CHAPTER XXX

FOOT BONES

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Abstract

Among the 199 foot remains inventoried to date in the Spy cave site, 10 specimens were potentially attributed to the Neandertal individuals Spy I and Spy II. The individual attribution of the metatarsals and pedal phalanges has remained unclear through the successive inventories contrary to those of the calcaneus and the talus, which articulates with the tibia Spy 9, and that were attributed to Spy II. Recently, a comprehensive review of the Spy site collections has notably reshaped the palaeoanthropological inventory; with regard to foot remains, two specimens have been removed from it. In this vein, five proximal lateral phalanges were selected for their patina and particular morphology in the Spy Neolithic collection which, with the eight specimens of the original collection, increases to 13 the number of foot bones potentially attributable to the Neandertals of the Spy cave site. In this chapter, we present a comparative study of this material, focusing on the metatarsals and the phalanges. They are compared to Neandertal specimens, Middle and Upper Palaeolithic modern humans, Neolithic series and recent humans by means of quantitative and qualitative analyses. Our results tend to exclude two of the three first metatarsals from the Neandertal original inventory and demonstrate that the five proximal phalanges recently extracted from the Neolithic collection are morphologically closely related to Neandertals. The Neandertal inventory would thus count 11 bones and fragments of foot bones. According to their morphological features, secondary anatomical connections, and their dimensions, they are attributed to the two adult Neandertals Spy I and Spy II.

INVENTORY OF FOOT BONES

Among the 199 foot remains inventoried to date in the Spy cave site, 10 specimens were potentially attributed to the Neandertal individuals Spy I and Spy II (Fraipont & Lohest, 1886, 1887; Twiesselmann, 1953, 1971). The left talus, Spy 18, articulates with the calcaneus, Spy 17, and articulates as well with the tibia Spy 9; these are attributed to the individual Spy II (Fraipont & Lohest, 1887; Twiesselmann, 1953). They have been well described (Leboucq, 1902; Fraipont, 1912, 1913, 1919, 1920; Morton, 1926), the talus having largely been integrated into more recent analyses relating specifically to the Neandertal talus or more widely to the hominin talus (e.g. Lisowsky, 1967; Day & Wood, 1968; Oxnard, 1972; Rhoads & Trinkaus, 1977; Gambier, 1981). The others are distal bones: 3 first metatarsals, 2 second metatarsals, 1 third metatarsal and 2 hallucal proximal phalanges. Because of the absence of direct articular contact and of available comparative studies, individual attribution of these distal bones has remained unclear through the successive inventories (Fraipont & Lohest, 1887; Fraipont, 1891; Twiesselmann, 1953, 1971). Trinkaus (1978) offers a brief review on this point and has delivered the only available study to date concerning the metatarsal and phalangeal remains from Spy. According to this author, "*[…] il y avait à Spy non seulement trois Néandertaliens, deux adultes (Spy 1 et Spy 2) et un enfant (Spy 3) (Twiesselmann, 1953, 1971), mais au moins trois Néandertaliens adultes et peut-être quatre ou cinq*". He added "*Quel que soit le nombre exact des individus, les os du pied prouvent avec certitude qu'il n'est plus nécessaire d'associer systématiquement les os postcrâniens avec les crânes de Spy 1 et Spy 2*". Recently, during a review of the material collected at the site, one proximal hallucal phalanx (Spy 425n) was found in the faunal material and determined as symmetrical to the Spy 25G specimen, bringing the number of possible Neandertal foot remains to 11. However, direct dating showed that it could not belong to this taxon, which thus excludes the Spy 25G specimen from the Neandertal inventory (Semal *et al.*, 2009, volume 1: chapter XVI). Lastly, one of the second metatarsals (Spy 25A) was also removed because of the nature of its fossilisation and its morphometric characteristics (Rougier *et al.*, this volume: chapter XIX); this specimen

was neither listed in the Twiesselmann (1971) inventory nor included in the Trinkaus analysis (1978) (see Rougier *et al.*, this volume: chapter XIX). Today, the original collection contains eight foot bones and fragments of foot bones that might be attributed to the adult Neandertals (Table 1; SF1 to SF6).

More generally, a review of the Spy cave site collections has notably reshaped the palaeoanthropological inventory (Rougier *et al.*, 2004, this volume: chapter XIX; Semal *et al.*, 2009, volume 1: chapter XVI). Pursuing in this vein, we went through the Neolithic foot material from the site (housed at the RBINS); among the remains (representing all the parts of the foot) we identified five proximal lateral phalanges (Spy 274e, 205b, 228b, 398d and 170d) which fossilisation recalled that of the Neandertal specimens and which robustness contrasted with that of the other proximal phalanges in this collection while recalling the morphology of Neandertal proximal lateral phalanges as described in the literature.

In view of these recent developments, a reassessment of the Spy metatarsal and pedal phalangeal bones was necessary. We aim here to provide new insights into their presumed association with the two Neandertal adults. In addition, we question the possible inclusion in the Neandertal inventory of the five phalanges extracted from the Neolithic material. Unfortunately, the necessary background is poor; there is little Neandertal material available for comparison and the interest in these anatomical segments among palaeoanthropologists is still limited. In general, studies have highlighted the robustness of the Neandertal foot bones as and when discoveries of Neandertal remains have occurred. To date, the study of the Shanidar material (Trinkaus, 1975, 1983) is the only synthesis on this matter, providing, in particular, new insights into Neandertal foot characteristics in the light of the numerous foot remains from the site. Concerning the distal segments, the robustness of the first metatarsal and proximal phalanges, with substantial development of their plantar areas of attachment, can be noted. More recently, Trinkaus & Hilton (1996) have pointed out that "[…] the Neandertals have moderately shorter proximal pedal phalanges with the middle (digits 2-4) phalanges having significantly wider diaphyses relative to the recent humans". However, concerning the hallucal column, the data in the case that interests us here must be used with caution since the Neandertal specimens considered in Trinkaus & Hilton (1996) included those from Spy. Thus, where the allocation of isolated bones in the Neandertal inventory is concerned, the results we propose for the Spy foot remains must be regarded a priori as pointers for further progress and as a first step towards a solution other than one that considers all the specimens as Neandertal because there is no evidence to the contrary.

MATERIALS AND METHOD

As there is no doubt over the attribution of both the talus and the calcaneus, our analysis focused on the five metatarsals and the hallucal proximal phalanx of the original Neandertal

Inventory number	*Bone*	*Side*	*State of preservation*	*Maturation*	*Attribution (Twiesselmann, 1971)*
25D	MTT 1	L	Complete	M	only one left MTT 1 listed; attributed to Spy II
25B	MTT 1	L	Complete	M	
25C	MTT 1	R	Complete	M	
23A	MTT 2	L	4/5 proximal fragment	M	Spy II
23B	MTT 3	R	1/2 proximal fragment	M	
25F	PP 1	R	Complete	M	Spy II
17	Calcaneus	L	Complete, eroded	M	Spy II
18	Talus	L	Complete	M	Spy II

Table 1. Inventory of the eight foot bones from the original Spy collection (RBINS).
MTT = Metatarsal; PP = Proximal phalanx; R = Right; L = Left; M = Mature.

collection, and the five proximal lateral phalanges extracted from the Neolithic material; concerning the talus and the calcaneus specimens, we provide pictures and their main classical dimensions in the supporting materials (ST1 and SF1-2). The comparative Neandertal sample included: Kiik-Koba 1 (Bonč-Osmolovskij, 1954), Shanidar 1, 3, 4, 6 and 8 (Trinkaus, 1975, 1983), Tabun C1 (McCown & Keith, 1939), La Ferrassie 1 and 2 (Heim, 1982), La Chapelle-aux-Saints 1 (Boule, 1912) and Krapina (n = 31) (Radovčić *et al.*, 1988). The anatomically modern human sample used for comparison included Middle Palaeolithic specimens from Qafzeh and Skhul (McCown & Keith, 1939; Vandermeersch, 1981), Upper Palaeolithic specimens from Pataud (Billy, 1975) and Cro-Magnon, a sample of Neolithic humans from the Mosan Valley (Maurenne, Hastière, Furfooz, Freyr, Goyet, Waulsort and Montaigle) (RBINS; database provided by Hélène Rougier and Isabelle Crevecoeur), a sample of French Neolithic remains (*Musée de l'Homme*, Paris) and a sample of recent humans (*Musée de l'Homme*, Paris). We studied the original material from La Ferrassie, La Chapelle-aux-Saints, Krapina, Pataud and Cro-Magnon and used the data from the literature for the other Palaeolithic fossils.

The study was carried out on the basis of both quantitative and qualitative data: (1) measurements as defined by Martin & Saller (1957) as well as the indices defined by Trinkaus (1978) and the calculation of cross-section areas; (2) X-rays, virtual symmetrisations, superimpositions and articulations of 3D reconstructed models - these models were provided by Patrick Semal (RBINS) under the TNT project (and are available on request at www.nespos.org); (3) direct qualitative observations of, in particular, the shape of the joint areas and the development of the tendon and ligament attachment areas.

RESULTS AND DISCUSSION

Both surface and radiological observations show that (1) ossification of each bone is complete, which bears out their attribution to mature individuals, and (2) there is no difference between the metatarsals that might be related to age.

Figure 1. Lateral view of the first metatarsals Spy 25B (a), Spy 25C (b), Pataud 6 (c), La Ferrassie 1 (d), Krapina 245 (e) and Spy 25D (f); the bones have been scaled so that their maximal lengths are equal in order to make comparisons of the concavity of their plantar border easier. Pictures of Spy and Krapina specimens by P. Semal, RBINS; pictures of Pataud 6 and La Ferrassie 1 by G. Berillon (courtesy of P. Mennecier, MNHN, Paris).

Specimens	*Maximal length*	*Articular length*	*Maximal height*	*Maximal width*	*Shaft height*	*Shaft width*	*Minimal height*	*Minimal width*	*Proximal articular height*	*Proximal articular width*
Kiik-Koba 1 (R)	59.3	63.0	35.6	23.6	13.6	16.4			34.5	17.0
Kiik-Koba 1 (L)	59.5	62.0	36.2	22.1	14.8	17.0			35.5	17.5
Tabun C1 (R)	51.0	49.5	22.0	18.5		13.4			21.2	16.2
Tabun C1 (L)	52.5	51.0		17.5	9.5	13.0			21.5	14.0
Shanidar 1 (R)		58.6			12.1	12.9			30.1	
Shanidar 1 (L)		60.6	33.3	22.2	12.9	13.7			31.1	15.9
La Ferrassie 1 (L)	67.7	64.8	36.3	27.0	13.0	17.1	12.8	17.1	31.6	17.8
La Ferrassie 2 (L)	56.4	54.6	28.8	19.6	10.0	13.0	9.5	13.6		14.0
Krapina 245	59.6	57.8	31.7		14.7	16.0	12.9	16.0	30.8	
Krapina 246					12.5	13.2	11.3	13.1		
Mean_NEA±SD	59.1±5.6	58.5±5.1	31.4±5.4	21.7±3.6	12.5±2.1	14.7±1.9	11.6±1.6	14.9±1.9	30.1±5.2	15.8±1.8
N	5	6	6	5	7	7	4	4	5	5
Skhul 3 (L)		58.0	30.5	22.0	13.5	14.5				
Skhul 4 (L)		64.5	29.0	23.0	15.0	17.2				
Qafzeh 3 (R)		60.7	28.9	19.9	14.5	14.3				
Qafzeh 8 (R)		62.7	29.3		14.3	15.8				
Qafzeh 8 (L)		63.0	29.8		14.6	15.0			29.5	13.5
Qafzeh 9 (R)		58.9	29.8		14.4	15.3			27.0	13.0
Pataud 6	58.9	57.2	26.6		12.0	11.1	10.9	11.9	26.2	
Cro-Magnon 1	66.2	65.3	29.9	19.2	12.7	12.0	11.5	12.8	29.0	17.2
Cro-Magnon 2	63.8	62.8	26.2		12.2	12.7	11.3	13.2		16.1
Mean_PMH±SD	63.0±3.7	61.3±3.1	28.9±1.6	21.0±1.8	13.6±1.2	14.0±2.0	11.2±0.3	12.6±0.7	27.9±1.6	14.9±2.0
N	3	8	8	4	8	8	3	3	4	4
Mean_NHS±SD	58.2±3.9	55.7±3.6	26.9±1.9	19.7±1.9	12.9±1.0	13.2±1.2	11.8±1.0	13.2±1.3	26.5±1.9	16.2±1.5
N	111	112	10	104	112	112	10	10	107	103
Spy 25D	55.7	53.4	27.1	20.1	11.5	13.7	10.6	13.9	25.9	15.9
Spy 25B	54.9	52.9	26.3		12.9	13.1	12.4	13.7	24.9	
Spy 25C	52.7	51.2	25.7		12.3	12.1	11.2	13.8	25.0	

The first metatarsal

The absolute dimensions (Table 2) of the three first metatarsals (Spy 25B, Spy 25C and Spy 25D) are small compared to the average values for recent modern and fossil humans. Their maximum dimensions (length, and width and height of the base) fall below the averages of the three comparative samples. Unlike Trinkaus (1978), we did not observe any clear differences in the robusticity index for both modern human samples and the Neandertal sample; Spy 25D falls in the middle of the range of variation as a whole. The Neandertal and modern human samples differ in: (1) the relative dimensions of the base (Maximal height / Articular length, Proximal articular height / Articular length, Cross-section area / Articular length) which are relatively larger in Neandertals; (2) the conformation of the shaft cross-section at mid-length (Shaft width / Shaft height) and at the minimal height (Minimal width / Minimal height) levels: in Neandertals, the shaft is broader than high especially at its minimal height level; (3) the proximal rugosity index. With regard to the base development and the shaft cross-section, Spy 25B and Spy 25C come close to modern humans. Spy 25D comes close to Neandertals in the morphology of the cross-section of the shaft only, with a shaft of greater breadth than height from mid-length to its minimum height level.

Specimens	*Distal maximal height*	*Distal maximal width*	*Maximal height / Articular length*	*Proximal articular height / Articular length*	*Shaft width / Shaft height*	*Minimal width / Minimal height*	*Maximal width / Maximal height*	*Cross-section area / Articular length*[(1)]	*Proximal rugosity index*[(2)]	*Robusticity index*[(2)]
Kiik-Koba 1 (R)	23.0	21.6	0.57	0.55	1.21				69.81	47.62
Kiik-Koba 1 (L)	23.6	22.3	0.58	0.57	1.15		0.61	10.13	77.65	51.29
Tabun C1 (R)	17.2	20.0	0.44	0.43			0.84		84.38	
Tabun C1 (L)	18.0	20.0		0.42	1.37					44.12
Shanidar 1 (R)	22.0	20.8		0.51	1.07					42.66
Shanidar 1 (L)	23.8	19.6	0.55	0.51	1.06		0.67	9.58	66.89	43.89
La Ferrassie 1 (L)	24.4		0.56	0.49	1.32	1.34	0.74	11.87	57.39	46.45
La Ferrassie 2 (L)	19.7		0.53		1.30	1.43	0.68	8.12		42.12
Krapina 245	22.0	24.3	0.55	0.53	1.09	1.24				53.11
Krapina 246										
Mean_NEA±SD	21.9±2.6	21.6±2.2	0.54±0.05	0.51±0.06	1.21±0.13	1.34±0.10	0.71±0.09	9.92±1.55	71.58±11.89	46.83±4.42
N	6	4	6	5	6	3	5	4	4	6
Skhul 3 (L)	20.7	22.5	0.53		1.07		0.72	9.08		48.28
Skhul 4 (L)	21.0	23.0	0.45		1.15		0.79	8.12		49.92
Qafzeh 3 (R)	18.8	24.6	0.48		0.99		0.69	7.44		47.45
Qafzeh 8 (R)	19.7	22.2	0.47		1.10					48.01
Qafzeh 8 (L)	20.2	22.8	0.47	0.47	1.03					46.98
Qafzeh 9 (R)	19.3	22.7	0.51	0.46	1.06					50.42
Pataud 6	20.8	20.5	0.47	0.46	0.93	1.09				40.38
Cro-Magnon 1			0.46	0.44	0.94	1.11	0.64	6.90	86.89	37.83
Cro-Magnon 2	21.9		0.42		1.04	1.17				39.65
Mean_PMH±SD	20.4±1.0	22.7±1.3	0.47±0.03	0.46±0.01	1.03±0.07	1.12±0.04	0.71±0.06	7.88±0.94		45.44±4.78
N	7	6	8	4	8	3	4	4		9
Mean_NHS±SD	20.4±2.2	21.1±1.7	0.49±0.08	0.48±0.10	1.03±0.08	1.12±0.07	0.72±0.03	7.46±0.72	78.23±5.74	46.88±2.71
N	111	108	10	107	112	10	10	10	10	112
Spy 25D	18.9	23.2	0.51	0.49	1.19	1.31	0.74	8.01	75.60	47.19
Spy 25B	19.9	20.6	0.50	0.47	1.02	1.10	0.71	7.30		49.15
Spy 25C	18.2		0.50	0.49	0.98	1.23				47.66

Table 2. (opposite page and above) Dimensions and indices of the Spy first metatarsals and comparative data. NEA: Neandertal; PMH: Palaeolithic modern humans; NHS: Neolithic *Homo sapiens*; (L): left side; (R): right side; SD: Standard deviation. [(1)] Cross-section area = Maximal height*Maximal width*π/4, assuming that the outline of the base is elliptic; [(2)] Trinkaus (1978).

Concerning the rugosity index, Spy 25D falls between the average values of the modern human and the Neandertal samples; it is to note that we found values very distinct from those provided by Trinkaus (1978).

From a qualitative point of view, in Neandertals, the plantar edge of the shaft is more concave than in modern humans, both fossil and recent; in modern humans, its proximal part is almost rectilinear. Among all Spy specimens, the former morphology is observed in the Spy 25D specimen only (Figure 1).

Finally, the left proximal hallucal phalanx Spy 25G, recently excluded from the Neandertal inventory, articulates perfectly with the Spy 25B specimen but not with the Spy 25D specimen.

Concerning possible associations of these metatarsals, Trinkaus (1978) noted: *"Les trois premiers métatarsiens sont trop différents pour ne pas provenir de deux individus [...]"*. If there is no doubt that the left first metatarsal Spy 25D and the right first metatarsal Spy 25C cannot be paired due to their clearly visible differences, we cannot exclude without further explanation that more discrete differences in size and shape between Spy 25C and Spy 25B could be related to their different state of preservation (Rougier *et al.*, this volume: chapter XIX). We therefore carried out a comparative examination, both direct and virtual, of their morphological features (Figure 2). This revealed many discrete differences between the two bones, in the shaft, the head and the base. In the shaft, they relate to the obliqueness of the medial edge, the orientation of the dorsal face, the proximo-distal evolution of the cross-section, the concavity of the medio-distal portion of the dorsal face, and the relief of the lateral area behind the head. The shaft of Spy 25B is more voluminous and its plantar face extends distally behind the head. In the head, the differences relate to the entire dorso-plantar orientation of the head and the position of the two dorsal tubers behind the dorsal edge of the joint area. Lastly, the bases are oriented in very different ways, with a marked concavity of the joint area for the medial cuneiform in the Spy 25B specimen. Because of these differences, these two metatarsals should be attributed to two different individuals.

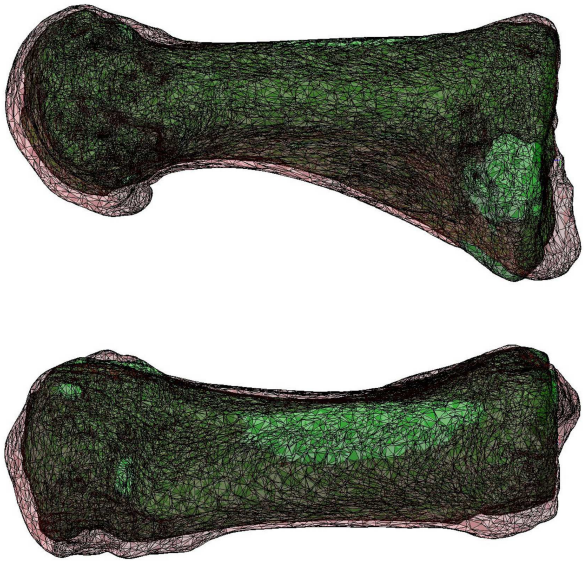

Figure 2. 3D superposition of the first metatarsals Spy 25B and Spy 25C, in pink and green respectively, in lateral view (top) and in dorsal view (bottom). See in transparency that differences concern all the parts of the metatarsals although they are more marked at the base and head level.

To conclude, the three first metatarsals appear to represent three adult individuals, which agrees with Trinkaus' conclusions (1978). Nevertheless, some of the metric and morphological data cast doubts on the attribution of all three to Neandertals: in every respect, specimens Spy 25B and Spy 25C are morphologically close to the modern human morphology. Taking into account the differences observed between the samples of modern humans and Neandertals, it does not seem plausible to keep them in the Neandertal collection of the Spy cave site. As far as the shape of the shaft is concerned, the Spy 25D specimen is morphologically more closely related to the Neandertal specimens of our comparative sample; therefore, in the current state of comparative analysis, we suggest that this specimen should be kept in the Neandertal

Figure 3. The Spy 23A second metatarsal (a: medial view, b: proximal view, c: dorsal view, d: plantar view, e: X-ray in dorsal incidence, f: horizontal cross-section). Note the relative development of the base, the plantar curvature of the shaft (a) and the wide depression at the medio-distal side of the base (d-f). Pictures, radiograph and cross-section by P. Semal, RBINS.

inventory. It may be recalled that Twiesselmann (1953) had already attributed a single left first metatarsal to the Neandertal material; this specimen could be Spy 25D.

The second metatarsal

The left second metatarsal specimen (Spy 23A) lacks the head, which limits metric comparisons (Table 3); the shaft is very plantarly curved. Its morphology corresponds to the morphology usually observed in Neandertal lateral metatarsals, with the extension of the joint areas and the plantar areas of attachment (*cf.* Trinkaus, 1983), the massive dimensions of the base that contrast with the diameters of the shaft and the rapid proximo-distal decrease in the diameters of the shaft (especially the medio-lateral diameter) (Figure 3). In modern humans, the base is relatively less massive with less extended joint areas and plantar areas of attachment, and the diameters of the shaft gradually decrease proximo-distally. These observations support the initial attribution of Spy 23A to a Neandertal individual (Fraipont & Lohest, 1887; Twiesselmann, 1953).

We noted a morphological characteristic in this specimen that could further support this attribution. It consists of a broad nonarticular depression located well forward at the limit between the base and the shaft of the bone (Figure 3d-f). In medial view, the proximal part makes up an area of contact that extends along the entire height of the base, while in the dorsal view, it is distally and laterally very oblique, at an angle of approximately 45° to the axis of the shaft. Its distal portion forms a large fossa, plantarly. This structure has never been described on the Spy specimen. We

Specimens	*Maximal height*	*Maximal width*	*Shaft height*	*Shaft width*	*Proximal articular height*	*Proximal articular width*
Kiik-Koba 1 (R)	24.4	18.6	10.7	9.1	20.1	17.2
Kiik-Koba 1 (L)	25.3	17.7	10.8	9.2	20.4	16.8
Tabun C1 (R)	19.0	13.5	7.0	6.5	18.5	11.4
Shanidar 1 (R)	22.4	19.8	9.5	8.3		16.5
Shanidar 1 (L)	23.7	19.4	10.4	9.0	21.0	17.6
La Ferrassie 1 (L)		17.6	9.6	8.3		13.6
La Ferrassie 2 (L)		18.4				15.3
Krapina 247.2	21.5					
Krapina 246.1			8.5	6.8		
Krapina 248.4			8.2	7.1		
Mean_NEA±SD	22.4±2.7	17.3±2.2	9.1±1.4	7.8±1.2	20.0±1.3	14.9±2.5
N	4	5	6	6	3	5
Skhul 4 (L)	24.0	14.2	14.0	8.5		
Qafzeh 8 (R)	23.9	18.8	11.0	10.0		
Qafzeh 8 (L)	23.8	16.9	10.8	9.1	22.0	13.5
Qafzeh 9 (R)		15.7	10.6	8.9	18.0	13.5
Pataud 6	18.8	13.3	9.6	7.0	16.1	11.4
Cro-Magnon 1	20.6	13.7	9.8	8.5	8.0	12.8
Mean_PMH±SD	21.8±2.5	14.8±1.5	11.0±1.8	8.4±0.8	16.0±5.9	12.8±1.0
N	4	5	5	5	4	4
Mean_NHS±SD		15.2±1.5	8.4±1.1	7.8±1.0	18.9±1.8	13.5±1.4
N		56	56	56	42	48
Spy 23A	23.8	19.1	9.6	8.8	19.7	15.6

Table 3. Dimensions of the Spy second metatarsal and comparative data. NEA: Neandertal; PMH: Palaeolithic modern humans; NHS: Neolithic *Homo sapiens*; (L): left side; (R): right side; SD: Standard deviation.

observed a similar morphology in La Ferrassie 1, bilaterally, and on the left foot of La Ferrassie 2 (the corresponding zone on the right-hand side could not be observed because it is encased in the sediment block in which it is still preserved). Heim (1982) had noted the presence of this fossa on the La Ferrassie specimens, which he associated with the adducted orientation of the hallux. On these specimens, we observed a close correspondence between this particular morphology observed on the medial face of the second metatarsal's base (similar to that of the Spy 23A specimen), and that of the lateral face of the first metatarsal's base. This correspondence ensures optimal congruence between the first and second metatarsals as well as a functionally coherent positioning of the two bones (see below, "Possible associations of the foot bones" section). Additional investigations are necessary to fully determine the nature of this structure (ongoing research). Nevertheless, for the subject that interests us here, and according to what we observed on the La Ferrassie fossils, this particular morphology of Spy 23A must be seen as a discrete non-pathological anatomical structure that corresponds to the lateral portion of the first metatarsal's base, that we have never observed before (among hundreds of bones of shod and unshod modern humans including fossil specimens), that has never been described to our knowledge in any modern human (past or present) and that we observed in two other Neandertal individuals out of no more than ten available specimens.

The third metatarsal

The right third metatarsal specimen (Spy 23B) lacks the distal portion of the corpus and the head, which limits metric comparisons (Table 4); the shape of the preserved portion indicates that the shaft was rectilinear. Similarly to the second metatarsal specimen, its morphology

Specimens	*Maximal height*	*Maximal width*	*Shaft height*	*Shaft width*	*Proximal articular height*	*Proximal articular width*
Kiik-Koba 1 (R)	23.4	18.4	11.7	7.4	20.2	18.3
Kiik-Koba 1 (L)	25.1	17.7	13.0	9.5	21.9	17.7
Tabun C1 (R)	19.0	13.0	8.0	6.0	18.0	14.0
Shanidar 1 (R)		19.8	9.2	7.7		16.3
La Ferrassie 1 (L)	21.9	16.4	9.7	7.2		17.4
La Ferrassie 2 (L)		16.1	8.3	6.8		15.3
Krapina 247.3	22.7	16.8	8.9	7.6	21.5	14.9
Krapina 247.4			8.7	7.0		
Krapina 247.1	21.8		8.4	7.2		
Mean_NEA±SD	22.3±2.0	16.9±2.1	9.5±1.7	7.4±0.9	20.4±1.8	16.3±1.6
N	6	7	9	9	4	7
Skhul 4 (L)	21.0	15.0	13.0			
Qafzeh 8 (R)	23.5	15.2				
Qafzeh 8 (L)	22.7	15.0	10.5	7.4	20.5	14.5
Qafzeh 9 (R)	21.1	15.1	10.0	8.4	14.0	13.5
Pataud 6	18.8	12.6	8.3	6.2	17.7	10.0
Mean_PMH±SD	21.5±1.8	14.6±1.1	10.4±1.9	7.3±1.1	17.4±3.3	12.7±2.4
N	5	5	4	3	3	3
Mean_NHS±SD		13.9±1.1	8.4±0.9	7.2±0.7	18.9±1.4	13.1±1.1
N		101	102	102	85	99
Spy 23B	21.8	16.4	9.6	8.0	18.1	15.5

Table 4. Dimensions of the Spy third metatarsal and comparative data. NEA: Neandertal; PMH: Palaeolithic modern humans; NHS: Neolithic *Homo sapiens*; (L): left side; (R): right side; SD: Standard deviation.

corresponds to the frequently observed morphology of Neandertal lateral metatarsals with the extension of the joint areas and the plantar areas of attachment (*cf.* Trinkaus, 1983), the massive dimensions of the base compared to the diameters of the shaft and the rapid proximo-distal decrease in the diameters of the shaft (Figure 4). In modern humans, the base is relatively less massive, and the shaft is medio-laterally flattened with a dorso-plantar diameter that gradually decreases proximo-distally. Although there are very few data, they support the initial attribution of Spy 23B to a Neandertal individual (Fraipont & Lohest, 1887; *contra* Twiesselmann, 1953).

Figure 4. The Spy 23B third metatarsal (a: lateral view, b: proximal view, c: dorsal view). Note the relative development of the base, the plantar attachment area, and the rectilinear shaft. Pictures by P. Semal, RBINS.

Figure 5. The Spy 25F proximal hallucal phalanx (a: dorsal view, b: plantar view, c: proximal view, d: medial view). Note the concavity of both the dorsal and plantar faces of the shaft (d). Pictures by P. Semal, RBINS.

The right proximal hallucal phalanx

The right proximal hallucal phalanx (Spy 25F) is complete and very well preserved (Figure 5). Its dimensions are large, well above the average values of the comparative samples (Table 5). In most of the absolute measurements, there is no clear difference between the Neandertal and the modern human samples we compared. Where the dimensions of the base are concerned, when scaled according to the lengths of the bones (see indices), some small differences are observed between Neandertals and modern humans: the base is slightly larger in Neandertals. However, for these variables, the Neandertal comparative sample is small, which limits the range of this observation. For these variables, the Spy 25F specimen comes close to the Neandertal specimens. Lastly, a comparison of the width and height at midshaft (Figure 6), as carried out by Trinkaus &

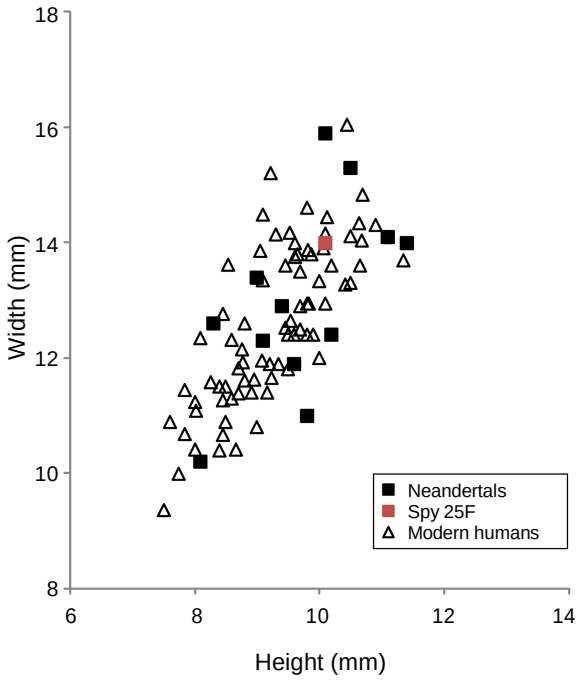

Figure 6. Proximal hallucal phalanx shaft width vs. shaft height of Neandertals, modern humans and Spy 25F.

Specimens	*Maximal length*	*Articular length*	*Shaft height*	*Shaft width*	*Maximal height*	*Maximal width*	*Minimal height*	*Minimal width*	*Proximal articular height*	*Proximal articular width*
Kiik-Koba 1 (R)		27.5	10.1	15.9	18.3	23.1			14.5	19.0
Kiik-Koba 1 (L)		28.0	10.5	15.3	18.0	23.6			13.6	18.8
Krapina 250.1	32.4	26.6	9.4	12.9	16.9	19.8	8.2	12.6	13.9	18.2
Krapina 250.2	29.0	24.2	8.1	10.2	14.8	17.7	7.0	10.2	12.5	16.8
Krapina 250.3		27.8	9.1	12.3	16.9		7.7	12.3		
Krapina 250.4		27.5	9.6	11.9			7.5	11.8		
La Ferrassie 1 (R)					13.6	19.7			12.1	15.1
La Ferrassie 2 (L)	28.1	23.2	9.8	11.0	16.0	19.3	6.8	12.5	12.6	17.8
Shanidar 1		28.1	10.2	12.4	18.9	20.4			14.4	18.4
Shanidar 3					18.1	22.1			15.5	20.2
Shanidar 4 (R)		27.2	11.1	14.1	18.6	21.7			15.3	19.0
Shanidar 4 (L)		27.7	11.4	14.0						
Shanidar 6		24.5	8.3	12.6	16.9	18.7			13.5	16.5
Shanidar 8		24.5	9.0	13.4	16.3	19.6			13.4	16.0
Tabun C1					15.0	16.2			13.8	15.7
Mean_NEA±SD	29.8±2.3	26.6±1.6	9.7±1.1	12.7±1.4	16.7±1.6	19.9±2.1	7.4±0.6	11.9±1.0	13.7±1.1	17.5±1.6
N	3	10	11	11	12	11	5	5	11	11
Pataud 6 (L)	31.0		9.6	11.6	15.2	16.7	7.7	11.4	14.4	16.6
Cro-Magnon 1 (L)	35.2		9.4	11.2	17.2	20.9	7.8	11.2	14.6	19.5
Mean_NHS±SD	32.1±3.0	27.6±2.7	9.2±0.9	12.7±1.4	15.8±1.4	19.3±1.9			13.7±1.5	18.0±1.8
N	57	58	58	58	55	57			50	52
Mean_RHS±SD	32.4±2.7		9.4±0.7	12.3±1.1	15.9±1.3	18.8±1.5	7.9±0.5	12.7±1.0	13.1±1.1	17.2±1.4
N	20		20	20	20	20	20	20	20	20
Spy 25F	35.5	31.5	10.1	14.0	19.5	22.1	9.2	15.0	19.2	17.1

Hilton (1996) but using a larger Neandertal sample than these authors, does not show any clear differences between the Neandertal and modern human samples (*contra* Trinkaus & Hilton, 1996). Spy 25F falls within the higher parts of both variations.

Figure 7. Medial view of the Spy 25F proximal hallucal phalanx (a), a Neandertal proximal hallucal phalanx (b, Krapina 250.1) and a modern human proximal hallucal phalanx (c). Phalanges have been scaled according to their maximal length. Note, on the Neandertal specimen, the rectilinear dorsal border and the very developed plantar areas of attachment compared to the modern human condition. With regard to this, Spy 25F closely resembles the modern human condition. Picture of the Krapina specimen by P. Semal, RBINS (courtesy of J. Radovčić, CNHM); picture of the modern human specimen by G. Berillon.

Specimens	*Distal height*	*Distal width*	*Maximal width / Maximal length*	*Maximal height / Maximal length*	*Maximal width / Articular length*	*Maximal height / Articular length*	*Distal width / Maximal length*	*Distal width / Articular length*	*Distal height / Distal width*
Kiik-Koba 1 (R)	10.5	20.4			0.84	0.67			0.51
Kiik-Koba 1 (L)	9.3	19.5			0.84	0.64			0.48
Krapina 250.1	7.6		0.61	0.52	0.74	0.64			
Krapina 250.2	8.7	14.6	0.61	0.51	0.73	0.61	0.50	0.60	0.60
Krapina 250.3	8.7	18.4				0.61			0.47
Krapina 250.4	10.3	17.7							0.58
La Ferrassie 1 (R)									
La Ferrassie 2 (L)	8.7	16.8	0.69	0.57			0.60		0.52
Shanidar 1	10.2	18.2			0.73	0.67			0.56
Shanidar 3									
Shanidar 4 (R)	9.2	17.2			0.80	0.68			0.53
Shanidar 4 (L)	9.5	17.8							0.53
Shanidar 6	9.5	16.0			0.76	0.69			0.59
Shanidar 8	8.8	16.9			0.80	0.67			0.52
Tabun C1									
Mean_NEA±SD	9.1±0.8	17.3±1.4	0.64±0.04	0.53±0.03	0.77±0.04	0.65±0.03			0.54±0.04
N	11	10	3	3	7	8			10
Pataud 6 (L)	10.2	15.2	0.54	0.49			0.49		0.67
Cro-Magnon 1 (L)	13.4	19.4	0.59	0.49			0.55		0.69
Mean_NHS±SD	9.9±1.1	16.7±1.6	0.60±0.04	0.49±0.04	0.70±0.05	0.58±0.06	0.52±0.04	0.61±0.05	0.59±0.04
N	56	56	56	54	57	55	56	56	56
Mean_RHS±SD	9.8±1.4	15.8±2.2	0.58±0.03	0.49±0.03			0.49±0.06		0.62±0.04
N	20	20	20	20			20		20
Spy 25F	13.3	19.9	0.62	0.55	0.70	0.62	0.56	0.63	0.67

Table 5. (opposite page and above) Dimensions and indices of the Spy proximal hallucal phalanx and comparative data. NEA: Neandertal; NHS: Neolithic *Homo sapiens*; RHS: Recent *Homo sapiens*; (L): left side; (R): right side; SD: Standard deviation.

From a qualitative point of view, we observed certain morphological features that distinguish the Neandertal specimens from modern humans (Figure 7): (1) at the base, the highly developed plantar areas of attachment (*cf.* Trinkaus, 1983); in lateral view, a shaft with (2) a rectilinear dorsal edge, especially at the proximal segment level, associated to a plantarly very concave plantar face. Given their relatively small absolute length, this gives a very particular profile to the Neandertal phalanges with, in particular, a marked plantar and distal slope of the long axis of their shaft whatever the height of their head. In comparison, Spy 25F has relatively small plantar areas of attachment and a shaft with a dorsally concave dorsal face, a morphology reminiscent of the modern human pattern. The morphology of the Spy 25F phalanx thus seems very particular, very large with a relatively wide base although the development of the plantar areas of attachment is limited. By default, this specimen should be kept in the Neandertal inventory, although its very particular morphology casts doubt on its attribution.

The lateral proximal phalanges

Preliminary observations prompted us to carry out further investigations on five lateral proximal phalanges originally allocated to the Neolithic collection of the Spy cave site (Figure 8). Given their dimensions, their estimated rank and laterality (the lateral plantar tuber is relatively more de-

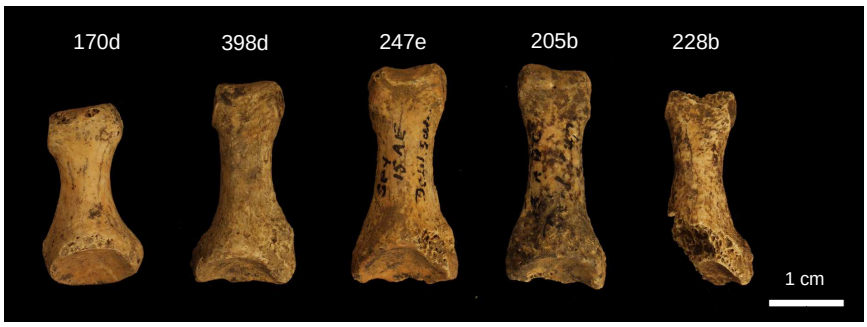

Figure 8. Dorsal view of the five lateral proximal phalanges extracted from the Neolithic collection of the Spy cave site. Inventory numbers are given above each specimen. Pictures by P. Semal, RBINS.

veloped than the medial, and the distal edge of the head is laterally and distally oriented), we suggest that these five phalanges may be attributed to a single individual. They are determined as follows: Spy 274e and Spy 205b represent respectively a left and a right proximal phalanx of digits 2-3; Spy 398d and Spy 228b represent respectively a left and a right proximal phalanx of digits 3-4; and Spy 170d represents a left proximal phalanx of digit 5.

Concerning the comparison of the height and width at mid-shaft (our comparison differs from that of Trinkaus & Hilton (1996) by pooling the lateral phalanges together, whatever their rank), we noted, like these authors, that the Neandertal group overlaps the upper part of the modern human variation and extends slightly beyond it (Figure 9). The five Spy specimens are projected at the intersection of both groups. The height, width and cross-section area of the base scaled to the length of the bones seem to be the most discriminating variables (Table 6); for these parameters, the phalanges come very close to the Neandertal lateral phalanges. Figure 10 illustrates the evolution of the cross-section area of the base with the length of the phalanges; all five Spy specimens are projected close to the limit of the modern human variation, and in the middle of the Neandertal sample.

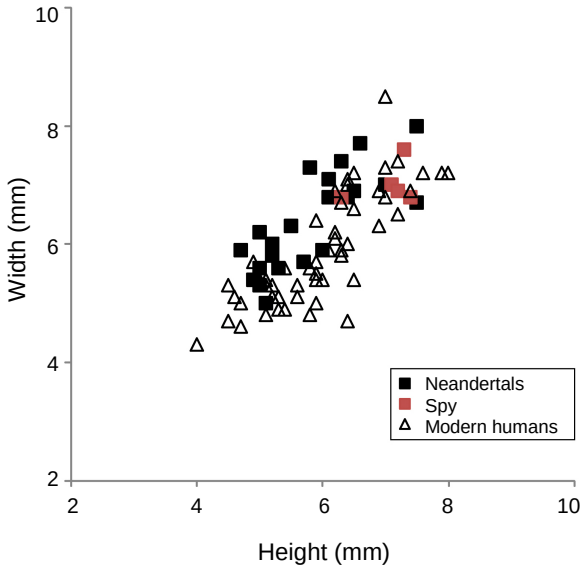

Figure 9. Lateral proximal pedal phalanx shaft width vs. shaft height of Neandertals, modern humans and the five Spy specimens.

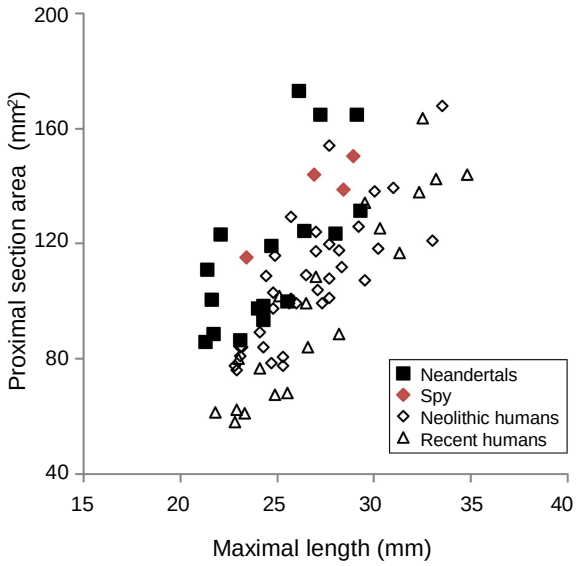

Figure 10. Proximal cross-section area vs. maximal length for lateral proximal phalanges of Neandertals, modern humans and the four Spy specimens. (Proximal cross-section area = Maximal height* Maximal width*π/4, assuming that the outline of the base is elliptic).

Specimens	*Maximal length*	*Maximal height*	*Maximal width*	*Shaft height*	*Shaft width*	*Minimal height*	*Minimal width*	*Proximal articular height*
Mean_NEA±SD	25.1±2.8	11.6±1.6	12.8±1.4	5.8±0.8	6.4±0.8	4.7±0.6	6.2±0.9	9.9±1.5
N	19	20	18	22	22	22	22	20
Mean_NHS±SD	26.6±2.7	11.2±1.0	12.1±1.5	6.2±0.8	6.0±1.0	4.7±0.5	6.0±0.9	9.3±0.9
N	36	36	36	36	36	36	36	36
Mean_RHS±SD	27.3±4.0	10.6±1.9	11.7±1.9	5.7±1.0	5.7±0.8	4.3±0.6	6.2±0.9	8.9±1.5
N	20	20	20	20	20	20	20	20
Spy 205b	28.4	13.3	13.3	7.1	7.0	5.8	7.0	10.5
Spy 274e	28.9	13.5	14.2	7.3	7.6	6.1	7.6	11.5
Spy 228b				7.4	6.8	5.2	6.8	
Spy 398d	26.9	13.1	14.0	7.2	6.9	5.7	6.9	10.8
Spy 170d	23.4	11.2	13.1	6.3	6.8	5.2	6.7	10.0

Specimens	*Proximal articular width*	*Distal height*	*Distal width*	*Maximal height / Maximal length*	*Maximal width / Maximal length*	*Distal height / Maximal length*	*Distal width / Maximal length*	*Distal height / Distal width*
Mean_NEA±SD	10.7±1.7	6.2±0.9	9.5±1.3	0.46±0.03	0.52±0.06	0.25±0.03	0.39±0.05	0.66±0.04
N	19	22	18	19	18	19	16	18
Mean_NHS±SD	10.4±1.1	5.7±0.8	8.7±1.1	0.42±0.03	0.45±0.03	0.21±0.02	0.33±0.03	0.66±0.05
N	36	36	36	36	36	36	36	36
Mean_RHS±SD	10.2±1.7	5.6±0.8	8.8±1.3	0.39±0.03	0.43±0.03	0.21±0.02	0.32±0.02	0.64±0.04
N	20	20	20	20	20	20	20	20
Spy 205b	12.2	7.0	9.8	0.47	0.47	0.25	0.35	0.71
Spy 274e	12.0	7.4	10.6	0.47	0.49	0.26	0.37	0.70
Spy 228b			9.3					
Spy 398d	11.6	6.9	9.5	0.49	0.52	0.26	0.35	0.73
Spy 170d	11.2	6.4	10.0	0.48	0.56	0.27	0.43	0.64

Table 6. Dimensions and indices of the Spy proximal lateral pedal phalanges and comparative data. NEA: Neandertal; NHS: Neolithic *Homo sapiens*; RHS: Recent *Homo sapiens*; (L): left side; (R): right side; SD: Standard deviation.

From a qualitative point of view, the bases of the lateral proximal phalanges of Neandertals display particular morphological traits that distinguish them from modern humans. It is well known that the plantar areas of attachment are very developed (*cf.* Trinkaus, 1983); we observed as well in lateral view that these areas are proximally projected compared to the dorsal margin of the proximal joint area (Figure 11). In the modern human sample, the plantar areas of attachment are relatively small and not projected proximally. The five Spy phalanges display the morphology observed in the comparative Neandertal sample.

These quantitative and qualitative observations, although preliminary, suggest that these five specimens may be attributed to an adult individual of the Neandertal inventory.

Possible associations of the foot bones

Between the first and the second metatarsals

Our examination of the bones from La Ferrassie 1 and 2 highlights a close correspondence between the conformation of the medial face of the second metatarsal base (similar to that of

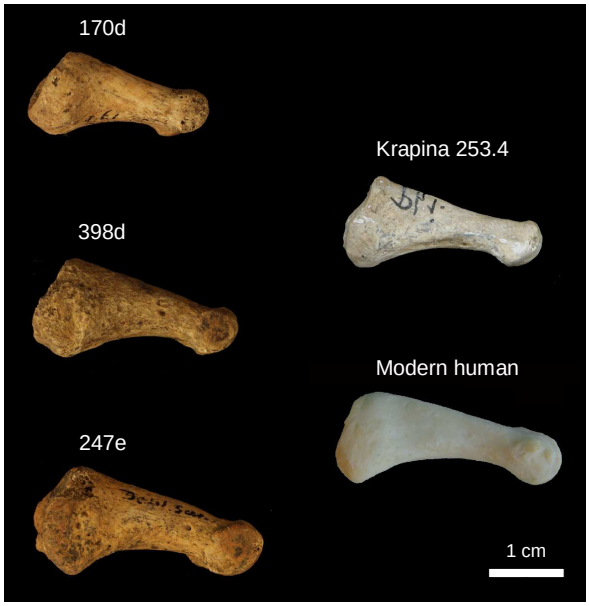

Figure 11. Medial view of the Spy left lateral proximal pedal phalanges, Krapina 253.4 (symmetrised) and a modern human lateral proximal pedal phalanx. The Spy specimens, with plantar areas of attachment that are well developed and proximally projected resemble the Krapina specimen. Pictures of the Spy specimens by P. Semal, RBINS; pictures of the Krapina (courtesy of J. Radovčić, CNHM) and modern human specimens by G. Berillon.

Spy 23A) and that of the lateral face of the first metatarsal base. On La Ferrassie 2, the contact is achieved thanks to joint areas that are mirror-shaped. On La Ferrassie 1, the congruence is achieved by a proximally located articular zone (on the right) or contact zone (on the left); in addition, to the fossa of the second metatarsal corresponds a highly developed area of attachment for the *m. fibularis longus* on the plantar face of the first metatarsal. When the tarso-metatarsal complex is rearticulated, these two mirror-shaped structures are perfectly embedded. In addition, for each individual of La Ferrassie, in the horizontal plane, the first cuneo-metatarsal joint is placed forward compared to the second, and the axes of the bodies of the first and second metatarsals are relatively parallel; in the frontal plane, the second metatarsal base is placed at the level of the dorsal portion of the first metatarsal base. This general architecture is similar to those of Shanidar 1, Tabun C1 and Kiik-Koba 1. It is therefore reasonable to assume that the particular contact between the first and second La Ferrassie metatarsals does not affect the structure of the foot, and should be seen as a bilateral non-pathological anatomical structure. It involves an evident morphological correspondence between the first and second metatarsal bases, on both sides. There is no such morphological correspondence between the Spy second metatarsal and any of the Spy first metatarsals (Figure 12).

Metrically, compared with the comparative Palaeolithic samples, the base of the Spy first metatarsals is too low compared to that of the second metatarsal: the average ratio of the first metatarsal height with the second metatarsal height is equal to 1.36 in Neandertals and 1.31 in modern humans, while it is equal to 1.14 for Spy 25D.

Considering these observations, none of the Spy first metatarsals can be associated with the second metatarsal (*contra* Fraipont & Lohest, 1887; Twiesselmann, 1953).

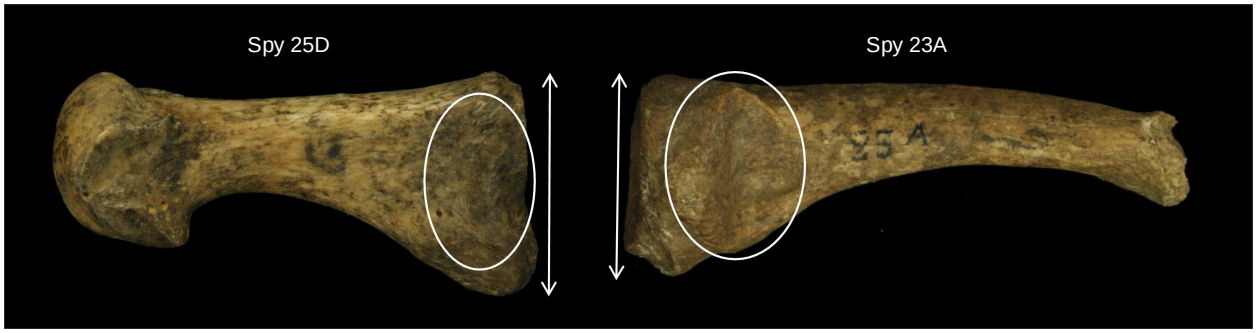

Figure 12. Lateral view of the first metatarsal Spy 25D and medial view of the second metatarsal Spy 23A. Note that neither their contact areas (circled) nor their maximal heights (arrows) are compatible. Pictures by P. Semal, RBINS.

Between the hallucal phalanx and the first metatarsals

The Spy 25F hallucal proximal phalanx articulates with none of the first metatarsals of the collection, neither directly nor virtually (with symmetrised left metatarsals) (*contra* Twiesselmann, 1953).

Between the second and the third metatarsals

On the left second metatarsal, Spy 23A, the joint area for the third metatarsal is single and concave while on the right third metatarsal, Spy 23B, the joint area for the second metatarsal is bipartite and concave (Figure 13). Given the usual morphological similarity between right and left pedal anatomy, this contrasts with what is expected for usually highly congruent metatarso-metatarsal joints such as those of humans.

In comparison with the relative dimensions of the second and third metatarsal bases in the Neandertals and modern human samples, the dimensions of the base of the Spy third metatarsal seem too small, especially in width, relatively to those of the second metatarsal: the average ratio of the second metatarsal width with the third metatarsal width is equal to 1.04 in Neandertals, 1.08 in modern humans, and 1.16 for the Spy specimens.

Lastly, the plantar curvature of the second metatarsal Spy 23A is marked while the shaft of the third metatarsal 23B is rectilinear. The shaft curvature of lateral metatarsals usually varies. Nevertheless, the difference appears too important for two contiguous metatarsals that would belong to the same individual.

Therefore, according to these observations, we believe that the second and third metatarsals from Spy cannot be associated with the same individual.

Concerning non-contiguous metatarsals and phalanges of the inventory, some hypothetical associations based on dimensional criteria can be proposed: the first (Spy 25D) and the third (Spy 23B) metatarsals on one hand, and the Spy 25F hallucal proximal phalanx and the Spy 23A second metatarsal on the other. Lastly, if the attribution of the lateral proximal phalanges to Neandertals is confirmed, these could belong to a unique individual and be associated with any other foot bones of the inventory.

Figure 13. Lateral view of the second metatarsal Spy 23A and medial view of the third metatarsal Spy 23B. Note (1) that neither their joint areas (dotted lines and curved segments) nor their maximal widths (arrows) are compatible and (2) the curvature of the second metatarsal shaft. Pictures by P. Semal, RBINS.

CONCLUSION: INDIVIDUAL ATTRIBUTION

On the basis of these new observations, the remaining eight foot bones of the original collection could represent at least four adult individuals. These observations converge with Trinkaus' conclusions (1978). However, based on the observations reported here, some may not be Neandertals, as Twiesselmann's inventories implied (Twiesselmann, 1953, 1971; *contra* Trinkaus, 1978). In the current state of progress of our investigations of the Neandertal material available for comparison and the available literature, we believe it is justified to keep the following specimens in the Neandertal inventory: the Spy 18 talus, the Spy 17 calcaneus, the Spy 23A second metatarsal and the Spy 23B third metatarsal; there are not enough consistent observations to allow either the Spy 25F hallucal proximal phalanx or the Spy 25D first metatarsal to be excluded from the Neandertal inventory. Lastly, five lateral proximal phalanges (Spy 274e, Spy 205b, Spy 228b, Spy 398d and Spy 170d), which we extracted from the Neolithic collection from the Spy cave site, may be added to this inventory. Our observations of the metatarsal and phalangeal material plead in favour of an attribution to two adult Neandertals, one larger than the other. Nevertheless, our conclusions do not support the individual attribution proposed by Twiesselmann (1953, 1971). The second metatarsal, Spy 23A, and the hallucal proximal phalanx, Spy 25F, that represent the largest individual could be associated with the talus, Spy 18, and the calcaneus, Spy 17, and would thus be attributed to Spy II. The first metatarsal, Spy 25D, and the third metatarsal, Spy 23B, would represent another individual, smaller, who could be Spy I. The five lateral proximal phalanges could be attributed to Spy I or Spy II.

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BIBLIOGRAPHY

BILLY G., 1975. Étude anthropologique des restes humains de l'Abri Pataud. *In*: H. MOVIUS (ed.), *Excavations of the Abri Pataud, Les Eyzies (Dordogne)*. Cambridge, Harvard University: 199-259.

BONČ-OSMOLOVSKIJ G. A., 1954. Skelet stopy i goleni iskopaemogo čheloveka iz grota Kiik-Koba. *Paleolit Kryma*, **3**.

BOULE M., 1912. L'homme fossile de La Chapelle-aux-Saints. *Annales de Paléontologie*, **7**: 85-192.

DAY M. H. & WOOD B. A., 1968. Functional affinities of the Olduvai Hominid 8 talus. *Man*, **3**: 440-454.

FRAIPONT C., 1912. L'astragale chez l'Homme moustérien de Spy. Ses affinités. *Bulletin de la Société d'Anthropologie de Bruxelles*, **31**: CXCV-CCXXVIII.

FRAIPONT C., 1913. *Sur l'importance des caractères de l'astragale chez l'homme fossile*. Liège, Université de Liège, Faculté des sciences: 66 p.

FRAIPONT C., 1919. Note préliminaire sur l'étude radiographique du pied chez les primates vivants et fossiles. *Bulletin de la Société d'Anthropologie de Bruxelles*, **34**: 163-168.

FRAIPONT C., 1920. Sur la structure intime de l'astragale chez les primates. *Bulletin de l'Académie royale de Belgique, Classe des Sciences*, **6** (5): 261-263.

FRAIPONT J., 1891. Les Hommes de Spy (la race de Canstadt ou de Néanderthal en Belgique). *Congrès international d'anthropologie et d'archéologie préhistoriques. Compte rendu de la dixième session à Paris, 1889*. Paris: 321-362.

FRAIPONT J. & LOHEST M., 1886. La race humaine de Néanderthal ou de Canstadt, en Belgique. Recherches ethnologiques sur des ossements humains, découverts dans des dépôts quaternaires d'une grotte à Spy et détermination de leur âge géologique. Note préliminaire. *Bulletin de l'Académie royale des Sciences de Belgique*, 3ème série, **XII**: 741-784.

FRAIPONT J. & LOHEST M., 1887. La race humaine de Néanderthal ou de Canstadt en Belgique. Recherches ethnologiques sur des ossements humains, découverts dans des dépôts quaternaires d'une grotte à Spy et détermination de leur âge géologique. *Archives de Biologie*, **7**/1886: 587-757.

GAMBIER D., 1981. *Étude de l'astragale chez les Néandertaliens*. Thèse de doctorat, Université Paris VI, 2 vol.: 148 p. + 33 pl.

HEIM J.-L., 1982. Les hommes fossiles de la Ferrassie. II. Les squelettes adultes (squelette des membres). *Archives de l'Institut de paléontologie humaine*, **38**: 272 p.

LEBOUCQ H., 1902. Ueber prähistorische Tarsusknochen. *Verhandlungen der Anatomischen Gesellschaft*, **16**: 143-150.

LISOWSKI F. P., 1967. Angular growth changes and comparisons in the primate talus. *Folia Primatologica*, **7** (2): 81-97.

MARTIN R. & SALLER K., 1957. *Lehrbuch der Anthropologie in systematischer Darstellung*. Stuttgart, Gustav Fischer Verlag.

MCCOWN T. D. & KEITH A. SIR, 1939. *The Stone Age of Mount Carmel. Volume II: The fossil human remains from the Levalloiso-Mousterian*. Oxford, Clarendon Press: 165 p.

MORTON D. J., 1926. Significant characteristics of the Neanderthal foot. *Natural History*, **26**: 310-314.

OXNARD C. E., 1972. Some African fossil foot bones: a note on the interpolation into a matrix of extant species. *American Journal of Physical Anthropology*, **37** (1): 3-12.

RADOVČIĆ J., SMITH F. H., TRINKAUS E. & WOLPOFF M. H., 1988. *The Krapina hominids. An illustrated catalog of the skeletal collection*. Zagreb, Yugoslavia, Mladost, Croatian Natural History Museum: 118 p.

RHOADS J. G. & TRINKAUS E., 1977. Morphometrics of the Neandertal talus. *American Journal of Physical Anthropology*, **46** (1): 29-44.

ROUGIER H., CREVECOEUR I., FIERS E., HAUZEUR A., GERMONPRÉ M., MAUREILLE B. & SEMAL P., 2004. Collections de la Grotte de Spy: (re)découvertes et inventaire anthropologique. *Notae Praehistoricae*, **24**: 181-190.

SEMAL P., ROUGIER H., CREVECOEUR I., JUNGELS C., FLAS D., HAUZEUR A., MAUREILLE B., GERMONPRÉ M., BOCHERENS

H., PIRSON S., CAMMAERT L., DE CLERCK N., HAMBUCKEN A., HIGHAM T., TOUSSAINT M. & VAN DER PLICHT J., 2009. New Data on the Late Neandertals: Direct Dating of the Belgian Spy Fossils. *American Journal of Physical Anthropology*, **138** (4): 421-428.

TRINKAUS E., 1975. *A functional analysis of the Neandertal foot*. Ph.D. Dissertation, University of Pennsylvania: 465 p.

TRINKAUS E., 1978. Les métatarsiens et les phalanges du pied des Néandertaliens de Spy. *Bulletin de l'Institut royal des Sciences naturelles de Belgique*, **51** (7): 1-18.

TRINKAUS E., 1983. *The Shanidar Neandertals*. New York, Academic Press: 502 p.

TRINKAUS E. & HILTON C. E., 1996. Neandertal pedal proximal phalanges: diaphyseal loading patterns. *Journal of Human Evolution*, **30** (5): 399-425.

TWIESSELMANN F., 1953. Belgique et Luxembourg. *In*: H. V. VALLOIS & H. L. MOVIUS (ed.), *Catalogue des Hommes Fossiles.* Comptes Rendus de la XIX[e] Session du Congrès Géologique International à Alger, 1952: 93-101.

TWIESSELMANN F., 1971. Belgium. *In*: K. P. OAKLEY, B. G. CAMPBELL & T. I. MOLLESON (ed.), *Catalogue of Fossil Hominids. Part II: Europe*. London, Trustees of the British Museum: 5-13.

VANDERMEERSCH B., 1981. *Les Hommes fossiles de Qafzeh (Israël)*. Cahiers de Paléoanthropologie. Paris, CNRS Éditions: 319 p.

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