Geometric morphometrics and the population diversity of Late Glacial horses in Western Europe (*Equus caballus arcelini*): phylogeographic and anthropological implications

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Abstract

In order to test the possibility of large migrations of wild horses between the North and the South of Western Europe during the Late Glacial, we addressed the population diversity in this area, especially during the Bölling/Alleröd periods. We based this appreciation upon the detailed morphology of the distal part of the metapodials. Landmark approaches were applied to archaeological and palaeontological samples from three distinct areas: Switzerland Plateau, Paris Basin, and Charente (France). Little differences of isometric size characterized the three regional samples. Multivariate analyses of shape (principal component analysis, discriminant, canonical variates and neural network analyses) revealed similar sets of complex shape features on both metacarpals and metatarsals. In addition, regional groups appeared clearly differentiated by well defined shape patterns, the functional implications of which remain to be established. These results evidence the existence of a regional structuration of populations (particularly clear on the CVA of both metacarpals and metatarsals) suggesting the absence of long distance migrations. Finally, it appears that the distinction between size and shape systematically operated by geometric morphometrics can provide better insights into the study of the mobility of ancient populations. Geometric morphometrics approaches such as 3D Procrustes superimpositions, appear therefore to be of great interest for archaeological purposes.
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1. Introduction

In a general way, wild horses have played an important role in the subsistence of human groups in Western Europe especially during the Late Glacial [14–20,48,51,56,58,74,75]. They were small sized horses,

belonging to the subspecies *Equus caballus arcelini* Guadelli [38].

In the Paris Basin, however, famous Magdalenian sites such as Pincevent (Seine-et-Marne) or Verberie (Oise), dated to the Dryas I-Bölling/Alleröd periods [67], for a long time suggested a subsistence overwhelmingly dominated by reindeers (*Rangifer tarandus* L.), with almost insignificant contributions from horses [2,3,33, 47,52,63]. Recently, excavations at Marolles-sur-Seine (Seine-et-Marne) provided bone assemblages dominated by horses [1,48] and balanced this picture, revealing that

either the reindeer or the horse have been alternatively the key-prey of the Magdalenian hunters, as it had been previously noticed in Germany [73,74]. A similar situation has also recently been stated for the first occupations of the Azilian culture in the Paris Basin (Bölling/Alleröd), namely from the site Le Closeau (Haut-de-Seine; [10,11]), with dominance of horses and of red deer, instead of reindeer.

These observations suggest possible (seasonal?) mobility of the Late Glacial horses into and out of the Paris Basin. A similar question has been solved some years ago for the reindeer in the Southwest and Centre of France on one hand, and in Western Germany from the other, where Fontana [34] and Weinstock [72,73] eventually demonstrated that populations were mainly resident. Weinstock especially used careful osteometric comparisons to indicate that reindeer populations from Northern Germany significantly differed from the ones in Southern Germany, Switzerland and Paris Basin. Such differences could be considered to result from restricted genic flows suggesting low interregional migration rates.

In the same perspective, we compare interregional morphological characteristics of the Magdalenian and Azilian wild horses in and South of Paris Basin, in order to determine if horse populations in this area belonged to resident populations or periodically came from southern areas. As references for southern areas, we took into consideration the Switzerland Plateau and the Northern Aquitain Basin, both characterised by the presence of large and well preserved Magdalenian horse bone assemblages [23,51,56].

Previous morphological and metrical analyses of equid limb bones [24,28,29] clearly indicated that good discrimination may be achieved with metapodials [27,30,31]. Moreover, together with teeth and phalanges, these bones are among the more frequent because of their resistance to taphonomic injuries [58], as confirmed by all of our study assemblages. Therefore, we first concentrated on metapodials, although teeth and phalanges are also studied in parallel [9].

Since most of metapodial diaphyses were broken by the Prehistoric humans for marrow consumption, we limited our investigations to the distal articular extremity which is also the most diagnostic part for both environmental and taxonomic interpretations [28].

Morphometric investigations at the population level ask for both a careful description and a high statistical power due to the generally low levels of morphological differentiation. Geometric morphometric approaches [4,13] have been recurrently shown to meet both requirements better than traditional morphometric approaches [62]. They furthermore have the additional benefit to allow for the direct visualization of shape deformations along biological directions such as size or along statistical ones such as canonical, principal or factorial axes. In order to recover the overall shape of metapodial extremities we used three-dimensional homologous landmark coordinates, analyzed by the mean of Procrustes superimposition approaches. Although new for the field of archaeozoology, particularly as applied to fragmented archaeological bone remains, such approaches have been shown to provide accurate results in many different fields (see for instance [54]).

2. Material and methods

2.1. Material and measurements

For the Paris Basin (Fig. 1), we used the large horse bone collections from the sites of Marolles-sur-Seine (Le Grand Canton; Tureau des Gardes; Table 1) and the smaller ones (almost one-hundred determined bones or less) of Verberie, Bonnières-sur-Seine and Le Closeau [7,8,15–20,50]. For the Switzerland Plateau, we revised the very large Magdalenian collections of the sites of Hauterive-Champréveyres (and Monruz, both dated to the very end of Dryas I and the early beginning of Bölling (Tables 1 and 2; [51,56]). In the same geographic area, Veyrier is composed of a small rockshelter discovered during the 1930s [46]. For the Northern Aquitain Basin, we investigated the site of Le Quéroy (Charente), which provided a chronological sequence dated from the Dryas I to the beginning of the Holocene, with numerous and well preserved horse bones (Table 1; [65,66]).

Except perhaps for Le Quéroy collection, all the assemblages can be considered as randomly sampled by both heavy taphonomic deflation [36] and dispersion, and by limited and scattered excavations of very large spreadings of horse carcass deposits. In addition, for all sites, bones have been drawn from different Magdalenian stratigraphic levels which can be considered as non-strictly contemporaneous at the scale of individual life of equids. Consequently, we considered that the probability of sampling both right and left metapodial (both either fore or rear limb) of the same individual was acceptably low, and we included in our study both right and left bones. Since the Procrustes superimposition process (see below) automatically reflects the objects, all the metacarpals or metatarals are transformed into left objects. Table 1 gives the sample sizes by areas and by anatomic segment: anterior and posterior metapodials extremities are almost evenly represented, except for the Paris Basin where metatarsals are slightly more numerous.

We selected 15 landmarks, using the distance measurements defined by Eisenmann [28], to which we added landmarks in order to cover the overall three-dimensional form of condyles. Three-dimensional coordinates were registered using a POLHEMUS 3Draw digitizer. The landmarks 1 and 2 (Fig. 2) correspond to
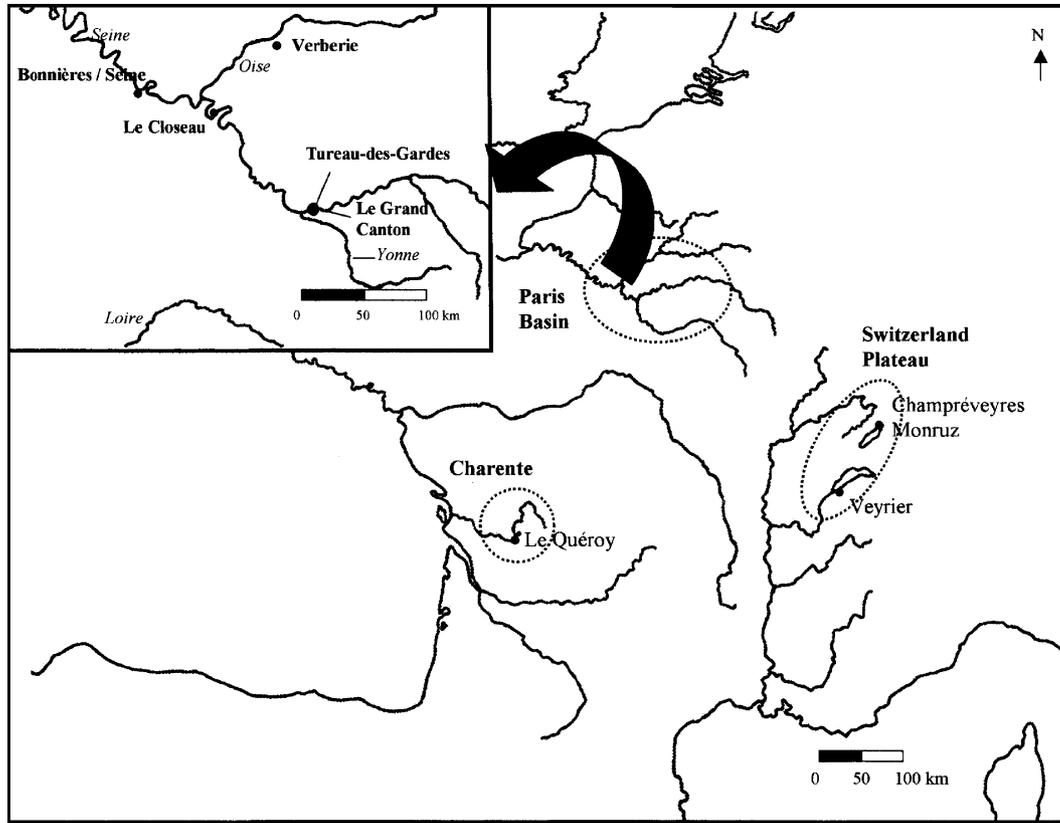
Fig. 1. Location of sites and regions.

the supra-articular tuberosities which are, respectively, on the medial and lateral borders. The landmarks 3–4–5–15–6–7–8–9–10–11, interlinked, describe the outline of the distal articular surface. The distance between the supra-articular tuberosities and the extremity of the distal condyle can be assessed by the links between 1–11 and 2–15 landmarks. The shape and the extension of the

sagittal crest are described by the 4–13–8 landmarks' link. The landmarks 11 to 15, which characterize the distal profile of the condyle, have been defined as follow: (1) landmarks 12 and 14 have been located at the cross-points between the root of the sagittal articular crest and the slight linear ripple (Fig. 3) which runs distally from lateral to medial edges of the articular surface; (2) beginning with these two landmarks, we subsequently determined the other ones so as to form a continuous line with all of them, 11 and 15 being located at the medial and lateral edges of the condyle, respectively, and 13 at the most distal point of the sagittal crest.

2.2. Morphometric and statistical analyses

Morphometric and statistical treatments followed three basic steps: (1) superimposition of the raw 3D coordinates to a common reference, (2) dimension reduction of the data, and (3) statistical analyses. These steps are detailed in the following paragraphs.

(1) Coordinates, contrarily to distances, are sensitive to translation and rotation of the reference system. Accordingly, raw coordinates were superimposed using a Procrustes Generalized Least-squares (GLS) superimposition algorithm [37,61]: the sum of

Table 1
Sample sizes at the region level

Areas	NISP	MNI	Metacarpals	Metatarsals
Charente [1]*			**10**	**13**
Le Quéroy	700	10	10	13
Switzerland Plateau [3]			**23**	**22**
Hauterive-Champréveyres	5000	21	2	1
Monruz	5000	**	18	18
Veyrier	1000	6	3	3
Paris Basin [6]			**22**	**35**
Le Closeau	500	6	0	1
Le Grand Canton	3700	117	3	9
Tureau-des-Gardes (5–6)	5000	**	7	7
Tureau-des-Gardes (10)	5000	61	12	15
Verberie	40	4	0	1
Bonnières/Seine	12	3	0	2
Sample size			**55**	**70**

*The number of sites per areas is indicated between brackets.
**In progress.

Table 2
Chronological datas per geographical areas

Areas	Sites	Lab code	Radiocarbon ages B.P.	Radiocarbon ages cal B.P.
Charente (France)	Le Quéroy (1)	Gif-5524	12 800 ± 140	15 870–14 352
		Gif-5325	12 590 ± 140	15 590–14 181
		Gif-5190	10 150 ± 180	12 390–11 201
Switzerland	Hauterive-Champréveyres (2)	UZ-2285	13 050 ± 155	16 267–14 520
		UZ-2283	12 950 ± 155	16 148–14 418
		UZ-2282	12 825 ± 155	16 000–14 331
		UZ-2286	12 780 ± 135	15 916–14 319
		UZ-2171	12 730 ± 135	15 856–14 281
		UZ-2175	12 630 ± 130	15 728–14 182
		UZ-2172	12 620 ± 145	15 737–14 163
		UZ-2177	12 600 ± 145	15 713–14 153
		UZ-2173	12 540 ± 140	15 633–14 134
		UZ-2174	12 510 ± 130	15 584–14 130
		UZ-2287	12 500 ± 145	15 592–14 119
Switzerland	Monruz (2)	ETH-6413	13 330 ± 110	16 541–15 066
		ETH-6421	13 140 ± 120	16 326–14 695
		ETH-6420	13 120 ± 120	16 302–14 669
		ETH-6418	13 110 ± 120	16 290–14 657
		ETH-6416	13 070 ± 130	16 256–14 594
		ETH-6417	13 030 ± 120	16 195–14 557
		ETH-6412	12 970 ± 110	16 111–14 501
		ETH-6415	12 900 ± 120	16 040–14 420
		ETH-6419	12 880 ± 120	16 016–14 404
Switzerland	Veyrier (3)	GrA-9703	12 560 ± 60	15 550–14 250
		Eth-3937	12 300 ± 130	15 450–14 050
		B–3787	12 310 ± 140	15 450–14 050
Parisian Basin	Le Closeau–L46 (4)			
		GrA-11664	12 350 ± 60	15 324–14 112
		GrA-11665	12 360 ± 60	15 488–14 115
Parisian Basin	Le Grand Canton (5)			
		Gif-9608	12 880 ± 80	15 590–14 840
		Gif-9606	12 195 ± 130	14 685–13 850
		Gif-9607	12 080 ± 115	14 490–13 745
		Gif-9609	11 420 ± 100	13 610–13 100
		OxA-3671	11 030 ± 105	13 056–12 834
		OxA-3139	12 650 ± 130	15 128–14 621
Parisian Basin	Tureau-des-Gardes–S.6 (6)	Ly 6988	12 290 ± 90	15 450–14 050
	Tureau-des-Gardes–S.10 (5)	AA44214	12 170 ± 130	14 660–13 830
Parisian Basin	Verberie (7)			
	Level II.1	Gif-A95453	12 430 ± 120	15 495–14 174
	Level II.2	Gif-A95454	12 950 ± 130	16 107–14 517
	Level II.3	Gif-A99106	12 520 ± 120	15 549–14 213
	Level II.3	Gif-A99421	12 300 ± 120	15 471–13 905
Parisian Basin	Bonnières/Seine		Magdalenian industry	

(1) J.-F. Tournepiche [66]; (2) D. Leesch [51]; (3) A. Bridault and C. Bémilli [19]; (4) P. Bodu [10]; (5) M. Julien and J.-L. Rieu [48]; (6) A. Bridault (personal communication); (7) B. Valentin et al. [68].

squared distances between homologous landmarks of each object and a reference configuration are iteratively minimized by translations and rigid rotations. At each iteration, the reference, which is taken as the mean configuration of the whole superimposed sample, is updated. Centroid size, defined as the square root of the sum of the squared distances between the center of the object and its landmarks [13], is eliminated from the superimposed coordinates by ratios. Geometrically, each object is therefore scaled to unit centroid size, centered and rotated in order to minimise its deviations from a reference object. At the end of the superimposition

process, the whole data set is represented by a size measure, a reference object called consensus which corresponds to the mean object over the whole sample, and a Procrustes residual matrix which contains the shape parameters of each object expressed as the differences in its coordinates relative to the consensus coordinates.

(2) In order to increase the power of discrimination methods and of statistical tests, the dimension of the shape space defined by the procrustes residuals was reduced. We followed the approach detailed in Baylac and Friess [6] and exemplified by instance in Dobigny et al. [25], Baylac et al. [5] and Friess
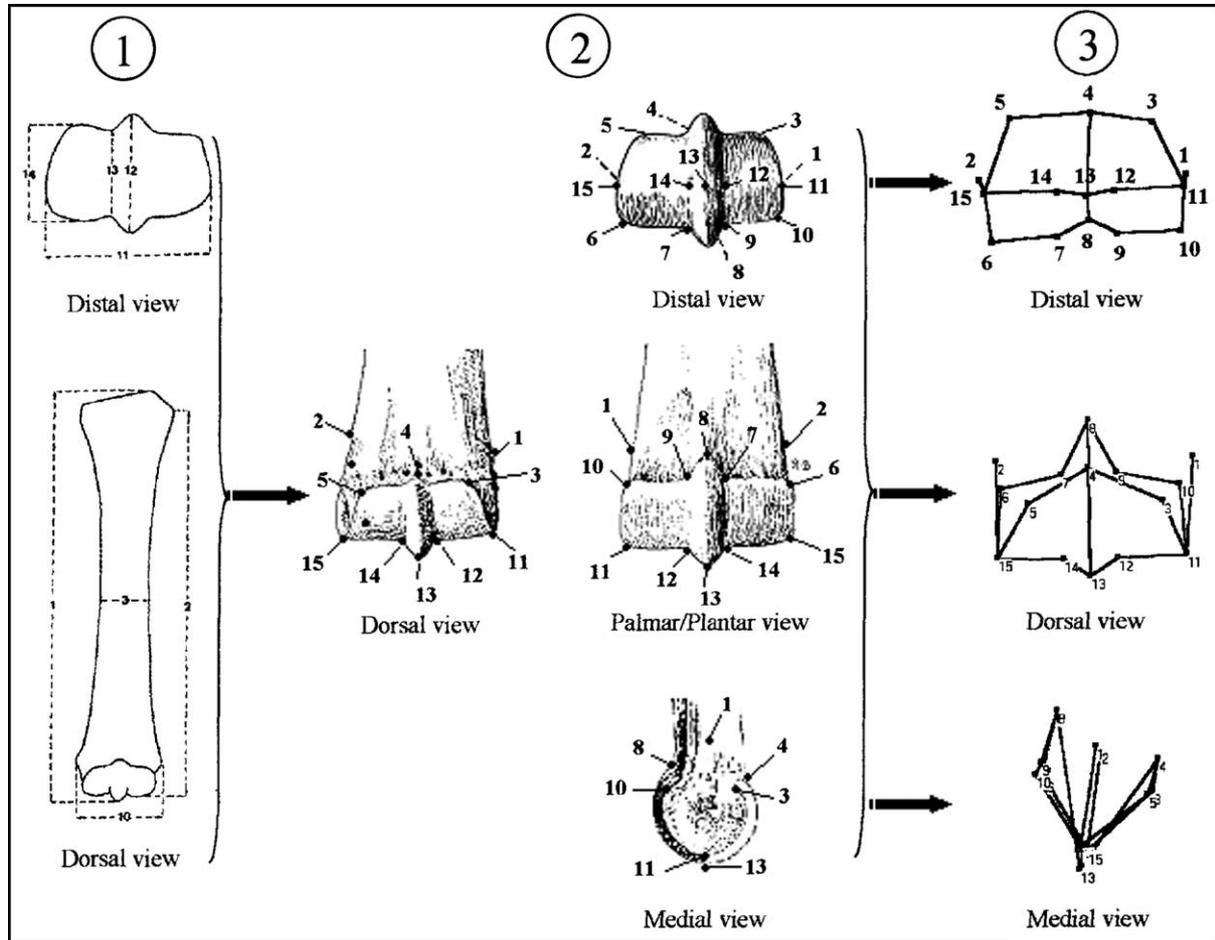
Fig. 2. Location of metapodials landmarks: (1) traditional measurements (dotted lines) of metapodials (V. Eisenmann [28]), (2) compared with location of landmarks (illustration R. Barone, 1986), (3) links between landmarks used to visualize the overall shapes.

and Baylac [35]. First, using a Principal Component Analysis (PCA), Procrustes residuals were transformed into a set of independent shape variates of decreasing magnitude [45]. The last components which did not carry a significant shape information were deleted. The number of deleted components was selected for each analysis in order to maximize

Fig. 3. View of the distal extremity of a metacarpal of an *Equus przewalskii* showing the slight linear ripple which runs distally from lateral to medial edges of the articular surface (cl. O.B.).

the correct cross-validated classification percentages [6].

(3) Principal Components – calculated at the preceding step – were plotted and analyzed to search for geographic patterns. We used concurrently Canonical Variate Analyses (CVA), discriminant functions and neural networks. PCA, which confounds the within- and between-group variabilities, was mostly used as an exploratory tool to evidence the patterns of heterogeneity of the total sample, and as a confirmatory tool to test for a possible bias of CVA due to the low sample sizes. Due to the lack of precise diachronic information (^{14}C calibration plateau during the Bölling period), we did not explore the within-locality variability. Although the knowledge of the patterns of variability at this level could bring interesting additional information, we believe that only large samples should be used for that purpose, perhaps reinforced by a concomitant analysis of the variability of recent specimens. Multiple discriminant analyses and neural networks were used to estimate the classification rates between regions and/or sites. Neural networks are now

becoming standard tools [25] due to their higher discriminative power than traditional linear approaches and due also to their fewer statistical assumptions [60]. All classification rates were estimated using cross-validated procedures which provide lower but unbiased estimates. Centroid size differences were tested by ANOVA. Since centroïd size is an isometric size parameter, superimposed shape coordinates are size-free but not allometry-free: they still include the possible allometries. No formal test for allometry could be done at the within-region or site levels due to the relatively low sample sizes. Instead, the importance of allometry in the analyses was estimated through plots of projections onto the different canonical and component axes versus centroid size.

We defined a set of links between landmarks in order to help to visualize the overall shape of condyles (Fig. 2). Two extreme shapes were then calculated and drawn, one for each axis extremity, thus depicting the shape variability along the corresponding direction. Deformations were amplified by a factor of 2 for better visualization. In all figures, extreme shapes (solid lines) were drawn against the mean shape or consensus (dotted lines) which plots always at the center of the factorial plane. The Procrustes superimposition and the deformations along principal axes were calculated using APS program (http://www.cpod.com/monoweb/aps/). Dimension reduction, statistical and pattern recognition analyses were done using the R statistical language [44,69–71] for Linux v. 1.81 (http://cran.r-project.org/) and specially devised MATLAB functions.

3. Results

3.1. Isometric size comparisons

At the regional level (Fig. 4A, C), only horses from Le Quéroy differ significantly both in the metacarpals ($F = 4.459$; $p = 0.016$: df $= 2/53$) and in the metatarsals ($F = 6.056$; $p = 0.004$; df $= 2/67$). They are larger than Paris Basin and Switzerland bones. At the site level (Fig. 4B, D), differences are significant in the metacarpals ($F = 3.849$; $p = 0.003$; df $= 6/49$; Le Quéroy, TDG and Verrier being larger than the others) but not in the metatarsals ($F = 1.588$; $p = 0.139$; df $= 9/60$).

3.2. Shape analyses

3.2.1. Principal component analyses

3.2.1.1. Metacarpals. The first plane of the PCA explains 45% of the total variance (Fig. 5). The

remaining axes, which do not show significant between-site differences, will not be discussed.

The first axis (28.6%) discriminates Le Grand Canton horses in the negative part, from the other sites taken together. Horses from Le Grand Canton and, to a smaller extent, those from Switzerland, display the following shape features (Table 3; Fig. 5, compare left to right small side illustrations):

(1.1) a more expanded articular extremity, especially in the medio-lateral direction and on the palmar face: on distal view, lateral landmarks, 5 and 6, and medial ones, 3 and 10, are all peripheral with reference to the consensus (dotted lines), mostly in the lateral and medial directions, distances with the respective consensus landmark being longer for 10 and 6 than for 3 and 5; by contrast, metacarpals from Le Quéroy and from the other sites of Paris Basin (positive values of F1) display, in distal view, a contraction with reference to both the consensus and Le Grand Canton bones;

(1.2) the distal medio-lateral linear ripple of the articular surface is approximately equidistant from the dorsal and palmar sides: on distal view, distances between 10–11 and 6–15 are approximately the same as distances between 11–3 and 15–5, respectively, whereas they are much shorter for the positive part of F1;

(1.3) a smaller proximal extension of the articular surface on both dorsal and palmar faces: on medial and dorsal views distances 5–15 and 6–15 on lateral side, and 10–11 and 3–11 on medial side are shorter than for both the consensus and bones of other localities;

(1.4) the palmar extension of the articular surface is larger than the dorsal one (dorsal view) for Le Grand Canton, whereas the other Paris Basin horses and Le Quéroy ones have a well balanced development of the articular surface on both sides;

(1.5) a more rounded shape for the condyle in medial view, both the landmarks 10 and 6 on palmar side and the landmarks 3 and 5 on the dorsal side being located distally with reference to the consensus; by contrast, in other sites, the medially viewed shape of the condyle appears more oval, as if proximo-distally stretched;

(1.6) supra-articular tuberosities (landmarks 1 and 2) are more proximal (medial and dorsal views); this entails both longer distances between these tuberosities and their respective distal extremities (high distances between 1–11 and 2–15 with reference to the consensus) and a more proximal location with reference to the level of the more proximal points of the sagittal crest (landmarks 4 and 8);

(1.7) supra-articular tuberosities are very slightly shifted towards the dorsal side (medial view).
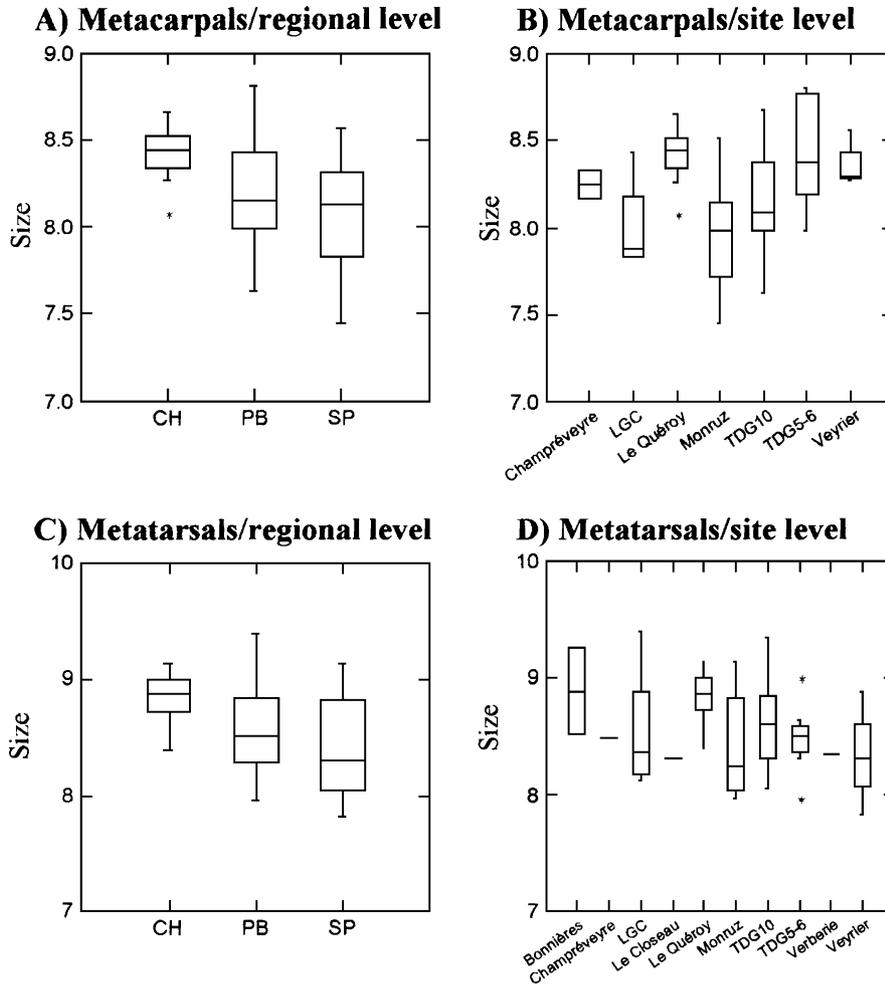
Fig. 4. Box plots of the centroid size differences for metacarpals and metatarsals at the regional and site levels. Abbreviations: CH = Le Quéroy (Charentes); PB = Paris Basin; LGC = Le Grand Canton; TDG = Tureau des Gardes; SP = Switzerland Plateau.

In short, the distal articular surfaces of metacarpals of Le Grand Canton horses tend to be transversally expanded, distally shortened and more rounded in medial view, whereas, in Le Quéroy (Charente) and, in a less clear-cut way, in the other sites of Paris Basin, they tend to be transversally contracted, well developed proximally on both dorsal and palmar sides and more oval in medial view. Sites of the Switzerland Plateau are intermediate.

The second axis (15.6%) only tends to segregate horses from Le Quéroy and Switzerland, in the negative half, from those of Paris Basin, including Le Grand Canton. The former are characterized by the following shapes (Fig. 5, compare lower to upper side illustrations):

(2.1) metacarpals from Le Grand Canton have a slightly wider articulation, especially on the palmar part (distal view); this feature reminds what was

observed on the first axis; here again, F2 opposes transversally elongated condyles (negative: Switzerland and Le Quéroy) to more rounded and contracted condyles (Paris Basin);

(2.2) the proximal edge of the articular surface on the palmar side has a "V"-like shape (dorsal view), whereas bones from Paris Basin show a "W"-like shape, with landmarks 7 and 9 located more distally relative to landmarks 6 and 10 (and to the consensus);

(2.3) the palmar extension of the articular surface is larger than the dorsal one (dorsal view), whereas Paris Basin horses have a well balanced development of the articular surface on both sides;

(2.4) a sagittal asymmetry of the crest and of the whole condyle (dorsal and distal views), the latter being distally oriented towards the lateral edge (mostly: landmark 4 shifting laterally and landmark 13 shifting medially);
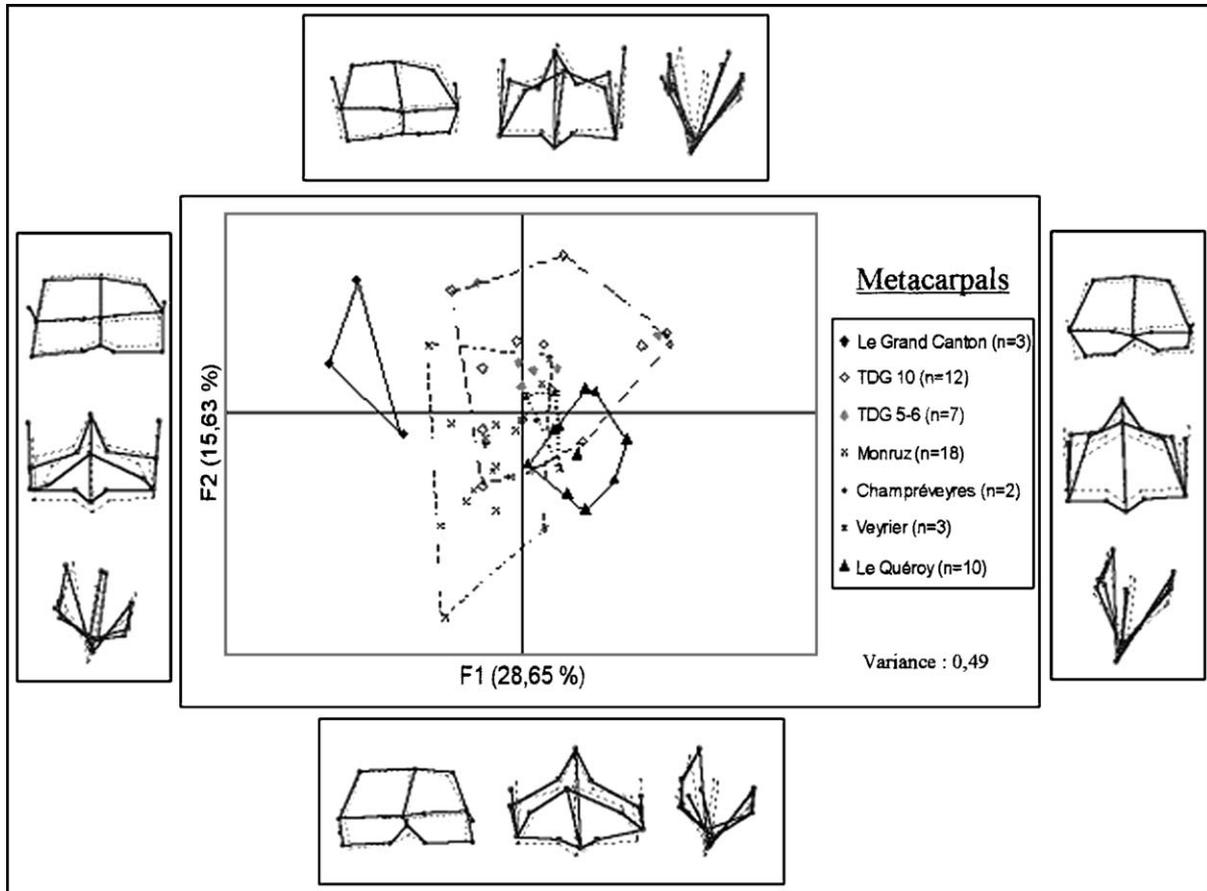
Fig. 5. Plots onto the first PCA plane for metacarpals. Symbols are for sites, while convex-hulls delineate regions. Extreme shapes are represented at both extremities of each PCA axis (left and right for the first axis, bottom and top for the second one). Extreme shapes are figured out by a solid line. Superimposed in dotted line, the consensus (or mean) shape.

(2.5) the supra-articular tuberosities are closer to the distal extremity with reference to both the consensus and the Paris Basin horses (dorsal and medial views), and to the most proximal points of the sagittal crest

(2.6) the supra-articular tuberosities are also shifted towards the palmar side (medial view).

In short, the second axis combines two new (2.2 and 2.4) features of shape variability to the four already observed onto F1. Both increase the importance of asymmetries, already suggested by (1.4) and (1.7), which are now of three kinds: dorsal and palmar extensions of the articular surfaces, medio-lateral orientation of the sagittal crest, and dorso-palmar shift of the supra-articular tuberosities. The Paris Basin horses differ from the other ones both by reverse asymmetries and by a "V"-shaped proximal edge.

Graphically (not illustrated), there was no relationship between the projections onto these principal components and size either at the between- or at the within-site levels. As a consequence, sites and regions

differ in both size and shape, but these differences apparently do not involve any allometric component.

3.2.1.2. Metatarsals. The first plane of the PCA explains about 41% of the total variance (Fig. 6). Here again, the remaining axes, which do not show significant between-site differences, will not be discussed.

The first axis (22.5%) depicts a variability which is shared by all the localities, and thus should be considered as the expression of an intrinsic variability of metatarsals of Late Glacial horses (Table 3; Fig. 6). For the negative part of the plane (left side illustration on Fig. 6, to be compared to the right one), it consists in:

(3.1) a general contraction of the articular extremity with reference to the consensus, all landmark points being internal with reference to the consensus on the distal view;

(3.2) a slight asymmetry of the condyle and of the sagittal crest, distally shifted towards the medial side (distal and dorsal views);

Table 3
Interpretations of PCA axes for metacarpals and metatarsals

	Metacarpal		Metatarsal	
Code	1	2	3	4
Multivariate factor	F1	F2	F1	F2
% Variance of the factor	28,6	15,6	22,5	18,4
Type of variability	Mainly inter-regional	Partly inter-regional	Mainly intra-regional	Partly inter-regional
Geogr. oppositions / Shape Features	LGC/others	others/PB	None	LGC-LCl-Sw/ rest of PB
icon	(1.1)	(2.1)		(4.1)
icon			(3.1)	
icon	(1.2)			
icon		(2.2)		(4.2)
icon	(1.3)			(4.3)
icon	(1.4)	(2.3)		
icon	(1.5)			(4.4)
icon		(2.4)	(3.2)	(4.5)
icon	(1.6)	(2.5)	(3.3)	(4.6)
icon	(1.7)	(2.6)	(3.4)	

Features of shape are summarized by icons in the first column, while numbers (code numbers plus feature numbers) between brackets refer to the text. Icons are drawn using the links of Fig. 2 (3).

(3.3) far more proximally located supra-articular tuberosities, which are thus both more distant from the respective distal extremities and more proximal than the most proximal point of the sagittal crest (dorsal and medial views);

(3.4) the supra-articular tuberosities are also very slightly shifted towards the dorsal side (medial view).

Though with large partial overlaps, the second axis (18.4%) separates more clearly the localities. This axis also emphasizes a large variability for the Paris Basin. Most of the horses from this region (i.e. Verberie, Bonnière-sur-Seine, Tureau des Gardes – sector 10 and some of Le Grand Canton) are gathered onto the positive side of F2, while most of the horses from Le Grand Canton and the single one from Le Closeau rather superimpose with horses from the Switzerland Plateau in the negative part of F2. Horses from Le Tureau des Gardes (sectors 5 and 6) are in an intermediate position, while those from Le Quéroy plot almost in the center of the plane.
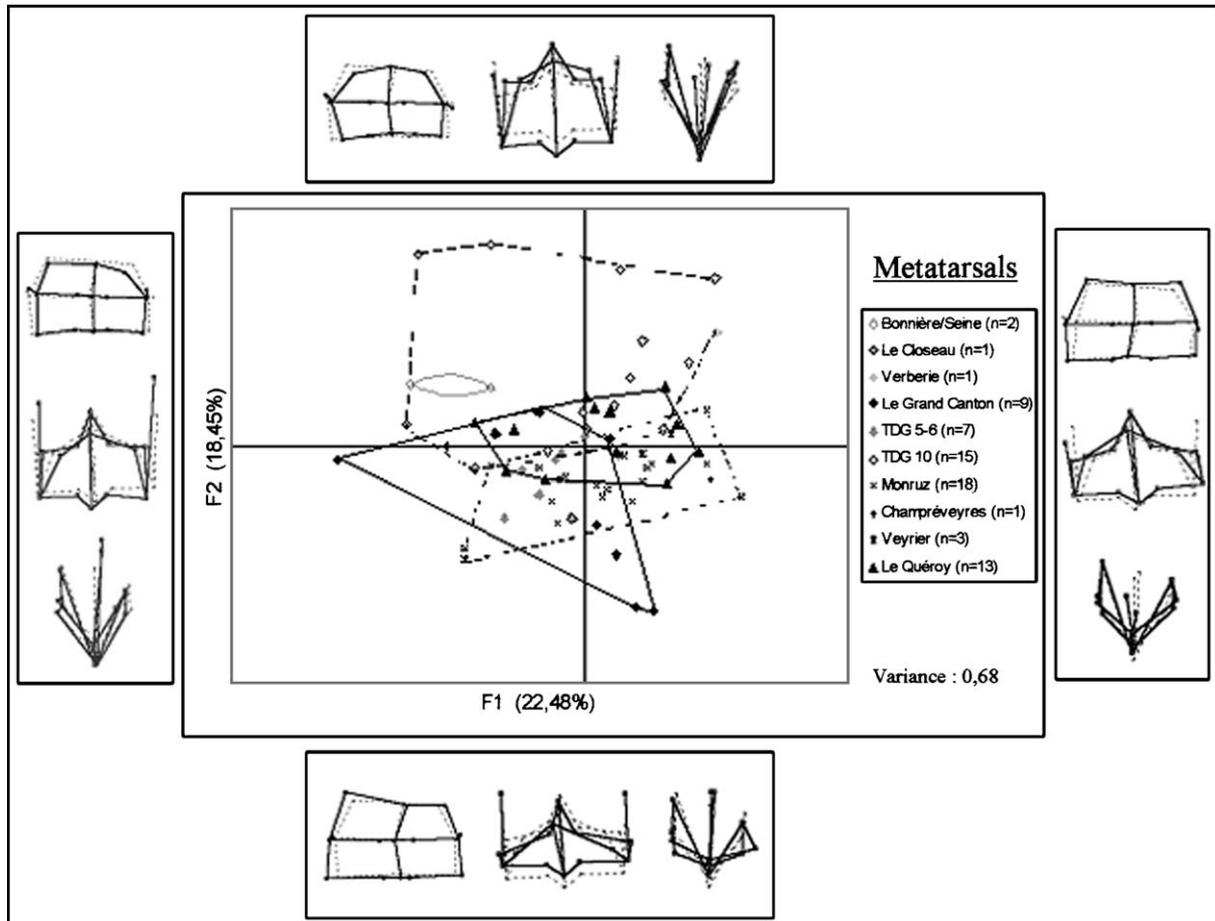
Fig. 6. Plots onto the first PCA plane for metatarsals. Otherwise see legend of Fig. 4.

Shape of the horse metatarsals of Switzerland and most of Le Grand Canton are characterized by (below in Fig. 6):

(4.1) a larger medio-lateral development of the articular condyle, mainly due to a lateral expansion (distal view);
(4.2) a ''V''-like shape (dorsal view) of the proximal edge of the articular surface on the palmar side (whereas bones from the other sites of the Paris Basin tend towards a ''W''-like shape, however, not so clearly expressed as for the metacarpals of the same sites; see Fig. 4, positive part of F2);
(4.3) a small expansion of the articular surface in the proximal directions on both dorsal and plantar sides (dorsal view);
(4.4) a more rounded shape for the condyle in medial view, with very distal positions for landmarks 10, 6, 3 and 5, whereas condyles of the other Paris Basin horses appear more proximo-distally stretched, as it was for the metacarpals (see Fig. 4);
(4.5) a slight sagittal asymmetry of the condyle (dorsal and distal views), the latter being distally oriented towards the lateral edge;
(4.6) slightly more proximal supra-articular tuberosities with reference to the level of both the consensus and the palmar termination of the sagittal crest (dorsal and medial views).

In short, on this second axis, horses from Le Grand Canton/Le Closeau and from Switzerland (and, to a smaller extent, from Tureau des Gardes 5–6 and Le Quéroy) are opposed to the rest of the horses from the Paris Basin by features similar to the ones observed for metacarpals on both F1 and F2 axis, i.e. a distal articular surface more transversally expanded, more distally shortened and more rounded in medial view, together with a slight sagittal asymmetry and a ''V''-shape for the proximal edge of the palmar articular surface.

Here again, there is no significant relationship between shape differences and size at the between- or at the within-site levels. The same conclusion may be proposed as for the metacarpals, i.e. that sites and regions differ in both size and shape, but that these differences do not seem to involve any allometric component.

3.2.2. Canonical variate and discriminant analyses; neural networks

For metacarpals and metatarsals, discriminant and canonical analyses were conducted, respectively, on the first six and on the first nine principal components. These component numbers are those which maximize the correct classification percentages obtained by cross-validation (Tables 4, 5 and 6). For neural networks,

Table 4
Cross-validated classification percentages obtained by linear discriminant analyses of metacarpal shapes

	Paris Basin (France)	Le Quéroy (Charente, France)	Switzerland Plateau	Sample size
Paris Basin	**91,30**	0,00	8,70	23
Le Quéroy	0,00	**80**	20	10
Switzerland Plateau	13,04	4,35	**82,61**	23

Lines = original memberships, columns = predicted memberships.

calculations were done with increasing numbers of components and the better and more parsimonious model (i.e. which maximized the classification rates with the smallest number of components) was selected. All analyses were done at the region level, Switzerland, Le Quéroy and the Paris Basin.

Previous PCA analyses on both metacarpals and metatarsals showed the great heterogeneity of the Paris Basin sample with the exception of most of the horses from Le Grand Canton, which always plot apart. Accordingly, the Paris Basin metatarsal sample has been divided into two sub-samples: Le Grand Canton and other localities. As there were only three metacarpals from Le Grand Canton, they were discarded (their distinctiveness and shape particularities were already well delineated on the first PCA axis; Fig. 5). In all cases, inclusion of size together with shape did not increase the quality of the discriminations, but even decreased them slightly. Therefore, the present results will deal only with shape. Features of shape have been already described for the PCA analyses, and will be used, where they apply, in the interpretations of the shape variability onto CVA axes. Both variabilities may in fact not be equivalent: CVA analyses describe the between-group variability after a preliminary normalization of the within-group one, while PCA analyses deal with the total (within and between) group variability.

3.2.2.1. Metacarpals. The MANOVA of shape was highly significant: Wilks = 0.2068, $F = 9.593$, df = 12/96, $p = 5.63 \times 10^{-12}$. The total percentage of cross-validated correct classification given by multiple discriminant analyses (84.6%) was high considering that we are dealing with archaeological samples of few specimens each. Table 4 summarizes the results for each region. Neural networks gave a roughly similar overall classification rate equal to 87.5%. These results show that regions may be considered to differ substantially. The two canonical axes explain 86.0% and 14.0% of variance, respectively.

Canonical variate plots (Fig. 7) showed that horses from Switzerland and Le Quéroy were almost completely separated by the first canonical axis from the Paris Basin ones. The former two areas were partly separated by
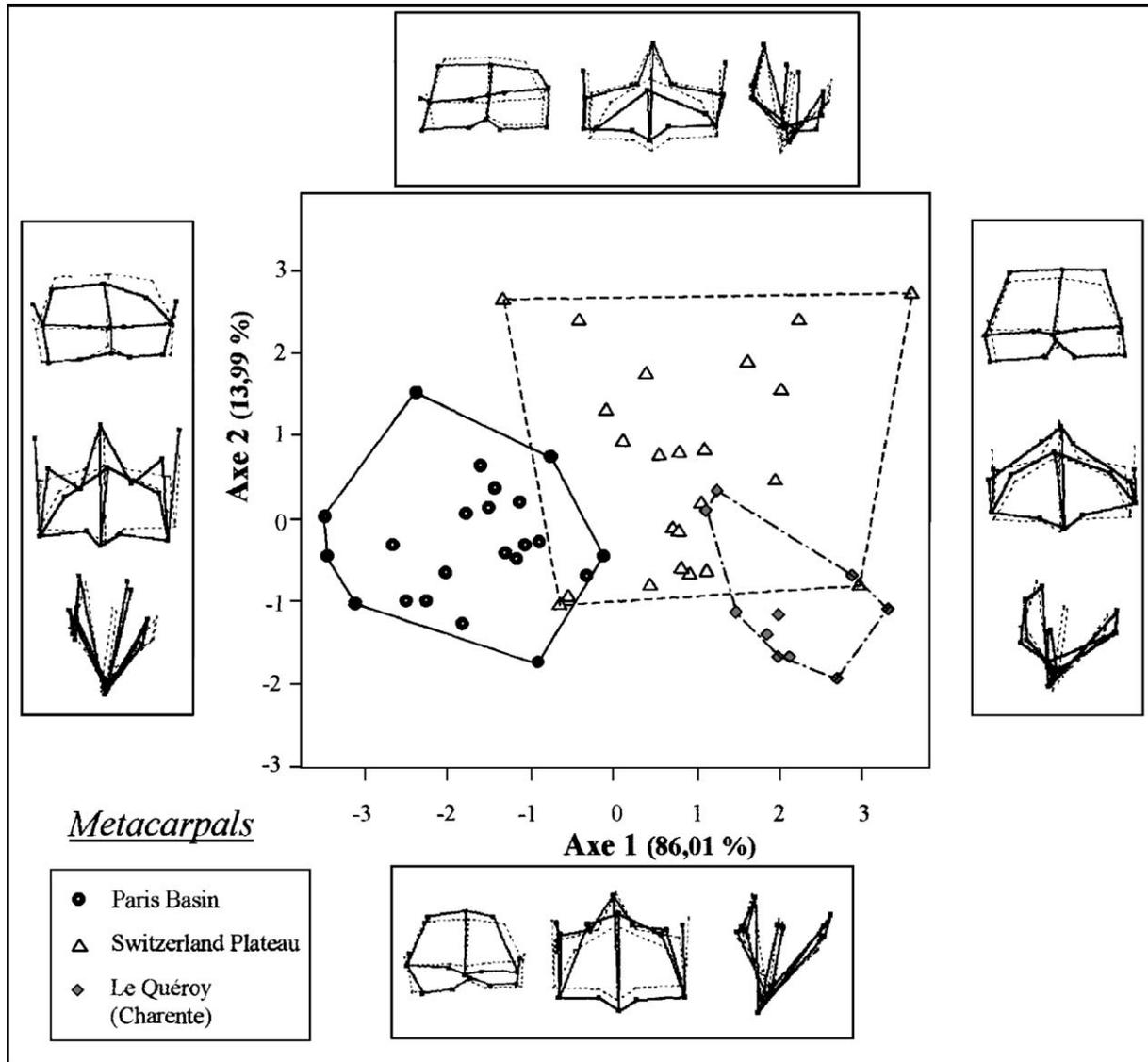
Fig. 7. Plots onto the first plane of a canonical variate analysis of metacarpals at the region level. Otherwise see legends of Fig. 4.

a combination of axes 1 and 2. Condyles from Paris Basin were characterized by (Table 5; Fig. 7, compare left to right small illustrations):

(5.1) a general contraction of the articular extremity, especially for its dorsal half (distal view), all landmarks being internally shifted;

(5.2) the "W"-like shape of the proximal edge of the articular surface on the palmar side (dorsal views), which sharply contrasts with the "V"-like shape for horses of Switzerland and Le Quéroy;

(5.3) an oval, proximo-distally stretched general shape for the distal condyle when observed in a medial view;

(5.4) a sagittal asymmetry of the crest and of the whole condyle (distal and dorsal views), which tends to be distally oriented towards the medial side, while it is distally oriented towards the lateral side for horses of Switzerland and Le Quéroy;

(5.5) a "pull in" shape for the distal profile of the condyle in dorsal view, the lateral and medial extremities of which (landmarks 11 and 15) are at a more distal level than the central parts of the articulation (landmarks 12 and 14), except the sagittal crest; for horses of Switzerland and Le Quéroy, the distal profile is more globally "convex", with 12–14 at a more distal level than 11–15;

(5.6) more proximal supra-articular tuberosities with reference to both the consensus and the most proximal points of the sagittal crest;

(5.7) dorsally shifted supra-articular tuberosities (medial view).

Table 5
Interpretations of CVA axes for metacarpals and metatarsals

	Metacarpal		Metatarsal	
Code	5	6	7	8
Multivariate factor	F1	F2	F1	F2
% Variance of the factor	86,1	14,0	59,8	27,9
% Correct classification	84,6		74,9	
Neuronal network rate	87,5		75,7	
Geogr. oppositions / Shape Features	BP/others	Sw/Quéroy	BP/others	LGC/BP Sw/Quéroy
⬡		(6.1)		(6.1)
⬡	(5.1)		(5.1)	
⬡		(6.2)		
⬡		(6.3)	(6.3)	
⬡	(5.2)		(5.2)	
⬡		(6.4)		(6.4)
⬡		(6.5)		
⬡	(5.3)	(6.6)	(5.3)	(6.6)
⬡	(5.4)			
⬡	(5.5)			(5.5)
⬡	(5.6)		(5.6)	
⬡	(5.7)		(5.7)	

Features of shape are summarized by icons in the first column, while numbers (code numbers plus feature numbers) between brackets refer to the text. Icons are drawn using the links of Fig. 2 (3).

Patterns of shape onto the second axis of Le Quéroy and, to a lesser extent, of the Paris Basin may be described as follows (Fig. 7, compare lower with upper small illustrations):

(6.1) a narrow transversal development of the palmar part of the articular surface (distal view);

(6.2) a thicker dorso-palmar development of the dorsal part of the articular surface (distal view);

(6.3) a slight palmar shift of the slight medio-lateral linear ripple in its medial half (distal view);

(6.4) a larger distal stretching of the articular surface (dorsal view);

(6.5) a well balanced development of dorsal and palmar parts of it, whereas the dorsal part is shorter than the palmar one for most of the Switzerland horses;

(6.6) a more proximo-distally elongated condyle (medial view) with reference to the more rounded one of the Switzerland horses.

In summary, Le Quéroy and to a lesser extent Paris Basin horses are characterized by a more massive and rounded shape of the distal condyles in distal view and proximo-distal elongation of the articular surface, especially on the dorsal side. Horses from the Switzerland display the reverse morphological patterns.

3.2.2.2. Metatarsals. The MANOVA results are highly significant: Wilks = 0.1149, F = 9.912, df = 27/170.03,

$p = 3.09 \times 10^{-16}$. The total percentage of cross-validated correct classification obtained by discriminant analyses (74.9%) or by neural networks (75.7%) was lower than those observed for the metacarpals. Percentages for each region (Table 6) are also lower with the single exception of Switzerland. The first three canonical axes of the CVA explain 59.8%, 27.9% and 13.1% of variance, respectively. The F1 × F2 plane, which will be the only one to be discussed, explains 86.9% of the variance.

Canonical variate plots (Fig. 8; Table 6) show that the first axis operates an almost perfect distinction between all the Paris Basin horses, including the Le Grand Canton/Le Closeau sites, from the ones of Le Quéroy and Switzerland. The former are characterized by the same features as for the metacarpals (5.1, 5.2, 5.5, 5.6 and 5.7). Though less pronounced, (5.3) is also common to both metacarpals and metatarsals of the Paris Basin. Pattern (6.3) of the second axis of the metacarpal analysis appears here with a symmetric expression, the slight medio-lateral linear ripple being shifted in its lateral (and not medial) half.

The second axis shows tendencies in shapes which globally distinguish on one hand, the horses of Le Grand Canton/Le Closeau from the other Paris Basin ones, and on the other the Switzerland from Le Quéroy ones. Nevertheless, these discriminations are incomplete, a result which is in accordance with the low classification rates already noticed. It must be stressed that individuals of Switzerland which plot inside the outline of Le Quéroy are coming from the three different sites (Veyrier, Monruz and Champréveyre). The morphological patterns which partly discriminate the populations on this second axis are the same as for the metacarpals in (6.1) (though more pronounced), (6.4) and (6.6). Although (6.2), (6.3) and (6.5) are not clearly detected for the metatarsal, the former features are sufficient to describe the same general tendencies for the Le Quéroy and Paris Basin metatarsals as those already observed with metacarpals, i.e. a less massive and rounded shape of the distal condyles in distal view,

Table 6
Cross-validated classification percentages obtained by linear discriminant analyses of metatarsal shapes

	Paris Basin (France)	Le Grand Canton (B.P., France)	Le Quéroy (Charentes, France)	Switzerland Plateau	Sample size
Paris Basin	**69,23**	11,54	3,85	15,38	26
Le Grand Canton	0,00	**69,23**	0,00	30,77	13
Le Quéroy	0,00	0,00	**55,56**	44,44	9
Switzerland Plateau	0,00	4,55	9,09	**86,36**	22

Lines = original memberships, columns = predicted memberships. Le Grand Canton has been separated out from the Parisian Basin for heterogeneity reasons (see text).
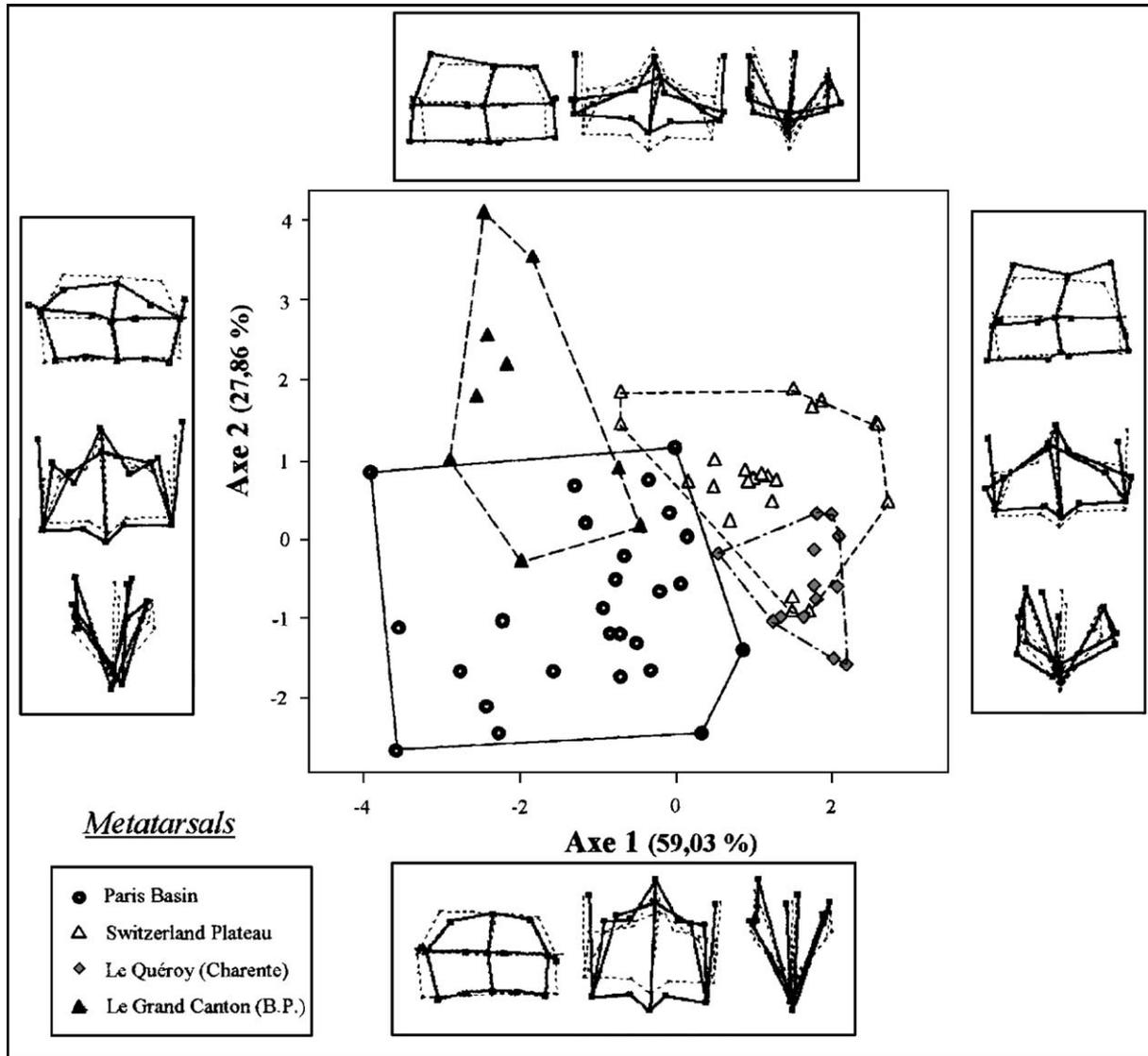
Fig. 8. Plots onto the first plane of a canonical variate analysis of metatarsals at the region level. Le Grand Canton specimens have been treated separately from the Paris Basin for reasons of shape heterogeneity (see text). Otherwise see legends of Fig. 4.

and a more important proximo-distal elongation of the articular surface. Switzerland and the Le Grand Canton/Le Closeau horses display the reverse patterns.

4. Discussion and conclusive remarks

4.1. Significance and evaluation of the morphological patterns evidenced by the morphometric analyses

Most patterns of shape are shared in common by PCA and CVA axes, a result which indicates that in the former, the between-group variability is dominating over the within one. As a consequence, CVA results, although coming from samples of restricted sizes, appear well grounded and fully interpretable. Remaining minor

discrepancies, such as patterns of asymmetry, will not be further analyzed.

In summary, at the regional level, size differences are low even for the Le Quéroy horses which have significantly larger metacarpal and metatarsal condyles. The relationships between time and centroid size cannot be assessed due to the lack of accuracy of radiocarbon calibrations for this period.

Canonical analyses of shape reveal very similar patterns of variability in metacarpals and metatarsals. Shape variations are particularly rich and diverse, since at least six main patterns of variability (Table 7) can be recognized (i.e. A–A′, C, D–E, F, G, I–J) describing three main morphological patterns: (1) A–A′, D and F are expressions of the general shape of the articular massif, either expanded/contracted (A–A′), or rounded/ elongated (D, F); (2) G expresses a medio-lateral

asymmetry (because of their association with, respectively, D and I, E and J may not be considered as true asymmetries); (3) The association of D and E expresses the seesaw motion of the articular surface from the anterior to the posterior part. In addition, the analyses pointed some local particularities, such as the variation in the shape of the edge of the articular surface (C).

4.2. Functional versus genetical implications

The distal ends of the metapodials are part of the extremely sophisticated fetlock joint where the springing action greatly depends on the elasticity of the suspensory ligament [43,64]. At that level, the two branches of the suspensory ligament run on the external sides of the sesamoids, while the intersesamoid ligament is located directly opposite to the metapodial sagittal crest. One may expect that shape modifications of the whole system (including the metapodial articular surface studied here) have some sort of functional reasons or implications. It is unknown, however, if static or dynamic mechanical constraints may actually act on the osteological detailed morphology and, if so, how, and to what extent. On the other hand, it is known that the main functions of the front and hind legs are not the same, since they involve, respectively, traction and propulsion. Yet in our study, the distal parts of both metacarpals and metatarsals show very similar associations of pattern variations for the two first axes of the shape analyses and, in addition, lead to very similar regional discriminations. It seems thus likely that the observed interpopulational variability results more from genetic control than from functional adaptations or mechanical constraints.

4.3. Diversity of the Late Glacial horses of Western Europe and archaeological implications

Almost all equid metapodials are clearly separated by the canonical analyses, between a septentrial group (Paris Basin) and a southern group (Switzerland Plateau and Charente by Le Quéroy site). The latter group also shows important differences in shape, although unrelated to the preceding ones. Even if the observed differences are less genetically determined than we believe (and more under the influence of mechanical constraints), they clearly evidence a regional populational fragmentation pattern for the studied Late Glacial horses of Western Europe. The fragmentation of the Magdalenian *E. caballus arcelini* into regional populations would not be surprising, since present day large ungulates in the tundra display the same pattern [22]. Today, this appears to be dependent on the existence of high demographic density [59] and of course, from the absence of large scale migrations. Our observations link up with other studies obtained for reindeer populations during the Late Glacial in Southern France, the Paris Basin, Northern Switzerland, Belgium and Germany [34,72]. Late Glacial mammoth species of Eurasia (namely, *Mammuthus trogontherii* and *Mammuthus primigenius*) also exhibit a similar complex mosaïc pattern [53]. All these observations are consistent with a 'plaid' structuration of mosaic landscapes of the so-called "Mammoth-Steppe" biome that occurred during the Late Glacial in Eurasia [40–42,49]. Our results on wild horses seem also to confirm the predictions of Guthrie about the existence of complex and diversified communities until the Bölling/Alleröd interstadial (between 13 000–12 000 years B.P.).

However, because they exhibit more variable morphological features, the horses of the Paris Basin seem to have a lesser homogeneity at the regional scale than those of southern areas. Indeed, some of the horses of Grand Canton and Le Closeau seem to differ from all the others of this region, and may have belonged to a distinct "population", even if this hypothesis is only supported by very restricted data samples. Because of the lack of resolution due to the ^{14}C calibration plateau during the Bölling and the early Alleröd periods, we do not know whether the various bone samples represent

Table 7
Summary of the between-sites and -regions patterns of shape highlighted by CVA analyses

Metacarpals and Metatarsals. Icons are drawn using the links of Fig. 2 (3).

contemporaneous populations or even whether each sample is composed of contemporaneous individuals. The larger diversity in shape may result from a stronger population instability through time related to immigrations of animals originating from different surrounding areas [9]. Two main factors could be involved. First, the warming trend at the end of the Late Glacial increased the sea level in the North (Baltic) and West (Channel), reducing terrestrial territories and pushing back horse populations from the Channel area to the southern and central part of France. Secondly, the sedges and graminoïds, which represented the main source of food for horses, should have been more sensitive to climatic fluctuations in northern areas than equids themselves [26,39]: during this instable period, the available amount of food could have played an important role in the distribution of high density horse populations.

4.4. Geometric morphometrics and archeology

Our study would not have been possible without the considerable background obtained using traditional morphometric approaches (see references in Sections 1 and 2): the choice of both the anatomic part to be investigated, and the landmarks themselves was crucial and relied upon the abundant previous osteological investigations on equids. But geometric morphometrics clearly surpasses the more traditional approaches since it allows for a better description and understanding of the variability patterns. It becomes thus easier to distinguish actual homologies from superficial resemblances. Still more to the point, our results show without ambiguity that 3D geometric morphometrics are fully usable even in such a demanding field as Archaeozoology. They highlight the potential interest of such approaches at the population level by simultaneously revealing an unexpectedly large variability for both metacarpals and metatarsals and by visualizing their main trends. Clearly, this points out that geometric morphometrics should not be considered only as a last-end approach, used after more traditional ones. Its ability to handle complex patterns of shape demonstrates on the contrary, that it should be used directly as an exhaustive comprehensive tool able to highlight morphological regions of potential interest. Bookstein [13] already pointed out its interest at the preliminary and exploratory steps of a study.

Another potential improvement over traditional morphometrics is the clear size and shape decomposition framework, although a similar framework was proposed first in the context of multivariate morphometrics through Mosimann's log-shape-ratios [12,57], which use also an isometric size definition [21,32,55].

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