CHAPTER XXXII

NON-METRIC TRAITS IN THE SPY REMAINS

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Abstract

The non-metric traits, cranial and post-cranial, of the Spy remains are described and compared with other Neandertals and modern humans. There are no non-metric traits belonging only to Neandertals, but certain traits are more frequent among Neandertals than among modern humans. Among these traits some are inherited and others are linked to environmental factors and there is, in particular, a reduction of non-metric hyperostotic traits over time.

INTRODUCTION

Since the discovery of Spy remains in a cave near Namur (Belgium) in 1886 by De Puydt and Lohest, few studies have been made of these remains alone (i.e. Fraipont & Lohest, 1887; Fraipont, 1891, 1927; Thoma, 1975; Trinkaus, 1978; Trinkaus & Ruff, 1989; Orban & Leguebe, 1990; Rougier *et al.*, 2004), even if they have been widely used in more general studies on Neandertal populations.

Non-metric traits, known also as *epigenetic*, *discrete* or *discontinuous* traits, are discontinuous skeletal variations which are not measurable. They are qualitative traits, not pathological, and are thus defined by their presence or absence in each individual and they are included in human variations. Non-metric traits have been widely studied on modern human skeletons and they have proven to be useful indicators of genetic relationships between and within populations, as well as of developmental processes (for a discussion see Hauser & De Stefano, 1989). On the contrary, although the presence or absence of discrete traits is mentioned in studies of fossil bones (i.e. Tillier *et al.*, 1989; Stefan & Trinkaus, 1998), very few studies have been done of non-metric traits on fossil humans in general and on Neandertals in particular (i.e. Tillier, 1987; Condemi, 1990-1991, 1992, 2001; Manzi *et al.*, 1996, 2000).

The aim of this paper is to describe non-metric traits, both cranial and post-cranial, on the Spy remains and then to discuss their significance.

MATERIALS AND METHODS

Among modern humans, non-metric traits are well known on the cranium, face and mandible and are included in Berry & Berry (1967), Ossenberg (1970), Sjøvold (1984), Reinhard & Rösing (1985) and Hauser & de Stefano (1989). By contrast, few papers present a list of post-cranial non-metric traits, none of which are recent (Finnegan, 1978; Saunders, 1978) and we thus present a short description of each trait (SI1).

In the following investigation we were able to examine 18 non-metric cranial traits and 20 post-cranial traits on the Spy specimens (Table 1). Where not expressly indicated, the traits are considered when present. If the parts concerned are either badly damaged or missing, no reference is made to the specimen for that particular trait. When possible, the non-metric traits on the Spy cranium will be discussed as an expression of hypostosis or hyperostosis, according to Ossenberg's (1969) classification, in order to analyse growth and developmental patterns in Neandertals in comparison with present human variation.

The etiology of these non-metric characters is subject to controversy and is a complex topic. If certain studies have shown a strong tendency toward inheritability of certain features (Saunders & Popovitch, 1978; Sjøvold, 1984), other studies have stressed the importance of environmental factors (Ossenberg, 1969; Corruccini, 1974). Indeed, multiple determinants (genetic and environmental) are probable for most

Skull			
Normae	*Non-metric traits*	*Normae*	*Non-metric traits*
Norma facialis	Metopic suture	*Norma lateralis*	Parietal foramen
	Supratrochlear foramen/notch		Extrasutural mastoid foramen
	Supraorbital foramen/notch		Suprameatal spine
	Frontal grooves		Suprameatal depression
	Supraorbital incisura mediana		Auditory torus
	Frontal foramen		
Norma verticalis	Coronal ossicle/s	*Norma occipitalis*	Ossicle/s at lambda
	Sagittal ossicle/s		Lambdoid ossicle/s
	Ossicle/s at bregma		Epipteric bone/s

Upper limb		*Lower limb*	
Bone	*Non-metric traits*	*Bone*	*Non-metric traits*
Clavicle	Coraco-clavicular joint	Femur	Exostoses in the trochanteric fossa
Scapula	Glenoid notch		Third trochanter
	Morphology of the axillary border		Hypotrochanteric fossa
Humerus	Septal aperture		Fossa of Allen
	Deltoid tuberosity		Tibial imprint
	Radial sulcus or spiral groove	Patella	Vastus notch
			Vastus fossa
		Tibia	*Tuberculum tendinis*
			Vertical crest
			Tibial squatting facets
		Talus	*Os trigonum*
			Talar squatting facets
			Trochlear extension surface
			Malleolar extension surface

Table 1. List of cranial and post-cranial non-metric traits; for a description, see text and SI1

of these non-metric traits (Grünenberg, 1952; Cheverud & Buikstra, 1981). Today research is oriented toward the influence of certain disorders linked to ontogenesis. The influence of homeogenes has been demonstrated thus illustrating a complex genetic determination (Tiret *et al.*, 1993; Crubézy *et al.*, 1999).

In the comparisons of Spy non-metric traits with Neandertals, pre-Neandertals, anatomically modern humans and Upper Palaeolithic specimens, observations were made on the original fossils. When references are to the available literature, this will be indicated. For a comparison with the modern human variation, data on recent European samples were collected from British, Dutch and Italian specimens (Vecchi, 1968; Berry, 1975; Perizonius 1979a, 1979b; Vienna & Manzi, 1987).

RESULTS AND DISCUSSION

Cranial non-metric traits

For reasons related to the state of preservation of the Spy fossils, our study concerns only a limited number of non-metric cranial traits which we compare to homologous regions on the Neandertals where these regions exist.

Hypostotic traits

Metopic suture (Figure 1)

On Spy 1 this suture is absent; on Spy 10, the part is not complete but the break is situated on the midline, indicating the presence of a metopic suture, which is visible near the coronal suture. On the four Neandertals (La Ferrassie 1, La Chapelle-aux-Saints 1, La Quina 5 and Guattari 1) where this feature may be observed, this suture does not appear. By contrast, it is very much in evidence among the pre-Neandertals (La Chaise abri Suard, S16 and S32) and the proto-Neandertals (La Chaise abri Bourgeois-Delaunay BD 17, Saccopastore 1); it is also present in the Levant on the Neandertal Amud 1 and on Qafzeh 9.

Coronal ossicle/s, *Sagittal ossicle/s and Ossicle/s at bregma*

Only Spy 1 exhibits this part of the cranium. No coronal ossicle is present. This is also the case on the La Chapelle-aux-Saints 1, La Ferrassie 1, La Quina 5 and Guattari 1 Neandertals. On La Quina 5 a small sagittal ossicle is observed, as well as on Saccopastore 1. All these bones are also absent on the fossils of Cro-Magnon and Abri Pataud 1.

Squamosomastoid suture persistence (Figure 2)

On Spy 1 the persistence of a squamosomastoid suture can be observed. This suture is not visible on Spy 10, but is clearly visible on all the Neandertals on which this part is preserved (Saccopastore 1, 2, La Chapelle-aux-Saints 1, La Quina 5, Guattari 1). This region is not complete on La Ferrassie 1 and Amud 1.

Epipteric bone/s

This feature is not observable on Spy 1 and no epipteric bone is present on Spy 10. It is also absent on the other Neandertals (La Ferrassie 1, La Chaise, Bourgeois-Delaunay, Saccopastore 2, Guattari 1, La Chapelle-aux-Saints 1, La Quina 5, Amud 1), except on Saccopastore 1, where it is present.

Hyperostotic traits

Frontal grooves

Present on Spy 1 and Spy 10, these grooves are also observable on La Ferrassie 1, La Quina 5 and Amud 1, but not on La Chapelle-aux-Saints 1. No data is available in regard to the pre-Neandertals. These grooves, however, are present on Abri Pataud 1, Cro-Magnon 1, 2 and 17 and on Qafzeh 9.

Frontal foramen

Two frontal foramina are observable on the two Spy fossils and they are also present on the four European Neandertals (La Ferrassie 1, La Chapelle-aux-Saints 1, La Quina 5, Guattari 1) as well as on Amud 1. No data is available in regard

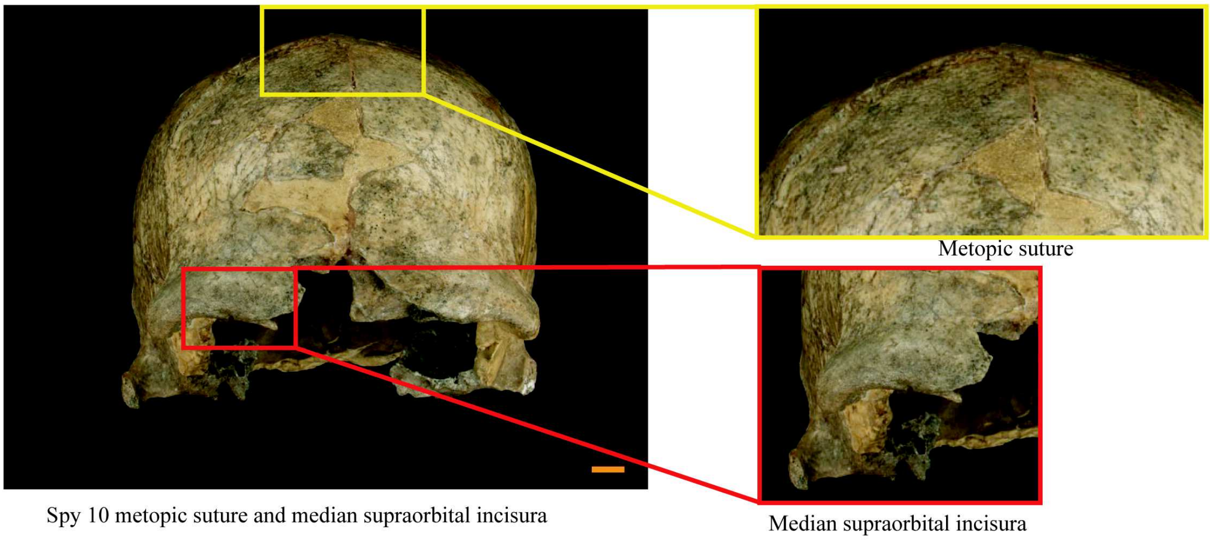


Figure 1. Non-metric traits on Spy 10 in *norma facialis* (Photo: P. Semal, RBINS).

to the pre-Neandertals. However these grooves are not present on Abri Pataud 1, Cro-Magnon 1, 2 and Qafzeh 9 but they are present on Cro-Magnon 17.

Supraorbital foramen/notch

On the two Spy fossils they are not observable. They are present on the four Neandertals on which this feature may be observed (La Ferrassie 1, La Chapelle-aux-Saints 1, La Quina 5, Guattari 1). It is not observable on Amud 1. By contrast it is present on Saccopastore 1 and 2.

Supratrochlear foramen/notch

On the two Spy fossils they are not observable. On the two Neandertals on which this region is present, they exist on Guattari 1 but not on La Ferrassie 1, nor may they be observed on Amud 1. A supratrochlear foramen or notch is absent on Abri Pataud 1, Cro-Magnon 1, 3 and 17 but present on Cro-Magnon 2.

Supraorbital incisura mediana (Figure 1)

It is present on the two Spy fossils but is observable only on La Quina 5, and is absent on the other three European Neandertals as well as on Amud 1. It is present on Cro-Magnon 2 and 17.

Suprameatal spine (Figure 2)

On Spy 1 and Spy 10 a suprameatal spine is present. It is also the case on the other Neandertals whose state of preservation permits observation of this feature (La Ferrassie 1, La Chapelle-aux-Saints 1, La Quina 5, Guattari 1, Saccopastore 1 and 2, La Chaise, Bourgeois-Delaunay). These features can also be observed on Cro-Magnon 1 and 2 and on Qafzeh 9.

Auditory torus (Figure 2)

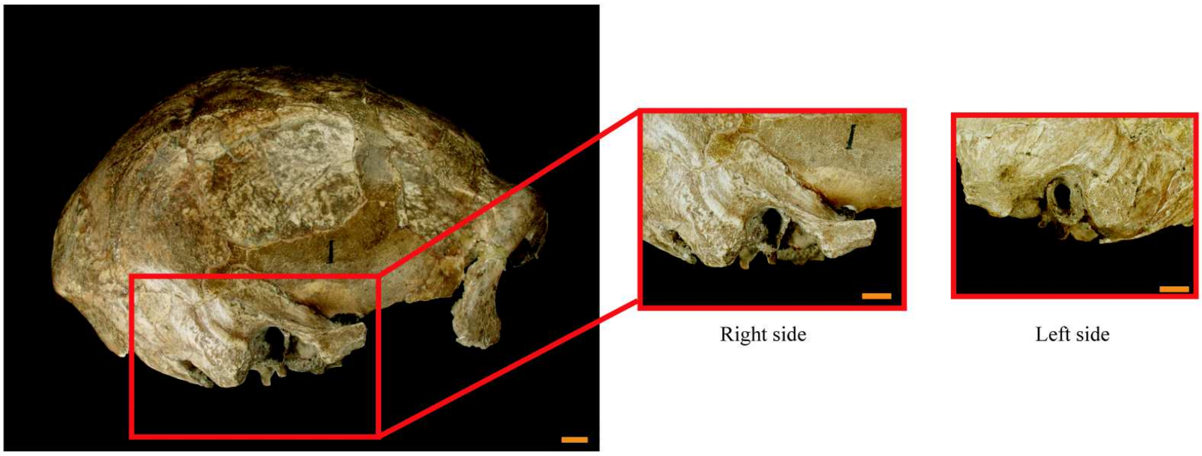
This feature is often regarded as pathological, but it is present on all the Neandertals, including the two fossils of Spy, as well as on pre-Neandertals and on fossils from the Upper Palaeolithic where the region on which this character may be observed is preserved.

The genetic determination of the torus is sharply contested. It is often attributed to long-term irritation and it is thus considered to be pathological. This feature is relatively uncommon among modern humans: its frequency varies from 0 % to 26.2 % (Corruccini, 1974; Zivanovic, 1979). The average frequency is situated at about 2.5 %.

Foramina and ossicles

Parietal foramen absent

On Spy 1 and Saccopastore 1 this foramen is absent. In Spy 10 it cannot be observed. On Neandertals (La Ferrassie 1, La Chapelle-aux-Saints 1, La Quina 5, Guattari 1) and the fossils from the Upper Palaeolithic (Cro-Magnon 1, 2, 3 and 17, Abri Pataud 1) it is also absent.



Right side

Left side

Spy 1 righ lateral view, squamomastoid suture persistence, supremeatal spine and auditory torus

Figure 2. Non-metric traits on Spy 1 in *norma lateralis* (Photo: P. Semal, RBINS).

Extrasutural mastoid foramen

No extrasutural foramen exists on Spy 1. This foramen is present on Spy 10. The expression of this feature is variable on Neandertals: it is present on La Ferrasssie 1, Saccopastore 1 and la Chaise Bourgeois-Delaunay, and absent on Saccopastore 2, Guattari 1, La Chapelle-aux-Saints 1, La Quina 5 and Amud 1. It is present on Qafzeh 9, Abri Pataud 1 and Cro-Magnon 1, 2 and 17.

Ossicle/s at lambda and *Lambdoid ossicle/s*

On Spy 1 an ossicle at lambda and on the lambdoid suture cannot be observed, since the part is missing. On Spy 10 no ossicles on lambda and on the suture are present. On all the Neandertals (La Chapelle-aux-Saints 1, La Ferrassie 1, La Quina 5, Guattari 1, Saccopastore 1, La Chaise Bourgeois-Delaunay), one or more ossicles on lambda and on the suture are present.

Post-cranial non-metric traits

Clavicle

Coraco-clavicular joint

The Spy remains display no coraco-clavicular articulation on the clavicles, as is the case with all Neandertal and Upper Palaeolithic remains. In modern humans, the frequency of this joint varies greatly and the European population displays the lowest frequency, less than 5 % (Cockshott, 1992; Gumina *et al.*, 2002) and it may be considered to be a genetic marker for population migrations (Cockshott, 1992). The absence of this trait on any known Neandertal and Upper Palaeolithic clavicles could be linked to a low frequency of this trait among these populations.

Scapula (Table 2, Figures 3 and 4, ST1)

Glenoid notch

The glenoid notch is present in more than 60 % of the Neandertal scapulae studied and it is

	Neandertal	Homo sapiens
Glenoid notch	61.10 %	73.33 %
Morphology of the axillary border: bisulcate	14.29 %	44.68 %
Morphology of the axillary border: ventral	10.71 %	48.94 %
Morphology of the axillary border: dorsal	75.00 %	6.38 %

Table 2. Percentages of each scapular trait in Neandertals and modern humans.

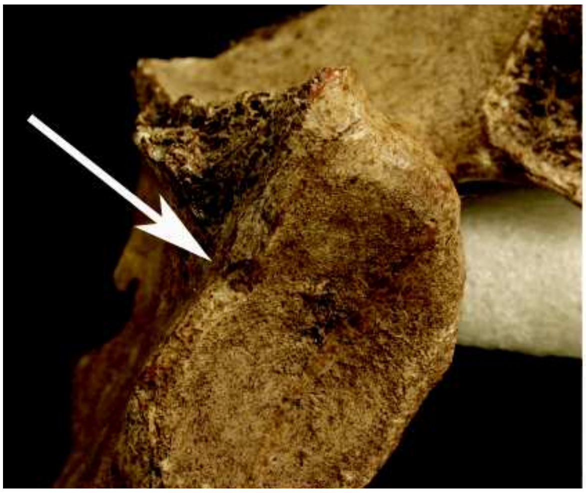


Figure 3. The glenoid notch (arrow) on the Spy 573a scapula in glenoid view (Photo: P. Semal, RBINS).

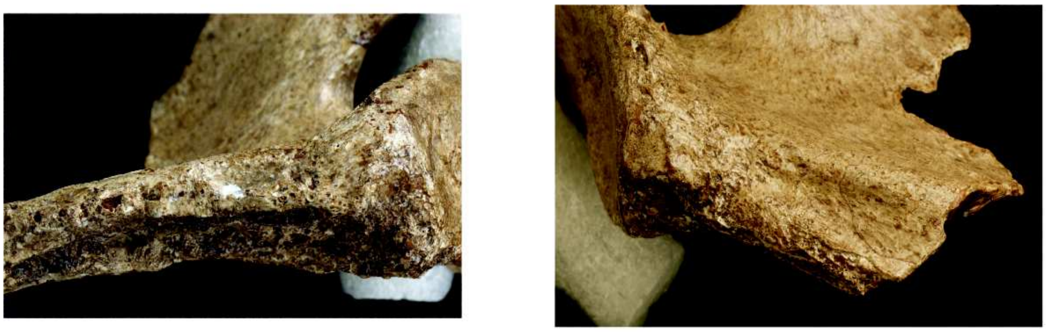


Figure 4. Morphology of the axillary border of the Spy 572a (left) and 573a (right) scapulae (Photo: P. Semal, RBINS).

present, but slightly, on both Spy scapulae, contrary to La Ferrassie 1, where this trait is present only on the right scapula. This frequency is somewhat lower than that among modern human fossils, which is slightly more than 70 %. In modern humans, the frequency of the glenoid notch is around 55 % (Prescher & Klümpen, 1997). In the area of the notch, the glenoid labrum is not fixed to the bony margin of the glenoid cavity, but bridges the notch itself (Prescher & Klümpen, 1997). Such an attachment of the labrum could make the shoulder joint less resistant to dislocating forces and may induce a Bankart lesion (Prescher & Klümpen, 1997).

The frequency of the glenoid notch in modern humans is less than in Neandertals and Upper Palaeolithic humans. However, it is slightly more frequent in Upper Palaeolithic remains than in Neandertals. This difference between all these human groups is not so wide and hence it is difficult to assert that it would reflect a different sensibility to the Bankart lesion among human groups.

Morphology of the axillary border

It has been repeatedly noted that the Neandertal axillary border displays a dorsal sulcus more frequently than a bisulcate or a ventral one, and our results fit well with this assertion, with 75 % of Neandertal scapulae showing a dorsal sulcus. However, the Spy 573a scapula displays a dorsal sulcus, contrary to the Spy 572a scapula, which seems to exhibits a ventral one. Anatomically modern human and Upper Palaeolithic remains, as well as modern humans, more often display a ventral sulcus, and among our modern human fossils the frequency we have found for the dorsal sulcus is lower than 10 %.

Many scholars (i.e. Trinkaus, 1977; Heim, 1982; Voisin, 2000) consider that the sulcus position depends on the musculature, and would reflect a pronounced development of the *teres minor* muscle, which would act as a lateral rotator of the humerus, and hence would produce greater efficiency in some movements, especially for the purpose of throwing objects. If this functional interpretation is correct, individuals like Kebara or Spy displaying two different morphologies on each scapula, would be associated with an unrealistically high specialisation between the right and left upper limb. Alternatively, the explanation which correlates the frequency of the dorsal sulcus and the robustness of the scapula (Odwak, 2006) is interesting because it fits well the asymmetry of the trait. Hence the dorsal sulcus on the Neandertal scapula would be the by-product of post-natal developmental history rather than a different upper limb use between these two human groups.

Humerus (Table 3, Figure 5, ST2)

Septal aperture

The septal aperture is common among Neandertals (Trinkaus *et al.*, 2006) and reaches a frequency of over 50 %, but no Spy humerus displays this perforation. However, this high frequency is in great part due to the Krapina humeri, 75 % of which display a septal aperture. Without the Krapina humeri, the frequency is lower and reaches 37.5 %, which is still high. This value corresponds to the highest one known in modern humans, which is between 3 and 35 % (Hrdlička, 1932; Singhal & Rao, 2007). Moreover, La Quina 5 (left), Shanidar 1 and the two Spy humeri, which lack a true septal aperture, display pinhole perforations of the thin septum (Vandermeersch & Trinkaus, 1995). On the contrary, in anatomically modern humans and Upper Palaeolithic humans the frequency reaches 10 % without the Taforalt population and 22 % when it is included.

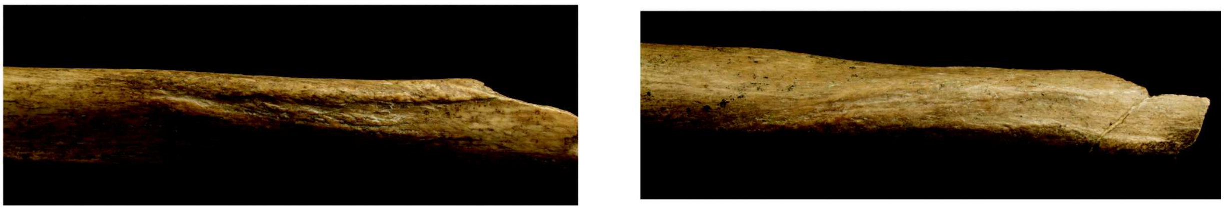
It has been commonly asserted that the septal aperture depends mainly on bone robustness and, by extension, is more frequent in females than in males. However, Hrdlička (1932) and Saunders (1978) demonstrated that this aperture is mostly inherited, even if bone robusticity and / or ulna morphology could moderate the genetic control (Benfer & McKern, 1966; Riesenfeld & Simon, 1975; Singhal & Rao, 2007). The high frequency of the septal aperture among Neandertals, with or without the Krapina humeri, could be a trait of this human group, and could,

	Neandertal	Homo sapiens
Septal aperture	53.57 %	22.22 %
Deltoid tuberosity	96.30 %	100.00 %
Radial sulcus	45.00 %	93.55 %

Table 3. Percentages of each humeral trait in Neandertals and modern humans.

Humerus Spy 5A

Humerus Spy 5B



Humerus Spy 14A

Humerus Spy 14B

Figure 5. Deltoid tuberosity of the Spy humeri (Photo: P. Semal, RBINS).

in a certain way, reflect some genetic homogeneity among them. Moreover, the earliest Upper Palaeolithic remains display the lowest frequency of the septal aperture (Trinkaus *et al.*, 2006), and hence could confirm the genetic differences between the two human groups.

This high frequency of the septal aperture would increase elbow extension (De Wilde *et al.*, 2004), which may affect the capacity to throw objects. Some other traits have been interpreted as enhanced movement forces, as the morphology of the scapula axillary border (but see the part about the scapula) and the great length of the clavicle (Voisin, 2000). In other words, all of these traits taken together should really increase the arm movement forces, especially during throwing.

Deltoid tuberosity

The deltoid tuberosity is present in all but one Neandertal (the right humerus of La Chapelle-aux-Saints 1) i.e. the frequency of the deltoid tuberosity among Neandertals is more than 95 %. In anatomically modern and Upper Palaeolithic humans the frequency is 100 %, which is higher than in modern humans. As roughness and size of muscle scar plastically respond to repetitive muscle use (Churchill & Smith, 2000), this high frequency of deltoid tuberosity among anatomical and Upper Palaeolithic humans, as well as among Neandertals, is due to the high level of physical activity in which these fossil populations were involved.

The radial sulcus

There are four humeri among the Spy remains, and the radial groove is present on two of them (14B and 14A). Moreover, among Neandertals, 45 % of the humeri display a radial sulcus. All anatomically modern human humeri and nearly all Upper Palaeolithic humeri display a radial sulcus, except for two Taforalt humeri. As Neandertal deltoid tuberosity is narrower than the one of modern humans (Endo, 1971), the Neandertal humerus shaft becomes more rounded than does the modern one. Hence the radial sulcus tends to flatten to the point of becoming invisible among Neandertals. In other words, the radial sulcus should be correlated to the morphology of the deltoid tuberosity.

Lower limb

Femur (Table 4, Figure 6, ST3)

Exostoses in the trochanteric fossa

Among the Neandertal femurs studied, only six, including Spy 16, display a trochanteric fossa and only two (La Ferrassie 1 right and Neandertal 1 right) display exostoses in the trochanteric fossa. However, even if the sample is very low, the frequency of this trait among Neandertals is very close to that of modern humans.

According to Saunders (1978) and Stirland (1996), this trait is much more frequent in old subjects than in young adults and seems related to a high level of physical activity. Since

	Neandertal	Homo sapiens
Fossa of Allen	16.70 %	26.32 %
Tibial imprint	0.00 %	47.06 %
Exostoses in the trochanteric fossa	33.33 %	26.31 %
Third trochanter	14.29 %	31.81 %
Hypotrochanteric fossa	68.75 %	35.71 %

Table 4. Percentages of each femoral trait in Neandertals and modern humans.

Figure 6. Hypotrochanteric fossa (white circle) on the Spy 8 femur in posterior view (Photo: P. Semal, RBINS).

Neandertals and, until recently, also modern humans, were involved in a high level of physical activity, the low level of frequency for the exostoses in the trochanteric fossa for these human groups leads us to suppose that most individuals died before reaching an elderly age.

Third trochanter

Like Fraipont & Lohest (1887), we do not recognize any third trochanter on Spy 8 and 16. It is present only on Krapina 213 and on the Neandertal 1 left femur (but on the latter, it is slightly pronounced). In other words, within Neandertals the frequency is lower than 15 %, which corresponds to the lower border of the frequency ranges in modern humans (Hrdlička, 1937). However, until the work of Trinkaus (1986) the third trochanter was considered to be characteristic of Neandertals but as showed by him, and as our work confirms it, the third trochanter is not a characteristic trait. The third trochanter became common in Europe with the emergence of Neolithic populations (Condemi, 2001). Palaeolithic remains also display a very low frequency of this trait (Condemi, 2001). The high frequency in our sample of Upper Palaeolithic remains is due to Taforalt.

Among modern humans, the frequency of this trait depends on geography (Hrdlička, 1937; Stirland, 1996), and there thus seems to be a genetic background, even if recent work shows that it depends more on environmental conditions, especially on a high level of physical activity. However, the high frequency of the third trochanter among the Taforalt population (known to display a high level of endogamy) and the low frequency among Neandertals show that the genetic component is an important part of the expression of this trait, more essential than previously thought.

Hence, the high frequency of this trait among Neolithic populations (Condemi, 2001) would be due to genetic flow from outside Europe and may reflect migrations of new populations.

Hypotrochanteric fossa

The hypotrochanteric fossa is present on the Spy 8 femur but absent on Spy 16. Among Neandertals, the hypotrochanteric fossa frequency is higher than 65 %. This frequency is much higher than in recent modern humans for which it is less than 50 % (Hrdlička, 1934; Saunders, 1978). This high frequency of the hypotrochanteric fossa among Neandertals led Heim (1974) to consider it to be a Neandertal apomorphy. If Middle and Upper Palaeolithic modern humans are considered together, the hypotrochanteric fossa frequency is similar to that found among extant modern humans. However, if we consider separately early anatomically modern remains such as Qafzeh and Skhul, the frequency rises to 100 % within the latter, whereas among Upper Palaeolithic remains this frequency is less than 30 %. This result is coherent with Condemi (2001), who observed a decrease of the hypotrochanteric fossa frequency from the Upper Palaeolithic until the modern period.

Numerous factors may account for this frequency change: (i) the hypotrochanteric fossa is associated with a high level of physical activity (Trinkaus, 1976); since this frequency decreases before the end of the Upper Palaeolithic, this interpretation seems to be doubtful, (ii) the hypotrochanteric fossa frequency reaches its maximum around the age of 19 and then decreases (Saunders, 1978). The frequency differences in Neandertals and early anatomically modern humans, compared to more recent humans, may reflect a younger age at death for the former group than for the latter one.

Fossa of Allen

Among all Neandertal remains studied, the fossa of Allen is present on Spy 8 only. This very low frequency among Neandertals, less than 17 %, could be underestimated because the anatomical part of the femur, where this trait is normally present, is very often eroded. Nearly 40 % of the femurs studied do not present a bone sufficiently well preserved to allow observations. With a frequency slightly higher than 25 % for the fossa of Allen among Taforalt femurs, these Upper Palaeolithic remains are closer to Neandertals than to more recent modern humans which reach a frequency of 70 % (Parsons, 1914; Meyer, 1924). This result confirms that the Allen fossa is not correlated to a squatting position as previously supposed. For Belcastro *et al.* (2006), the frequency change between the Pleistocene and modern human populations may reflect a change in mechanical stress related to flexion/extension of the hip joint.

Tibial imprint

The Spy femur, like other Neandertal femurs, does not display any tibial imprint. On the contrary, among Taforalt femurs, nearly 50 % display a medial tibial imprint This trait depends on two factors: the presence of a *tuberculum tendinis* on the tibia and a frequent use of a hyperflexed position of the knees, like the one used during squatting. Other traits on Neandertal remains show the usual hyperflexed position of the knees, as well as on the Taforalt population (squatting facets on talus, etc.). The *tuberculum tendinis* is not frequent on Neandertal remains and hence could explain the absence of a tibial imprint on the Neandertal femur.

Patella (Table 5, Figure 7, ST4)

Vastus notch

More than 70 % of Neandertal patellae, including the unique Spy 19 patella, display a vastus notch, a frequency which is much higher than that among modern humans, where it is around 6 % (Anderson, 2002). The two Skhul IV patellas, as well as the two of Dolní Věstonice 3, display a vastus notch (McCown & Keith, 1939; Trinkaus & Jelínek, 1997) and more than half the Taforalt remains also display this trait. Since the vastus notch may be, to a certain degree, inherited (Angel *et al.*, 1987; Scapinelli & Capasso, 2000), its high frequency among the Taforalt population is coherent with the high level of endogamy (Ferembach, 1960) of this population. Hence, its high frequency among Neandertals may reflect some genetic homogeneity and isolation in regard to modern humans.

Vastus fossa

More than 50 % of Neandertal patellae display a vastus fossa, including that of Spy (Spy 19). This frequency is much higher than that

	Neandertal	Homo sapiens
Vastus notch	72.72 %	57.50 %
Vastus fossa	45.00 %	55.00 %

Table 5. Percentages of each patellar trait in Neandertals and modern humans.

Figure 7. Vastus notch and vastus fossa on the supero-lateral angle of the Spy 19 left patella in anterior view (Photo: P. Semal, RBINS).

found on modern humans, which is around 6 %. As this trait is very often associated with the vastus notch, it would thus be also inherited.

Moreover, 25 % of Neandertal patellae display both the vastus notch and the vastus fossa and only 20 % display the vastus fossa alone. As for the vastus notch, the high frequency of the vastus fossa would be characteristic of Neandertals as is also the high frequency of the vastus fossa and vastus notch on the same bone.

Tibia (Table 6, ST5)

Tuberculum tendinis

No Neandertal remains studied display a *tuberculum tendinis*. As this tubercle is responsible for the tibial imprint (Kostick, 1963) on the distal epiphysis of the femur, usually when the knee is in hyperflexed position, its absence explains that there is no tibial imprint on the Neandertal femur. On the contrary, this trait is present on 20 % of the Taforalt tibiae, and fits well the frequency of the tibial imprint on the femur.

As this tubercle is the insertion point of a rare component of the semimembranous muscle (Cave & Porteous, 1958), the high frequency of the *tuberculum tendinis* among the Taforalt population is coherent with the high level of endogamy described for it (Ferembach, 1960).

Vertical crest

There is no vertical crest, neither on the Spy 9 tibia nor on the totality of Neandertal remains studied, contrary to Upper Palaeolithic tibias where this trait reaches a frequency higher than 60 %. According to Mafart (1984), this trait would be acquired, but our observations are not compatible with such a hypothesis and correspond better to that of a genetic control.

	Neandertal	Homo sapiens
Tuberculum tendinis	0.00 %	20.00 %
Vertical crest	0.00 %	63.40 %
Tibial squatting facet: lateral	58.30 %	43.20 %
Tibial squatting facet: medial	9.01 %	0.00 %
Tibial squatting facet: double	0.00 %	2.86 %

Table 6. Percentages of each tibial trait in Neandertals and modern humans.

Tibial squatting facets

Spy's unique tibia does not display any squatting facets. However, more than half of Neandertal tibias display such squatting facets, which is coherent with Trinkaus' (1975) results. The lateral facet is much more frequent than the medial one, which is present only on La Ferrassie 1, and there is no double facet within Neandertals. In Upper Palaeolithic humans, nearly half of the population displays a lateral squatting facet. Among the samples, there is no medial facet and only one double facet (or 2.86 %). The high frequency of squatting facets among Neandertals and Upper Palaeolithic remains is coherent with a frequent hyperflexed position of the ankle, and may be due to a frequent use of the squatting position. However, these traits could also be associated with frequent long walks on hard surfaces (Ari *et al.*, 2003), which is coherent with the hunter-gatherer behaviour of these populations.

Talus (Table 7, Figure 8, ST6)

Os trigonum

An *os trigonum* does not exist, neither on Neandertal remains, nor on Middle and Upper Palaeolithic anatomically modern humans. As the frequency of this bone is around 10 % in extant modern humans and may even reach 50 % in some populations (Anwara & Nicholl, 2005; Wansbrough & Eyres, 2007), its absence in past populations is difficult to explain. If this bone is the result of a non fusion of an accessory ossification centre it may reflect a genetic shift between modern humans and earlier remains. On the contrary, if the *os trigonum* is the result of a traumatic event, this would signify a shift in behaviour or in bone structure between earlier *Homo* and modern humans.

Talar squatting facets

More than 60 % of Neandertal taluses display a lateral talar squatting facet, but not the only talus from Spy (Spy 18), and in Upper Palaeolithic remains this frequency is less than 5 %. By contrast, the medial talar squatting facet is absent in all the Neandertal remains studied and its frequency is low in Upper Palaeolithic populations, less than 5 %.

	Neandertal	Homo sapiens
Os trigonum	0.00 %	0.00 %
Lateral talar squatting facet	61.50 %	4.70 %
Medial talar squatting facet	0.00 %	4.70 %
Medial malleolar extension surface	88.20 %	95.50 %
Medial extension of the trochlear surface	42.90 %	39.10 %
Lateral extension of the trochlear surface	64.70 %	45.70 %

Table 7. Percentages of each talar trait in Neandertals and modern humans.

Figure 8. The Spy 18 talus in lateral (left), superior (center) and medial (right) views (Photo: I. Crevecoeur, RBINS).

Trochlear and malleolar extension surfaces

Among these three articular extensions, the Spy talus, as Trinkaus (1975) has already noted, displays only the malleolar extension surface. These extensions of the articular surface are frequent in modern human as in Neandertals. The malleolar extension surface is slightly more frequent in Upper Palaeolithic than in Neandertal specimens, whereas the two other extensions are more frequent in Neandertals than in modern humans.

Trochlear and malleolar extension surfaces as squatting facets are associated with a hyperflexed posture, such as frequent use of a squatting position for rest. However, the high frequency of these characters among Neandertal taluses could also be a possible response to a mechanical stress through increase of the articular surfaces, hence allowing a better force distribution at the ankle joint (Castellana & Malgosa, 1993). This interpretation is somewhat better because numerous populations frequently used a squatting position and these extensions and articular facets could be rare. Moreover, Neandertals are known to be heavily built and hence force distribution at the ankle joint would have to be more extended.

DISCUSSION AND CONCLUSION

For reasons that relate to the state of preservation of the Spy fossils and of the Neandertals, our study concerns only a limited number of skeletal variations and does not deal with the Neandertal population as a whole. The result is a partial and necessarily insufficient perspective in regard to the diachronic analysis of Neandertals. For this reason the results we have obtained are difficult to interpret in terms of a strictly evolutionary schema. Indeed, if the Neandertals are characterized by a series of derived (apomorphic) morphological traits, which progressively increase during the Middle Palaeolithic, we cannot adopt an identical reasoning for the non-metric characters.

By contrast, Neandertal crania show non-metric traits at a frequency which is different than that observed on modern humans. This is particularly the case for the auditory torus, the suprameatal spine and depression as well as the surnumerary ossicles. There is a tendency toward reduction of hyperostotic and hypostotic traits. We may consider the first case to be a phenomenon of gracilization of the cranial skeleton from pre-Neandertals to Neandertals and, in the second case, a possible modification of certain ontogenetic parameters, relating for example to bone growth. The suturary or surnumerary ossicles, considered to be hypostotic traits, are often observable among pre-Neandertals with great frequency. For Sergi (1933-1934) and Manzi *et al.* (2000), they result from an "ontogenic stress" due to a disproportion in speed and duration between cerebral growth and bone growth, having as a consequence acute intra-cranial pressure at the level of the sutures.

On the basis of a better sample, certain of the non-metric traits might serve as excellent indicators for studies of growth and would permit us to demonstrate shifts in development, as has been done for more recent populations (Crubézy, 1991).

Post-cranial traits could be divided into two groups: (i) traits which are essentially inherited, even if certain environmental factors could have some influence (morphology of the axillary border, septal aperture, radial sulcus, third trochanter, hypotrochanteric fossa, vastus notch, vastus fossa, tuberculum tendinis), (ii) traits which are essentially induced by environmental factors and / or behaviour (glenoid notch, deltoid tuberosity, exostosis in trochanteric fossa, fossa of Allen, tibial imprint, tibial squatting facets, talar squatting facets, trochlear and malleolar extension surface).

Among inherited traits, four of them (septal aperture, radial sulcus, vastus notch and vastus fossa) display a frequency in Neandertals which is significantly different from that of modern humans and Upper Palaeolithic remains. These traits, and their frequency, suggest some genetic homogeneity within the Neandertal population permitting us to distinguish it from modern humans, but without allowing us to decide whether these populations correspond to one or two species. Moreover, the septal aperture associated with the great length of the clavicle among Neandertals could increase throwing forces.

Among traits induced by environmental factors, four (tibial imprint, tibial squatting facets, talar squatting facets, trochlear and malleolar extension) may be associated with the hyperflexed position of lower limb joints (Trinkaus, 1975). These traits could be associated with a frequent use of a squatting rest position. However, according to Ari *et al.* (2003), the so-called tibial and talar squatting facets could also be due to frequent long walks on hard surfaces. Whatever the explanation, the results imply that Neandertal and Upper Palaeolithic humans display the same behaviour.

The Spy remains display a similar expression pattern of discrete traits to that of other Neandertals. However, the septal aperture, the tibial squatting facets and the talar squatting facets do not display the same pattern of expression. The septal aperture, which is frequent within Neandertal remains, is absent on Spy humeri. As this trait is genetically controlled, its absence on the Spy remains may reflect some genetic differences between Neandertal populations. In other words, according to DNA testing, Neandertals are not a homogeneous population (Caramelli *et al.*, 2006; Orlando *et al.*, 2006). The Spy tibia and talus do not display any squatting facets, which are traits related to behaviour, even if trochlear and malleolar extension surfaces are present on Spy.

In summary, we observe no non-metric traits belonging only to Neandertals, but certain traits are more frequent among Neandertals. Throughout the course of Neandertal evolution, we observe a process for the cranium, not of augmentation – as is the case with certain morphological traits – but of reduction of non-metric hyperostotic traits from the period of the most ancient to that of the most recent fossils.

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