CHAPTER XXVII

HAND BONES

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Abstract

The Spy site has yielded 265 complete and fragmented human hand bones. Fourteen are found in the original collection from the 1886-1887 excavations. The remainder have been identified during a revision of all faunal collections from the site.

The original collection inventory mentions nine metacarpals and four proximal phalanges. An additional metacarpal from the original collection was not identified as such, but as a costal fragment. The Neandertal attribution of the thirteen identified hand remains and their association with the two adult Neandertal skeletons had never been questioned. However, the discovery of over 200 other hand bones (mature and immature), largely associated with a Neolithic burial present at Spy, brings into question the homogeneity of the original collection and raises the possibility that Neandertal hand bones may be present among the more recently discovered remains.

In this chapter, we present a comparative morphometric study of the Spy hand bones. They are compared to Neandertal specimens, Middle and Upper Palaeolithic modern humans and Neolithic series by means of uni- and multivariate statistical analyses. Our results demonstrate the taxonomic heterogeneity of the original collection; metacarpal Spy 25E possesses modern morphological and biometric characteristics, and the immature metacarpal Spy 22B may be of Neolithic age. Additionally, we were able to associate some hand bones of the original collection based on robustness, symmetry and secondary anatomical connection criteria, resulting in seven of the ten metacarpals and three of the four proximal phalanges to be attributed to the same individual, Spy II. Among the newly discovered bones, four proximal phalanges and five middle phalanges have been clearly isolated according to their morphology and dimensions. They exhibit a clear Neandertal conformation and may be associated with the Spy II skeleton. Direct ^{14}C dating of one of these middle phalanges (Spy 430a) confirms the results of the comparative analysis.

INVENTORY OF THE HAND BONES

A total of 265 complete or fragmented hand bones have been inventoried to date from the Spy cave site. Among these, fourteen are found in the original collection from 1886-1887 and thirteen of them were attributed to the Neandertal specimens Spy I and II without distinction. In their first publication, Fraipont & Lohest (1887) described only nine hand bones. The other four were recognised later among a group of undetermined hand and foot bone fragments and were labeled during the unpublished inventory made in 1935 at the Royal Belgian Institute of Natural Sciences (RBINS). In the first version of the Catalogue of Fossil Hominids, Twiesselmann (1953) listed the full collection and gave a precise attribution for most of the hand bones to either the Spy I or the Spy II specimen. Finally, we identified one metacarpal among the costal remain assemblage of the origin-al collection and today, this collection contains ten metacarpals and four proximal phalanges, as listed in Table 1.

The 251 new hand bone remains were discovered and identified during the 2004-2006 revision of all the faunal collections from the various excavations at Spy. These faunal remains had been stored in several Belgian institutions (RBINS, Royal Museums of Art and History, *Université de Liège* and *Musée Archéologique de Namur*) and in private collections gathered through former clandestine excavations (like the Beaufays & Carpentier collections). Supporting Table 1 (ST1) contains the inventory of all the newly recognised mature and immature hand bone remains.

The discovery of such a large amount of new hand bones, associated mostly with the Neolithic burial identified at Spy, raises the double

	Bone	Side	Preservation State	Maturation	Inventory	Notes
20I	MTC V	L	Distal extremity missing	M	3	Inventoried as a costal fragment
21A	MTC II	R	Complete	M	1	
21B	MTC III	R	Distal extremity missing	M	1	
21C	MTC IV	R	Distal extremity missing	M	1	
21D	MTC III	L	Proximal half	M	1	
22A	MTC II	L	Fragment	M	1	Refits with 25I and 25K
22B	MTC II	R	Complete	I	2	Inventoried as a left MTC III
22C	MTC IV	L	Complete	M	1	
24A	PP IV	R	Complete	M	1	
24B	PP V	R	Complete	M	1	
24C	PP II	L	Complete	M	1	
25E	MTC III	L	Distal extremity missing	M	2	
25H	PP I	R	Complete	M	2	
25I	MTC II	L	Proximal extremity	M	1	Refits with 22A and 25K
25J	MTC I	L	Part of the proximal extremity	M	2	
25K	MTC II	L	Distal extremity	M	1	Refits with 22A and 25I

Table 1. Inventory of the fourteen hand bones from the original Spy collection (RBINS).
Inventories: 1 = Fraipont & Lohest, 1887; 2 = Catalogue of the RBINS from 1935; 3 = Newly identified hand bone.
MTC = Metacarpal; PP = Proximal phalanx; R = Right; L = Left; M = Mature; I = Immature.

issue of the homogeneity of the original collection and the possible presence of Neandertal hand bones among the new remains. Previous studies of Neandertal specimens have emphasised differences in the characteristics of the carpus, the metacarpals and the phalanges of this group compared to anatomically modern humans (e.g. Boule, 1911; Suzuki & Takai, 1970; Musgrave, 1971, 1973; Trinkaus, 1983). Some of these traits could represent autapomorphies in relation to biomechanical advantages (Musgrave, 1971; Aiello & Dean, 1990; Churchill, 2001; Niewoehner, 2001). Therefore, we compared all the hand bone remains from Spy with samples from Neandertals, Middle and Upper Palaeolithic modern humans, Neolithic humans from the Mosan Valley and extant humans. We performed uni- and multivariate statistical analyses in order to identify Neandertal morphometric characteristics among the hand bones from Spy and to test the homogeneity of the original collection.

MATERIALS AND METHODS

The Neandertal comparative sample (NEAND) includes hand bone remains from European and Asian specimens: Amud 1 (Suzuki & Takai, 1970), Oliveira 1 (Trinkaus *et al.*, 2007), Kebara 2 (Vandermeersch, 1991), Kiik-Koba 1 (Vlček, 1975), Krapina (n = 68), La Chapelle-aux-Saints 1 (Boule, 1911), La Ferrassie 1 & 2 (Heim, 1982), Neandertal 1 (Smith *et al.*, 2006), Regourdou 1, Saint-Césaire 1, Shanidar 3 – 6 (Trinkaus, 1983), Tabun C1 (McCown & Keith, 1939), and Vindija 300. The measurements of the La Chapelle-aux-Saints, Krapina, Saint-Césaire and Vindija hand bone remains were taken on the original fossils. For Regourdou 1, the acquisition of metrical data was achieved with ArteCore on 3D reconstruction models (STL files) of the hand bones available in the NESPOS Database (2008).

The modern human comparative samples include data from:

a. Middle Palaeolithic modern humans (MPMH) from the Qafzeh and Skhul populations (McCown & Keith, 1939; Vandermeersch, 1981);

b. Upper Palaeolithic human remains (UPMH) from Abri Lafaye, Abri Pataud, Barma del Caviglione, Cro-Magnon (data for the latter three

Metacarpals										
	Rank	*Side*	*LMAX*	*LART*	*PH*	*PB*	*MH*	*MB*	*DH*	*DB*
25J	MTC I	L	-	-	18.04	16.12	-	-	-	-
21A	MTC II	R	66.95	62.48	18.88	20.54	9.70	8.82	15.77	18.06
22A	MTC III	L	66.38	63.18	17.52	19.81	9.14	8.66	14.98	17.83
21B	MTC III	R	-	-	13.56	15.75	9.10	8.68	-	-
21D	MTC III	L	-	-	15.49	16.11	8.94	8.60	-	-
21C	MTC IV	R	-	-	14.04	13.40	8.02	7.58	-	-
22C	MTC IV	L	55.94	55.18	13.45	12.33	7.45	7.21	13.03	15.28
20I (°)	MTC V	L	-	-	-	*14.30*	*6.62*	*7.84*	-	-
749a (*)	MTC I	R	43.95	41.74	15.63	15.04	8.85	12.42	10.96	16.48

Proximal Phalanges												
	Rank	*Side*	*LMAX*	*LART*	*PH*	*PAH*	*PB*	*PAB*	*MH*	*MB*	*DH*	*DB*	*DAB*
25H	PP I	R	28.66	25.75	12.79	11.19	17.74	14.86	7.62	10.36	8.54	13.68	13.38
426a	PP II	R	36.05	33.80	13.00	10.36	17.00	13.15	6.68	11.30	8.38	13.45	12.29
24C	PP II	L	37.00	35.00	12.80	10.30	17.93	13.82	6.60	11.10	8.62	13.03	12.04
748a	PP III	L	41.95	39.60	13.48	11.40	17.65	13.80	6.95	11.50	8.89	14.77	12.90
747a	PP IV	R	-	-	-	-	-	-	6.13	10.50	8.50	13.65	11.60
24A	PP IV	L	40.29	39.65	12.52	10.52	15.66	12.86	7.09	10.34	7.83	13.10	11.31
766a	PP IV	L	39.94	38.97	13.10	-	16.20	12.65	6.25	11.18	8.46	*13.00*	*11.20*
24B	PP V	R	32.91	31.58	11.68	9.83	15.75	11.97	5.45	10.00	7.48	11.90	10.74

Middle Phalanges												
	Rank	*Side*	*LMAX*	*LART*	*PH*	*PAH*	*PB*	*PAB*	*MH*	*MB*	*DH*	*DB*	*DAB*
165k	MP II	L	-	-	9.85	7.50	14.53	12.85	5.30	8.93	-	-	-
430a	MP III	R	26.46	25.97	10.77	7.75	15.52	13.47	5.46	9.37	6.46	12.86	11.24
390a	MP III	L	26.96	25.90	10.64	7.88	15.19	13.76	5.64	9.33	6.45	12.40	11.32
484a	MP IV	R	26.27	25.24	9.51	7.54	14.16	12.71	5.05	8.77	5.51	11.78	11.04
222b	MP V	R	19.88	19.08	8.08	6.19	11.49	10.45	4.93	7.68	4.47	9.36	8.77

(°) Shaft and proximal extremity deformed by a fracture.
(*) The Neandertal attribution of this specimen is uncertain.

Table 2. Measurements (in mm) of the Spy Neandertal metacarpals and phalanges (specimens from the original collection and newly identified remains). Bones and side abbreviations are as in Table 1. MP = Middle phalanx; LMAX = Maximal length; LART = Articular length; PH = Proximal height; PB = Proximal breadth; PAH = Proximal articular height; PAB = Proximal articular breadth; MH = Midshaft height; MB = Midshaft breadth; DH = Distal height; DB = Distal breadth; DAB = Distal articular breadth. Numbers in italics and underlined are estimated.

are from Trinkaus, pers. com.), Dolní Věstonice (Sládek *et al.*, 2000; Trinkaus *et al.*, 2000), Gruta do Caldeirão (Trinkaus *et al.*, 2001), Mladeč (Trinkaus *et al.*, 2006), and Nazlet Khater (Crevecoeur, 2008);

c. Neolithic humans of the Mosan Valley (NEOM) from Hastière (Petite Caverne, Caverne M and Trou Garçon), Maurenne (Caverne de la Cave) and Furfooz (Trou du Frontal), stored at the RBINS.

For some comparisons, a fifth group of recent modern humans (RMH) was considered. It consisted of data from a Gallo-Roman Necropolis in France (Baigl *et al.*, 1997). The identifications and measurements of the Mosan Neolithic and recent human hand bones were done by

the author. The ranks of the proximal phalanges (PP) were determined according to their respective lengths (PP III ≥ PP IV > PP II > PP V) (Susman, 1976) and the morphology of their extremities (Landsmeer, 1955; Musgrave, 1971; Case & Heilman, 2006). For statistical reasons, the proximal phalanges of the third and fourth ranks were combined in the comparative database, as were the middle and distal phalanges of the second to fifth ranks.

The measurements used are those defined by Martin (Bräuer, 1988) for the carpus and by Musgrave (1970) for the metacarpals and phalanges. The dimensions of all the Spy Neandertal hand bone remains are listed in Table 2.

The morphometric characteristics of the Spy hand bones were studied by means of uni-, bi- and multivariate analyses. Adjusted Z-scores (Maureille *et al.*, 2001) were computed to com-
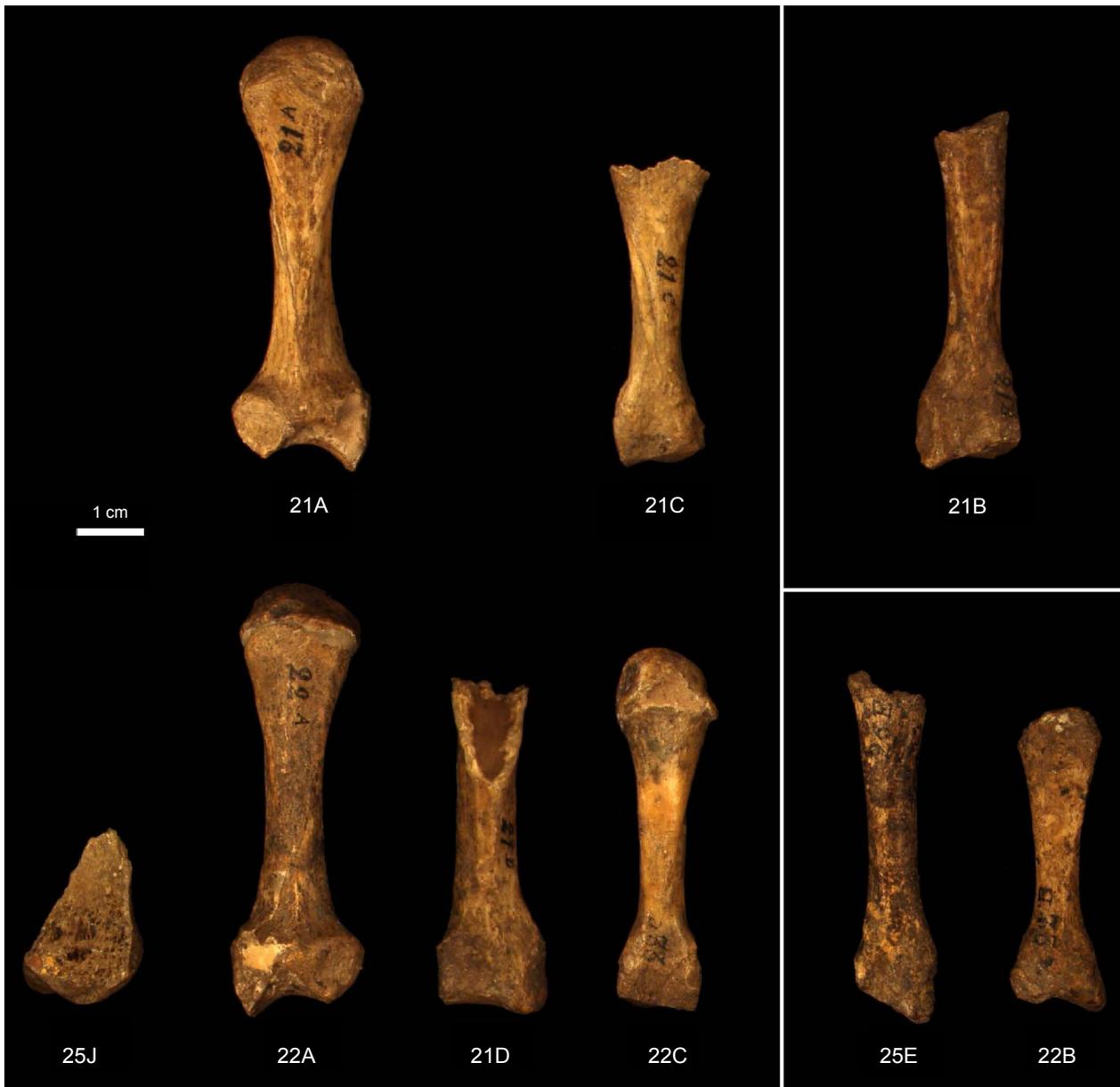

Figure 1. Dorsal view of the metacarpals inventoried in the original Spy collection. Inventory number is shown below each specimen. The white lines separate bones that are proposed to be associated (see text).

pare the dimensions of the Spy remains to the means and standard deviations of the comparative groups. This method is based on Student's t-test, which takes into account the size of the comparative groups and maximises the variation range for small sample sizes. Principal component analyses (PCA) were performed with Stat*lab* (STAT*lab*, 1991). Each variable was first tested for normality. We used size-adjusted dimensions, computed using the Darroch & Mosimann (1985) definition of shape, in the multivariate analyses (see Jungers *et al.* [1995] for the relevance of size adjustment).

RESULTS AND DISCUSSION

Carpal bones

All carpal bones from Spy come from the new revision of the faunal remains. With regard to absolute dimensions, they all fall within the range of variation of the modern human samples. There are few significant differences in dimensions between the Neandertal and modern human carpal bones (Villemeur, 1994). The most distinctive Neandertal morphological characteristics are located on the trapezium, the capitate and the hamate. The tubercle of the trapezium and the hamulus on the hamate are more developed than those of modern humans. The proximo-distal length and the radio-ulnar thickness of these processes are significantly bigger (Musgrave, 1971; Villemeur, 1994). The Neandertal trapezia exhibit a condyloid surface for the carpo-metacarpal joint of the first metacarpal, whereas the articulation has a saddle shape in modern humans (Oberlin *et al.*, 1997). Finally, the capitate-metacarpal articulation of the Neandertals is characterised by a parasagittal orientation of the surface of the second metacarpal (60° ± 10.8°, n = 8; Niewoehner *et al.*, 1997), which may represent a biomechanical advantage in bending (Churchill, 2001).

The nine capitate bones found in the faunal collections all exhibit a distal orientation of the capitate-second metacarpal facet similar to that of contemporary samples. The angles range from 32° to 44° (37.44° ± 4°, n = 9). The hamate bones from Spy have moderate hamuli similar to the development observed among the Mosan Neolithic samples. They all fall within the lower part of the Neandertal range of vari-

ation for the width and height of the hamulus. The same observation can be made for the tubercle of the trapezium, which is poorly developed compared to that of Neandertal samples. In addition, all of the trapezia possess a saddle-shaped articular surface for the first metacarpal.

Therefore, the metrical and morphological comparative analyses show that none of the newly recognised carpal bones from Spy exhibit Neandertal features.

Metacarpals

The ten metacarpals of the original collection are illustrated in Figures 1 and 2.

Spy 25J is the proximal extremity of a left pollical metacarpal (MTC I). Although its preservation state is very fragmentary, it shows some metrical and morphological Neandertal characteristics. The height of the proximal surface (PH = 18.04 mm) falls well outside of the Mosan Neolithic range of variation (12.66 ± 1.32 mm, n = 114), whereas it is included in the Neandertal range of variation (17.12 ± 1.32 mm, n = 9). Moreover, its proximal articular surface does not exhibit the saddle shape of modern humans. In lateral view, the trapezium facet is nearly flat rather than concave. This morphology is common among Neandertal specimens, whose proximal surfaces vary from slightly concave to convex, forming a condyloid articu-

Figure 2. Dorsal and palmar views of the left fifth metacarpal Spy 20I previously inventoried as a costal fragment in the original collection.

lation in the latter case (Musgrave, 1971; Vlček, 1975; Oberlin *et al.*, 1997).

The two second metacarpals (MTC IIs) present in the original collection (21A and 22A) are symmetrical. Their dimensions are very similar, as is the morphology of their articular surfaces and midshafts. They are characterised by wide distal and proximal extremities and by a sharp *crista dorsalis* running up the proximal quarter of the shaft in posterior view. This crest is not uncommon among modern humans, but it is usually not as sharply defined as it is in Neandertal specimens (Musgrave, 1971; Trinkaus, 1983). The width of the extremities also reflects a Neandertal conformation. Figure 3 illustrates the adjusted Z-scores of the dimensions of the Spy MTC IIs in relation to both the Neandertal and Mosan Neolithic ranges of variation. Spy 22A and Spy 21A possess a similar profile for each measurement. They align with the Neandertal range of variation for all measurements, while they fall outside of the 95 % confidence limit of the Mosan Neolithic group for the breadth of the head. Spy 22A falls at the upper limit of the NEOM sample for the breadth of the proximal end and for the height of the distal extremity. These results suggest that both MTC IIs are Neandertal specimens and that they belong to the same individual.

There are three metacarpals from the third rank (MTC III) in the original collection (Spy 21B, Spy 21D and Spy 25E). They exhibit different particularities regarding their morphology and dimensions. Previous studies of fossil MTC IIIs have identified specific features that distinguish Neandertal specimens from those of modern humans (e.g. Suzuki & Takai, 1970; Villemeur, 1994; Niewoehner *et al.*, 1997). The proximal extremity of the Neandertal third metacarpal is characterised by reduced development of the styloid process and its more lateral projection with regard to the longitudinal axis of the bone (Villemeur, 1994; Niewoehner, 2001). In addition, the articular facet of the capitate is oriented more proximally compared to the modern human morphology (Villemeur, *ibid.*). The three MTC IIIs of Spy show different patterns. Both Spy 21B and Spy 21D have strong proximal extremities with a reduced styloid process projected medially, but Spy 25E exhibits a modern human morphology with a marked styloid process in a parasagittal orientation (Figure 4).

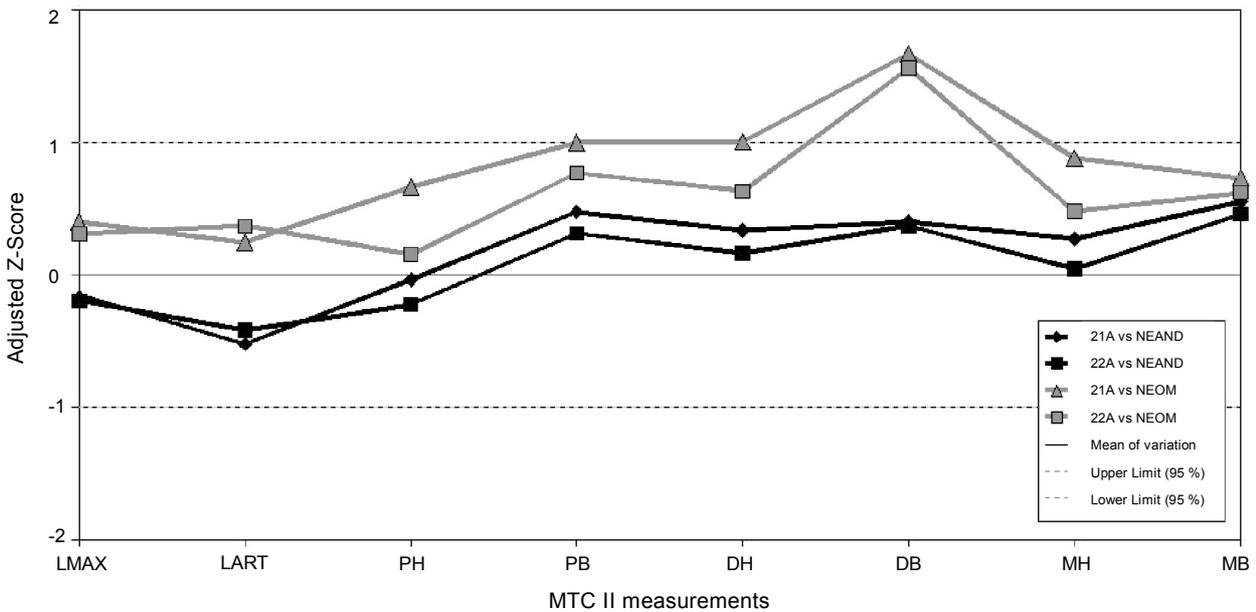Cross-sections of the bones at the levels of the midshaft and proximal extremity, obtained

Figure 3. Adjusted Z-scores of the second metacarpal dimensions of Spy 21A and Spy 22A compared to both the Neandertal (NEAND) and Mosan Neolithic (NEOM) ranges of variation. Zero represents the mean and +1/-1 represent the upper and lower 95 % limits of variation, respectively. Variable abbreviations are as in Table 2.
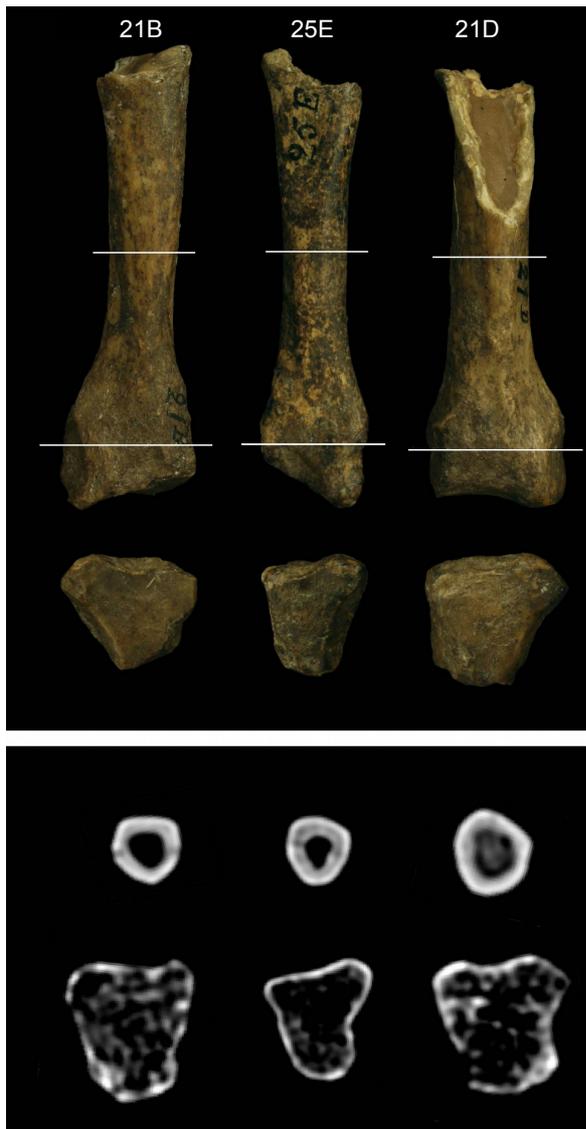
Figure 4. Morphological (above, dorsal and proximal view) and cross-sectional (below) comparison of the three third metacarpals from the original Spy collection. White lines indicate the levels of the cross-sections represented below.

via medical CT scanner (SOMATON Sensation 64), also indicate the similarity between Spy 21B and Spy 21D compared to Spy 25E. However, despite their similarities with Neandertal MTC IIIs, Spy 21B and Spy 21D probably do not belong to the same individual. Their dimensions and the morphology of their proximal articular surfaces (Figure 4) are not symmetrical. Furthermore, there is no suitable secondary connection between Spy 21B and the second metacarpal Spy 21A, whereas Spy 21D

and Spy 22A fit together. These two MTC IIIs from the original collection probably represent two different Neandertal individuals.

The proximal dimensions of Spy 25E confirm the modern human nature of this bone, which falls within the Mosan Neolithic range of variation shown in Figure 5. The bivariate plot illustrates a difference in allometry of the MTC III proximal end dimensions between the Neandertal group and all the Pleistocene and re-cent modern human samples. Neandertals pos-sess a proportionally greater proximal breadth (PB) relative to the proximal height (PH) than modern humans. In Figure 5, only Tabun C1 shows the proximal proportions of modern hu-mans. This position may be explained by the temporal distance between this earlier specimen and later Neandertals, suggesting that some Neandertal derived characteristics were not totally fixed.

The two metacarpals of the fourth rank (MTC IV), Spy 21C and Spy 22C, are symmet-rical. Neandertal MTC IVs are characterised by wide extremities, especially the distal ones. The most complete fourth metacarpal (Spy 22C) pos-sesses a secondary anatomical connection with the Spy 21D third metacarpal and falls outside of the Mosan Neolithic range of variation for the breadth of the head (DB: Spy 22C = 15.28 mm; NEOM = 12.54 ± 1.03 mm, n = 91). The dimen-sions of the proximal extremity are also in the upper part of the Neolithic range of variation, as is the case for the other (less complete) MTC IV from Spy (Spy 21C). Unfortunately, the most distinguishing part (the distal extremity) is broken in this latter metacarpal. Morphologic-ally, Neandertal MTC IVs show some particular-ities, notably in the orientation of the proximal end (Bonč-Osmolovskij, 1941). The base is situ-ated within the longitudinal axis of the bone, whereas among modern humans, the proximal extremity is projected laterally. Spy 21C and Spy 22C show the Neandertal disposition.

The last metacarpal identified in the ori-ginal collection is an immature MTC of the second rank, Spy 22B. It was described as an incomplete third metacarpal in the 1935 cata-logue. However, the morphology of its distal end is clearly immature (unfused), and the prox-
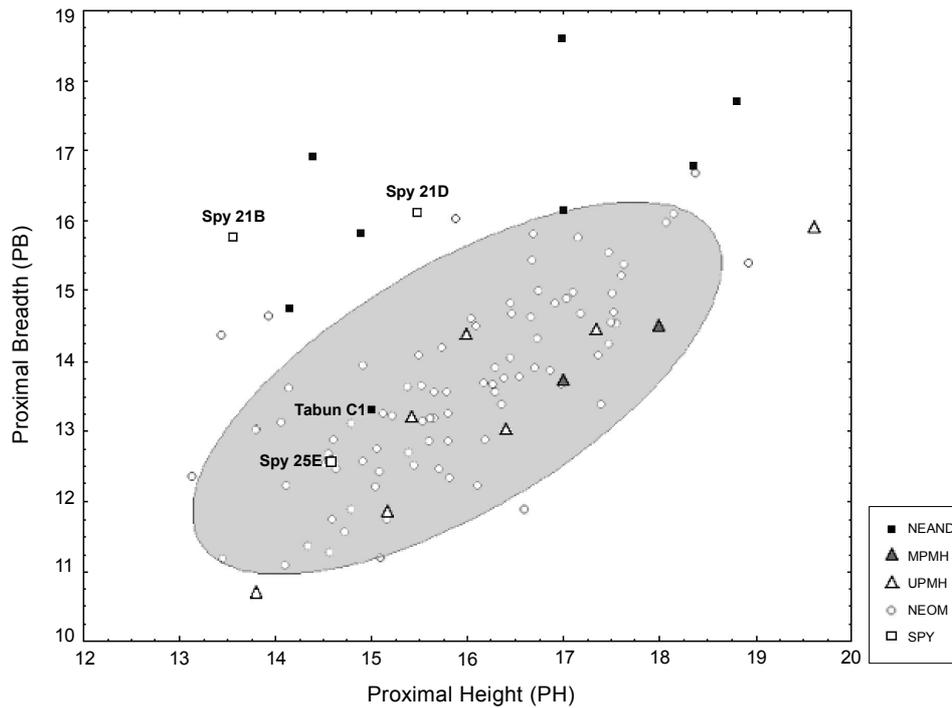
Figure 5. Bivariate plot of the proximal breadth versus the proximal height of the third metacarpals from Spy and the comparative group samples. NEAND = Neandertals; MPMH = Middle Palaeolithic Modern Humans; UPMH = Upper Palaeolithic Modern Humans; NEOM = Mosan Neolithic humans.

imal extremity belongs to an MTC II. Furthermore, we recognised among the faunal remains an immature MTC III (Spy 398l) of the same side and maturation state that fits perfectly with the articular surface of Spy 22B. The dating of this unvarnished bone provided a Neolithic age for this immature MTC III and therefore, by association, for Spy 22B (Semal *et al.*, volume 1: chapter XVI). This result confirms our hypothesis that the original "Neandertal" hand bone collection was heterogeneous.

Finally, one additional metacarpal is present in the original collection but had not been identified yet. Spy 20I is a left metacarpal from the fifth rank whose proximal extremity is damaged and whose distal extremity is broken off (Figure 2). This bone was identified as a costal fragment in the 1935 catalogue. This error could be related to the presence of a healed fracture at the level of the proximal half of the bone. The diaphysis is deformed and crushed from the middle of the medial face to the tip of the lateral part of the proximal extremity. A bony crest of 8 mm is present distal to mid-diaphysis on the

Figure 6. Right first metacarpal Spy 749a in dorsal (D), palmar (P), medial (M) and lateral (L) views.

postero-lateral side of the diaphysis. The morphology of the diaphysis, which is similar to that of the other Neandertal metacarpals from Spy, and the consistency of the secondary anatomical connection of the medial articular surface of Spy 20I with the Spy 22C fourth metacarpal support the attribution of this bone to one of the adult Neandertals.

Among the forty-eight newly discovered metacarpal remains, only one is of ambiguous taxonomic status: the right first metacarpal Spy 749a (Figure 6; SF1). The other metacarpals display modern morphologies, and their dimensions fall within the range of variation of the Mosan Neolithic sample. However, attribution to the Neolithic burial cannot be stated with certainty when dealing with very fragmentary pieces.

The first metacarpal Spy 749a comes from the private collection of M. Beaufays, which has also yielded two new Neandertal phalanges (see below). It is quite complete with the exception of the palmar side of the distal end. The measurements of this MTC I are within the lower part of the Neandertal range of variation, except for its distal height. On the other hand, the proximal height of Spy 749a falls outside of the upper limit of the Mosan Neolithic sample range. However, regarding this latter value, Spy 749a is still close to the NEOM range of variation, whereas Spy 25J is totally outside of it (Figure 7).

Focusing on the morphology of Spy 749a, there is a small flange on the distal half of the lateral side of the shaft at the level of the insertion of the *M. opponens pollicis*. Neandertal MTC I bones show a well-developed lateral crest at that same level of the shaft, forming a distinct spatula in some specimens, such as Kiik-Koba 1 (Vlček, 1975; Oberlin *et al.*, 1997). The expression of this crest is variable among Neandertals. This characteristic has also been observed on modern human first metacarpals (Kimura, 1976), but the radial breadth is significantly higher (Maki & Trinkaus, 2011) in Neandertals. Spy 749a exhibits a radial projection of the *M. opponens pollicis* insertion of 7.49 mm, which aligns with the Neandertal variation (Radial breadth = 7.8 ± 0.9 mm, n = 10; Maki & Trinkaus, 2011).
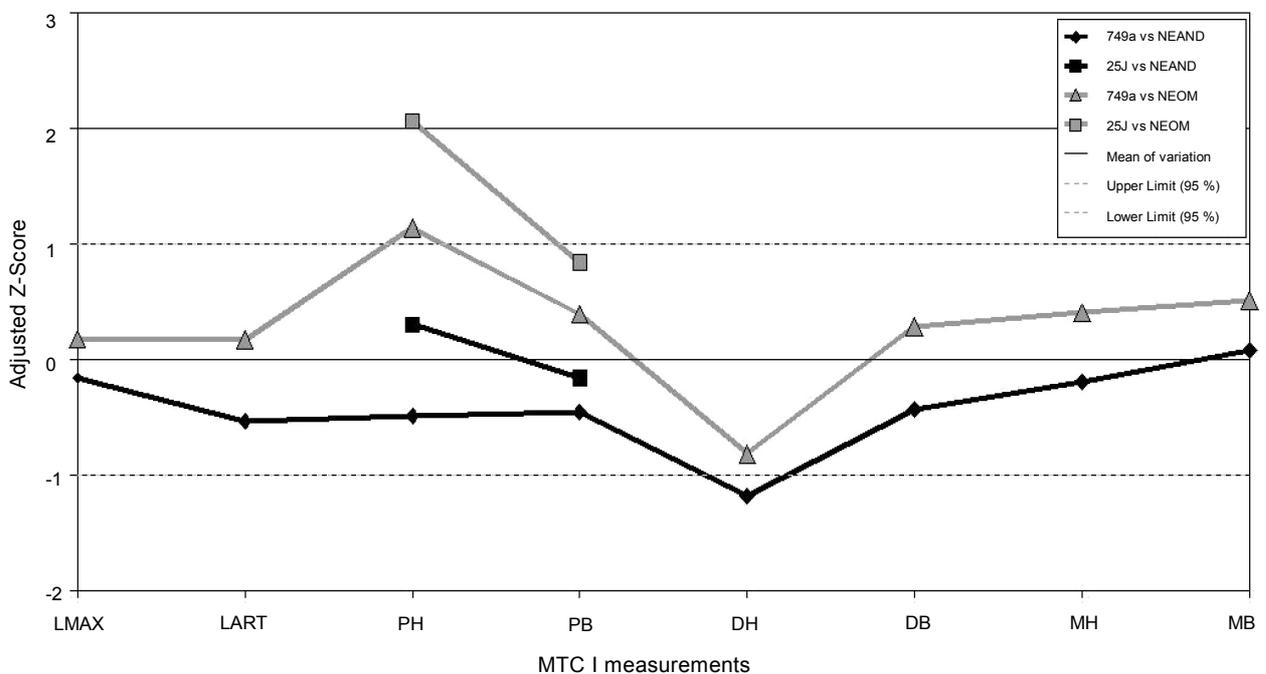

Figure 7. Adjusted Z-scores of the first metacarpal dimensions of Spy 749a and Spy 25J compared to both the Neandertal (NEAND) and Mosan Neolithic (NEOM) ranges of variation. Zero represents the mean and +1/-1 represent the upper and lower 95 % limits of variation, respectively. Variable abbreviations are as in Table 2.

The proximal articular surface of Spy 749a shows a saddle shape common among anatomically modern humans, which differs from the morphology of Spy 25J. Therefore, even if some metrical and morphological features point to Neandertal characteristics, it is difficult to ascertain the taxonomic affinities of Spy 749a. Furthermore, multivariate analyses on size-adjusted variables do not solve the problem, since the other new MTC I bones from Spy, whose morphological features are clearly modern, lie close to the Neandertal group, as does Spy 749a.

Proximal phalanges

Neandertal proximal phalanges are characterised by a relatively short diaphysis with wide maximal and articular distal and proximal extremities (Bonč-Osmolovskij, 1941; Musgrave, 1971, 1973; Villemeur, 1994). The lateral tubercle of the proximal end of the second proximal phalanx is very pronounced, and its expan-sion may double the diameter of the base (Musgrave, 1971). Given these remarkable characteristics, there is little doubt about the Neandertal affinities of the four proximal phalanges in the original collection (Spy 25H, 24C, 24B and 24A; Figure 8). Additionally, the revision of the Spy collections has yielded four Neandertal specimens among the seventy-three new proximal phalanges identified (Spy 426a, 748a, 766a and 747a; Figure 8).

Spy 25H is a right proximal phalanx of the pollex (PP I). Compared to the recent and Neolithic samples, this phalanx is short and possesses wide extremities. Its distal articular breadth (DAB = 13.38 mm) lies outside the NEOM range of variation (10.88 ± 0.91 mm, n = 71). We performed a PCA analysis on six size-adjusted dimensions (LART, PH, PB, MH, DH, DB, DAB). The first three principal components account for 72.65 % of the total variance. The clustering of the samples is best illustrated by the first and third axes (PC1 and PC3)

Figure 8. Dorsal view of all Neandertal proximal phalanges identified at Spy. Inventory number is shown below each specimen. The white line separates bones proposed to be associated (see text).
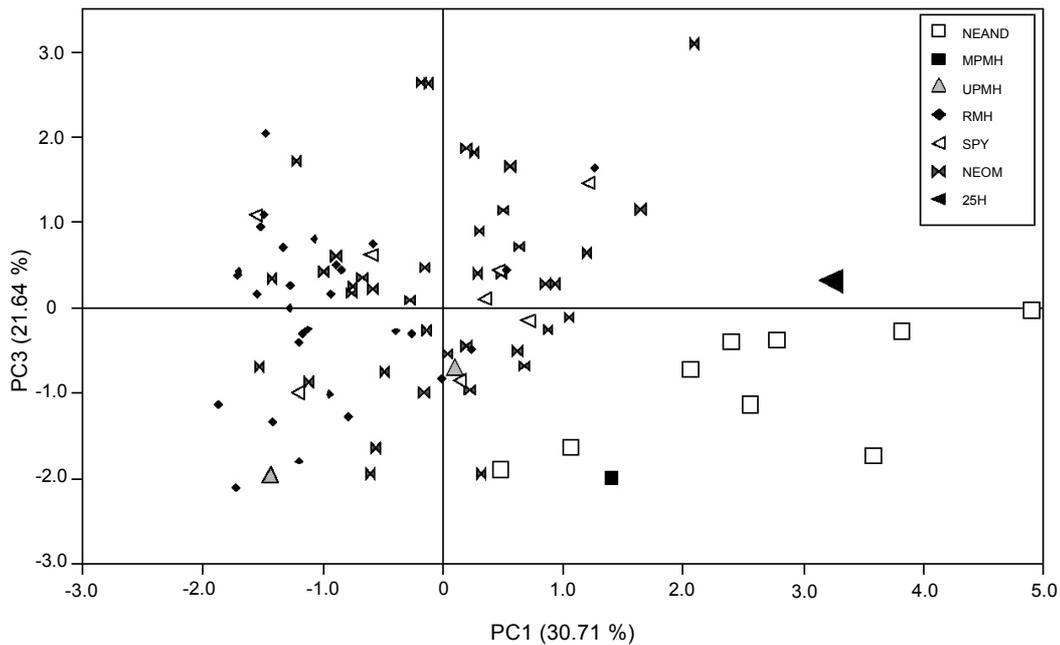
Figure 9. Bivariate plot of the first and third principal components of the PCA analysis on size-adjusted measurements of the first proximal phalanges. Variables used: LART, PH, PB, MH, DH, DB & DAB. Variable abbreviations are as in Table 2, and comparative group denominations are as in Figure 5. RMH = Recent modern humans.

in Figure 9. Neandertal specimens and Spy 25H are isolated from the recent and past modern human samples in the lower right quadrant. This position is due to the combination in Neandertal PP Is of a small articular length (LART) and distal height (DH) in relation to a wide distal articular breadth (DAB). This result confirms the Neandertal characteristics described above and attests to the Neandertal affinities of Spy 25H compared to the other PP Is found at Spy.

Spy 24C, a second proximal phalanx (PP II), possesses the Neandertal morphometrical traits described by Musgrave (1971). The proximal extremity is wide, with a well-developed and laterally projected tubercle. The distal end has large articular and maximal breadths. The characteristics that distinguish Neandertal PP IIs from those of modern humans are illustrated by the adjusted Z-scores in Figure 10.

The dimensions of Spy 24C, Spy 426a and Spy 264a are compared to the range of variation of the Mosan Neolithic sample. The latter two specimens are newly recognised human PP IIs from the faunal collections. Spy 426a presents the same morphometrical characteristics as Spy 24C. Although the proximal tubercle is broken, the di-

mensions of the proximal and distal articular facets are similar to those of Spy 24C. This is also true for the morphology of its shaft, which shows visible radial torsion. The adjusted Z-scores of these two phalanges (Spy 24C and Spy 426a) confirm their similarity. Moreover, their positions on the diagram (Figure 10) correspond to the Neandertal pattern, with a proportionally small length in relation to the breadth and height of the entire phalanx. They also show the flattening of the shaft with relatively small medial height (MH) in relation to the other dimensions. These differences with modern human morphology are all the more evident when compared to the curve of Spy 264a, which represents a robust Neolithic PP II.

In addition to the metrical traits, there are some differences between Neandertal and modern human PP IIs in the morphology of their distal ends, which are demonstrated by Spy 24C and Spy 426a. These characteristics are present in all proximal phalanges from rank II to V. As illustrated in SF2, Neandertal distal extremities have a trapezoidal shape rather than a rectangular one. The articular surface is hardly visible on the dorsal surface of the bone, whereas in modern human proximal phalanges the articular facet overflows between the two sides of the trochlea
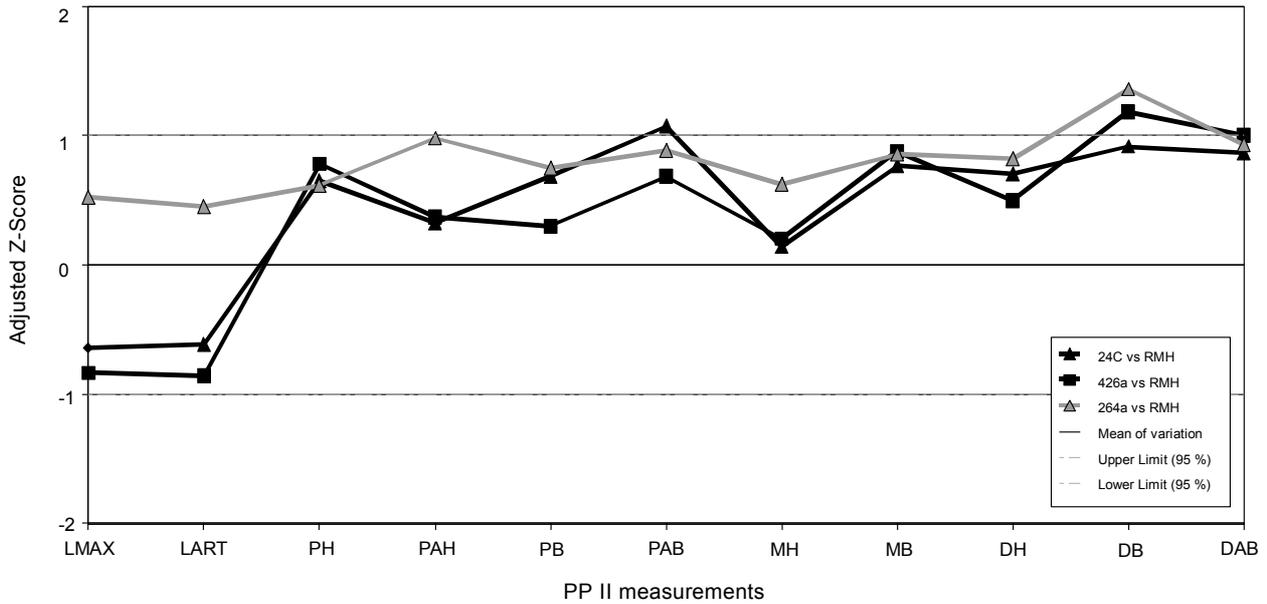
Figure 10. Adjusted Z-scores of the second proximal phalanges Spy 24C, Spy 426a and Spy 264a compared to the Mosan Neolithic range of variation. Zero represents the mean and +1/-1 represent the upper and lower 95 % limits of variation, respectively. Variable abbreviations are as in Table 2.
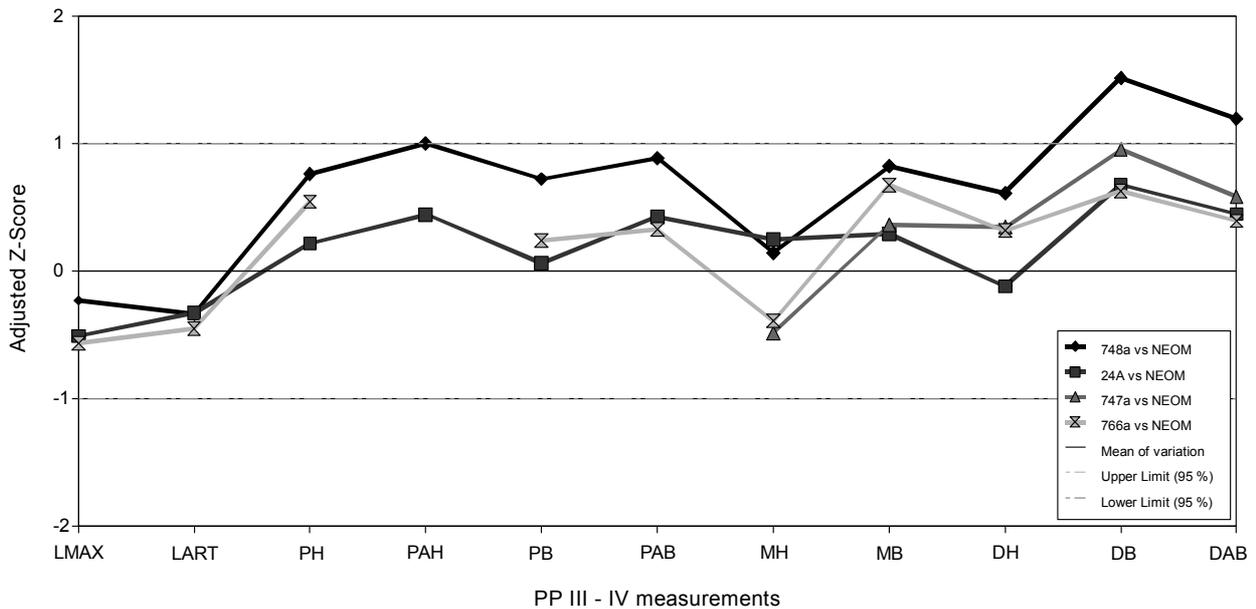

Figure 11. Adjusted Z-scores of the third and fourth proximal phalanges Spy 24A, Spy 747a, Spy 748a and Spy 766a compared to the Mosan Neolithic range of variation. Zero represents the mean and +1/-1 represent the upper and lower 95 % limits of variation, respectively. Variable abbreviations are as in Table 2.

onto the dorsal side and shows a concave outline. In addition, the development of the trochlea is more pronounced among modern humans. Neandertals have a more flattened and smooth distal articular surface.

The metrical differences between Neandertals and modern humans for the third and fourth proximal phalanges are less obvious. There is one proximal phalanx attributed to the fourth rank in the original collection, Spy 24A.

Its dimensions lie within the Neandertal and Neolithic ranges of variation. However, its pattern of small length compared to distal breadth and the palmo-dorsal flattening of the distal extremity correspond to Neandertal characteristics (Figure 11). Furthermore, the distal end of Spy 24A exhibits the same morphological features shown by the distal extremities of Neandertal proximal phalanges (*cf.* SF2). Therefore, even if uni- and multivariate analyses cannot distinguish clearly between Neandertal and modern human PP III-IVs, it is likely that this PP IV belongs to a Neandertal individual.

Three other proximal phalanges from the third and fourth ranks, which present Neandertal metrical and morphological features, have been identified in the faunal remains: Spy 748a (PP III), Spy 747a (PP IV) and Spy 766a (PP IV). Their overall dimensions, illustrated in the adjusted Z-score diagram of Figure 11, show a clear Neandertal pattern with a proportionally small length, palmo-dorsal flattening of the midshaft and of the distal end, and wide maximal and articular distal breadths. For Spy 748a, the latter two dimensions fall outside the Neolithic range of variation. The morphology of the distal end is also consistent with the Neandertal conformation. In addition, Spy 747a and Spy 766a are most likely symmetrical, which implies that Spy 24A belongs to a more gracile Neandertal individual.

The last proximal phalanx from the original collection is Spy 24B (PP V). It exhibits a clear ulnar deviation of the distal extremity, which is a distinctive feature of phalanges from the fifth rank. As with the previously discussed Spy Neandertal phalanges, Spy 24B is small with wide extremities and a flattened midshaft. The maximal and articular breadths of the distal extremity (DB = 11.9 mm; DAB = 10.74 mm) fall beyond the upper limit of the Mosan Neolithic range of variation (9.48 ± 0.72 mm, n = 74 and 8.57 ± 0.75 mm, n = 73, respectively). No other fifth proximal phalanx with Neandertal characteristics has been identified in the newly recognised human remains from Spy.

Figure 12. Dorsal, proximal, distal and palmar views (from top to bottom) of all newly identified Neandertal middle phalanges. Inventory number is shown above each specimen.

Middle and distal phalanges

No middle or distal phalanges were inventoried in the original collection. The revision of the faunal collections has revealed the presence of sixty-two complete and fragmented middle phalanges (MP) and thirty distal ones (DP). Few descriptions of Neandertal middle phalanges have closely investigated their characteristics. They are said to be short with wide heads and bases (Bonč-Osmolovskij, 1941; Musgrave, 1971; Heim, 1982). Given these criteria, five new Neandertal MPs have been identified among the sixty-two MPs found in the faunal remains (Spy 165k, 222b, 390a, 430a and 484a; Figure 12).

Compared to the Mosan Neolithic sample, these phalanges are relatively short with wide extremities, which give them a rectangular shape rather than the trapezoidal shape exhibited by modern human middle phalanges (SF3). Among the different measurements, the distal articular breadth is the most discriminatory, as illustrated in Figure 13.

The middle phalanges of the second to fourth ranks are pooled together for each comparative sample because there is an important metrical overlap between these digits, making it hard to identify isolated phalanges. Spy 390a, 430a and 484a clearly fall within the Neandertal range of variation and outside of all the modern human comparative groups for the distal articular breadth. Spy 165k has a broken distal end, but the dimensions and morphology of its proximal extremity and midshaft are similar to those of the other three. In addition, the morphological and metrical proximity of these four Neandertal MP II-IVs suggests that they belong to the same individual and allows us to determine their ranks. Spy 390a and Spy 430a are symmetrical and attributed to the third rank. Spy 165k possesses a wider proximal extremity and a wider shaft than Spy 484a, which suggests that Spy 165k belongs to the second rank whereas Spy 484a belongs to the fourth rank. Direct ^{14}C dating has been achieved on Spy 430a, which confirms its ancient age (33,940 +220, -210 BP; GrA-32630), although
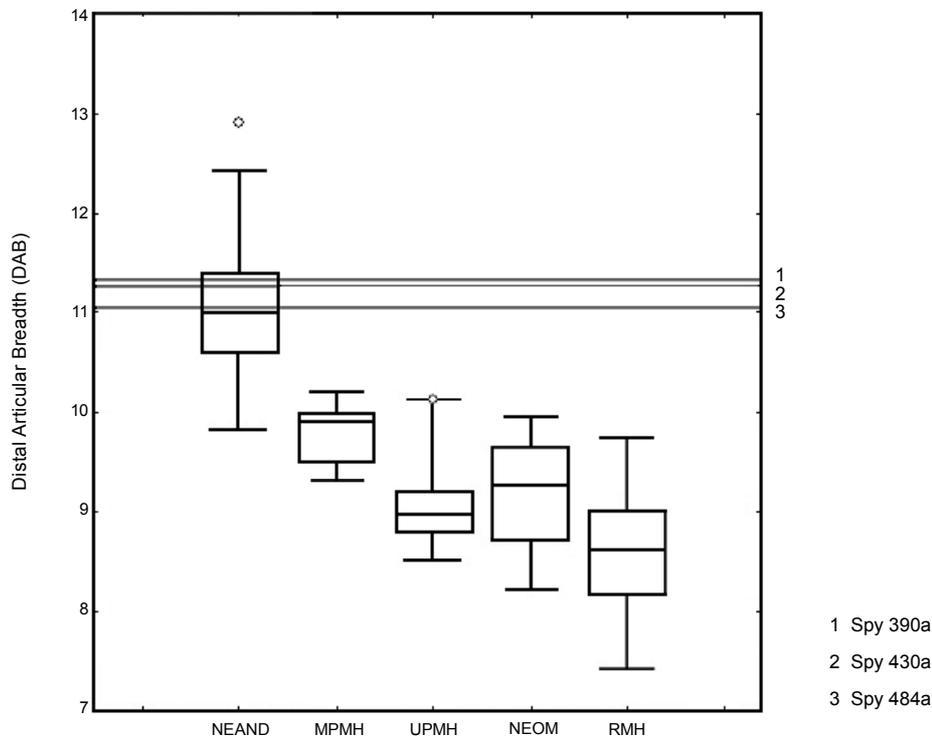

Figure 13. Box and whisker plots of the distal articular breadth (DAB) of the second to fourth middle phalanges for Spy 390a, Spy 430a and Spy 484a and the comparative samples. Box plots display the median, 25th-75th and 5th-95th percentiles. Comparative group denominations are as in Figures 5 and 8.
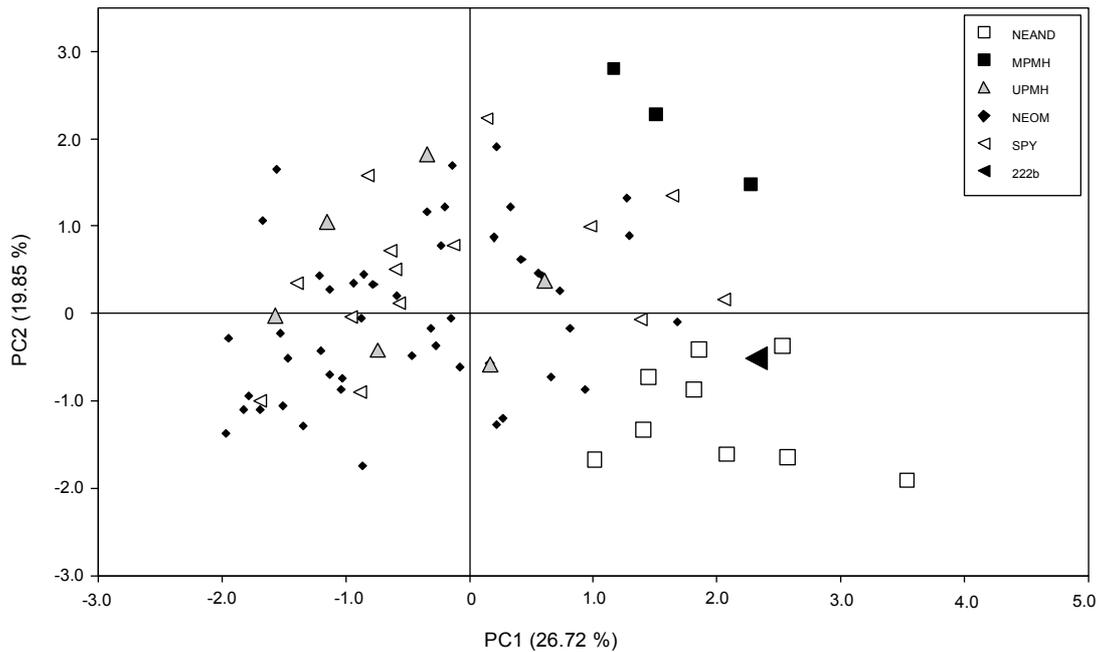
Figure 14. Bivariate plot of the first two principal components of the PCA analysis on size-adjusted measurements of the fifth middle phalanges. Variables used: LART, PH, PAH, PB, PAB, MH, MD, DH, DB & DAB. Comparative group denominations are as in Figure 5.

it appears to have undergone some contamination (Semal *et al.*, volume 1: chapter XVI). The last MP, Spy 222b, shows an ulnar deviation typical of the fifth digit. Univariate analyses give less clear results regarding the differences between Neandertal and modern human MP Vs. However, when multivariate analysis is performed on ten size-adjusted measurements, Spy 222b is included in the Neandertal group (Figure 14).

Neandertal distal phalanges have been more widely investigated, since they present clear differences regarding the shape and dimensions of their distal ends (Musgrave, 1973; Trinkaus, 1983). Furthermore, the Neandertal pollical distal phalanx is longer than that of modern humans and possesses a very broad distal end. It is also characterised by a strong ulnar deflection of the shaft in relation to the proximal extremity (Musgrave,

	Bone	Side	Preservation State	Maturation	Collection	Notes
414d	PP II	R	Proximal extremity	M	RBINS	Refits with 426a
426a			Distal half		RBINS	Refits with 414d
747a	PP III	R	Proximal extremity missing	M	Beaufays	
748a	PP IV	R	Complete	M	Beaufays	
766a	PP IV	L	Sub-complete	M	Carpentier	
165k	MP II	-	Distal extremity missing	M	RBINS	
390a	MP III	L	Complete	M	RBINS	Symmetric to 430a
430a	MP III	R	Complete	M	RBINS	Symmetric to 390a
484a	MP IV	-	Complete	M	RBINS	
222b	MP V	R	Complete	M	RBINS	

Table 3. Inventory of the nine Neandertal hand phalanges newly identified among the faunal remains from Spy. Abbreviations are as in Tables 1 and 2.
For further information on the Beaufays & Carpentier collections, see Semal *et al.*, volume 1: chapter II.

1971; Trinkaus, 1983; Smith, 2000). However, despite these visible particularities, no Neandertal distal phalanges were identified among the thirty newly recognised distal phalanges from Spy.

CONCLUSIONS

The reassessment of the Spy hand bones provides new insight into their supposed association with the two Neandertal adults as well as into the composition of the original human collection. Table 3 lists all the newly recognised hand bones for which there is conclusive evidence for a Neandertal taxonomic attribution (see also SF1). This brings the number of Neandertal hand bones discovered at Spy up to twenty-two, with at least two individuals represented.

The preservation state of the Spy Neandertal hand bones and their morphometrical study allow us to propose individual associations for these bones. Several observations suggest that the most complete infra-cranial skeleton belongs to a robust Neandertal specimen, probably Spy II (Rougier *et al.*, this volume: chapter XIX). The results of our study are consistent with this hypothesis; among the twenty-two metacarpals and phalanges identified, nineteen may be associated with the same individual given their similar robustness. The association criteria are based on morphological features (i.e. symmetrical bones)

and on secondary anatomical connections (inter-metacarpal, metacarpo-phalangeal and inter-phalangeal connections). Finally, the following association scheme (Figure 15) can be proposed for both Neandertal individuals.

In Figure 15, question marks suggest some doubts regarding the first metacarpals Spy 25J and Spy 749a, as well as the first pollical phalanx Spy 25H. The morphology of Spy 25H is similar to that of the proximal phalanges belonging to the most complete individual; however, the lack of a secondary connection leaves uncertainties about the individual association. The same question arises for the two MTC Is, but Spy 25J is clearly a Neandertal bone. If we consider Spy 749a to be a Neandertal MTC I, then there is no doubt about the attribution of Spy 25J to Spy II since it is more robust than, and not symmetrical to, Spy 749a. On the other hand, if Spy 749a is a modern MTC I, then the attribution of Spy 25J to either Neandertal individual is possible.

Through our reassessment of the Spy hand bones, we have also confirmed the presence of Neandertal autapomorphies in these anatomical parts. Previously described Neandertal hand bone characteristics (e.g. Musgrave, 1971; Trinkaus, 1983) were found among the metacarpal and phalangeal remains attributed to the Spy Neandertal adults, and allow relevant discrimination between modern human and Ne-
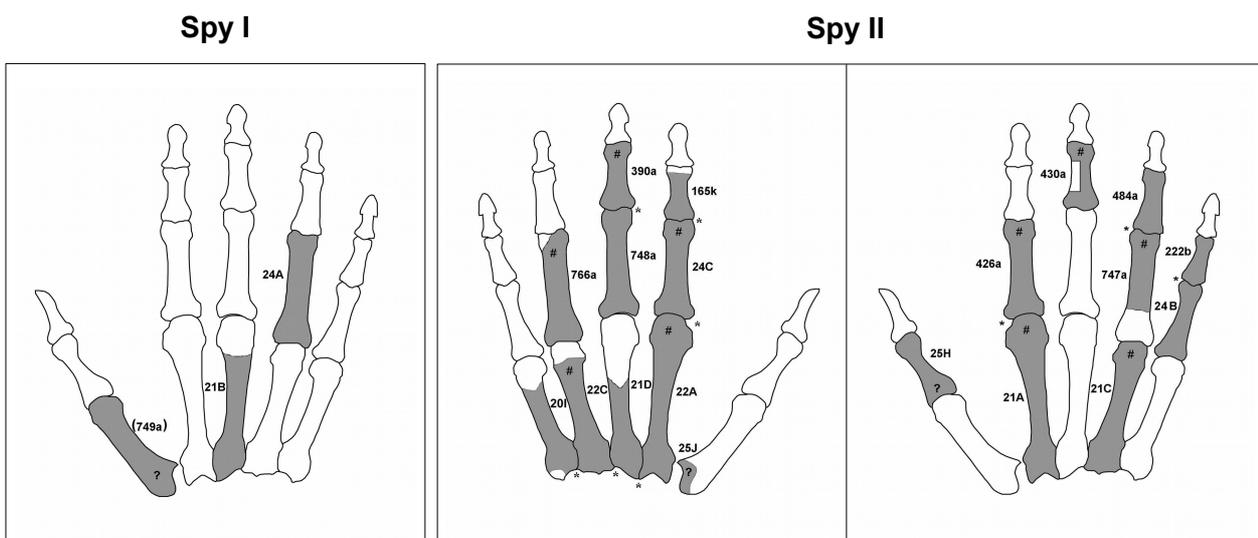
Spy I **Spy II**

Figure 15. Proposed conservation scheme of the hand bones for both Spy Neandertal individuals.
= symmetrical bone preserved; * = secondary anatomical connection; ? = uncertainty about the attribution.

andertal specimens. These discriminative features are mostly related to differences in conformation that are independent of size. Regarding the Neandertal metacarpals from Spy, the morphology, orientation and shape of the articular surfaces of the proximal ends, in addition to differences in the width of their distal extremities, distinguish Neandertal remains from modern human ones. The proximal phalanges show a peculiar pattern of small length, wide extremities and flattening of their shafts and distal ends (Figures 10 and 11). Moreover, the overall morphology of their distal extremities is very discriminatory (*cf.* SF2). Finally, the Neandertal middle phalanges are small, with strong proximal articular breadths, very wide distal extremities and proportionally flattened and narrow shafts compared to modern human MPs. All of these features give Neandertal middle phalanges a peculiar conformation (SF3). In addition, distal articular breadth appears to be a relevant variable to distinguish between Neandertal and modern human MPs. Further studies are now needed to determine whether the Neandertal derived features that concern the conformation of the proximal and middle phalanges are related to biomechanical or environmental adaptations.

The newly discovered Spy hand bones (SF1), their number and their association with the Neandertal individuals raise the question of the intentional nature of the deposit. Hand bone articulations are among the most labile (Duday *et al.*, 1990), and their persistence at the time of discovery suggests that the deposition of at least the skeleton described as "lying on the right side, with one hand against the mandible" (De Puydt & Lohest, 1887) might be primary and intentional. Unfortunately, no precise drawing of the spatial organisation of the hand bones was made in the field. De Puydt & Lohest (1887) stated that both individuals were quite incomplete. However, as underlined by Rougier *et al.* (this volume: chapter XIX), bones from different anatomical parts are represented for each individual.

There are thus good indications that both skeletons in Spy cave may actually have been (sub-)complete, as suggested by Hrdlička (1930), and that the observation made by De Puydt & Lohest was a consequence of their excavation techniques. This is also supported by the first results from the reassessment of the Spy collections (Rougier *et al.*, 2004) and by the discovery of so many new Neandertal hand bones. Although the primary and/or intentional character of the deposit at Spy may never be proven, the consistency of the identified hand bones gives credibility to the description given by M. Lohest for the position of the most complete skeleton.

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