Chapter 11

A Preliminary Approach to the Neanderthal Speciation by Distance Hypothesis: A View from the Shoulder Complex

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Abstract Neanderthal extinction is still under debate and there are two main schools of thought on this topic: (1) Neanderthals and modern humans are two distinct species and (2) Neanderthals and modern humans are a single species, with or without two subspecies. Recently, a new hypothesis has risen up, which takes into account arguments from both schools: the Neanderthal speciation by distance (i.e. Voisin 2006c). This hypothesis is based on a morphological cline from East to West in Neanderthal populations. In other words, the farther those populations lived to the west, the more they displayed pronounced Neanderthal characters. The aim of this study is to test the speciation by distance hypothesis in Neanderthal in regard to the shoulder complex. The shoulder girdle displays a morphological cline from East to West, but only for architectural characters and not for functional ones. This cline could be better explained by a result of a speciation by distance induced by genetic drift than by a different response to any physical activities. This study tends to confirm the speciation by distance model for Neanderthal, even if more studies are needed to confirm it firmly.

Keywords Geographical cline • Europe • Near East • Shoulder girdle • Clavicle • Scapula

Introduction

Neanderthal extinction is still under debate and there are two main schools of thought on this topic: (1) Neanderthals and modern humans are two distinct species (i.e., Rak 1993; Hublin et al. 1996; Stringer and McKie 1996; Bermùdez de Castro et al. 1997; Krings et al. 1997; Stringer 1998, 2002; Bocquet-Appel and Demars 2000; Hublin 2000; Arsuaga et al. 2001; Bräuer 2001; Schillaci and Froehlich 2001; Rak et al. 2002; Harvati 2003; Harvati et al. 2004); and (2) Neanderthals and modern humans are a single species, with or without two subspecies (i.e. Thoma 1965; Trinkaus 1983, 1991; Smith et al. 1989a, 2005; Smith 1991; Smith and Trinkaus 1991; Frayer 1992; Wolpoff et al. 2000; Relethford 2001, 2003; Ahern et al. 2002; Curnoe and Thorne 2003). But recently, a new hypothesis has risen up, which takes into account arguments from both schools: the Neanderthal speciation by distance (Moncel and Voisin 2006; Voisin 2006c).

Extreme examples of speciation by distance are "ring species" or speciation by circular overlap. "Ring species provide dramatic evidence that normal genetic divergence within one species can build up to a sufficient level to generate two species" (Ridley 2004: 388). Among vertebrates, fully convincing examples of ring species are few and include the Californian salamander *Ensatina eschscholtzii* (Ridley 2004), the herring gull *Larus argentatus* and lesser black-backed gull *Larus fuscus* (Mayr 1974), and the greenish warbler *Phylloscopus trochiloides* (Irwin et al. 2001a, 2005). In central Siberia, two distinct forms, *P. trochiloides viridanus* and *P. trochiloides plumbeitarsus,* are sympatric without interbreeding (Fig. 11.1), and therefore may be considered two species. These two forms are nevertheless connected by a chain of interbreeding populations encircling the Tibetan plateau to the south (*P. trochiloides ludlowi, P.t. trochiloides, P.t. obscuratus*), and traits change gradually in consecutive populations (Irwin et al. 2001a). There is no obvious species boundary along this chain, and the two terminal "species" *viridanus* and *plumbeitarsus* are connected by gene flow (Irwin et al. 2001b).

Between the two forms living in central Siberia, morphological traits change gradually in consecutive populations encircling the Tibetan plateau, in the same manner as those of western to eastern Neanderthals. Thus, just before the spread of modern humans into Europe about 40,000 years ago, there was a chain of Neanderthal populations throughout Europe and the Near East, more or less connected by

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S. Condemi and G.-C. Weniger (eds.), *Continuity and Discontinuity in the Peopling of Europe: One Hundred Fifty Years of Neanderthal Study*, Vertebrate Paleobiology and Paleoanthropology, DOI 10.1007/978-94-007-0492-3_11,

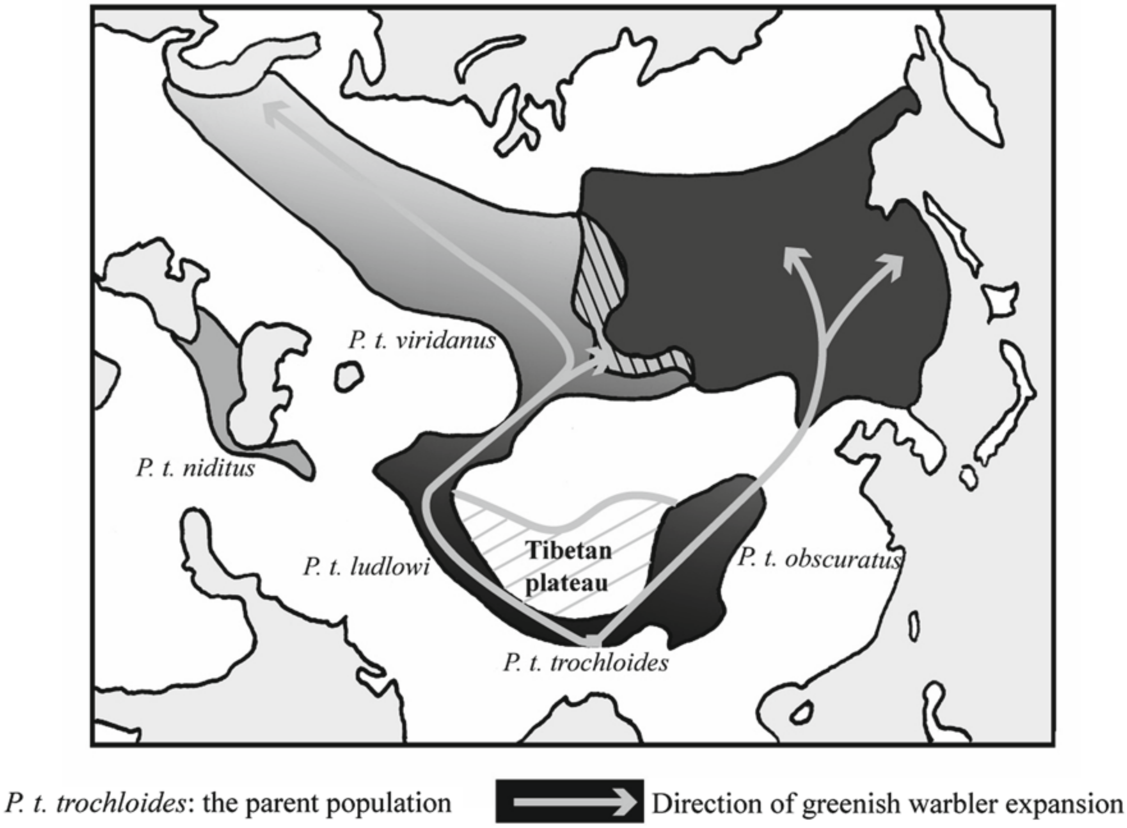

Fig. 11.1 The greenish Warblers (*Phylloscopus trochiloides*) ring species. The break in the population in west China is inferred to be recent and caused by deforestation (After Irwin et al. 2001a and Voisin 2006c)

Table 11.1 Summary of Neanderthal characteristics in West Europe and Near-East

West Europe	Near-East
Pronounced Neanderthal characters: *"Hyper Neanderthal" morphology*	Slightly pronounced Neanderthal characters: *"Hypo Neanderthal" morphology*
No Neanderthal characters within first post-Neanderthal populations.	Neanderthal characters within first post-Neanderthal populations.

gene flow (the gene flow rate would have varied as the ice sheets expanded and receded) and displaying a morphological cline from East to West. In other words, in the west part of the Neanderthal distribution area, human groups are characterized by pronounced Neanderthal characters and in the East part, populations are characterized by slightly pronounced Neanderthal characters (Table 11.1). Moreover, Neanderthal features seem to subsist in Central Europe and Near East post-Neanderthal populations (i.e. Smith et al. 1989b, 2005; Frayer 1992; Wolpoff et al. 2001, 2004; Trinkaus et al. 2003a, b; Janković et al. 2006; Ahern 2006; Hawks 2006).

The aim of this study is to test the speciation by distance hypothesis in Neanderthal in regard to the shoulder complex. I used shoulder girdle bones because they are the most characteristic of Neanderthal postcranial ones (Heim 1974, 1982; Vandermeersch 1981; Voisin 2004, 2006a) and also because the upper limb capacities depend on the shoulder complex. More extensive studies are currently in progress both on cranial and postcranial evidence and also on teeth (Voisin and Condemi, in press). The present work is more a preliminary report than a full conclusive paper and its aim is to show that a morphological cline clearly existed in Neanderthal populations and affected special features.

Materials and Methods

Materials

We studied 18 Neanderthal scapula and 17 clavicles (Table 11.2), which were completed for some characters by additional individual data from the literature. The sample is completed by 33 clavicles and 29 scapulas of modern humans (MH) (*Homo sapiens sapiens*) from several parts of the world (Europe 10, Africa 7, North America 5, Asia 7, unknown 4 (the last four, only for clavicles)). These

Table 11.2 Fossil remains used in this study

Clavicle	Scapula
Régourdou (L) and (R)	/
La Ferrassie I (L)[a] and (R)[a]	La Ferrassie I (L)[a] and (R)[a]
Neanderthal (R)	Neanderthal (R)
/	Spy (L) and (R)
La Chapelle-aux-Saints (L)[a]	/
Krapina 142 (R)[a]	Krapina 125 (L)[a]
Krapina 143 (R)[a]	Krapina 127 (R)[a]
Krapina 144 (R)[a]	Krapina 128 (R)[a]
Krapina 145 (R)[a]	Krapina 129 (R)[a]
Krapina 149 (R)[a]	Krapina 130 (L)[a]
Krapina 153 (L)[a]	Krapina 131 (L)[a]
Krapina 154 (L)[a]	Krapina 132 (R)[a]
Krapina 155 (L)[a]	Krapina 134 (R)[a]
Krapina 156 (L)[a]	Krapina 135 (R)[a]
/	Vindija 209 (L)
Kebara (L) and (R)	Kebara (L) and (R)
/	Tabun I (L)[a]

(L) and (R) mean respectively left and right

[a] Original remains

specimens are housed in the Département "*Hommes, Natures, Sociétés*" *du Musée de l'Homme*, Paris (France), the *Institut de Paléontologie Humaine*, Paris (France), the Croatian Natural History Museum, Zagreb (Croatia), and the *Institut Royal des Sciences Naturelles de Belgique,* Bruxelles (Belgium).

Methods

Study of the Clavicles

Due to its complexity, the morphology of the clavicle will be approached in regard to its curvatures. When projected on two perpendicular planes, one cranial and one dorsal, the clavicle morphology can be decomposed in elementary curvatures, as shown in Fig. 11.2.

The middle arc of curvature is estimated according to Olivier's method (1951a) as the proportion between the length of the chord and the height of the curvature (Fig. 11.2):

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

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

Three other characters will also be used: the total length (measured with a calliper as the greatest length of the bone), the presence or absence of a costo-clavicular ligament insertion, or costal tuberosity, and of a subclavius sulcus.

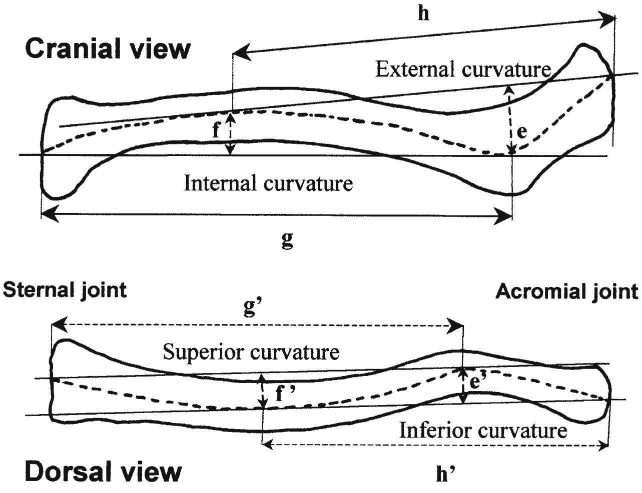

Fig. 11.2 Determination of curvatures on a right clavicle of *Pan troglodytes* (Olivier 1951a)

Study of the Scapulas

As the majority of the scapula remains are damaged, only three measurements could be used on most fossils:

The glenoid fossa index:
(Breadth of the glenoid fossa/height of the glenoid fossa) × 100.

The breadth and the height of the glenoid fossa are measured as suggested by Martin (1928). This method is less precise than that proposed by Vallois (1928–1946), but as most works on Neanderthal used the Martin technique, I will also use it for obtaining data comparable with those of other authors.

The scapula neck index (Larson 1995):
Neck length/root square (breadth of the glenoid fossa × height of the glenoid fossa) × 100.

This index is associated to arm movement, especially to the abduction function of the infraspinatus (Larson 1995). Neck length is the minimum width of the infraspinous fossa (between A and B) at the neck of the scapula (Fig. 11.3), measured with a caliper.

The angle A:
It is the angle between glenoid great axis and the ventral bar (the prominent buttress just medial to the axillary border on the ventral surface of the scapula). This angle is correlated to the axillo-glenoid angle (Stern and Susman 1983) and its measure does not need a complete scapula, which is very rare in fossil records. The higher the angle values, the more the glenoid fossa is oriented cranially.

The morphology of the axillary border and the associated sulcus:
Ventral, bisculate, or dorsal. This character is associated to arm movements and could be the result of a high muscle activity or could have a more phylogenetic relationship

(Trinkaus 1977; Heim 1982; Frayer 1992; Odwak 2006; Trinkaus 2006, 2008).

The measurements and distribution of the variables have been computed with ViStat 6.4 ® (Young 2001). Graphics showing the range of variation of each variable are represented by the mean and +/− two times standard deviation.

Fig. 11.3 Neck length or the minimum width of the infraspinous fossa (From A to B) (After Larson 1995)

Results

The Clavicle

Curvatures in Cranial View

In superior view, all fossil clavicles studied here are distributed within the range of variation of modern human ones (Fig. 11.4, Table 11.3) and there is no evidence for a cline for this feature. This result shows that Neanderthal clavicles, in superior view, are less S-shaped than classically described (Boule 1911–1913; Patte 1955; Heim 1974, 1982; Vandermeersch and Trinkaus 1995) and display no differences with modern human ones in cranial view. This result is confirmed by other recent works (Voisin 2000, 2001, 2004, 2006a).

Curvatures in Dorsal View

In dorsal view, modern human clavicles can be classified into three morphological groups (Fig. 11.5), or types, according to Olivier's studies on more than 800 clavicles from Europe, Africa, America, and Australia (Olivier 1951b, 1954, 1955; Olivier et al. 1954). Type I possesses only an inferior curvature, and is the most frequent. 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 at the acromial end. Type III clavicles show a superior curvature at the acromial end, and none at the sternal part. Type III clavicles are by far the least frequent form (Olivier 1951b, 1954, 1955; Olivier et al. 1954).

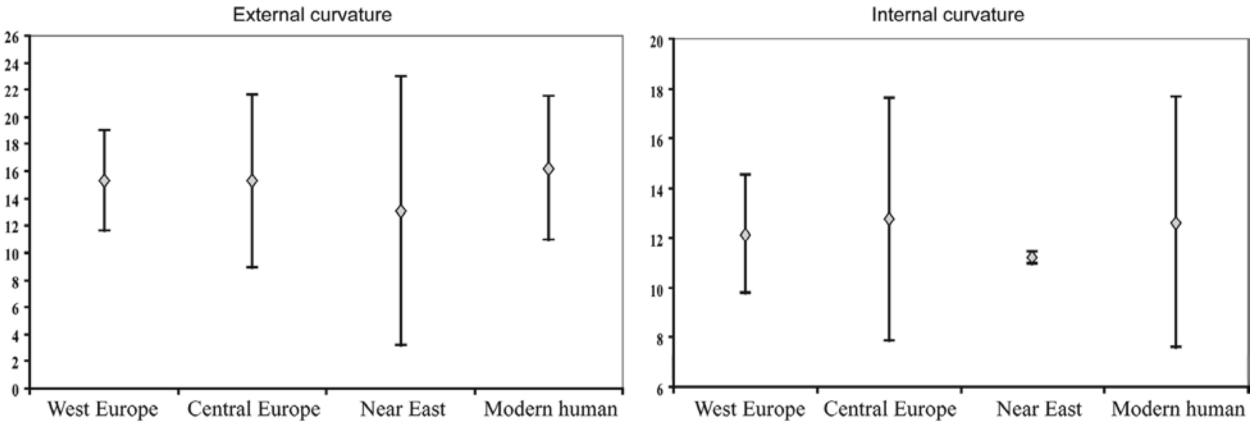

Fig. 11.4 Mean and range of variation of clavicle curvatures in cranial view in West Europe, Central Europe, and Near-East Neanderthals

Table 11.3 Values of clavicle curvatures in superior view

Individual	External curvature	Internal curvature	Region
Régourdou (R)	14.46	10.00	West Europe
Régourdou (L)	13.16	11.86	
La Ferrassie 1 (R)	14.22	13.24	
La Ferrassie 1 (L)	17.65	12.32	
Neanderthal (R)	16.67	13.16	
La Chapelle-aux-Saints (L)	/	12.24	
Mean	**15.23**	**12.14**	
Krapina 142 (R)	17.40	16.70	Central Europe
Krapina 143 (R)	13.90	12.10	
Krapina 154 (L)	14.10	11.40	
Krapina 149 (R)	20.00	/	
Krapina 144 (R)	12.00	/	
Krapina 155 (L)	18.10	/	
Krapina 153 (L)	10.80	10.30	
Krapina 145 (L)	/	11.30	
Krapina 156 (L)	/	14.70	
Mean	**15.19**	**12.75**	
Kebara (L)	16.51	11.11	Near-East
Kebara (D)	9.52	11.29	
Mean	**13.02**	**11.20**	
Modern Human Standard deviation/Mean	2.65/16.12	2.52/12.62	

Table 11.4 Values of clavicle curvatures in dorsal view

Individual	Inferior curvature	Superior curvature	Region
Régourdou (R)	7.41	8.04	West Europe
Régourdou (L)	3.03	3.21	
La Ferrassie 1 (R)	5.41	5.83	
La Ferrassie 1 (L)	8.23	2.61	
Neanderthal (R)	7.41	6.18	
La Chapelle-aux-Saints (L)	7.37	/	
Mean	**6.48**	**5.17**	
Krapina 142 (R)	6.9	5.9	Central Europe
Krapina 143 (R)	6.3	0	
Krapina 154 (L)	6.3	6.6	
Krapina 149 (R)	13.3	/	
Krapina 144 (R)	9.3	/	
Krapina 155 (L)	6.8	/	
Krapina 153 (L)	3.8	3.9	
Krapina 145 (L)	/	7.2	
Krapina 156 (L)	2.2	/	
Mean	**6.86**	**4.72**	
Kebara (L)	4.94	0	Near East
Kebara (R)	3.38	0	
Mean	**4.16**	**0**	
Modern human standard deviation/mean	2.37/4.98	1.70/1.15	

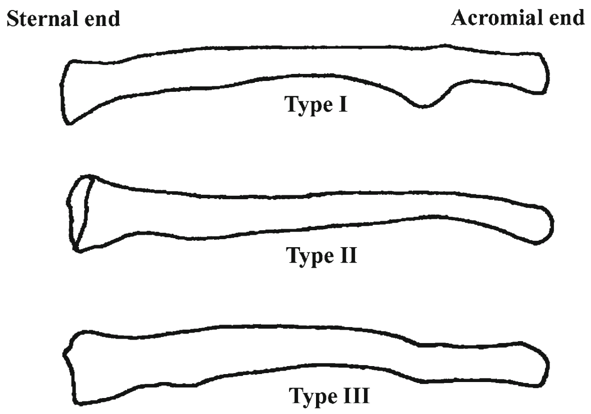

Fig. 11.5 The three types of modern human clavicles (For a definition, see text and Voisin 2006a)

Nearly all clavicles that do not belong to modern or Upper Paleolithic humans display two curvatures in dorsal view: an inferior one at their acromial extremity and a superior curvature at their sternal extremity (Voisin 2004, 2006a, 2008). However, some modern human clavicles display two curvatures in dorsal view, but their morphology is different from that of Neanderthal (Voisin 2004, 2006a, 2008). The superior curvature, when present, is less pronounced and less frequent in modern humans (Table 11.4). Moreover, some Neanderthal clavicles (Régourdou left and right, La Ferrassie I right, Krapina 153 and 154) display a superior curvature that is even more pronounced than the inferior one (Table 11.4). However, Kebara (right and left) and Krapina 143 display a modern morphology, showing only the inferior curvature. As a whole, 78% of Neanderthal clavicles show two curvatures in dorsal view (Voisin 2004, 2006a, 2008), and none with only one curvature are from West Europe.

The Length

Neanderthal clavicles have an average length similar to that of Upper Paleolithic and modern human ones (Voisin 2004, 2006a) (Table 11.5). However, Neanderthal populations are heterogeneous for this character (Fig. 11.6, Table 11.5) and clavicles from Western Europe are longer than those from Krapina and those from the Near East. This observation, confirmed by other authors (Trinkaus 1983; Nara 1994), may show that Neanderthal clavicles display a trend toward a reduction in size from West to East, even if Kebara clavicles stand close to western Neanderthal values.

Table 11.5 Clavicle total length values

Individual	Total length	Region
Régourdou (R)	152.0	West Europe
Régourdou (L)	146.0	
La Ferrassie 1 (R)	173.5	
La Ferrassie 1 (L)	178.0	
Neanderthal (R)	140.0	
Mean	**157.9**	
Krapina 153 (L)	145.0	Central Europe
Krapina 142 (R)	149.0	
Krapina 143 (R)	130.9	
Krapina 154 (L)	118.0	
Mean	**135.7**	
Kebara (L)	162.0	Near East
Kebara (R)	150.5	
Shanidar 3 (R)[a]	149.0	
Shanidar 1 (L)[b]	150.0	
Tabun 1 (R)[c]	135.0	
Tabun 1 (L)[c]	135.0	
Mean	**146.9**	

[a, b] From Trinkaus (1981, 1982)

[c] From Heim (1982)

Costal Tuberosity and Subclavius Sulcus

All Neanderthal clavicles studied here display both a costal tuberosity and a subclavius sulcus, except Krapina 153 and 149, which do not show respectively any costal tuberosity or subclavius sulcus. These two characters display no clinal variation in Neanderthal populations, and their frequencies are close to that of modern humans (Table 11.6).

Table 11.6 The presence or the absence of the costal tuberosity and the subclavius muscle in Neanderthals

Individual	Costal tuberosity	Subclavius sulcus
Shanidar 1 (L)[a]	Present	Present
Shanidar 1 (R)[a]	Present	?
Shanidar 3 (R)[a]	Present	?
Kebara (L)	Present	Present
Kebara (R)	Present	Present
Tabun 1 (L)	Present	/
Tabun 1 (L)	Present	/
Krapina 153	Absent	Present
Krapina 143 (R)	Present	?
Krapina 142 (R)	Present	Present
Krapina 156 (L)	Present	Present
Krapina 155 (L)	/	Present
Krapina 144 (R)	/	/
Krapina 145 (R)	Present	Present
Krapina 149 (R)	/	Absent
Krapina 154 (L)	Present	Present
Krapina 157 (L)	Present	/
Régourdou (R)	Present	Present
Régourdou (L)	Present	Present
La Ferrassie I (R)	Present	Present
La Ferrassie I (L)	Present	Present
La Chapelle-aux-Saints (L)	Present	/
Neanderthal (R)	/	Present
Neanderthal frequency (in%)	**94.73**	**92.86**
Modern human frequency (%)	**93.9**	**81.8**

/ Character not observable because part of the bone is missing

? No information available from literature

[a] From Trinkaus (1982, 1983)

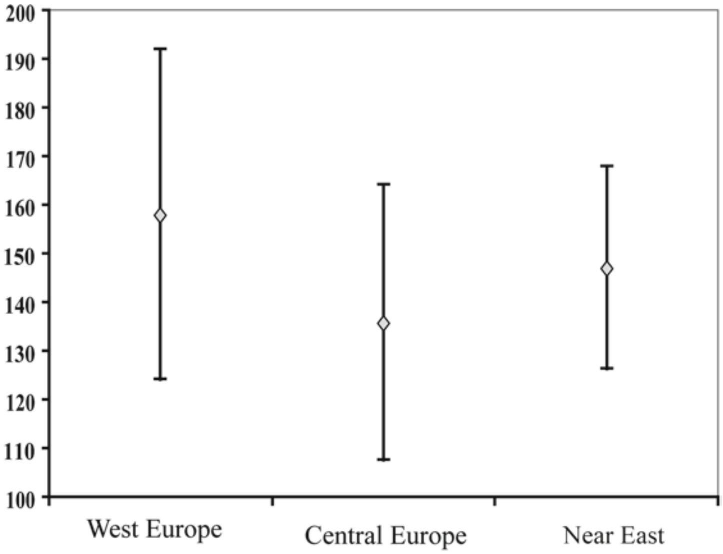

Fig. 11.6 Mean and range of variation of clavicle length in West Europe, Central Europe, and Near-East Neanderthals

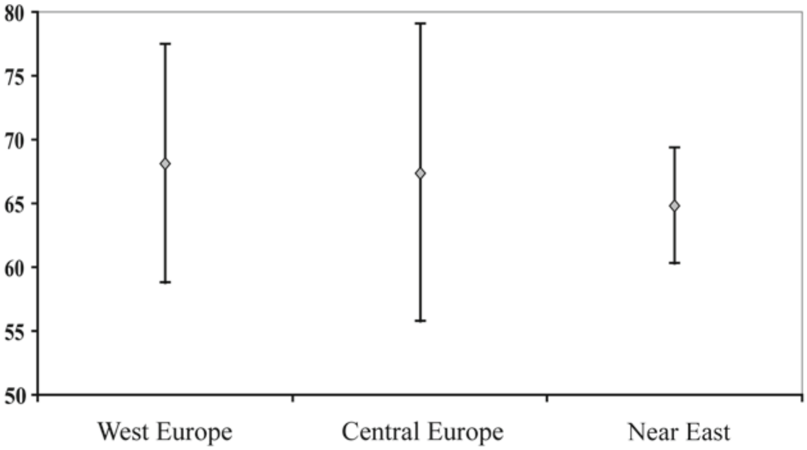

Fig. 11.7 Mean and range of variation of the glenoid index in West Europe, Central Europe, and Near-East Neanderthals

However, the two characters, taken together, are more frequent than on modern clavicles. In other words, it is more frequent to find the costal tuberosity and the subclavius sulcus on the same clavicle in Neanderthals (91.7%) than in modern humans (75.8%).

The Scapula

The Glenoid Index

The glenoid index, which is narrower in Neanderthals than in modern humans (i.e. Stewart 1962; Heim 1974, 1982; Voisin 2000; Trinkaus 2006), does not show any clear variation between Neanderthals in general and any clinal variation in particular (Fig. 11.7, Table 11.7).

The Scapula Neck Index

The scapula neck index seems to show slight differences from East to West (Table 11.7, Fig. 11.8). The average index is higher in Near East than in central or West Europe. In the Near East, the values are closer to those of modern humans (Voisin 2000). But, for this index, the data comes from only two scapulas from the same individual, Kebara, so that it is still impossible to conclude that the arm movement capacities are different between European and Near-East Neanderthals.

Angle *A*

The angle between glenoid axis and the ventral bar, or angle *A*, seems to be higher in Central European populations than in those of the Near East and West Europe (Table 11.7, Fig. 11.9). Nevertheless, Neanderthal populations are not homogenous for this character, which, at the same time, shows no evidence of an East to West morphological cline. However, the Kebara left value does not seem accurate, this scapula having possibly suffered during the time it spent underground (Vandermeersch 1991).

Table 11.7 Data for the glenoid and scapula neck index as well as for angle *A* (angle between glenoid axis and ventral bar). Some glenoid index values are taken from Vandermeersch (1981, 1991) and Trinkaus (2006)

Individual	Glenoid index	Scapula neck index	Angle *A*
Kebara (R)	63.9	91.6	148.0
Kebara (L)	61.5	93.5	133.0
Shanidar 1 (L)	65.8		
Tabun 1 (L)	65.5	89.5	141.5
Amud 1	67.5		
Mean	**64.8**	**91.5**	**140.8**
Krapina 127 (R)	65.4	75.2	155.0
Krapina 129 (R)	61.5	67.1	147.0
Krapina 125 (L)	68.0	81.4	148.0
Krapina 132 (R)	67.1	73.7	146.5
Krapina 130 (L)	77.3	86.2	147.0
Krapina 131 (L)	63.3	91.3	149.0
Krapina 133 (R)	69.1	90.2	
Vindija 209 (L)	77.0		138.5
Mean	**68.6**	**80.7**	**147.3**
Ferrassie I (R)	68.1	77.1	132.5
Ferrassie I (L)	65.2	80.8	141.0
Spy (L)	75.0	93.8	
Spy (R)	72.3	83.2	135.0
Neanderthal (R)	63.2	81.1	145.0
Mean	**68.8**	**83.2**	**138.4**
Modern human (standard deviation/mean)	**4.0/80.3**	**6.8/83.6**	**5.3/146.4**

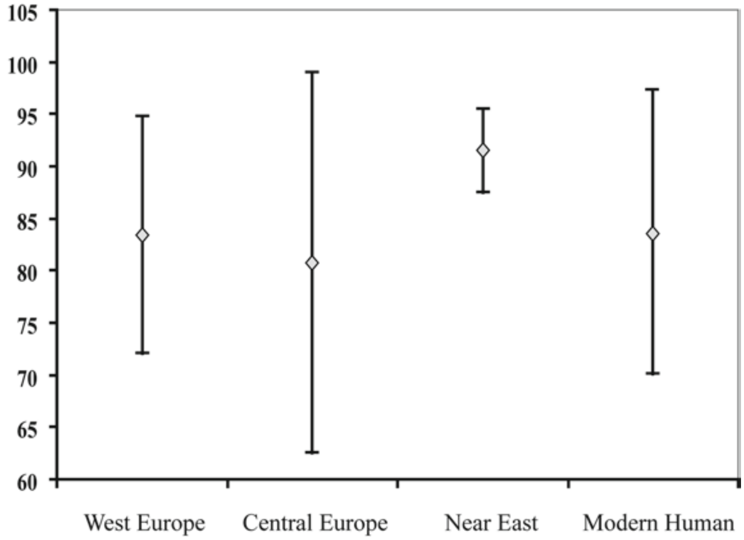

Fig. 11.8 Mean and range of variation of the scapula neck index in West Europe, Central Europe, and Near-East Neanderthals

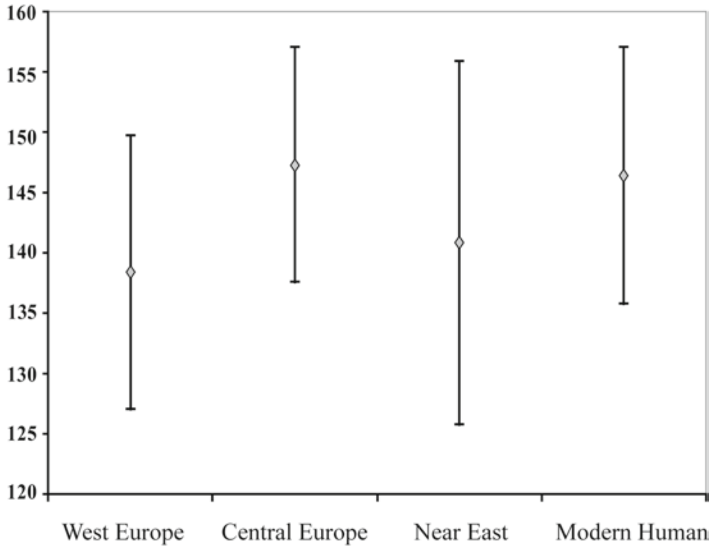

Fig. 11.9 Mean and range of variation of the angle between glenoid axis and the ventral bar, or angle A in West Europe, Central Europe, and Near-East Neanderthals and in modern humans

The Axillary Border

The morphology of the axillary border, and especially the position of the axillary sulcus (ventral, bisulcate, or dorsal), of the Neanderthal scapula has been well described and studied because of its possible distinctiveness between Neanderthals and Modern Humans and/or its relations to arm movements (i.e. Boule 1911–1913; Vallois 1928, 1932, 1946; Stewart 1962, 1964; Heim 1974, 1982; Trinkaus 1977, 1982, 1983; Vandermeersch 1981; Voisin 2000; Busby 2006; Odwak 2006; Trinkaus 2006). For a long time, a sulcus in dorsal position was considered as characteristic of Neanderthals (Boule 1911–1913; Vallois 1928, 1932, 1946; Stewart 1962, 1964) in comparison to modern humans, which were considered to possess only a ventral one, or sometimes a dorsal as well as a ventral one (bisulcate scapula). More recent works show that, in some modern human populations, it is possible to find a dorsal sulcus with a high frequency (Heim 1974, 1982; Trinkaus 1977, 1982, 1983, 2006; Vandermeersch 1981; Odwak 2006). Moreover, some Neanderthal scapulas also display the bisulcate type, and some also only possess a ventral sulcus. The bisulcate type is more frequent in Near East Neanderthal populations than in others (Table 11.8). Moreover, only a small proportion of scapulas from Central Europe have no dorsal sulcus, and none are known from West Europe. In other words, the distribution of the axillary border morphology is not homogenous within Neanderthal populations.

Table 11.8 The position of the axillary sulcus on Neanderthal scapulae. Some morphological data are taken from Boule (1911–1913), Fraipont (1927), Trinkaus (1982, 1983, 2006), Vandermeersch (1991), Frayer (1992) and Odwak (2006)

Ventral	Bisulcate	Dorsal	Percent (%)[a]
	Shanidar 3 (R)		37.5
		Shanidar 1 (L)	
		Shanidar 2 (L)	
		Shanidar 4 (R)	
		Tabun 1 (L)	
		Amud 1	
	Kebara (L)		
	Kebara (R)		
	Krapina 125 (L)		20
Krapina 127 (R)			
		Krapina 128 (R)	
		Krapina 129 (R)	
		Krapina 130 (L)	
		Krapina 131 (L)	
		Krapina 132 (R)	
		Krapina 134 (R)	
		Krapina 135 (R)	
		Vindija 209 (L)	
		La Ferrassie 1 (R)	0
		La Ferrassie 1 (L)	
		La Ferrassie 2 (R)	
		Neanderthal (R)	
		Spy (R)	
		Spy (L)	

[a] Frequencies, in percentage of non dorsal axillary sulcus

Discussion

The Clavicle

In Neanderthal, clavicle length and curvatures in dorsal view show a clinal variation from East to West. Clavicles may display only one curvature in dorsal view in the Near-East, contrary to those of western Neanderthals, which always display two. At the same time, clavicles become longer from East to West (with the exception of Kebara). Curvatures in dorsal view are associated to shoulder architecture (Voisin 2006a, b). As the costoclavicular ligament limits horizontal and vertical clavicle movements at the sternoclavicular joint, an elongation of this latter ligament increases the mobility and weakness of the joint and involves greater muscular control, exerted by the subclavius muscle. An important superior curvature permits to associate a high scapula with respect to the thorax and a clavicle with its medial end nearly parallel to the manubrium (Fig. 11.10). This condition avoids the elongation of the costoclavicular ligament. In other words, two pronounced curvatures in dorsal view are associated to scapulas located higher on the thorax than scapulas associated to clavicles with only an inferior curvature (Voisin 2004, 2006a, b). Hence, the curvatures cline within Neanderthals, in dorsal view, allows concluding the scapula position becomes progressively higher on the thorax from East to West within this population.

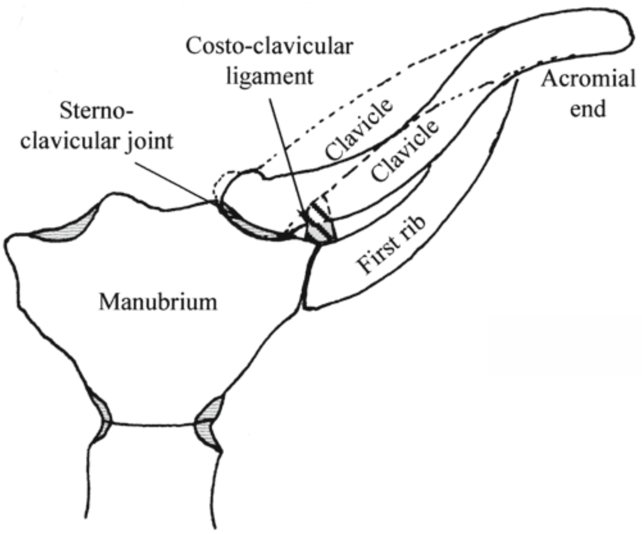

Fig. 11.10 Clavicles associated with a high scapula in regard to the thorax. *Dotted line*, human clavicle (with a unique inferior curvature); *full line*, great ape clavicle (with two curvatures in *dorsal view*). Note the costo-clavicular length difference with the two types of clavicle (After Voisin 2006b)

In the Near East, Neanderthal shoulder architecture is very similar to that of modern humans, whereas it becomes clearly different from ours in West Europe. Moreover, for a same shoulder breadth, the more the scapula sits high on the thorax, the longer is the clavicle. Thus, the geographic cline in clavicle length observed in this study is consistent with the dorsal curvatures cline.

At the same time, some clavicle characters do not display any geographical cline, like the curvatures in superior view and the subclavius sulcus and costal tuberosity frequencies. As demonstrated previously (Voisin 2006a, b), curvatures in superior view are related to arm movements, especially arm elevation, which are needed for both carrying and throwing objects like spears. There does not seem to be any difference in arm movement capacity from East to West in Neanderthal populations. The subclavius sulcus and costal tuberosity are present on most Neanderthal clavicles, and the frequency of these two characters is higher than in modern humans (Voisin 2000). As the scapula glenoid index, this character could be considered as a Neanderthal character, and may be due to a higher level of physical activities than in modern humans (Ray 1959; Jit and Kaur 1986).

Clavicle characters showing an East to West morphological cline are architectural, and, on the contrary, characters not displaying any morphological cline are functional.

The Scapula

Among scapula characters, the narrower morphology of the Neanderthal glenoid fossa is well known (i.e. Vallois 1928, 1932, 1946; Heim 1974, 1982; Trinkaus 2006). According to Churchill and Trinkaus (1990) and Trinkaus (2006), this narrower morphology "is related to habitual degrees of loading in medial and lateral hyperrotation of the glenohumeral articulation" (Trinkaus 2006, p. 344). This morphology is associated to peculiar arm movements and characteristic of Neanderthals and, as several other clavicle functional characters, the glenoid fossa morphology does not display any East to West cline.

The minimum width of the infraspinous fossa at the neck of the scapula, or scapula neck, determine the extension of the subscapularis fossa (Larson 1995) and also the importance of the infraspinous fossa, even on fragmentary remains (Voisin 2000). This index shows no clinal variation from East to West, and subsequently there is no variation of the subscapularis and infraspinous fossa along the Neanderthal distribution area. Furthermore, variation in Neanderthals does not differ from that of modern humans (Voisin 2000). In other words, the infraspinous and subscapularis muscles display no variation from West to East in Neanderthal populations, and are similar to those of modern humans. As other shoulder girdle functional characters, the minimum width of the infraspinous fossa at the neck of the scapula does not display any clinal variation.

The angle A, between the glenoid fossa and ventral bar, is correlated to the axillo-glenoid angle (Stern and Susman, 1983) and give a good overview of the orientation of the glenoid fossa. The orientation of the glenoid fossa is associated to arm movements for locomotion and/or manipulation. Central Europe and Near-East Neanderthals seem to have very similar values for this angle. On the contrary, these values tend to be lower in Western Europe. This difference could be explained by the fact that the scapula is situated higher on the thorax in Western than in Near-East or Central Europe Neanderthals. With lesser values, the glenoid fossa would have been oriented less cranially than in modern humans or in Eastern Neanderthals, and compensate for the elevation of the scapula in Western Neanderthals.

The morphology of the axillary border displays a morphological cline from West to East. According to several authors like Smith (1976), Trinkaus (1977), and Odwak (2006), it is an acquired character because the three types of sulci exist within Neanderthal, even on the same site like Krapina. Trinkaus (1977) suggest that the dorsal sulcus increases the attachment of the area for *Teres minor*. This latter muscle, along with infraspinatus, is a primary lateral rotator of the humerus and helps retaining the humeral head in the glenoid fossa. As Odwak (2006) wrote, this morphology may reflect overall osseous changes related to muscular hypertrophy and muscle re-orientation as well as to robusticity. The elevation of the shoulder in Neanderthals, as their clavicles show it, could be responsible for a reorientation of the shoulder muscles and especially the *Teres minor*. Thus, the morphological cline observed for the axillary sulcus may reflect the elevation of the shoulder girdle and the muscle hypertrophy that characterize Neanderthal populations. Even if this variation of the axillary sulcus is not genetically determinated, it reflects the Neanderthal shoulder architecture and it is more a by-product of the shoulder elevation than a real adaptation.

Thus, like clavicle curvatures, scapula traits associated to arm movement do not present any clinal variation from East to West and are homogenous within Neanderthal population. On the contrary, scapula characters in relation to shoulder architecture display an East to West cline.

Conclusion

A geographical cline in some characters of the shoulder girdle architecture seems to be evident from East to West in Neanderthal populations. Because of the scarcity of the remains at our disposal, it is not possible to draw any firm conclusion yet, and more studies, some of them in progress now, are needed on the subject. However, characters which seem to display a geographical gradient from East to West in Neanderthal populations are architectural, like clavicle morphology in dorsal view. On the contrary, functional characters, like clavicles curvatures in superior view, do not show any geographical cline.

Functional characters could be the result of various activities, and thus differences could be explained by behavior changes. On the contrary, architectural characters are mostly inherited and thus seem to be less a response to any physical activities than a result of a speciation by distance induced by genetic drift.

More studies are needed to conclude about the geographical cline from East to West in Neanderthal populations, but this first work shows that a geographical cline probably exists and is more a matter of architecture than a matter of function.

Acknowledgments I would first like to thank Silvana Condemi for her proposal to participate in the "150 years of Neanderthal discoveries – Early Europeans – continuity & discontinuity." I would also thank Professors Dominique Grimaud-Hervé, Jakov Radovcić, and Philippe Menecier, who allowed me to work, respectively, on the collections of the *Institut de Paléontologie Humaine* (Paris, France), the Croatian Natural History Museum (Zagreb, Croatia), and the *Département des collections du Musée de l'Homme* (Paris, France).

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