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Reconstructing the functional traits of the horses from the tomb of King Childeric

Pauline Hanot[a,*], Sylvain Gerber[b], Claude Guintard[c,d], Anthony Herrel[e], Laurent Verslype[f], Raphaël Cornette[b]

[a] *Department of Archaeology, Max Planck Institute for the Science of Human History, Kahlaische Straße 10, D-07745, Jena, Germany*
[b] *UMR 7205 « Institut de Systématique, Évolution, Biodiversité » (CNRS, MNHN, UPMC EPHE), Muséum National d'Histoire Naturelle, Sorbonne Universités 45 rue Buffon, 75005, Paris, France*
[c] *Unité d'Anatomie Comparée, Ecole Nationale Vétérinaire de l'Agroalimentaire et de l'Alimentation, Nantes Atlantique - ONIRIS, Route de Gachet, CS 40706, 44307, Nantes cedex 03, France*
[d] *Groupe d'Études Remodelage osseux et bioMatériaux (GEROM), Université d'Angers Unité INSERM 922 LHEA/IRIS-IBS, 4 rue Larrey CHU d'Angers, Angers, France*
[e] *UMR 7179 « Mécanismes Adaptatifs et Évolution » (CNRS, MNHN), Muséum National d'Histoire Naturelle, Sorbonne Universités 57 rue Cuvier CP 55, 75005, Paris, France*
[f] *Faculté de Philosophie, Arts et Lettres (FIAL)/Centre de Recherches d'archéologie Nationale (CRAN), Institut des Civilisations, Arts et Lettres (INCAL), Université Catholique de Louvain, Place Blaise Pascal 1, B-1348, Louvain-la-Neuve, Belgium*

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ABSTRACT

The Merovingian period sees the emergence of the saddle horse as a critical component of the military forces. This increased importance is generally thought to be associated with a particular attention paid to horse breeding, which contributed to preserve the large size they acquired during Roman period. In spite of the Early Middle Ages being considered as a turning point in the history of their usage in Western Europe, its impact on the morphological traits of the horses remain largely unexplored. Privilege of the warrior elite, the horse is also a marker of social rank when associated to human burials. The royal tomb of Childeric the 1st (Tournai, Belgium), considered as the most lavish of the western Germanic world, revealed the presence of twenty-one skeletons of equids, deposited in peripheral pits. Here we use 3D geometric morphometrics to characterize the morphological traits and possible function of these equids using shape variation and covariation analyses of the limb bones. We found close phenotypic proximities with modern racehorse specimens. However, differences in magnitude of morphological integration between them suggest specificities in the functional features of the archaeological horses and probably reflect variation in the degree of artificial selection. Our results demonstrate the importance of accurately exploring the complete shape of bones to describe the morphological characteristics of past animals. Our results also illustrate the interest of not only investigating shape variation, but also covariation patterns, in order to address functional questions and in trying to detect possible markers of artificial selection on past horses.

1. Introduction

Horses and humans share a long history of interaction from the initial domestication to the standardization of modern breeds. Indeed, the horse has played a key socio-economic role in numerous past societies and has been molded through artificial selection in order to suit human activities (Clutton-Brock, 1992; Kelekna, 2009). This artificial breeding is known to have largely impacted its morphological traits (Seetah et al., 2016), producing the large range of extant breeds (Denis, 2012; Lizet, 1989; Mulliez, 1983). Historical and iconographic sources are most commonly exploited to assess the ranges of use and associated morphologies of past horses, and to better document breeding and selection techniques (Bautier and Bautier, 1980; Hyland, 1990; Lorans, 2018; Toynbee, 1973; White, 1970). However, bones, besides being generally the only lasting remains from these past horses, can be regarded as the most objective and direct testimony of their morphology. Furthermore, the skeleton, which constitutes the rigid structure of all vertebrates, also plays an important functional role (Polly, 2008) by supporting the body

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* Corresponding author.
E-mail addresses: hanot@shh.mpg.de, pauline.hanot@mnhn.fr (P. Hanot).

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mass, contributing to movements through articulations or muscle attachments (Biewener, 2003, 1990) and by remodeling according to external and muscular constraints (Currey, 2003; Lanyon et al., 1979; West-Eberhard, 1989). Knowing that selective breeding in horses was partly performed on criteria of conformation and harmony, but also largely on performance and usage criteria (Kelekna, 2009), developing approaches using bone shape to address functional questions is of great interest.

Usually, size and robusticity estimations are computed using linear measurements of the bone length and width (Audoin-Rouzeau, 1994; Brauner, 1916; Kiesewalter, 1888; May, 1985), and exploited to describe the shape variation in horses over time, or from site to site. However, these approaches are often considered as insufficient for describing the morphological and functional diversity of populations (Forest, 1998), especially knowing that function generally impacts the whole morphology of bones (e.g. articular surfaces, muscle attachments, diaphyseal curvature; Botton-Divet et al., 2016; Lanyon, 1980; Milne, 2016). In this respect, approaches able to quantify the complete bone shape without excessive redundancy (Zelditch et al., 2012), such as geometric morphometrics (Bignon et al., 2005; Seetah et al., 2014), appear as a useful tool for contributing to understand the relationships between form and function (Cooke and Terhune, 2015). Specifically, the study of the correlation between morphometric variables is often used in evolutionary biology to investigate function: indeed, the functional interactions between anatomical elements (e.g. bones involved in a common functional task) contribute to produce shape covariation between them (Olson and Miller, 1958; Wagner and Altenberg, 1996; Young and Hallgrímsson, 2005). The patterns of morphological integration within a skeleton can thus be considered as partly reflecting the functional constraints associated with the usage and life-style of the animal (Botton-Divet et al., 2018; Hanot et al., 2017b, 2018; Martín-Serra et al., 2015). Although rarely explored on the microevolutionary scale, shape covariations are prone to be also impacted by artificial selection, as already demonstrated in extant domestic equids. Indeed, selective breeding, especially for function, has been shown to influence bone shape integration in terms of patterns and magnitude (Hanot et al., 2017b, 2018).

Through its chronological dimension, archaeological material constitutes an ideal support to observe rapid morphological changes and micro evolutionary processes over time and may, thus, allow to enrich our knowledge about past usages and breeding. In this study, we focus on a period which constituted a turning point in the history of the use of horses by humans in Western Europe, the Merovingian age (5th–8th century A.D.). By 476 A.D., the end of the Western Roman Empire entailed a political restructuration of the territory with the establishment of successive regional states ruled by barbarian kings. Among them, the Frankish kingdom, ruled over by the Merovingian dynasty, emerged as the most stable and influential entity, extending progressively their control to most of Western Europe (Wood, 2014). Exploiting the widely recognized Frankish equestrian prowess, cavalry emerged as a major component of the armies during the Merovingian period (Bachrach, 1972; Halsall, 2003; Lebedynsky, 2001). More generally, the role played by the horse became preponderant in riding, pulling vehicles or as a pack animal (Bachrach, 1972; Cross, 2011). The great importance of this animal in human activities is generally used to explain the conservation of the large size horses acquired during Roman period (140 cm in average in Europe against a mean of 120–130 cm during the Iron Age; Arbogast et al., 2002; Audoin-Rouzeau, 1994). This phenomenon, which contrasts with what happened for other taxa of domestic livestock (Clavel and Yvinec, 2010), is generally explained by the persistence of breeding techniques used during the Roman era (Arbogast et al., 2002), but also by potential crossbreeding with large horses from Eastern Europe (Audoin-Rouzeau, 1994). In any case, this would suggest that a particular attention was paid to horse breeding and selection during the Merovingian period. The role of the horse appears to be also symbolic at that time, judging from the presence of horse remains in several tombs from the middle of the 5th to the 6th century in Germania, and to a lesser extent on the left bank of the Rhine (Billoin et al., 2008; Gabriel et al., 1991; Guillaume et al., 2004; Müller-Wille, 1970; Oexle, 1984; Putelat et al., 2017; Truc, 2008). Horses were probably sacrificed and deposited as psychopomps in charge of guiding the souls of the deaths to the beyond ("Valhalla" in the Nordic and Germanic mythologies; Rech, 2007; Salin, 1957; Steuer, 2003; Werner, 1988). These deposits seem to be the privilege of the elite showing that, besides the likely religious role of their presence in tombs, they were probably also an ostentatious way to manifest the high social status of the owner of the burial (Dierkens et al., 2008; Wagner, 2005). The archaeological material associated to the deceased systematically stresses his warrior nature, including weapons and pieces of equipment for saddle horses (Baillif-Ducros and Yvinec, 2015; Dierkens et al., 2008; Müller-Wille, 1970; Oexle, 1984). This, coupled with the fact that these horses were described as mainly middle-aged males or gelded (Oexle, 1984), made some authors considered them as formerly used for riding, particularly for warfare (Ghenne-Dubois, 1991; Wagner, 2005).

In this study, we focus on the Merovingian tomb considered as the most lavish of the western Germanic world: the tomb of Childeric the 1st (Brulet et al., 1991; Kazanski and Périn, 1988; Périn and Kazanski, 2007; Quast, 2015). King of the Salian Franks and governor of the province of Belgica Secunda (northwestern Gaul), Childeric is considered as the first Merovingian king (Ewig, 2006; Zöllner and Schmidt, 1970). He died in 482 and his son, Clovis, succeeded him. His grave was discovered in 1653 in Tournai (now Belgium; Fig. 1), near the church of Saint-Brice, and further excavations revealed the presence of twenty-one equids in three pits located around the king's burial (Brulet et al., 1991). Their proximity to the grave, their stratigraphic position, and the associated radiocarbon dates (460–520 AD) suggest that these skeletons were related to the royal tomb (Gilot, 1991) and would result from a collective sacrifice (Brulet, 1997). Considering that these horses could have belonged to the royal herd (Brulet, 1997) or having been specially selected for the ritual sacrifice (Fern, 2005), they might be a suitable example to detect potential marks of artificial selection.

In the present study, we use 3D geometric morphometrics (GM) to characterize the morphological and functional traits of the horses found at Childeric's burial. We first confirm their specific identification: indeed, although rare, donkey and hybrid remains were registered in contemporaneous sites from the North of Gaul (Yvinec and Lepetz, 2002). Next, we characterize the morphology of these animals including their morphological variation in comparison to modern specimens of various breeds and explore the patterns of shape covariation between bones. This approach could allow us to address questions about the function and use of the horses found in the tomb of Childeric.

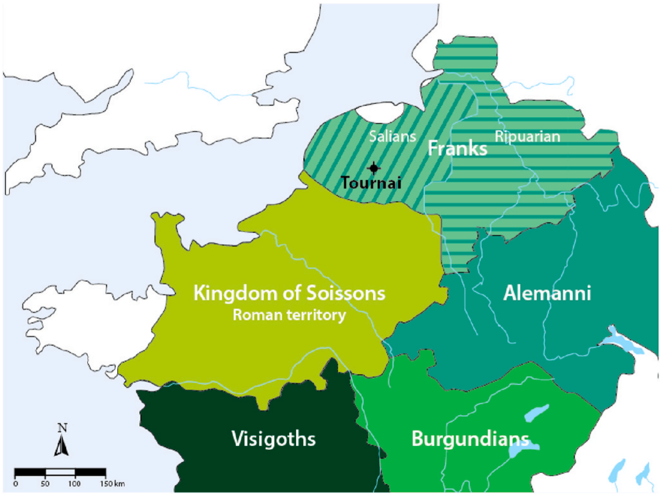

Fig. 1. Division of northern Gaul at the death of Childeric (482) and geographical location of the city of Tournai.

2. Material and methods

2.1. Material

The analyses include the bones of 12 complete or sub-complete skeletons from the site of Saint-Brice, Tournai (see Supplementary material 1). Indeed, of the 21 specimens collected on the site, four are immature (with not fully fused epiphyses) and five are too fragmented to be taken into account.

A reference sample of 122 modern specimens is also included (Table 1; see Supplementary material 1). Using a comparative sample is common in zooarchaeology (Cornette et al., 2015; Guillaud et al., 2015) as it may allow one to detect phenotypic proximities between modern and archaeological forms. These modern skeletons, which are housed in the collections of several European institutions, are all adults (with fully fused epiphyses).

2.2. Acquisition of data and geometric morphometrics

The geometric morphometric study concerns the 16 main bones of the appendicular skeleton (scapula, humerus, radio-ulna, metacarpal bone, coxal bone, femur, tibia, calcaneus, talus, metatarsal bone, proximal, middle, and distal anterior and posterior phalanges). The 3D coordinates of anatomical landmarks were recorded using a Microscribe 3D digitizer. The landmark protocol follows that defined by Hanot et al. and of which the repeatability was tested (Hanot et al., 2017a). Note, however, that some landmarks were removed from the analyses due to the fragmented nature of some bones (see Supplementary material 2).

A Generalized Procrustes Analysis (GPA) was performed on the landmark data of each bone in order to remove non-shape variation due to differences in position, scale, and orientation of the configurations (Rohlf and Slice, 1990). Next, a Principal Component Analysis (PCA) was performed on the Procrustes residuals to reduce the dimensionality of the multivariate datasets (Baylac and Frieß, 2005; Jolliffe, 2002; Krzanowski, 1988, 1987). New independent variables (Principal Components, PCs) maximizing the variance within the data were thus produced. GPA and PCA were performed using the R language" (R Core Team, 2015) and the "Rmorph" library (Baylac, 2014).

The differences between males and females were tested using a MANOVA performed on the shape data of each bone. When significant, a two-way MANOVA was used to assess the impact of sexual dimorphism on the observed differences between the groups/breeds. Due to the small number of geldings in the modern sample, their potential impact on the shape variation was not assessed.

Allometry was assessed for each bone using multivariate regressions of the shape variables (90% of the total variation) on the log10-transformed centroid sizes. Allometric effects were removed by extracting the residuals from the multivariate regression models (Monteiro, 1999) for the bones displaying a significant influence of size on shape. Given the small size of the sample, only a global multivariate regression on the whole sample was feasible (i.e., mixing males and females, and breeds).

Table 1
List and sample sizes of the breeds included in the analyses.

Species	Breed	Breed's aptitude	Sample size
E. caballus	Arabian	Riding-endurance race	4
E. caballus	Thoroughbred	Riding-sprint race	2
E. caballus	Selle Français	Riding-jump race	3
E. caballus	Trotteur français	Riding-trotting race	1
E. caballus	Lusitano	Riding-dressage	1
E. caballus	Unknown (riding horse)	Riding	1
E. caballus	Boulonnais	Draft	1
E. caballus	Percheron	Draft	2
E. caballus	Nordiker	Draft	2
E. caballus	Clydesdale	Draft	2
E. caballus	Shire	Draft	1
E. caballus	Unknown (pony)	–	2
E. caballus	Shetland pony	Riding, light draft	4
E. caballus	Icelandic	Riding	4
E. caballus	Camargue	Riding	1
E. caballus	Pottok	Riding	3
E. caballus	Mongol	Riding, pack, draft	4
E. caballus	Konik	Riding, light draft	1
E. przewalskii	–	–	15
E. asinus	Egyptian	–	2
E. asinus	Poitou	–	6
E. asinus	Asinara	–	1
E. asinus	Unknown	–	34
E. asinus×*E. caballus*	Unknown	–	17
E. caballus×*E. asinus*	Unknown	–	8

2.3. Species classification

The k-Nearest Neighbors (k-NN) algorithm was used on the bones from Tournai in order to confirm their attribution to horses. This method classifies an object in a group taking into account its k-NN using Euclidian distances after a leave-one-out cross validation (Ripley, 1996; Venables and Ripley, 2002). This approach was previously developed on a modern reference sample of domestic horses, donkeys, and hybrids and has demonstrated its potential for the specific identification of archaeological equid remains (Hanot et al., 2017a). This study, performed on the 16 main limb bones, enabled the correct classification of modern specimens with a rate of 77–94% according to the bone. Here, we retained the same parameters (i.e. the amount of variation included in the analyses, and number of Nearest-Neighbors taken into account in the classification process), except for the bones for which the fragmented nature of the archaeological remains required adjusting the sets of landmarks. In these cases, new parameters were defined to allow for the best classification rates. The k-NN classifications were performed using the library "class" (Venables and Ripley, 2002).

2.4. Shape variation

When the specific attribution was confirmed, a more complete study of the shape variation was carried out on the skeletons from Tournai with a refined comparative sample (see Supplementary material 1).

2.4.1. Shape variance

The morphological homogeneity of the archaeological sample was evaluated by comparing its shape variance to that of the extant horse breeds included in our study. To do so, the Procrustes variance sum of the diagonal elements of the group covariance matrix (Zelditch et al., 2012) of each bone was computed for the skeletons from Tournai and for each group of modern breeds. For convenience, the race breeds and the draft ones were respectively grouped, as defined by the International Federation for Equestrian Sports on the basis of functional and genetic criteria. Pairwise comparisons were then performed between the archaeological sample and each modern group in order to assess and compare their respective shape variance. This analysis was run using the "Geomorph" library (Adams and Otárola-Castillo, 2013).

2.4.2. Morphological comparison with extant breeds

The distribution of the data in shape space was displayed by plotting the two first PCs. The plots were performed using the "Rmorph" library (Baylac, 2014). Visualizations of the shapes associated with extreme parts of the PC axes were produced using a 3D photogrammetric model (from the bones of the modern specimen: CV9 - ONIRIS-Nantes AC). The photographs were taken from various angles using a Canon EOS 700D and the 3D reconstructions were computed on the software Agisoft PhotoScan (© 2014 Agisoft LLC, 27 Gzhatskaya st., St. Petersburg, Russia). The "Landmark" software (Wiley et al., 2005) was then used to obtain the landmarks coordinates of the 3D model. The shape deformation along the PCs was finally visualized using a Thin Plate Spline (TPS) deformation of the consensus surface, using the “Morpho” library (Schlager, 2016).

In order to summarize the total shape variation and to better visualize potential morphological proximities between the archaeological sample and modern breeds, an unrooted Neighbor-Joining tree (N-J tree) was created for each bone morphospace. The trees were computed from the Euclidean distances between the mean shape of each group. Here again, the race and draft breeds were grouped due to the small sample size. The mean shapes were computed for each group using the “Morpho” library (Schlager, 2016). The N-J trees were created using the “ape” library (Paradis et al., 2004).

2.5. Shape covariation

In order to better understand what underlies the shape variation of the limb bones from Tournai, we explored their covariation patterns. The covariation between within-limb adjacent bones (e.g. humerus and radio-ulna) was examined, known to largely result from the sharing of common function through articulations, muscles or ligaments (Botton-Divet et al., 2018; Fabre et al., 2014; Hallgrímsson et al., 2002). The covariation between the serially homologous bones (e.g. humerus and femur), considered as mainly related to developmental factors, was also studied. Indeed, in tetrapods, the fore- and hind limb elements are produced by the expression of a same developmental program (Hall, 1995). This produces shape covariation which is prone to be modified in response to functional requirements (e.g. functional divergence between the fore- and hind limbs due to specialization of one of them; Hallgrímsson et al., 2009; Nemeschkal, 1999; Young and Hallgrímsson, 2005).

2.5.1. Visualization of covariation patterns

We first applied Two-Blocks Partial Least Squares analyses (2B-PLS) on pairs of bones from the archaeological and modern samples. This method generates a covariance matrix based on the two datasets and extracts the main axes of covariation (Bookstein et al., 2003; Rohlf and Corti, 2000). The covariation between the within-limb connected bones was explored in order to detect functional interactions (Hanot et al., 2018). Partial Least Squares (PLS) coefficients were computed to assess the statistical significance and magnitude of the covariation using the “Geomorph” library (Adams and Otárola-Castillo, 2013). When the test provided significant covariation signal, the first PLS axes were generated and plotted for each block. The shape changes associated with the PLS axes were visualized by TPS deformation of the consensus surface, in the same way as for the PCA. 2B-PLS were performed using the “Rmorph” library (Baylac, 2014) and TPS deformation using the “Morpho” one (Schlager, 2016). The visualization displayed in Fig. 6 was obtained using AVIZO (VSG, Burlington, MA, USA) from the meshes of the extremes shapes of PLS axes.

Once again, for better legibility, unrooted Neighbor-Joining trees were created based on the Euclidean distances between the group centroids obtained from the PLS scores.

2.5.2. Magnitude of morphological integration

The magnitude of morphological integration between the bones of the skeletons from Tournai was assessed using Covariance Ratios (CR; Adams, 2016), computed from the pairwise covariances between variables. The CR measures the degree of modularity between datasets, a modular pattern being considered significant when the observed statistics is small compared to the distribution of values obtained under the null hypothesis of random associations of variables. Although this approach is unfit to signify the absence of covariation (unlike an integration test), we decided to use this approach because it appears as the only way to assess the intensity of morphological integration on a small sample thanks to its relative insensitivity to sample size (Adams, 2016; Evans et al., 2017; Muñoz-Muñoz et al., 2016). Indeed, its value reflects the intensity of integration, with high values corresponding to a strong degree and low values (close to zero) to a low degree (or even absence) of covariation. The analyses were computed using the function modularity.test included in the “Geomorph” library (Adams and Otárola-Castillo, 2013).

In order to compare the magnitude of covariation between datasets, we used the procedure proposed by Adams and Collyer (2016) to compute z-scores. This statistic test calculates the standard deviation (effect size) of a measure of integration (here CR values) obtained from different samples according to their respective expected value under the null hypothesis of no integration. This approach allows for the comparison between measures of integration from datasets displaying different expected values due to variations in the number of variables and sample size. Two-sample tests were also performed to know if the degree of integration was significantly different between datasets. These analyses were computed using the function compare.pls implemented in the “Geomorph” library (Adams and Otárola-Castillo, 2013) that we adapted to make it applicable to CR values.

For all the analyses previously described, test results were considered as significant when p-values (p) were below 0.05.

It should be noted that, due to the absence of the phalanges and tarsal bones in some archaeological skeletons, the sample size was too small to assess the intensity of integration in the most distal parts.

3. Results

3.1. Classification

The full set of correct classification rates and their associated retained parameters are presented in Supplementary material 3. For the archaeological assignment, we decided to retain only the bones providing correct classification rates of over 80%. Each specimen was identified on the basis of the predominant attribution from available bones. On this basis, the results assign all the skeletons from Tournai to horses, with an average correct classification rate of 88% (see Supplementary material 3). This result allows us to refine our comparative sample to horses only for the following analyses.

3.2. Shape variation

3.2.1. Shape variance

There is no significant difference in Procrustes variance between the bones from Tournai and those from modern groups, except in rare cases in which the Procrustes variance is systematically lower in the archaeological sample than in the modern groups (Table 2). This relative morphological homogeneity enables us to group the archaeological specimens in the following analyses.

3.2.2. Morphological comparison with extant breeds

The MANOVA performed on the shape data of horses indicates that the differences in shape between sexes were generally not significant, except for the scapula, radio-ulna, coxal bone and proximal posterior phalanx ($p < 0.05$). However, according to the two-way MANOVA, no interaction is highlighted between the differences among modern groups and sexual differences for these bones.

The PCA plots globally show a clear separation between the draft horses and the other modern groups along the first axis (Fig. 2). This axis mainly explains a differential degree of robusticity of the bones, with draft horses being associated with robust shapes. In all cases, the horses from Tournai are characterized by slender bones, pooling with most of the modern groups, in contrast to draft horses.

According to the Euclidean distances between the mean shape of the groups, the archaeological specimens from Tournai are in most cases closer to racehorses (the closest for nine out of 16 bones, among the two closest for 11 bones) and to a lesser extent, to Mongolian and

Table 2
Procrustes variance and p-values obtained from the pairwise comparisons between the archaeological sample (Tournai) and each modern group (significant differences in bold; $p < 0.05$).

	Scapula		Humerus		Radius		Metacarpal bone	
	Variance	P-value	Variance	P-value	Variance	P-value	Variance	P-value
Tournai	3.18E-02	–	1.51E-03	–	4.90E-04	–	3.62E-04	–
Race	1.42E-02	2.78E-01	1.65E-03	6.95E-01	6.46E-04	5.48E-01	5.25E-04	5.05E-01
Icelandic	1.27E-02	1.92E-01	2.02E-03	2.78E-01	1.26E-03	**2.90E-02**	6.71E-04	3.45E-01
Mongolian	8.35E-03	1.40E-01	1.81E-03	4.89E-01	4.34E-04	8.67E-01	4.28E-04	8.29E-01
Pottok	1.10E-02	1.64E-01	1.37E-03	7.75E-01	5.44E-04	8.91E-01	2.29E-04	6.91E-01
Przewalski	1.19E-02	1.32E-01	1.91E-03	2.50E-01	6.10E-04	6.14E-01	4.00E-04	8.79E-01
Shetland	1.23E-02	1.90E-01	1.60E-03	8.57E-01	6.67E-04	6.06E-01	4.93E-04	6.76E-01
Draft	2.87E-02	6.04E-01	3.35E-03	**1.00E-03**	1.94E-03	**1.00E-03**	1.79E-03	**1.00E-03**
	Proximal anterior phalanx		**Middle anterior phalanx**		**Distal anterior phalanx**		**Coxal bone**	
	Variance	**P-value**	**Variance**	**P-value**	**Variance**	**P-value**	**Variance**	**P-value**
Tournai	1.81E-03	–	9.00E-02	–	2.39E-02	–	8.87E-03	–
Race	2.39E-02	4.06E-01	6.42E-02	5.97E-01	1.21E-01	**4.70E-02**	7.82E-03	7.59E-01
Icelandic	3.30E-03	5.25E-01	1.04E-02	3.44E-01	1.32E-02	5.18E-01	1.48E-02	1.53E-01
Mongolian	1.80E-03	9.93E-01	1.06E-02	3.35E-01	8.44E-03	4.60E-01	5.73E-03	3.77E-01
Pottok	2.01E-03	9.31E-01	2.04E-02	3.29E-01	1.79E-02	7.11E-01	9.68E-03	8.46E-01
Przewalski	2.73E-03	7.35E-01	1.07E-02	2.36E-01	1.58E-02	7.16E-01	9.22E-03	8.99E-01
Shetland	6.83E-03	3.29E-01	1.16E-02	3.20E-01	1.74E-02	6.61E-01	1.62E-02	7.90E-02
Draft	4.02E-02	1.23E-01	1.49E-02	2.96E-01	2.78E-02	7.99E-01	1.68E-02	**4.00E-02**
	Femur		**Tibia**		**Talus**		**Calcaneus**	
	Variance	**P-value**	**Variance**	**P-value**	**Variance**	**P-value**	**Variance**	**P-value**
Tournai	2.50E-03	–	7.87E-04	–	5.02E-02	–	3.52E-03	–
Race	2.34E-03	8.26E-01	7.27E-04	8.30E-01	6.52E-03	1.52E-01	4.86E-03	2.21E-01
Icelandic	2.43E-03	9.33E-01	9.97E-04	5.69E-01	8.55E-03	2.44E-01	5.03E-03	2.13E-01
Mongolian	1.43E-03	2.94E-01	5.78E-04	5.69E-01	4.04E-03	9.80E-02	4.82E-03	2.79E-01
Pottok	2.36E-03	8.89E-01	5.51E-04	5.44E-01	4.66E-03	9.20E-02	3.29E-03	8.27E-01
Przewalski	2.67E-03	8.04E-01	9.32E-04	6.02E-01	6.74E-03	1.66E-01	5.41E-03	5.40E-02
Shetland	2.35E-03	8.89E-01	6.24E-04	6.74E-01	6.66E-03	1.88E-01	3.74E-03	8.59E-01
Draft	5.59E-03	**1.00E-03**	2.33E-03	**1.00E-03**	6.87E-03	2.77E-01	4.54E-03	3.68E-01
	Metatarsal bone		**Proximal posterior phalanx**		**Middle posterior phalanx**		**Distal posterior phalanx**	
	Variance	**P-value**	**Variance**	**P-value**	**Variance**	**P-value**	**Variance**	**P-value**
Tournai	2.87E-04	–	2.17E-03	–	5.84E-03	–	8.85E-03	–
Race	3.93E-04	9.12E-01	2.81E-03	4.80E-01	1.30E-02	**2.80E-02**	1.49E-02	3.64E-01
Icelandic	4.47E-04	8.21E-01	2.51E-03	7.74E-01	1.15E-02	2.31E-01	6.96E-03	7.22E-01
Mongolian	2.77E-04	9.89E-01	2.34E-03	8.92E-01	9.14E-03	4.16E-01	1.41E-02	3.46E-01
Pottok	/	/	2.02E-03	8.95E-01	1.24E-02	1.46E-01	/	/
Przewalski	5.69E-03	**3.50E-02**	2.24E-03	9.26E-01	1.08E-02	1.20E-01	4.34E-02	2.53E-01
Shetland	3.64E-04	9.10E-01	4.55E-03	5.80E-02	8.21E-03	5.91E-01	9.61E-03	8.91E-01
Draft	1.55E-03	5.60E-01	5.05E-03	**1.00E-03**	1.53E-02	**6.00E-03**	1.07E-02	7.00E-01

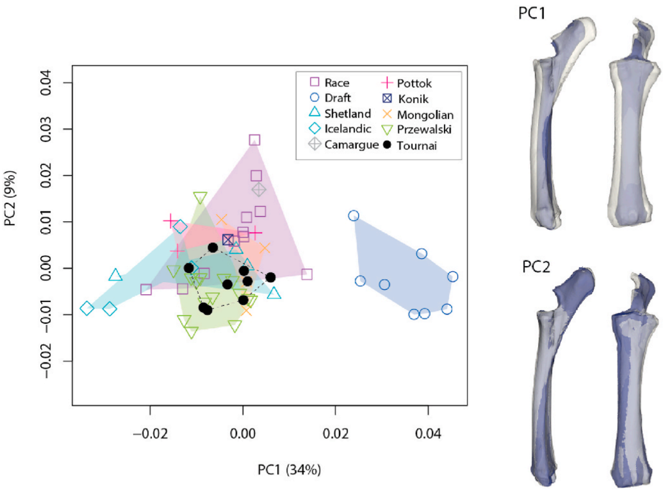

Fig. 2. Scatter plot of the two first PCs of the PCA performed on the radio-ulna shape data, with visualizations of the shape changes associated (in blue: extreme negative; in white: extreme positive). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Przewalski's horses (among the two closest for respectively nine and eight bones). Distances computed on allometry-free shape data provide similar results (see Supplementary material 4).

This result led us to refine the study of shape variation and reduce the comparative sample to racehorses only. The PCAs performed on girdles (scapula and coxal bone), talus, calcaneus and distal phalanges do not show structure among modern breeds, nor any greater phenotypic closeness between the specimens from Tournai and one or another extant breed (see Supplementary material 5). On the contrary, PCAs performed on the long bones reveal a clearer separation of the breeds along the first axes (Fig. 3; Supplementary material 5), in spite of the small number of representatives of each modern group. Indeed, the first Principal Component (PC1) corresponds for most of the bones to a degree of slenderness-robusticity (PC2 for the humerus), along with the extant breeds are structured according to a common trend: Arabian horses are systematically grouped in the part of the axis corresponding to slender bones, at the opposite from French Saddle horses which display more robust bones; as for Thoroughbreds, they tend to pool with French Saddle horses (particularly on the humerus and femur –stylopods-, and on the radio-ulna and tibia –zeugopods-; Fig. 3D), and display a more intermediate position on the distal bones (Fig. 3B). This tendency for Thoroughbreds to be closer to Arabian horses is strengthened for the proximal phalanges by contrast with the robusticity of those of French Saddle horses (Fig. 3C).

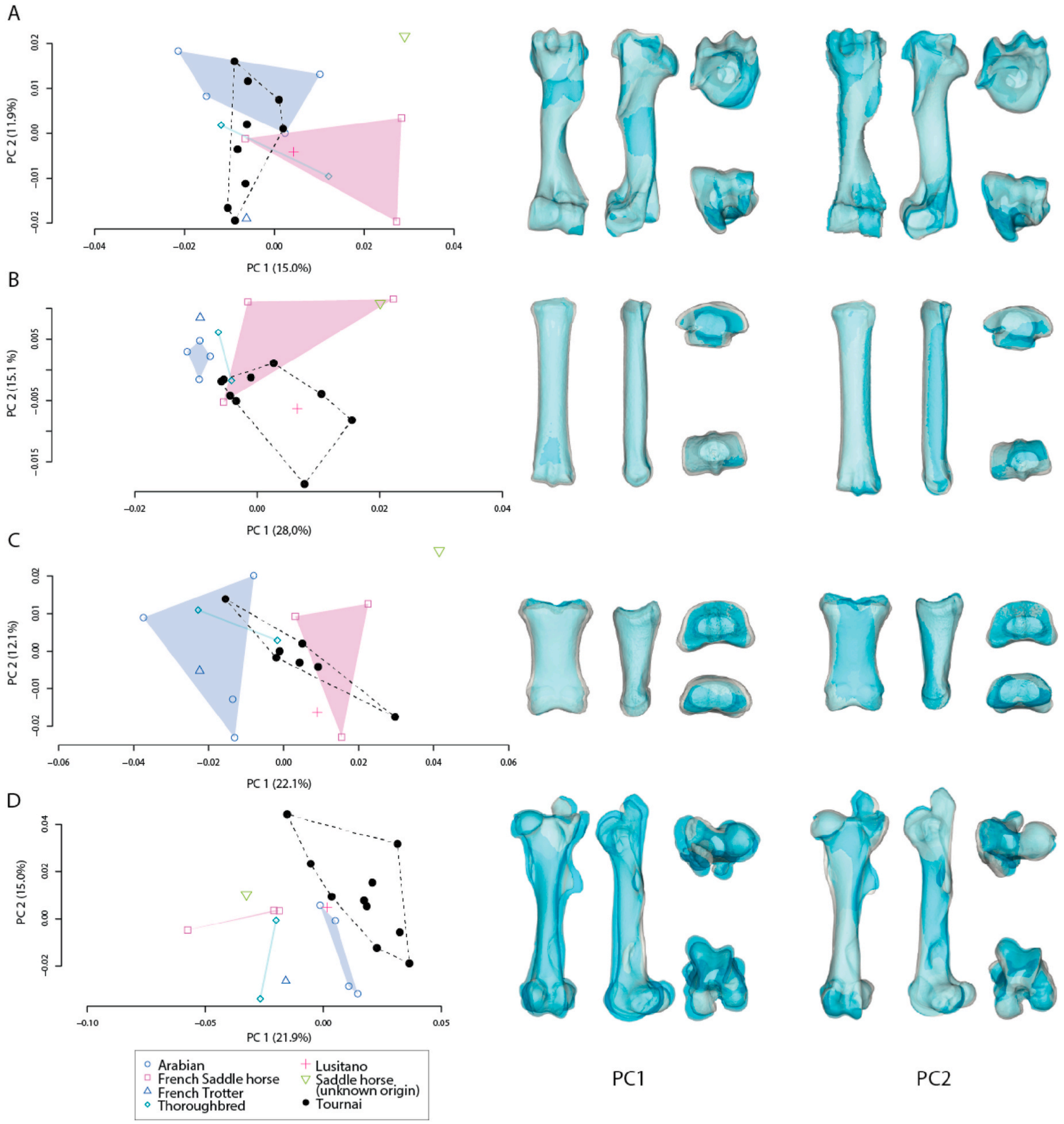

Fig. 3. Scatter plot of the two first PCs of the PCA performed on the humerus (A), metacarpal bone (B), proximal anterior phalanx (C), femur (D) shape data, with visualizations of the shape changes associated (in cyan: extreme negative; in white: extreme positive). The modern comparative sample is reduced to racehorses. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Concerning the archaeological sample from Tournai, they display slender stylo- and zeugopods and pool with Arabian horses (Fig. 3D; Supplementary material 5), except for the humerus for which they occupy the entire variation described by PC2 (Fig. 3A). This trend changes for the autopodial parts (metapodial bones and proximal phalanges) with a greater proximity to the robust bones of French Saddle horses (Fig. 3B and C).

3.3. *Shape covariation*

3.3.1. *Visualization of covariation patterns*

A significant covariation signal was obtained for five of the studied pairs of bone (humerus/radio-ulna, radio-ulna/metacarpal bone, coxal bone/femur, femur/tibia and proximal/middle distal phalanges). In all of the computed plots, draft horses clearly separate from breeds displaying more slender bones with which the specimens from Tournai pool (Fig. 4). This position along the covariation axes corresponds to relatively reduced attachment areas for muscles and ligaments by comparison with the draft horses (Hanot et al., 2018).

The values of distances between the centroid of each group reveal, as for the shape variation, a greater proximity of the specimens from Tournai to racehorses (the closest for three out of five cases, among the two closest in all of them) and to a lesser extent, to Mongolian and Przewalski's horses (among the two closest in two cases). Distances computed on allometry-free shape data provide similar results (see Supplementary material 6).

Here again, the result led us to refine the study of shape variation and reduce the comparative sample to racehorses only for PLS analyses. A significant covariation signal was obtained for only three of the studied pairs of bones (femur/tibia, tibia/metatarsal bone and metacarpal/metatarsal bone; Fig. 5). As in the PCAs, the main axis of covariation is related to a degree of slenderness-robusticity with a separation between

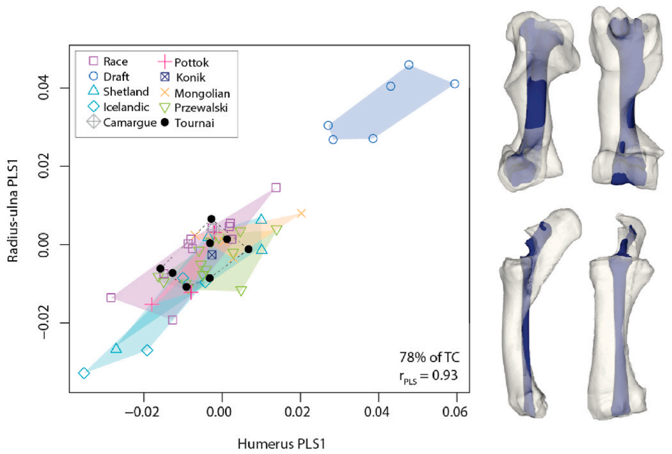

Fig. 4. Scatter plot of the first PLS axis describing shape covariation between humerus and radio-ulna, with visualizations of the shape changes associated (in blue: extreme negative; in white: extreme positive). TC: total covariation; rPLS: PLS correlation coefficient. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Arabian and French Saddle horses (with main areas of covariation located on muscle attachments in femur and tibia; Fig. 6). The archaeological specimens from Tournai clearly pool with Arabian horses in the main covariation axis between the femur and tibia, corresponding to relatively slender bones and reduced attachments areas (Fig. 5B). The trend is similar when considering the covariation between the tibia and metatarsal bone (Fig. 5C), in spite of the archaeological specimens presenting a more intermediate position. However, this trend is reversed when considering the covariation between metapodials with a grouping of the specimens from Tournai with French Saddle horses displaying more robust bones (Fig. 5A).

3.3.2. Magnitude of morphological integration

The magnitude of integration within the appendicular skeleton of the specimens from Tournai was compared to that of racehorses, the extant specimens displaying the most similar phenotype. The analyses were also conducted on the Przewalski's horses from our sample due to their recurring proximity to the specimens from Tournai and as representatives of horses which have not been submitted to artificial selection (see Supplementary material 7). The CR-associated permutation tests are significant within the archaeological sample, with CR values lower than one, showing that the degree of covariation is higher within than between bones (Fig. 7). The only exceptions concern the covariation between the coxal bone and the femur, and between the femur and the tibia. The covariation between the scapula and coxal bone in the specimens from Tournai is significantly lower than between the other pairs of serial homologous bones (see Supplementary material 7). Conversely, the strongest values are associated with the covariation between serial long bones as in both riding and Przewlski's horses, but some variation could be noticed between their respective patterns. Indeed, CR values associated with covariation in humerus/femur and radio-ulna/tibia pairs are higher in the archaeological than in the modern sample of riding horses (with a significant difference between z-scores for the radio-ulna/tibia pair). On the contrary, the integration pattern in extant racehorses is characterized by strong covariation between metacarpal and metatarsal bones revealed by high CR and z-score values, significantly higher than all the other pairs of bones. This produces an increase in the degree of covariation from proximal to distal serial homologous long bones that we do not observe in the specimens from Tournai. Similarly, the shape covariation between the metacarpal and metatarsal bones in Przewalski horses is significantly lower than that between the more proximal pairs of serially homologous bones (humerus/femur and radio-ulna/tibia).

Concerning the covariation between the connected within-limb bones, we observe a higher degree of morphological integration within the fore- than within the hind limb in the archaeological sample, whereas it is not the case in the modern one. The absence of significant covariation in two pairs of bones (coxal bone/femur and femur/tibia) in the skeletons from Tournai contrasts with the high values observed in the extant riding horses. Moreover, the covariation between humerus and radio-ulna is significantly higher in archaeological than in both modern riding and Przewalski's horses (with CR and z-scores values among the highest of their skeleton).

In each group and for most of the bones, the multivariate regressions of shape on centroid size do not show significant allometry. Thus, we can assume that allometry does not contribute to an increase of the morphological integration between the bones.

4. Discussion

According to the specific classification results, the skeletons discovered around the tomb of Childeric are morphologically close to horses, which is in agreement with the general assumption based upon our knowledge of the symbolic importance of this animal in Frankish funerary practices (Wagner, 2005). More precisely, the study of shape variation reveals a phenotypic similarity between the horses from Tournai and the extant racehorses of our sample. Specifically, the horses from Tournai tend to pool with Arabian horses concerning stylopods and zeugopods, corresponding to slender bones by comparison with the other race horses. This result is in accordance with those obtained using traditional morphometrics, by Gabriel et al. (1991) on the same specimens, and in Merovingian horses in general (Baillif-Ducros and Yvinec, 2015). However, the pattern observed in autopodial parts (metapodial bones and proximal phalanges) differs from that of proximal bones, with a greater proximity to race breeds displaying more robust bones (French Saddle horses here).

In our modern breeds, the structure of the shape variation seems to correspond to what is known about their functional specificities: indeed, the slenderness of the proximal bones (which are those including most of the muscular attachments) in Arabian horses, bred for endurance, could be related to their lower muscular mass in comparison with other breeds, especially Thoroughbreds, selected for high-speed locomotion (Crook et al., 2008). On the contrary, Thoroughbreds display relatively slender autopods (especially in comparison with French Saddle horses), probably as a better adaptation for sprinting (Hall, 2008; Hildebrand et al., 1995). However, in order to better assess the potential influence of function on the previously described shape variation, and then try to apply it by analogy to the archaeological specimens, we examined the patterns of covariation.

The main axes of covariation between horse limb bones have already been described as reflecting functional interactions (Hanot et al., 2018). Thus, the position of the archaeological specimens along these axes (previously shown as being probably largely related to muscular or ligament development) could partly indicate some functional similarities to either current group. The PLS analyses corroborate the results obtained from shape variation data and show a close proximity between the horses from Tournai and the race breeds, suggesting functional affinities between them. This sharing of morphological features nowadays found in modern-day breeds selected for saddle and racing activities is in accordance with the assumption, based on symbolic and archaeological evidence, that these horses may have been riding horses (Ghenne-Dubois, 1991; Wagner, 2005).

The PLS analyses in which the comparative sample is reduced to racehorses show a similar distribution of the specimens compared to what is observed on the first axes of the PCA performed on the same subsample (mostly according to the differential degree of robusticity of their bones). This indicates that the covariation between bones significantly contributes to their variation pattern (Klingenberg, 2014). The fact that the main areas of covariation between intra-limb connected

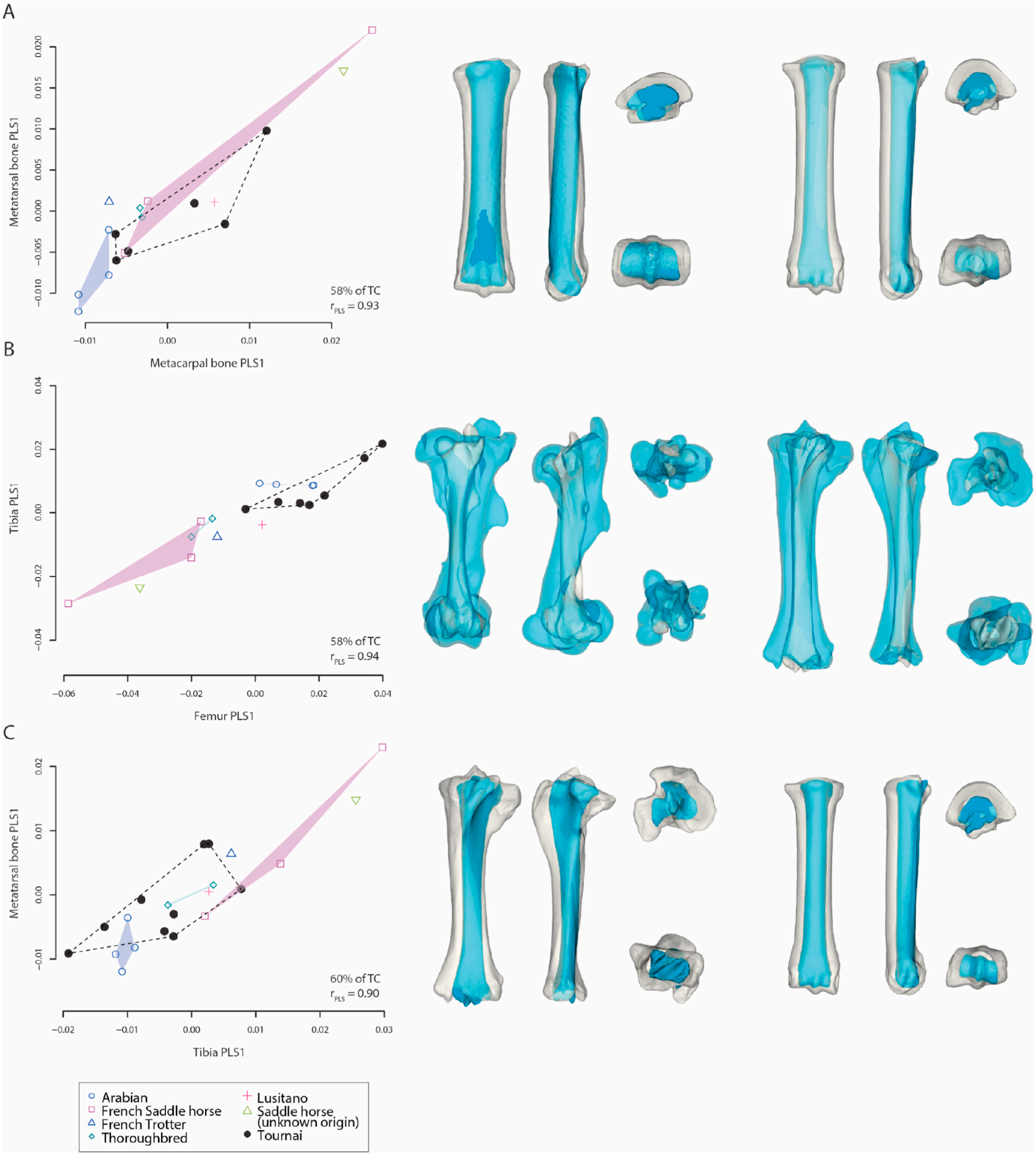

Fig. 5. Scatter plot of the first PLS axis describing shape covariation between metacarpal and metatarsal bones (A), femur and tibia (B), tibia and metatarsal bone (C), with visualizations of the shape changes associated (in blue: extreme negative; in white: extreme positive). TC: total covariation; rPLS: PLS correlation coefficient. The modern comparative sample is reduced to racehorses. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

stylopods/zeugopods correspond to muscular attachments confirms the role of functional factors in producing covariation. This allows us to more reliably interpret their slenderness in the specimens from Tournai as related to function, especially muscle characteristics: indeed, this suggests a muscular development more comparable to horses bred for endurance, such as Arabian horses, than to horses bred for sprinting and jumping (Thoroughbreds and French Saddle horses in our sample), known to display a greater muscle mass (Crook et al., 2008).

Conversely, the archaeological horse autopods differ from those of Arabian ones by their robusticity. This could be related to a specific functional requirement for the specimens from Tournai knowing that robust bones could allow to better resist to weight-bearing stresses (Martín-Serra et al., 2015, 2014). Their potential role as “war horses”, a use which no longer exists today, could have for instance required specific functional traits and may explain this specificity. However, the PLS analyses performed on the metatarsal bone tend to show that the covariation with the metacarpal bone contributes more to the robusticity than that with the tibia in the specimens from Tournai. In other words, this robusticity seems to be more driven by the covariation with the serial homologous bone (metacarpal) than the within-limb connected one (tibia). It is generally hypothesized that the shared developmental origin of fore- and hind limbs in tetrapods contributes to produce morphological integration between serially homologous elements whereas within-limb connected bones are supposed to constitute functional modules (Hallgrímsson et al., 2002; Young and Hallgrímsson, 2005). According to this hypothesis, developmental factors would

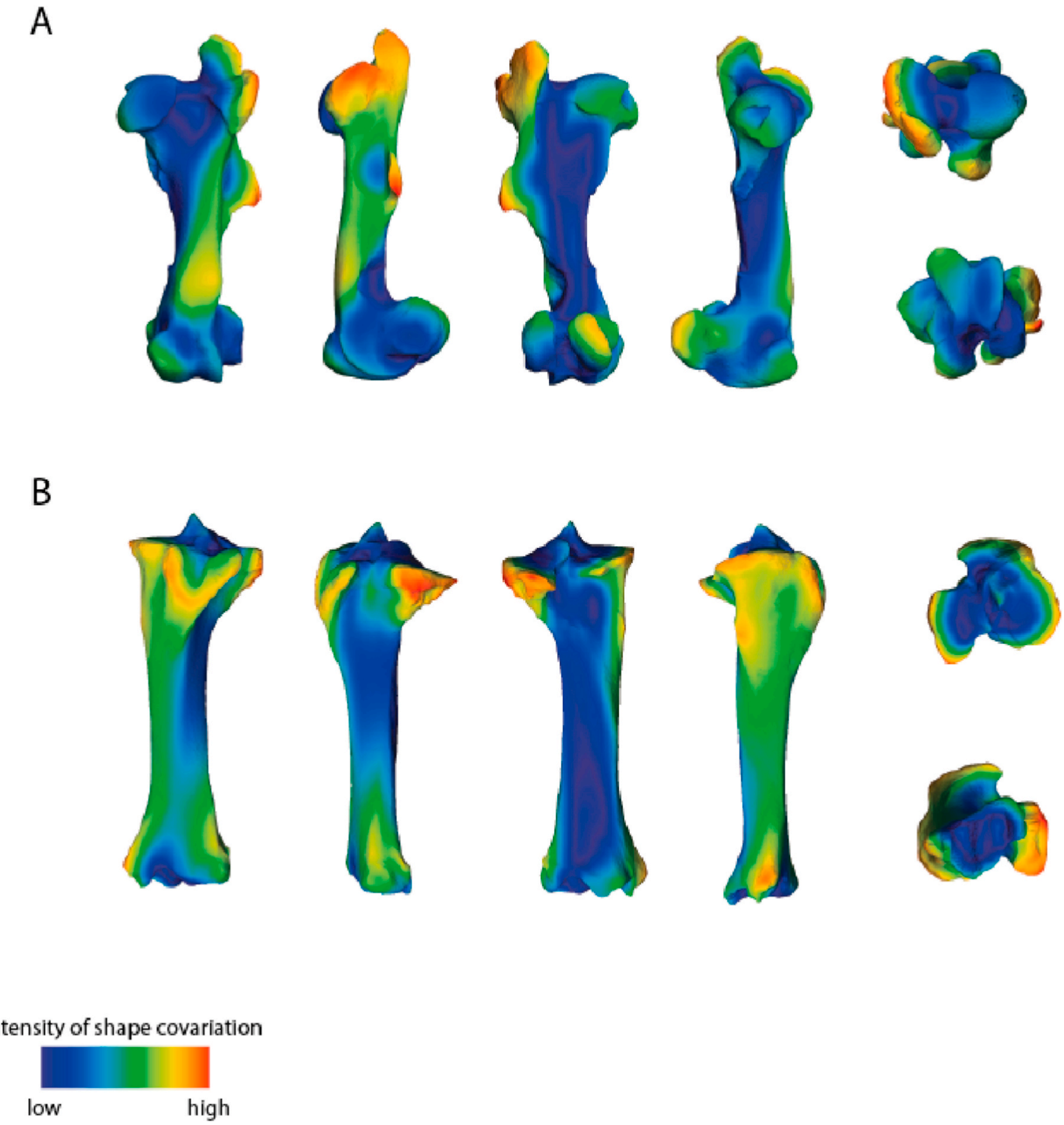

Fig. 6. Anatomical location and intensity of the shape deformation associated with the first PLS axes describing shape covariation between femur (A) and tibia (B). The shape associated with the negative part of the axes was colored according to its distance to the positive part (blues areas corresponding to the closest surfaces and red ones to the furthest surfaces). The main areas of covariation (in red) correspond to the gluteal muscles on the femur and to the flexor digitorum longus on the tibia. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

mostly contribute to the robusticity of the metatarsal bone with respect to functional ones in the specimens from Tournai. Conversely, both covariations with tibia and metacarpal bone are related with the metatarsal robusticity in French Saddle horses suggesting that the developmental signal would match functional requirements. Therefore, the ancestral covariation due to developmental factors would be potentially more strongly conserved in the limbs of the specimens from Tournai, and may be driving the morphological variation of metapodial bones. This aspect differs from Arabian horses, to which they are, however, morphologically close when comparing proximal bones. Artificial selection for high-speed locomotion may have contributed to a radical elongation of the autopods in some modern breeds (such as Thoroughbreds or Arabian horses), in order to increase the length of strides, minimize the moment of inertia and improve elastic storage with elongated distal tendons (Biewener, 1998; Hall, 2008; Hildebrand, 1987; Hildebrand et al., 1995). In this sense, a lower degree of artificial selection for functional traits in the specimens from Tournai (particularly high-speed running) could explain this difference.

In order to investigate the morphological impact of artificial selection, we studied the magnitude of morphological integration as a way to detect potential patterns related to locomotor specializations. A previous study performed on carnivores brought out the intensification of morphological integration between fore- and hind limb bones from proximal to distal parts of the limbs in cursorial taxa, in contrast with non-cursorial ones (Martín-Serra et al., 2015). A similar finding was observed in our sample of modern racehorses with a stronger degree of covariation between metapodials than in most proximal pairs of bones. The significantly low magnitude of shape covariation between the metacarpal and metatarsal bones in Przewalski's horses tends to confirm the idea that artificial selection for high speed running locomotion would contribute to increase the integration within this module. The lower degree of covariation between the metapodials observed in the

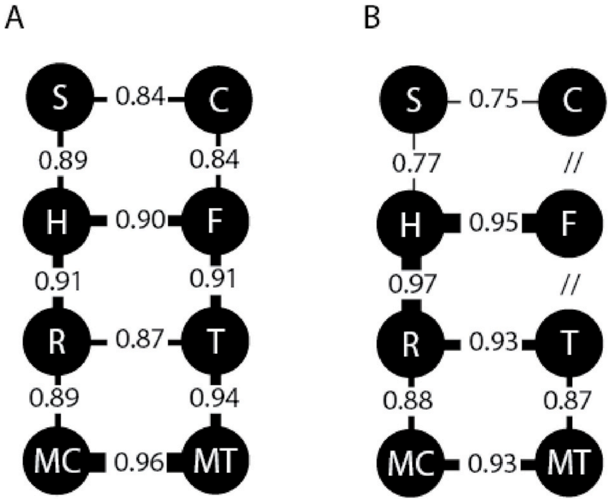

Fig. 7. Graphical models of the CR coefficients obtained on the appendicular bones of modern racehorses (A) and horses from the site of Tournai (B). The line thickness is proportional to the coefficient values (the boldest lines corresponding to the strongest intensity of covariation). Abbreviations: S, scapula; H, humerus; R, radio-ulna; MC, metacarpal bone; C, coxal bone; F, femur; T, tibia; MT, metatarsal bone;//, non-significant covariation.

specimens from Tournai could therefore be related with a lesser degree of running specialization (which appears as concomitant with the previously observed robusticity of their metapodials). Concerning the strong degree of covariation between the humerus and radio-ulna in the archaeological sample, it echoes the fact that their humerus is not characterized by its gracility unlike the other stylo- and zeugopods. This could suggest that the function of this anatomical area could have a particular importance in the locomotion of the horses from Tournai. Knowing that the forelimb plays a key role in support in most tetrapods, this particularity (as well as the robusticity of their autopods) could for instance reveal a specific use of these horses related to weight-bearing capacity. Moreover, the fact that the forelimbs play a major role in deceleration as well (by contrast with hind limbs which contribute more to acceleration; Heglund et al., 1982; Pasi and Carrier, 2003) is congruent with a lower degree of high-speed running specialization than in modern breeds such as Thoroughbreds or Arabian horses.

Although not being the predominant one, we should mention the proximity of the horses from Tournai to the Mongolian and Przewalski's horses, two distinct populations genetically related because having interbred in the past (Bowling et al., 2003; Goto et al., 2011; Orlando et al., 2013). This closeness with horses from Central Asia recalls the context of large population movements having occurred since the beginning of the 5th century (Aillagon, 2008). Indeed, the pressure from the Huns resulted in widespread migrations of peoples and armies from East to Western Europe, which suggests probable crossbreds between horses (Audoin-Rouzeau, 1994). Moreover, the presence of morphological features close to those of Eastern populations also questions the origin of the horses chosen to be buried with Childeric, considering the influence of traditions from Central and Eastern Europe on the tumulus-burial itself (Kazanski and Périn, 2005).

5. Conclusion

The aim of this study was to investigate the morphological and functional traits of equid skeletons found near to the tomb of the Merovingian king Childeric the 1st. Phenotypic similarity to modern racehorses was demonstrated and supported by a comparable position along axes of covariation. This suggests that the horses from Tournai, generally supposed to have been used for riding, especially as "war horses", display similar morphological and functional traits as do extant breeds selected for racing. More precisely, the horses from Tournai share with the Arabian horses from our sample the gracility of their stylopods and zeugopods, potentially related to a reduced muscle development. Conversely, the robusticity of their autopods distinguishes them from Arabians and could be related to a specific functional requirement or to a lower degree of artificial selection. Finally, variation and covariation patterns within the forelimbs suggest the particular importance of their role, possibly related to a particular importance of the support function in these Merovingian horses.

This study illustrates the interest of using 3D GM approaches for an accurate and complete description of bone shape variation. In the present study, this approach allowed us to highlight some specific areas of variation and covariation in bone shape, where traditional methods would only describe variation in slenderness-robusticity. The results also demonstrate the relevance of not only exploring shape variation, but also covariation, in order to address functional questions and to try to evaluate potential signatures of artificial selection on past animals. As illustrated by this study, the particular symbolic status of the domestic horse, which may contribute to the discovery of complete skeletons in archaeological sites, appears as an opportunity to conduct such investigations. However, this kind of approach would deserve to be carried out more broadly, not only on complete skeletons, but also on smaller sets of bone remains belonging to a same individual. It should however be reminded that describing the morpho-functional features of an animal through the study of its skeletal remains represents only one step towards a better knowledge of its past usage. Indeed, a number of past uses no longer exist today, limiting any inference from the comparison with modern examples. Similarly, it is reasonable to assume that the past morphological standards do not correspond to the current ones, or even that no morphological standard was defined for a specific use in the past. Therefore, this kind of morpho-functional information will benefit from being discussed in a broader context along with archaeological and historical data. Similarly, the bone shape analysis need to be included in a wider framework along with functional studies concerning muscle physiology, development, biomechanics and genetics (Mcnulty and Vinyard, 2015).

Future studies including a larger sample of contemporaneous skeletons (especially from non-ritual deposits) would be of great interest to assess the morphological variation of the Merovingian horses in general, and to detect potential differences in integration patterns. Moreover, the comparison between archaeological sites from different periods should be performed in order to see a potential evolution of covariation patterns over time, until the emergence of modern breeds. Specially, the comparison with specimens from other archaeological contexts assumed to have been used for riding in warfare could contribute to a better characterization of the morpho-functional features of the mounted war horses, use which no longer exists today. Such approaches would demonstrate the interest to study archaeological material in order to observe morphological changes and micro evolutionary processes over time.

Declaration of competing interest

☐ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.jas.2020.105200.

References

Adams, D.C., 2016. Evaluating modularity in morphometric data: challenges with the RV coefficient and a new test measure. Methods Ecol. Evol. 7, 565–572. https://doi.org/10.1111/2041-210X.12511.

Adams, D.C., Collyer, M.L., 2016. On the comparison of the strength of morphological integration across morphometric datasets. Evolution 70, 2623–2631. https://doi.org/10.1111/evo.13045.

Adams, D.C., Otárola-Castillo, E., 2013. geomorph: an R package for the collection and analysis of geometric morphometric shape data. Methods Ecol. Evol. 4, 393–399. https://doi.org/10.1111/2041-210X.12035.

Aillagon, J.-J. (Ed.), 2008. Rome and the Barbarians: the Birth of a New World. Skira.

Arbogast, R.-M., Clavel, B., Lepetz, S., Méniel, P., Yvinec, J.-H., 2002. Archéologie du cheval, des origines à la période moderne en France. Errance, Paris.

Audoin-Rouzeau, F., 1994. La taille du cheval en Europe de l'Antiquité aux temps modernes, Fiches d'ostéologie animale pour l'archéologie. Série B: mammifères. APDCA, Juan-les-Pins.

Bachrach, B.S., 1972. Merovingian Military Organization. University of Minnesota Press, Minneapolis, pp. 481–751.

Baillif-Ducros, C., Yvinec, J.-H., 2015. Le cheval de monte aux VI^{e}-VII^{e} siècles en Gaule du nord. Croisement de données archéologiques et ostéologiques. Archéopages 41, 14–19.

Bautier, R.-H., Bautier, A.-M., 1980. Contribution à l'histoire du Cheval au Moyen-Âge: L'élevage du Cheval. Bibliothèque nationale.

Baylac, M., 2014. Rmorph : a R Geometric and Multivariate. Morphometrics Library.

Baylac, M., Frieß, M., 2005. fourier descriptors, procrustes superimposition, and data dimensionality: an example of cranial shape analysis in modern human populations. In: Slice, D.E. (Ed.), Modern Morphometrics in Physical Anthropology, Developments in Primatology: Progress and Prospects. Springer Science & Business Media, New York, pp. 145–165. https://doi.org/10.1007/0-387-27614-9_6.

Biewener, A.A., 2003. Animal Locomotion. Oxford University Press.

Biewener, A.A., 1998. Muscle-tendon stresses and elastic energy storage during locomotion in the horse. Comp. Biochem. Physiol. B Biochem. Mol. Biol. 120, 73–87. https://doi.org/10.1016/S0305-0491(98)00024-8.

Biewener, A.A., 1990. Biomechanics of mammalian terrestrial locomotion. Science 250, 1097–1103.

Bignon, O., Baylac, M., Vigne, J.-D., Eisenmann, V., 2005. Geometric morphometrics and the population diversity of Late Glacial horses in Western Europe (*Equus caballus arcelini*): phylogeographic and anthropological implications. J. Archaeol. Sci. 32, 375–391. https://doi.org/10.1016/j.jas.2004.02.016.

Billoin, D., Châtelet, M., Putelat, O., Thiol, S., 2008. La nécropole mérovingienne à tumuli d'Hégenheim (Haut-Rhin). In: Guillaume, J., Peytremann, E. (Eds.), L'Austrasie. Sociétés, Économies, Territoires, Christianisation. Actes Des XXVIe Journées Internationales D'archéologie Mérovingienne, Nancy, 22-25 Sept. 2005. Presses universitaires de Nancy, Nancy, France, pp. 269–281.

Bookstein, F.L., Gunz, P., Mitterœcker, P., Prossinger, H., Schæfer, K., Seidler, H., 2003. Cranial integration in Homo: singular warps analysis of the midsagittal plane in ontogeny and evolution. J. Hum. Evol. 44, 167–187. https://doi.org/10.1016/S0047-2484(02)00201-4.

Botton-Divet, L., Cornette, R., Fabre, A.-C., Herrel, A., Houssaye, A., 2016. Morphological analysis of long bones in semi-aquatic mustelids and their terrestrial relatives. Integr. Comp. Biol. 56, 1298–1309. https://doi.org/10.1093/icb/icw124.

Botton-Divet, L., Houssaye, A., Herrel, A., Fabre, A.-C., Cornette, R., 2018. Swimmers, diggers, climbers and more, a study of integration across the mustelids' locomotor apparatus (carnivora: mustelidae). Evol. Biol. 45, 182–195. https://doi.org/10.1007/s11692-017-9442-7.

Bowling, A.T., Zimmermann, W., Ryder, O., Penado, C., Peto, S., Chemnick, L., Yasinetskaya, N., Zharkikh, T., 2003. Genetic variation in Przewalski's horses, with special focus on the last wild caught mare, 231 Orlitza III. Cytogenet. Genome Res. 102, 226–234. https://doi.org/10.1159/000075754.

Brauner, A., 1916. Materialy k poznaniu domashnikh zhivotnykh Rossii. 1. Loshad'kurgannykh pogrebenij Tiraspol'skago uezda, Khersonskoj gub. Equus goschkewitchi, mihi. Mém. Société Impériale D'agriculture Russ. Méridionale 86, 49–184.

Brulet, R., 1997. La tombe de Childéric et la topographie funéraire de Tournai à la la fin du V^{e} siècle. In: Clovis, Histoire et Mémoire. Presses de l'Université Paris-Sorbonne, Paris, France, pp. 59–78.

Brulet, R., Collin, B., Nisco, G. de, Dewanckel, G., Hulst, A. d, 1991. Les fouilles du quartier Saint-Brice à Tournai: l'environnement funéraire de la sépulture de Childéric. Departement d'archéologie et d'histoire de l'art.

Clavel, B., Yvinec, J.-H., 2010. L'archéozoologie du Moyen Âge au début de la période moderne dans la moitié nord de la France. In: 30 ans d'archéologie médiévale en France. Un bilan pour un avenir. CRAHM, Caen, pp. 71–87.

Clutton-Brock, J., 1992. Horse Power: A History of the Horse and the Donkey in Human Societies. Harvard University Press, Cambridge.

Cooke, S.B., Terhune, C.E., 2015. Form, function, and geometric morphometrics. Anat. Rec. 298, 5–28. https://doi.org/10.1002/ar.23065.

Cornette, R., Herrel, A., Stoetzel, E., Moulin, S., Hutterer, R., Denys, C., Baylac, M., 2015. Specific information levels in relation to fragmentation patterns of shrew mandibles: do fragments tell the same story? J. Archaeol. Sci. 53, 323–330. https://doi.org/10.1016/j.jas.2014.10.020.

Crook, T.C., Cruickshank, S.E., McGowan, C.M., Stubbs, N., Wakeling, J.M., Wilson, A. M., Payne, R.C., 2008. Comparative anatomy and muscle architecture of selected hind limb muscles in the Quarter Horse and Arab. J. Anat. 212, 144–152. https://doi.org/10.1111/j.1469-7580.2007.00848.x.

Cross, P.J., 2011. Horse burial in first millennium AD Britain: issues of interpretation. Eur. J. Archaeol. 14, 190–209.

Currey, J.D., 2003. The many adaptations of bone. J. Biomech. 36, 1487–1495.

Denis, B., 2012. Les races de chevaux en France au XVIIIe siècle. Et les idées relatives à leur amélioration. Situ Rev. Patrim. 18 https://doi.org/10.4000/insitu.9677.

Dierkens, A., Le Bec, C., Périn, P., 2008. Sacrifice animal et offrandes alimentaires en Gaule mérovinienne. In: Archéologie du sacrifice animal en Gaule romaine: Rituels et pratiques alimentaires. M. Mergoil, Montagnac, pp. 279–299.

Evans, K.M., Waltz, B.T., Tagliacollo, V.A., Sidlauskas, B.L., Albert, J.S., 2017. Fluctuations in evolutionary integration allow for big brains and disparate faces. Sci. Rep. 7, 40431. https://doi.org/10.1038/srep40431.

Ewig, E., 2006. Die Merowinger und das Frankenreich. W. Kohlhammer Verlag.

Fabre, A.-C., Goswami, A., Peigné, S., Cornette, R., 2014. Morphological integration in the forelimb of musteloid carnivorans. J. Anat. 225, 19–30. https://doi.org/10.1111/joa.12194.

Fern, C., 2005. The archaeological evidence for equestrianism in early Anglo-Saxon England, c. 450-700. Anglo-sax. Engl. 100, 450–700.

Forest, V., 1998. De la hauteur au garrot des espèces domestiques en archéozoologie. Rev. Médecine Vét. 149, 55–60.

Gabriel, A., Mees, G., Collin, B., 1991. Etude morphométrique des chevaux mérovingiens. In: Les Fouilles Du Quartier Saint-Brice à Tournai. L'environnement Funéraire de La Sépulture de Childeric, Collection d'archéologie Joseph Mertens. Publications d'Histoire de l'Art et d'Archéologie de l'Université catholique de Louvain, Louvain-la-Neuve, pp. 35–46.

Ghenne-Dubois, M., 1991. Les inhumations de chevaux et les trouvailles de Saint-Brice. In: Les Fouilles Du Quartier Saint-Brice à Tournai. L'environnement Funéraire de La Sépulture de Childeric, Collection d'archéologie Joseph Mertens. Publications d'Histoire de l'Art et d'Archéologie de l'Université catholique de Louvain, Louvain-la-Neuve, pp. 49–70.

Gilot, E., 1991. Datations au 14^{C}. In: Les Fouilles Du Quartier Saint-Brice à Tournai. L'environnement Funéraire de La Sépulture de Childeric, Collection d'archéologie Joseph Mertens. Publications d'Histoire de l'Art et d'Archéologie de l'Université catholique de Louvain, Louvain-la-Neuve, pp. 47–49.

Goto, H., Ryder, O.A., Fisher, A.R., Schultz, B., Pond, K.L., Nekrutenko, A., Makova, K.D., 2011. A massively parallel sequencing approach uncovers ancient origins and high genetic variability of endangered przewalski's horses. Genome Biol. Evol. 3, 1096–1106. https://doi.org/10.1093/gbe/evr067.

Guillaud, E., Cornette, R., Béarez, P., 2015. Is vertebral form a valid species-specific indicator for salmonids? The discrimination rate of trout and Atlantic salmon from archaeological to modern times. J. Archaeol. Sci. 65, 84–92. https://doi.org/10.1016/j.jas.2015.11.010.

Guillaume, J., Rohmer, P., Waton, M.-D., 2004. Une tombe de cheval. In: Trésors Mérovingiens d'Alsace. La Nécropole d'Erstein (VIe-VIIe Siècle Après J.-C.), Fouilles Récentes En Alsace. Editions des Musées de Strasbourg, Strasbourg, pp. 56–57.

Hall, B.K., 2008. Fins into Limbs: Evolution, Development, and Transformation. University of Chicago Press.

Hall, B.K., 1995. Homology and embryonic development. In: Hecht, M.K., Macintyre, R. J., Clegg, M.T. (Eds.), Evolutionary Biology, Evolutionary Biology. Springer US, pp. 1–37. https://doi.org/10.1007/978-1-4615-1847-1_1.

Hallgrímsson, B., Jamniczky, H., Young, N.M., Rolian, C., Parsons, T.E., Boughner, J.C., Marcucio, R.S., 2009. Deciphering the palimpsest: studying the relationship between morphological integration and phenotypic covariation. Evol. Biol. 36, 355–376. https://doi.org/10.1007/s11692-009-9076-5.

Hallgrímsson, B., Willmore, K., Hall, B.K., 2002. Canalization, developmental stability, and morphological integration in primate limbs. Am. J. Phys. Anthropol. 119, 131–158. https://doi.org/10.1002/ajpa.10182.

Halsall, G., 2003. Warfare and Society in the Barbarian West, 450-900. Routledge, Londres-New York.

Hanot, P., Guintard, C., Lepetz, S., Cornette, R., 2017a. Identifying domestic horses, donkeys and hybrids from archaeological deposits: a 3D morphological investigation on skeletons. J. Archaeol. Sci. 78, 88–98. https://doi.org/10.1016/j.jas.2016.12.002.

Hanot, P., Herrel, A., Guintard, C., Cornette, R., 2018. The impact of artificial selection on morphological integration in the appendicular skeleton of domestic horses. J. Anat. 232, 657–673. https://doi.org/10.1111/joa.12772.

Hanot, P., Herrel, A., Guintard, C., Cornette, R., 2017b. Morphological integration in the appendicular skeleton of two domestic taxa: the horse and donkey. Proc. R Soc. B 284, 20171241. https://doi.org/10.1098/rspb.2017.1241.

Heglund, N.C., Cavagna, G.A., Taylor, C.R., 1982. Energetics and mechanics of terrestrial locomotion. III. Energy changes of the centre of mass as a function of speed and body size in birds and mammals. J. Exp. Biol. 97, 41–56.

Hildebrand, M., 1987. The mechanics of horse legs. Am. Sci. 75, 594–601.

Hildebrand, M., Goslow, G.E., Hildebrand, V., 1995. Analysis of Vertebrate Structure. John Wiley & Sons, New York.

Hyland, A., 1990. *Equus*: the Horse in the Roman World. B.T. Batsford, London.

Jolliffe, I.T., 2002. Principal component analysis. In: Springer Series in Statistics, Second ed. Springer-Verlag, New York.

Kazanski, M., Périn, P., 2005. La tombe de Childéric: un tumulus oriental?. In: Mélanges Jean-Pierre Sodini. Travaux et Mémoires. na, Paris, France, pp. 287–298.

Kazanski, M., Périn, P., 1988. Le mobilier funéraire de la tombe de Childéric 1er ; état de la question et perspectives. Rev. Archéologique Picardie 3, 13–38. https://doi.org/10.3406/pica.1988.1528.

Kelekna, P., 2009. The Horse in Human History. Cambridge University Press, Cambridge.

Kiesewalter, L., 1888. Skelettmessungen am Pferde als Beitrag zur theoretischen Grundlage der Beurteilungslehre des Pferdes (Leipzig).

Klingenberg, C.P., 2014. Studying morphological integration and modularity at multiple levels: concepts and analysis. Phil. Trans. R Soc. B 369, 20130249. https://doi.org/10.1098/rstb.2013.0249.

Krzanowski, W.J., 1988. Principles of Multivariate Analysis: A User's Perspective. Oxford University Press, Inc., New York, NY, USA.

Krzanowski, W.J., 1987. Cross-validation in principal component analysis. Biometrics 43, 575–584. https://doi.org/10.2307/2531996.

Lanyon, L.E., 1980. The influence of function on the development of bone curvature. An experimental study on the rat tibia. J. Zool. 192, 457–466. https://doi.org/10.1111/j.1469-7998.1980.tb04243.x.

Lanyon, L.E., Magee, P.T., Baggott, D.G., 1979. The relationship of functional stress and strain to the processes of bone remodelling. An experimental study on the sheep radius. J. Biomech. 12, 593–600. https://doi.org/10.1016/0021-9290(79)90079-4.

Lebedynsky, I., 2001. Armes et guerriers barbares au temps des grandes invasions: IVe au VIe siècle apr. J.-C. Editions Errance.

Lizet, B., 1989. La Bête noire: À la recherche du cheval parfait. Les Editions de la MSH, Paris, France.

Lorans, E. (Ed.), 2018. Le cheval au Moyen Âge. Presses universitaires François-Rabelais.

Martín-Serra, A., Figueirido, B., Palmqvist, P., 2014. A three-dimensional analysis of the morphological evolution and locomotor behaviour of the carnivoran hind limb. BMC Evol. Biol. 14, 129.

Martín-Serra, A., Figueirido, B., Pérez-Claros, J.A., Palmqvist, P., 2015. Patterns of morphological integration in the appendicular skeleton of mammalian carnivores. Evolution 69, 321–340. https://doi.org/10.1111/evo.12566.

May, E., 1985. Widerristhöhe und Langknochenmasse bei Pferden–ein immer noch aktuelles Problem. Z. Für Säugetierkd. 50, 368–381.

Mcnulty, K.P., Vinyard, C.J., 2015. Morphometry, geometry, function, and the future. Anat. Rec. 298, 328–333. https://doi.org/10.1002/ar.23064.

Milne, N., 2016. Curved bones: an adaptation to habitual loading. J. Theor. Biol. 407, 18–24. https://doi.org/10.1016/j.jtbi.2016.07.019.

Monteiro, L.R., 1999. Multivariate regression models and geometric morphometrics: the Search for Causal factors in the analysis of shape. Syst. Biol. 48, 192–199. https://doi.org/10.1080/106351599260526.

Müller-Wille, M., 1970. 1970–1971: Pferdegrab und Pferdeopfer im frühen Mittelalter. Ber. Van Rijksd. Voor Het Oudheidkd. Bodemonderz. 20–21.

Mulliez, J., 1983. Les Chevaux du Royaume. Histoire de l'élevage du cheval et de la création des haras,. Montalba, Paris.

Muñoz-Muñoz, F., Carreira, V.P., Martínez-Abadías, N., Ortiz, V., González-José, R., Soto, I.M., 2016. Drosophila wing modularity revisited through a quantitative genetic approach. Evolution 70, 1530–1541. https://doi.org/10.1111/evo.12975.

Nemeschkal, H.L., 1999. Morphometric correlation patterns of adult birds (Fringillidae: Passeriformes and Columbiformes) mirror the expression of developmental control genes. Evolution 53, 899–918. https://doi.org/10.2307/2640730.

Oexle, J., 1984. Merowingerzeitliche Pferdebestattungen–Opfer oder Beigaben. Frühmittelalterliche Stud. 18, 122–172.

Olson, E.C., Miller, R.L., 1958. Morphological Integration. University of Chicago Press, Chicago.

Orlando, L., Ginolhac, A., Zhang, G., Froese, D., Albrechtsen, A., Stiller, M., Schubert, M., Cappellini, E., Petersen, B., Moltke, I., Johnson, P.L.F., Fumagalli, M., Vilstrup, J.T., Raghavan, M., Korneliussen, T., Malaspinas, A.-S., Vogt, J., Szklarczyk, D., Kelstrup, C.D., Vinther, J., Dolocan, A., Stenderup, J., Velazquez, A.M.V., Cahill, J., Rasmussen, M., Wang, X., Min, J., Zazula, G.D., Seguin-Orlando, A., Mortensen, C., Magnussen, K., Thompson, J.F., Weinstock, J., Gregersen, K., Røed, K.H., Eisenmann, V., Rubin, C.J., Miller, D.C., Antczak, D.F., Bertelsen, M.F., Brunak, S., Al-Rasheid, K.A.S., Ryder, O., Andersson, L., Mundy, J., Krogh, A., Gilbert, M.T.P., Kjær, K., Sicheritz-Ponten, T., Jensen, L.J., Olsen, J.V., Hofreiter, M., Nielsen, R., Shapiro, B., Wang, J., Willerslev, E., 2013. Recalibrating Equus evolution using the genome sequence of an early Middle Pleistocene horse. Nature 499, 74–78. https://doi.org/10.1038/nature12323.

Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20, 289–290. https://doi.org/10.1093/bioinformatics/btg412.

Pasi, B.M., Carrier, D.R., 2003. Functional trade-offs in the limb muscles of dogs selected for running vs. fighting. J. Evol. Biol. 16, 324–332. https://doi.org/10.1046/j.1420-9101.2003.00512.x.

Périn, P., Kazanski, M., 2007. La tombe de Childéric, le Danube et la Méditerranée. In: Villes et Campagnes En Neustrie, Europe Médiévale. M. Mergoil, Montagnac, pp. 29–57.

Polly, P.D., 2008. Adaptive zones and the pinniped ankle: a three-dimensional quantitative analysis of carnivoran tarsal evolution. In: Mammalian Evolutionary Morphology, Vertebrate Paleobiology and Paleoanthropology Series. Springer, Dordrecht, pp. 167–196. https://doi.org/10.1007/978-1-4020-6997-0_9.

Putelat, O., Koziol, A., Bocherens, H., Guintard, C., 2017. Les chevaux de la nécropole d'Odratzheim « Sandgrube » (Bas-Rhin). Étude archéozoologique et ostéométrique. In: Le Cheval Au Moyen Age, Perspectives Historiques. Presses Universitaires François-Rabelais, Tours, pp. 319–344.

Quast, D., 2015. Das Grab des fränkischen Königs Childerich in Tournai und die Anastasis Childerici von Jean-Jacques Chifflet aus dem Jahr 1655, Monographien des Römisch-Germanischen Zentralmuseums. Verlag Schnell & Steiner Regensburg, Mainz.

R Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rech, M., 2007. Pferdeopfer-Reiterkrieger: Fahren und Reiten durch die Jahrtausende; Begleitpublikation zur gleichnamigen Ausstellung im Focke-Museum/Bremer Landesmuseum vom 5.12. 2006 bis 25.3. 2007, im Gustav-Lübcke-Museum Hamm vom 22.04. 2007 bis 29.7. 2007, im Museum Burg Linn, Krefeld, vom 26.8. 2007 bis 2.12. 2007. Habelt.

Ripley, B.D., 1996. Pattern Recognition and Neural Networks. Cambridge University Press, Cambridge.

Rohlf, F.J., Corti, M., 2000. Use of two-block partial least-squares to study covariation in shape. Syst. Biol. 49, 740–753. https://doi.org/10.1080/106351500750049806.

Rohlf, F.J., Slice, D., 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. Syst. Biol. 39, 40–59. https://doi.org/10.2307/2992207.

Salin, E., 1957. La civilisation merovingienne, d'apres les sepultures les textes et le laboratoire.

Schlager, S., 2016. Morpho: Calculations and Visualisations Related to Geometric Morphometrics.

Seetah, K., Cardini, A., Barker, G., 2016. A 'long-fuse domestication'of the horse? Tooth shape suggests explosive change in modern breeds compared with extinct populations and living Przewalski's horses. Holocene 26, 1326–1333.

Seetah, K., Cucchi, T., Dobney, K., Barker, G., 2014. A geometric morphometric re-evaluation of the use of dental form to explore differences in horse (*Equus caballus*) populations and its potential zooarchaeological application. J. Archaeol. Sci. 41, 904–910. https://doi.org/10.1016/j.jas.2013.10.022.

Steuer, H., 2003. Pferdegräber. Reallexikon Ger. Altertumskunde 23, 50–96.

Toynbee, J.M.C., 1973. Animals in Roman Life and Art. Thames and Hudson, London, UK.

Truc, M.-C., 2008. Trois riches tombes du VIe siècle sur le site de La Tuilerie à Saint-Dizier (Haute-Marne). In: Guillaume, J., Peytremann, E. (Eds.), L'Austrasie. Sociétés, Économies, Territoires, Christianisation. Actes Des XXVIe Journées Internationales D'archéologie Mérovingienne, Nancy, 22-25 Sept. 2005. Presses universitaires de Nancy, Nancy, France, pp. 313–329.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, Fourth. Springer, New York.

Wagner, G.P., Altenberg, L., 1996. Perspective: complex adaptations and the evolution of evolvability. Evolution 50, 967–976. https://doi.org/10.2307/2410639.

Wagner, M.-A., 2005. Le cheval dans les croyances germaniques: paganisme, christianisme et traditions. Honoré Champion, Paris, France.

Werner, J., 1988. Adelsgräber von Niederstotzingen bei Ulm und von Bokchondong in Südkorea: Jenseitsvorstellungen vor Rezeption von Christentum und Buddhismus im Lichte vergleichender Archäologie; vorgetragen in der Klassensitzung am 11. Dezember 1987. Verlag d. Bayer. Akad. d. Wiss.

West-Eberhard, M.J., 1989. Phenotypic plasticity and the origins of diversity. Annu. Rev. Ecol. Syst. 20, 249–278. https://doi.org/10.1146/annurev.es.20.110189.001341.

White, K.D., 1970. Roman Farming. Cornell University Press, Ithaca, N.Y.

Wiley, D.F., Amenta, N., Alcantara, D.A., Ghosh, D., Kil, Y.J., Delson, E., Harcourt-Smith, W., Rohlf, F.J., John, K.S., Hamann, B., 2005. Evolutionary morphing. In: Proceedings of IEEE Visualization 2005. Presented at the VIS 05. IEEE Visualization, 2005. IEEE, Minneapolis, pp. 431–438. https://doi.org/10.1109/VISUAL.2005.1532826.

Wood, I., 2014. The Merovingian Kingdoms 450-751. Routledge.

Young, N.M., Hallgrímsson, B., 2005. Serial homology and the evolution of mammalian limb covariation structure. Evolution 59, 2691–2704. https://doi.org/10.1554/05-233.1.

Yvinec, J.-H., Lepetz, S., 2002. Presence d'especes animales d'origine mediterraneennes en France du nord aux periodes romaine et medievale: actions anthropiques et mouvements naturels'. In: Mouvements Ou Deplacements Depopulations Animales En Mediterranee Au Cours de l'Holocene. BAR International Series, pp. 33–42.

Zelditch, M.L., Swiderski, D.L., Sheets, H.D., 2012. Geometric Morphometrics for Biologists: A Primer. Academic Press.

Zöllner, E., Schmidt, L., 1970. Geschichte der Franken bis zur Mitte des sechsten Jahrhunderts. Beck.