

Krapina and Other Neanderthal Clavicles : A Peculiar Morphology?

Jean-Luc Voisin

► **To cite this version:**

Jean-Luc Voisin. Krapina and Other Neanderthal Clavicles: A Peculiar Morphology?. *Periodicum Biologorum*, 2006, 108 (3), pp.331-339. <halshs-00352689>

HAL Id: halshs-00352689

<https://halshs.archives-ouvertes.fr/halshs-00352689>

Submitted on 13 Jan 2009

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Krapina and Other Neanderthal Clavicles: A Peculiar Morphology?

JEAN-LUC VOISIN

USM 103
Institut de Paléontologie Humaine
1 rue René Panhard
75013 Paris
E-mail: jeanlucv@mnhn.fr
jeanlucvoisin2004@yahoo.fr

Key words: Clavicle, Shoulder,
Evolution, *Homo habilis*, *Homo ergaster*,
Homo antecessor, Neanderthal

Received April 27, 2006.

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

Even 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-

TABLE 1

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

Middle Palaeolithic Neanderthal (Nd)	Upper Palaeolithic humans (UP)	
Régourdou (R)	Abri Pataud (R)* Omo I KSH (L) Qafzeh 9 (L)	
Régourdou (L)	Taforalt (Taf)	
Kebara 2 (R)	Taf V-6* (R)	Taf XIIIa* (L)
Kebara 2 (L)	Taf XXIII* (L)	Taf VIII-3bis* (L)
La Ferrassie I (R)*	Taf XIX-3a* (L)	Taf XXVa* (R)
La Ferrassie I (L)*	Taf V-24* (L)	Taf IX-39* (L)
Neanderthal (R)	Taf XI-AR* (R)	Taf XIIIb* (R)
Krapina 153 (L)*	Taf XVa* (L)	Taf XVIIa* (R)
Krapina 142 (R)*	Taf XVc* (L)	Taf XVI-15* (R)
Krapina 143 (R)*	Taf XVII-26* (R)	Taf XVI* (R)
Krapina 154 (L)*	Taf XVIII-6* (R)	Taf XIV* (L)
Krapina 145 (R)*	Taf 24-5* (R)	Taf XIX-3* (R)
Krapina 145 (R)*	Taf XXVc* (L)	
Krapina 155 (L)*		
Krapina 149 (R)*		
Krapina 144 (R)*	Lower Palaeolithic	
Krapina 156 (L)*	<i>Homo antecessor</i>	<i>Homo ergaster</i>
La Chapelle-aux-Saints (L)*	Gran Dolina ATD6-50	KNM-WT 15000
	<i>Homo habilis</i>	
	OH 48	

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): $e / h \cdot 100$
- The sternal curvature (internal one): $f / g \cdot 100$

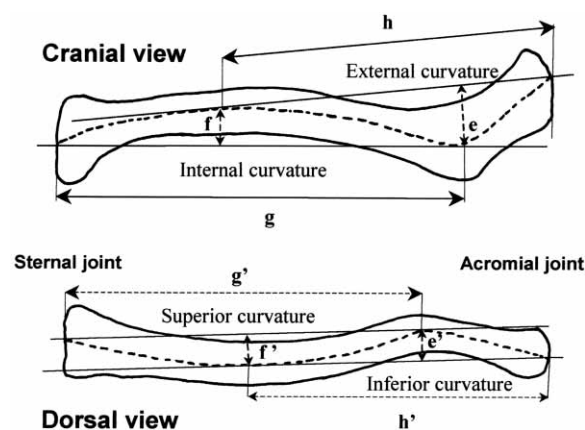


Figure 1. Measurements of clavicle curvatures (34). Example on a right clavicle of Pan troglodytes.

Dorsal plane:

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

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 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 its 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

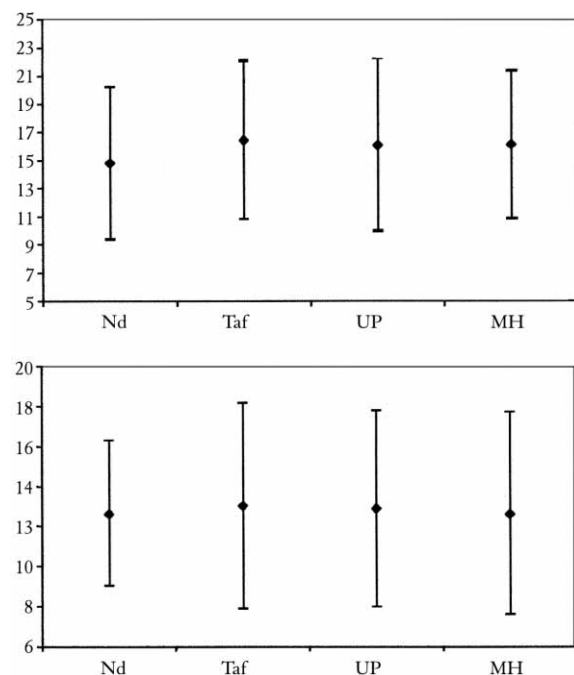


Figure 2. Mean and range of variation of clavicle curvatures in superior view in Neanderthal, Tafone, Upper Palaeolithic remains and Modern Human. Above: external curvature; Beneath: internal curvature.

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 curvature	External curvature
Upper Palaeolithic		
Abri Pataud	9.7	12.1
Omo I KSH (L)	13.1	14.56
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
<i>Homo ergaster</i>		
KNM-ER15 000 (R)	13.1	14.6
KNM-ER15 000 (L)	15.3	14.7
<i>Homo antecessor</i>		
ATD-6 50 (R)	12.4	18.7
<i>Homo habilis</i> 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					INTERNAL CURVATURE				
Sample statistics					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
<i>Sample Differences</i>					<i>Sample Differences</i>				
DiffMean = 0.060		StErr = 0.765		Var = 7.942 (Pooled)	DiffMean = -0.250		StErr = 0.668		Var = 6.205 (Pooled)
<i>Significance test</i>					<i>Significance test</i>				
Test Result	T = 0.078	df = 54.0	P = 0.9381		Test Result	T = -0.374	Df = 55.0	P = 0.7097	
Sample statistics					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
Taf	21	16.429	2.824	7.974	Taf	21	13.000	2.567	6.587
<i>Sample Differences</i>					<i>Sample Differences</i>				
DiffMean = -0.314		StErr = 0.758		Var = 7.372 (Pooled)	DiffMean = -0.384		StErr = 0.709		Var = 6.449 (Pooled)
<i>Significance test</i>					<i>Significance test</i>				
Test Result	T = -0.414	Df = 52.0	P = 0.6803		Test Result	T = -0.542	Df = 52.0	P = 0.5901	
Sample statistics					Sample statistics				
	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
<i>Sample Differences</i>					<i>Sample Differences</i>				
DiffMean = -1.317		StErr = 0.795		Var = 7.091 (Pooled)	DiffMean = -0.002		StErr = 0.690		Var = 5.335 (Pooled)
<i>Significance test</i>					<i>Significance test</i>				
Test Result	T = -1.657	Df = 48.0	P = 0.1041		Test Result	T = -0.002	Df = 48.0	P = 0.9981	

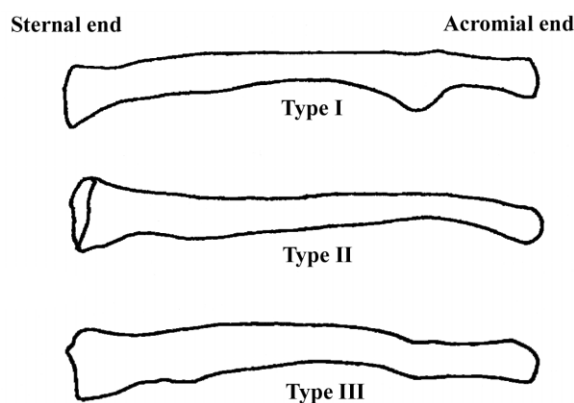


Figure 3. The three type of modern human clavicle (for a definition see text).

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.

	Individual	Inferior curvature	Superior curvature	
Upper Palaeolithic	Abri Pataud	6.9	0	
	Omo I KSH (L)	4.3	3.6	
	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 XI-AR (R)	5.7	0	
	Taf XVa (L)	5.3	0	
	Taf XVc (L)	0	0	
	Taf XVII-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 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 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	
<i>Homo ergaster</i>		KNM-ER15 000 (R)	5.0	7.4
	KNM-ER15 000 (L)	5.3	8.1	
<i>Homo antecessor</i>	ATD6-50 (R)	8.8	5.4	
<i>Homo habilis</i>	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 (Régourdou, 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 CURVATURE				
Sample statistics					Sample statistics				
	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 Differences					Sample Differences				
DiffMean = 0.620 StErr = 0.671 Var = 6.249 (Pooled)					DiffMean = -0.148 StErr = 0.473 Var = 3.035 (Pooled)				
Significance test					Significance test				
Test Result T = 0.924 df = 55.0 P = 0.3595					Test Result T = -0.314 Df = 54.0 P = 0.7550				
Sample statistics					Sample statistics				
	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 Differences					Sample Differences				
DiffMean = 0.939 StErr = 0.689 Var = 6.098 (Pooled)					DiffMean = -0.100 StErr = 0.485 Var = 3.015 (Pooled)				
Significance test					Significance test				
Test Result T = 1.362 Df = 52.0 P = 0.1790					Test Result T = -0.206 Df = 52.0 P = 0.8376				
Sample statistics					Sample statistics				
	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 Differences					Sample Differences				
DiffMean = 1.100 StErr = 0.719 Var = 6.021 (Pooled)					DiffMean = 3.538 StErr = 0.661 Var = 4.714 (Pooled)				
Significance test					Significance test				
Test Result T = 1.530 Df = 49.0 P = 0.1325					Test Result T = 5.349 Df = 47.0 P = p <.0001				

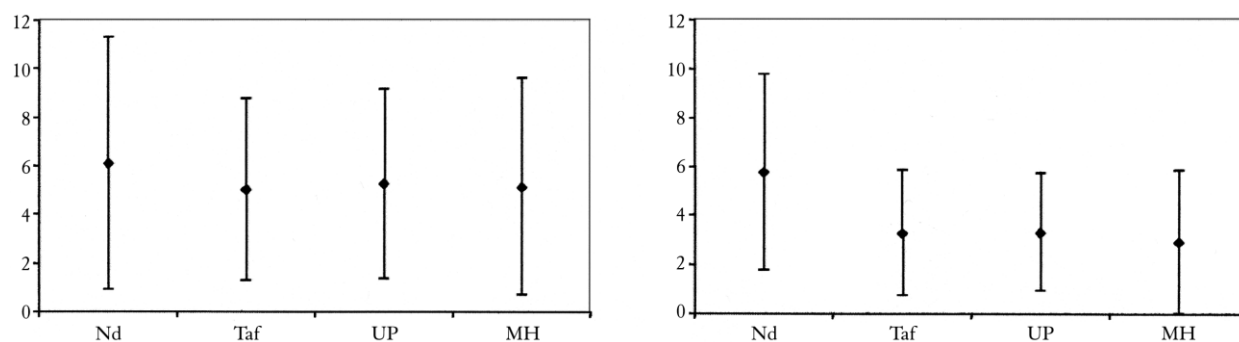


Figure 4. Mean and range of variation of clavicle curvature in dorsal view in Neanderthal, Taforalt, Upper Palaeolithic remains and Modern Human. Left: inferior curvature; right: superior curvature.

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

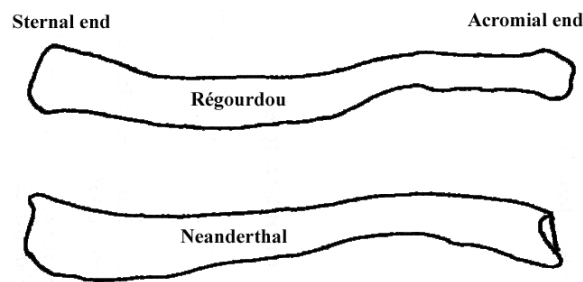


Figure 5. Neanderthal clavicle morphology in dorsal view (scale not respected).

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

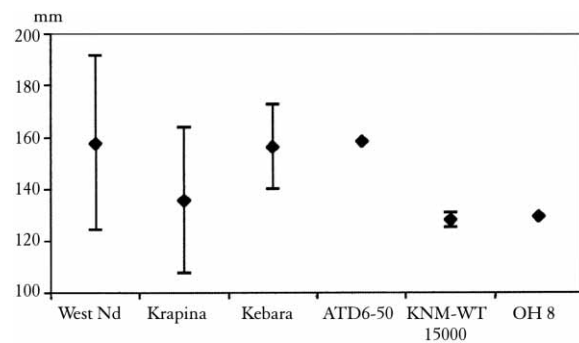


Figure 6. Middle and Lower Palaeolithic clavicle length.

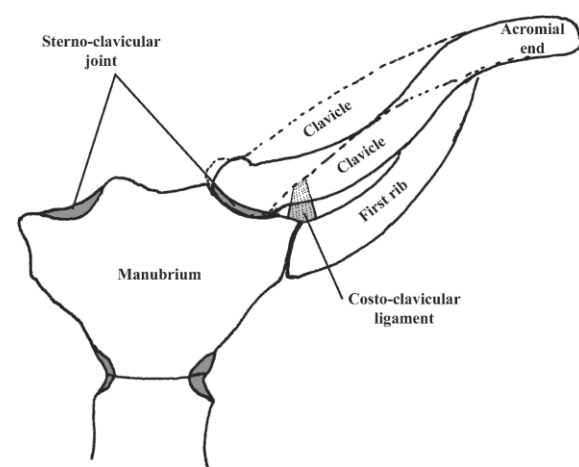


Figure 7. Clavicles associated with a high scapula in regard to the thorax. Dotted line: modern human clavicle. Full line: Neanderthal clavicle. Note the elongation of the costo-clavicular ligament in modern human if associated to a scapula situated high in regard to the thorax (from 25, 26).

TABLE 7

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

CLAVICLE LENGTH				
Sample statistics				
	N	Mean	StDev	Var
MH	33	145.197	9.973	99.468
UP	23	148.717	12.631	159.548
<i>Sample Differences</i>				
DiffMean = -3.520	StErr = 3.024	Var = 123.945 (Pooled)		
<i>Significance test</i>				
Test Result	T = -1.164	df = 54.0	P = 0.2495	
Sample statistics				
	N	Mean	StDev	Var
MH	33	145.197	9.973	99.468
Nd	11	149.536	17.358	301.295
<i>Sample Differences</i>				
DiffMean = -4.339	StErr = 4.229	Var = 147.522 (Pooled)		
<i>Significance test</i>				
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	<i>Homo habilis</i> , <i>Homo ergaster</i> , <i>Homo antecessor</i> , 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.

Acknowledgements: I would first like to thank David Frayer for its invitation to participate to this special Krapina issue. I also everyone who supported my work, and my wife for her unconditional support.

REFERENCES

1. BROCA P 1869 L'ordre des Primates. Parallèle anatomique de l'Homme et des singes. *Bull Soc Anthropol* 2^{ème} série, Tome IV: 228–401
2. PARSON F G 1917 On the modern English clavicle. *J Anat and Physiol* 51: 71–93
3. KLEIWEG DE ZWAAN J P 1931 La clavicle des javanais de l'est de Java. *L'Anthropologie (Paris)* 41: 273–287
4. TERRY R J 1932 The clavicle of the American Negro. *Am J Phys Anthropol* 16: 351–379
5. APOSTOLAKIS G 1934 La clavicle de l'Homme. *Arch Anat Histol Embryol* 18: 169–180
6. OLIVIER G 1951 Anthropologie de la clavicle. *Bull Mém Soc Anthropol* 10^{ème} série: 67–99
7. OLIVIER G 1954 Anthropologie de la clavicle. *Bull Mém Soc Anthropol* 10^{ème} série: 144–153
8. OLIVIER G 1955 Anthropologie de la clavicle. *Bull Mém Soc Anthropol* 10^{ème} série: 282–302
9. OLIVIER G, CAPLIEZ S 1957 Anthropologie de la clavicle. *Bull Mém Soc Anthropol* 10^{ème} série: 225–261
10. OLIVIER G, CARRÈRE P 1953 Types de clavicles. Variations et corrélations. *C.R. Ass Anat (Bordeaux)*: 248–254
11. OLIVIER G, CHABEUF M, LALUQUE P 1954 Anthropologie de la clavicle. *Bull Mém Soc Anthropol* 10^{ème} série: 35–46
12. RAY L J 1959 Metrical and non-metrical features of the clavicle of the Australian Aboriginal. *Am J Phys Anthropol* 17: 217–226
13. LONGIA G S, AGARWAL A K, THOMAS R J, JAIN P N, SAXENA S K 1982 Metrical study of rhomboid fossa of clavicle. *Anthrop Anz* 40: 111–115
14. JIT I, KAUR H 1986 Rhomboid fossa in the clavicles of North Indians. *Am J Phys Anthropol* 70: 97–103
15. MURPHY A M C 1994 Sex determination of prehistoric New Zealand Polynesian Clavicles. *New Zealand J Archaeol* 16: 85–91
16. SCHULTZ A H 1930 The skeleton of the trunk and limbs of higher primates. *Hum Biol* 2: 303–438
17. OLIVIER G 1953 La clavicle du Semnopithèque. *Mammalia* 17: 173–186
18. CAVE A J E 1961 Nature and morphology of the costoclavicular ligament. *J Anat* 95: 170–179
19. JENKINS F A 1974 The movement of the shoulder in clavicate and aclavicate Mammals. *J Morph* 144: 71–84

20. JENKINS F A, DUMBROWSKI P J, GORDON E P 1978 Analysis of the shoulder in brachiating spider monkeys (*Ateles geoffroyi*). *Am J Phys Anthropol* 48: 65–75
21. LJUNGGREN A E 1979 Clavicular function. *Acta Orthop Scand* 50: 261–268
22. HARRINGTON M A, KELLER T S, SEILER J G, WEIKERT D R, MOELJANTO E, SCHWARTZ H S 1993 Geometric properties and the predicted mechanical behaviour of adult human clavicles. *J Biomech* 26: 417–426
23. VOISIN J-L, BALZEAU A 2004 Structures internes claviculaires chez Pan, Gorilla et Homo. Méthode d'analyse et résultats préliminaires. *Bull et Mém de la Soc Anthropol* 16: 5–16
24. VOISIN J-L 2004 Clavicule : approche architecturale de l'épaule et réflexions sur le statut systématique des néandertaliens. *C. R. Palevol* 3: 133–142
25. VOISIN J-L 2001 Evolution de la morphologie claviculaire au sein du genre *Homo*, conséquence architecturale et fonctionnelle sur la ceinture scapulaire. *L'Anthropologie (Paris)* 105: 449–468
26. VOISIN J-L 2000 *L'épaule des hominidés. Aspects architecturaux et fonctionnels, références particulières à la clavicule*. Ph.D., Museum National d'Histoire Naturelle, Paris.
27. HEIM J L 1982 Les hommes fossiles de la Ferrassie II. *Arch Inst Paléontol Hum* 38: 1–272
28. HEIM J L 1982 Les enfants néandertaliens de la Ferrassie. Etude anthropologique et analyse ontogénique des hommes de neandertal. Masson, Paris.
29. VANDERMEERSCH B, TRINKAUS E 1995 The postcranial remains of the Regourdou 1 Neandertal: the shoulder and arm remains. *J Hum Evol* 28: 439–476
30. SANKHYAN A R 1997 Fossil clavicle of a middle Pleistocene hominid from the central Narmada valley, India. *J Hum Evol* 32: 3–16
31. BOULE M 1911-13 L'Homme fossile de la Chapelle-aux-Saints. *Ann Paleontol* 6, 7, 8: 111–172, 21–192, 1–70
32. RADOVČIĆ J, SMITH F H, TRINKAUS E, WOLPOFF M 1988 The Krapina hominids an illustrated catalog of skeletal collection. Mladost publishing house and Croatian Natural History Museum, Zagreb.
33. VANDERMEERSCH B 1981 Les Hommes fossiles de Qafzeh (Israël). C.N.R.S édition, Paris.
34. OLIVIER G 1951 Technique de mesure des courbures de la clavicule. *C.R. Ass. Anat.* XXXIXe Réunion (Nancy) 69: 753–764
35. YOUNG F 2001 ViSat 6.4 on www.visualstats.org
36. HEIM J L 1974 Les Hommes fossiles de la Ferrassie (Dordogne) et le problème de la définition des Néandertaliens classiques. *L'Anthropologie (Paris)* 78: 81–112
37. PATTE E 1955 *Les Néandertaliens*. Masson, Paris.
38. NAPIER J R 1965 Reply to Tobias, New discoveries in tanganyika, their bearing on hominid evolution. *Curr Anthropol* 6: 402–403
39. WALKER A, LEAKEY R 1993 The post cranial bones. In: Walker A, Leakey R (eds) *The Narikotome Homo erectus skeleton*. Springer-Verlag, Berlin, p 95–160
40. TRINKAUS E 1983 *The Shanidar Neandertals*. Academic Press, New York.
41. NARA T 1994 Etude de la variabilité de certains caractères métriques et morphologiques des néandertaliens. Ph.D., Université de Bordeaux I, Talence.
42. VOISIN J-L 2000 La clavicule humaine : adaptation à la station érigée? *Biom Hum et Anthropol* 18: 15–22
43. WOLPOFF M, MANNHEIM B, MANN A, HAWKS J, CASPARI R, ROSENBERG K R, FRAYER D W, GILL G W, CLARK G 2004 Why not the Neanderthals? *World Archaeology* 36: 527–546
44. VOISIN J-L (In Press) Speciation by distance and temporal overlap: a new approach to understanding Neanderthal evolution. In: Harvati K, Harrison T (eds) *Neanderthals revisited: new approaches and perspectives*. Kluwer Academic Press.
45. MONCEL M-H, VOISIN J-L (in press) «Les industries de transition» et le mode de spéciation des groupes néandertaliens en Europe entre 40–30 ka. *C. R. Palevol*
46. VANDERMEERSCH B 1991 La ceinture scapulaire et les membres supérieurs In: Bar-Yosef O, Vandermeersch B (eds) *Le squelette Moustérien de Kebara 2*. CNRS édition, Paris, p 157–178
47. BAR-YOSEF O, VANDERMEERSCH B 1991 Premiers Hommes modernes et néandertaliens au Proche-Orient : chronologie et culture. In: Hublin J J, Tillier A M (eds) *Aux origines d'Homo sapiens*. P.U.F., Paris, p 217–250
48. FEREMBACH D 1959 Les restes humains épipaléolithiques de la grotte de Taforalt (Maroc oriental). *C.r. Hebd. Séanc. Acad. Sci., (Paris)* 248: 3465–3467
49. FEREMBACH D 1960 Les Hommes du mésolithiques d'Afrique du Nord et le problème des isolats. *Bolm Soc Port Cienc Nat* 8: 1–16