 140 (R) 9.3 / Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4		Taf IX-39 (L)	6.6	0
Taf XVI-15 (R) 4.5 3.1 Taf XVI (R) 6.3 3.3 Taf XIV (L) 0 0 Taf 24-5 (R) 3.1 0 Taf XIX-3 (R) 3.4 5.97 Taf XXVc (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 143 (R) 6.3 0 Krapina 144 (R) 6.3 6.6 Krapina 155 (L) 6.3 6.6 Krapina 145 (R) 7.2 Krapina 144 (R) 9.3 / Krapina 156 (L) 2.2 / La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4		Taf XIIIb (R)	3.3	3.6
Taf XVI (R) 6.3 3.3 Taf XIV (L) 0 0 Taf 24-5 (R) 3.1 0 Taf XIX-3 (R) 3.4 5.97 Taf XXVc (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 144 (R) 6.3 6.6 Krapina 145 (R) 7.2 Krapina 145 (R) 7.2 Krapina 146 (R) 9.3 / Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4		Taf XVIIa (R)	0	2.5
Taf XIV (L) 0 0 0 Taf 24-5 (R) 3.1 0 Taf XIX-3 (R) 3.4 5.97 Taf XXVc (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 143 (R) 6.3 0 Krapina 144 (R) 6.3 6.6 Krapina 145 (R) 7.2 Krapina 145 (R) 9.3 / Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4		Taf XVI-15 (R)	4.5	3.1
Taf 24-5 (R) 3.1 0 Taf XIX-3 (R) 3.4 5.97 Taf XXVc (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 143 (R) 6.3 0 Krapina 149 (R) 13.3 / Krapina 149 (R) 13.3 / Krapina 145 (R) 9.3 / Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4		Taf XVI (R)	6.3	3.3
Taf XIX-3 (R) 3.4 5.97 Taf XXVc (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 144 (R) 6.3 6.6 Krapina 145 (R) 7.2 Krapina 145 (R) 7.2 Krapina 144 (R) 9.3 Krapina 156 (L) 2.2 La Chapelle-aux-Saints (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4		Taf XIV (L)	0	0
Taf XXVc (L) 0 1.5 Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 143 (R) 6.3 0 Krapina 149 (R) 13.3 / Krapina 145 (R) / 7.2 Krapina 145 (R) 9.3 / Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4		Taf 24-5 (R)	3.1	0
Neanderthals Régourdou (R) 7.4 8.0 Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 143 (R) 6.3 0 Krapina 154 (L) 6.3 6.6 Krapina 149 (R) 13.3 / Krapina 145 (R) / 7.2 Krapina 144 (R) 9.3 / Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints (L) 7.37 Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4		Taf XIX-3 (R)	3.4	5.97
Régourdou (L) 3.0 3.2 Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 143 (R) 6.3 0 Krapina 154 (L) 6.3 6.6 Krapina 149 (R) 13.3 / Krapina 145 (R) / 7.2 Krapina 145 (R) 9.3 / Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints (L) 7.37 Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4		Taf XXVc (L)	0	1.5
Kebara (L) 4.9 0.0 Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 144 (R) 6.3 0 Krapina 154 (L) 6.3 6.6 Krapina 149 (R) 13.3 / Krapina 145 (R) / 7.2 Krapina 145 (R) 9.3 / Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints (L) 7.37 Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4	Neanderthals	Régourdou (R)	7.4	8.0
Kebara (R) 3.4 0.0 La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 143 (R) 6.3 0 Krapina 154 (L) 6.3 6.6 Krapina 149 (R) 13.3 / Krapina 145 (R) / 7.2 Krapina 144 (R) 9.3 / Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints (L) 7.37 Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4		Régourdou (L)	3.0	3.2
La Ferrassie 1 (R) 5.4 5.8 La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 143 (R) 6.3 0 Krapina 154 (L) 6.3 6.6 Krapina 149 (R) 13.3 / Krapina 145 (R) / 7.2 Krapina 144 (R) 9.3 / Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4		Kebara (L)	4.9	0.0
La Ferrassie 1 (L) 8.2 2.6 Neanderthal (R) 7.4 6.2 Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 143 (R) 6.3 0 Krapina 154 (L) 6.3 6.6 Krapina 145 (R) / 7.2 Krapina 145 (R) / 7.2 Krapina 145 (R) / 7.2 Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4		Kebara (R)	3.4	0.0
Neanderthal (R)		La Ferrassie 1 (R)	5.4	5.8
Krapina 153 (L) 3.8 3.9 Krapina 142 (R) 6.9 5.9 Krapina 143 (R) 6.3 0 Krapina 154 (L) 6.3 6.6 Krapina 149 (R) 13.3 / Krapina 145 (R) / 7.2 Krapina 144 (R) 9.3 / Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4		La Ferrassie 1 (L)	8.2	2.6
Krapina 142 (R) 6.9 5.9 Krapina 143 (R) 6.3 0 Krapina 154 (L) 6.3 6.6 Krapina 149 (R) 13.3 / Krapina 145 (R) / 7.2 Krapina 144 (R) 9.3 / Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4		Neanderthal (R)	7.4	6.2
Krapina 143 (R) 6.3 0 Krapina 154 (L) 6.3 6.6 Krapina 149 (R) 13.3 / Krapina 145 (R) / 7.2 Krapina 144 (R) 9.3 / Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4 antecessor		Krapina 153 (L)	3.8	3.9
Krapina 154 (L) 6.3 6.6 Krapina 149 (R) 13.3 / Krapina 145 (R) / 7.2 Krapina 144 (R) 9.3 / Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4 antecessor		Krapina 142 (R)	6.9	5.9
Krapina 149 (R) 13.3 / Krapina 145 (R) / 7.2 Krapina 144 (R) 9.3 / Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4 antecessor		Krapina 143 (R)	6.3	0
Krapina 145 (R) / 7.2 Krapina 144 (R) 9.3 / Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4 antecessor		Krapina 154 (L)	6.3	6.6
Krapina 144 (R) 9.3 / Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4 antecessor		Krapina 149 (R)	13.3	/
Krapina 155 (L) 6.8 Present Krapina 156 (L) 2.2 / La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4 antecessor		Krapina 145 (R)	/	7.2
Krapina 156 (L) 2.2 / La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4 antecessor		Krapina 144 (R)	9.3	/
La Chapelle-aux-Saints / 7.37 (L) Mean 6.3 4.4 Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4 antecessor		Krapina 155 (L)	6.8	Present
(L) Mean Standard deviation Homo ergaster KNM-ER15 000 (R) KNM-ER15 000 (L) Mean 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) ATD6-50 (R) ATD6-50 (R) ATD6-50 (R)		Krapina 156 (L)	2.2	/
Standard deviation 2.8 3.0 Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4 antecessor		·	/	7.37
Homo ergaster KNM-ER15 000 (R) 5.0 7.4 KNM-ER15 000 (L) 5.3 8.1 Homo ATD6-50 (R) 8.8 5.4 antecessor 5.4		Mean	6.3	4.4
KNM-ER15 000 (L) 5.3 8.1 <i>Homo</i> ATD6-50 (R) 8.8 5.4 <i>antecessor</i>			2.8	3.0
KNM-ER15 000 (L) 5.3 8.1 <i>Homo</i> ATD6-50 (R) 8.8 5.4 <i>antecessor</i>	Homo ergaster	KNM-ER15 000 (R)	5.0	7.4
Homo ATD6-50 (R) 8.8 5.4 antecessor	0		5.3	
		OH48 (L)	4.6	2.7

slightly pronounced superior curvature, and thus look nearly straight. On the contrary, Taf XIX-3 shows two pronounced curvatures in dorsal view, the superior one being larger than in modern human ones (Table 5). Whatever the morphology of this peculiar bone, the overall morphology of Taforalt clavicles is not very different from that of modern human (Table 6), with only a somewhat higher frequency of type II (Table 4).

All Neanderthal clavicles display two curvatures in dorsal view (Figure 4 and Table 5): an inferior one at their lateral extremity and a superior one at their medial extremity (Figure 5), but Kebara and Krapina 143 display a modern morphology, showing only the inferior curvature. In other words, 78% of Neanderthal clavicles show two curvatures in dorsal view, contrary to modern humans where this proportion is 15%. Moreover, the morphology of modern human clavicle with two curvatures in dorsal view is not comparable to that of Neanderthal clavicles. When present, the superior curvature is less pronounced in modern man than in Neanderthal (Table 6). Furthermore, in some Neanderthal clavicles (Regourdou, left and right, La Ferrassie I, Krapina 153 and 154) the superior curvature is more pronounced than the inferior one (Table 5), which is never the case in modern human.

Clavicles belonging to *Homo habilis*, *Homo ergaster* and *Homo antecessor* are in morphology very similar to Neanderthal ones. Moreover, in the two Nario-Kotome clavicles the superior curvature is more pronounced than the inferior one, like in some Neanderthal clavicles. OH48, the only *Homo habilis* clavicle known, displays also two curvatures in dorsal view, even if they are underestimated because of the bad conservation state of this fossil (Table 5).

Clavicle length

Neanderthal clavicles have an average length similar to that of Upper Palaeolithic ones (Table 7) and modern humans ones. However, the Neanderthal population is heterogeneous for this character (Figure 6). Neanderthal clavicles from Western Europe are longer than those from Krapina. This observation, confirmed by others author (40, 41), may show that Neanderthal clavicles display a trend toward a reduction in size from west to east. On the contrary, the Taforalt and other Upper Palaeolithic populations are homogenous for this character.

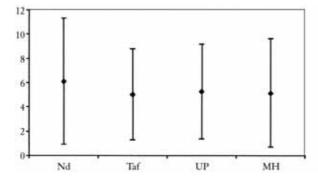
DISCUSSION

In superior view, clavicles from *Homo habilis* to modern human do not show great differences between them. In peculiar, Neanderthal clavicles are not more S-shaped than modern human as it had been previously asserted. In fact, Neanderthal clavicle just give an impression of being more S-shaped because of their great length in Western Europe. As shown by previous works (24–26, 42), clavicle morphology in superior view is essentially related to the ability of arm elevation. This ability allowed not only to climb, but also to throw, to carry or manipulate heavy objects.

TABLE 6

T-test comparing the inferior and superior curvatures between Neanderthal, modern human, Upper Palaeolithic and Taforalt remains for a confidence interval level of 95%.

INFERIOR CURVATURE SUPERIOR CURV				RIOR CURVA	TURE				
Sample star	tistics				Sample sta	tistics			
	N	Mean	StDev	Var		N	Mean	StDev	Var
MH	33	4.982	2.373	5.631	MH	33	1.146	1.698	2.884
UP	24	4.362	2.666	7.109	UP	23	1.295	1.804	3.255
Sample Dif DiffMean =		Err = 0.671	Var = 6.24	49 (Pooled)	Sample Di DiffMean		Err = 0.473	Var = 3.0	35 (Pooled)
Significance Test Result		df = 1	55.0 P	= 0.3595	Significano Test Result		.314 Df =	54.0 P =	= 0.7550
Sample star	tistics				Sample sta	tistics			
	N	Mean	StDev	Var		N	Mean	StDev	Var
MH	33	4.982	2.373	5.631	MH	33	1.146	1.698	2.884
Taf	21	4.043	2.616	6.846	Taf	21	1.246	1.796	3.226
Sample Dif DiffMean =		Err = 0.689	Var = 6.09	98 (Pooled)	Sample Di DiffMean		Err = 0.485	Var = 3.0	15 (Pooled)
Significance Test Result		62 Df =	52.0 P	= 0.1790	Significanc Test Result		.206 Df =	52.0 P =	= 0.8376
Sample star	tistics				Sample sta	tistics			
	N	Mean	StDev	Var		N	Mean	StDev	Var
Nd	18	6.082	2.599	6.755	Nd	16	4.684	2.936	8.617
MH	33	4.982	2.373	5.631	MH	33	1.146	1.698	2.884
Sample Dif DiffMean =		Err = 0.719	Var = 6.02	21 (Pooled)	Sample Di DiffMean		Err = 0.661	Var = 4.7	14 (Pooled)
Significance Test Result		30 Df =	49.0 P	= 0.1325	Significano Test Result		49 Df =	47.0 P =	= p <.0001



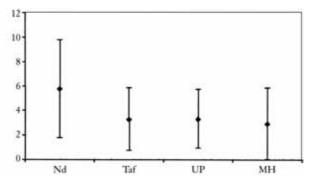


Figure 4. Mean and range of variation of clavicle curvature in dorsal view in Neanderthal, Taforalt, Upper Palaeolithic remains and Modern Human. Left: inferior curvature; right: superior curvature.

On the other hand, two groups may be distinguished among clavicles of the genus *Homo* in dorsal view. The first is characterized by clavicles with two curvatures in dorsal view and includes all *Homo* species studied here (*Homo habilis*, *Homo ergaster*; *Homo antecessor* and Neanderthal) except modern human. The second group is

characterized by clavicles showing only the inferior curvature in dorsal view and includes only modern human.

The morphology of the clavicle in dorsal view is related to the position of the scapula in regard to the thorax (25, 26). Indeed the superior curvature allows the sternal extremity of the clavicle to be parallel to the manubrium

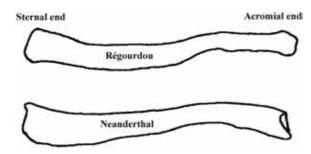


Figure 5. Neanderthal clavicle morphology in dorsal view (scale not respected).

and at the same time allows the acromial extremity, and thus the scapula, to sit high on the thorax. As the sternal extremity is parallel to the manubrium, the subclavier muscle as well as the costo-clavicular ligament remain short. Thus the mobility of this extremity remains low (Figure 7) and keeps the possibility of luxation of the sterno-clavicular joint very low. Hence, a clavicle with two pronounced curvatures in dorsal view is associated with a scapula high on the thorax. On the contrary, a clavicle with only the inferior curvature is associated with a scapula sitting low on the thorax (Table 8). This low position of the scapula in regard to the thorax is thus a modern human apomorphy.

Moreover, all Neanderthal clavicles in western Europe show two curvatures in dorsal view, whereas Krapina 143, display a modern morphology in Central Europe. In the Near East, this is also the case of Kebara 2 (right and left). There seems to be a morphological gradient from West to East in the Neanderthal clavicle. The morphology of this bone becomes in fact more and more

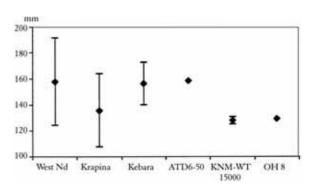


Figure 6. Middle and Lower Palaeolithic clavicle length.

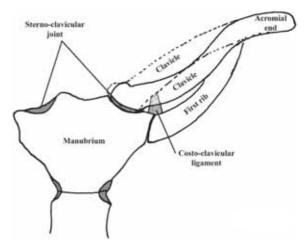


Figure 7. Clavicles associated with a high scapula in regard to the thorax. Dotted line: modern human clavicle. Full line: Neanderthal clavicle. Note the elongation of the costo-clavicular ligament in modern human if associated to a scapula situated high in regard to the thorax (from 25, 26).

TABLE 7

T-test comparing clavicle length between Neanderthal, modern human and Upper Palaeolithic remains for a confidence interval level of 95%.

CLAVICLE LENGTH	· I			
Sample statistics				
	N	Mean	StDev	Var
MH	33	145.197	9.973	99.468
UP	23	148.717	12.631	159.548
Sample Differences DiffMean = -3.520	StErr = 3.024	Var = 123.945 (Pooled)		
Significance test Test Result	T = -1.164	df = 54.0	P = 0.2495	
Sample statistics				
F	N	Mean	StDev	Var
MH	33	145.197	9.973	99.468
Nd	11	149.536	17.358	301.295
Sample Differences DiffMean = -4.339	StErr = 4.229	Var = 147.522 (Pooled)		
Significance test Test Result	T = -1.026	Df = 42.0	P = 0.3107	

TABLE 8

Relation between clavicle morphology in dorsal view and scapula position inside genus *Homo*.

	Two curvatures in dorsal view	Inferior curvature only
Human species	Homo habilis, Homo ergaster, Homo antecessor, Neanderthal	Modern human
Scapula position in regard to the thorax	High	Low

modern toward the east. More clavicles are necessary to conclude that a gradient does really exist, but such a gradient has already been found in several other Neanderthal characters (43–45). In other words, if this gradient in clavicle shape existed, the more Neanderthal populations lived east, the more their scapulas were situated lower on their thorax until they reached modern position in the Near East.

The Neanderthal elevation of the scapula in regard to the thorax allows to explain the extreme length of the western Neanderthal clavicle. For a similar thoracic diameter, the more the scapula is high on the thorax, the more the clavicle is elongated, and the extreme length of this bone in western Neanderthals is neither the consequence of an extraordinary thorax width (27, 29, 36, 37, 46), nor an extraordinary length of the trapezius and sternocleidomastodeus insertions (47). The peculiar morphology of some of Taforalt clavicles (Taf XIX-3, Taf XVIIa, Taf XXVc) and the high proportion of type II among them can be explained by the high level of endogamy that seemed to exist within that population (48, 49). In other words, this high endogamy permitted the apparition of an atavistic character. Similarly, modern human clavicle morphology could be the result of genetic drift within a small population, which was probably the case of the first anatomically modern humans.

The shorter length of Krapina clavicles in regard of those of Western Neanderthals and Kebara may not be due to the older age of Krapina remains, because old western remains like ATD6-50 fit well within the Western Neanderthal variation and numerous other characters display a West to East cline in Neanderthal populations (44, 45). Hence, Krapina shorter clavicles may be explained by their eastern situation in regard to »classical Neanderthal«, and Kebara may be a peculiar individual for this character, but more clavicles from central Europe and Near East are needed to conclude.

CONCLUSION

The shape of the clavicle is approached by projecting curvatures in two perpendicular plans. In superior view, clavicle morphology is very similar from *Homo habilis* to modern humans. Hence, Neanderthal clavicles are not more S-shaped than modern human ones.

In dorsal view, two kinds of clavicle shapes exist. The first one is characterized by two curvatures in dorsal view and the second one by only one curvature and corresponds to Upper Palaeolithic remains and modern human. The clavicle morphology in dorsal view is correlated to the scapula position in regard to the thorax and the results are summarized in Table 8. The modern human clavicle, and the shoulder architecture associated, is unique and thus the Neanderthal shoulder is not peculiar in regard to older human remains.

The length and shape of the Neanderthal clavicle become more and more modern as fossils come from localities situated farther east, and become quite modern in the near east, at the oriental border of Neanderthal's distribution area. This west to east cline in clavicle morphology, which still needs confirmation, is matched by similar clines in other Neanderthal characters. A series of facts which suggest a speciation by distance for this human group as few authors (44,45) has already proposed.

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