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# Equids in Time and Space

*Papers in Honour of Véra Eisenmann*

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## 12. Western European Late Glacial horse diversity and its ecological implications

*Olivier Bignon & Véra Eisenmann*

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*Late Glacial Horses have been studied by applying conventional and geometric morphometrics to archaeological and palaeontological samples. All archaeological collections belong to the end of the Oldest Dryas and the Bölling pollen chronozones (13 000 – 12 000 years BP). The palaeontological collection covers the Late Glacial period (circa 15 000 – 10 000 years BP). Wild horse (*Equus caballus arcelini*) populations of three distinct areas: Switzerland Plateau (archaeological samples), Paris Basin (archaeological samples, France) and Charente (palaeontological samples, France) were compared. The results evidence: 1. similarity of ground/hooves interactions (as shown by the third phalanges), in spite of different regional topographical contexts, 2. clear differences between regional populations (as based on the metapodials). The first point seems related to horse preferences for bank river and/or marshy habitats. The second - to low genetic flux exchanges and absence of large scale migrations. It suggests that the characteristic mosaic traits (or at least some of them) of the Mammoth-Steppe have lingered until around 12 000 BP in Western Europe. The higher diversity in Paris Basin very likely results from superimposition of recapture waves originating in different, more northern, or central areas.*

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### **Introduction**

At the end of the Pleistocene, after the last maximum glacial (around 18 000 BP), the Late Glacial (15 000 to 10 000 BP) is known to be a very unstable climatic period (Grootes *et al.* 1993; Magny 1995; Stuiver *et al.* 1995). Many ice core samples from Greenland have recorded in detail the large and quick fluctuations of the climate that appears to never find an equilibrium (Björck *et al.* 1998). The major climatic transitions correlate well with the European chronozones sequence (pollen zone boundaries; Fig. 1). But in addition to these large signals, the temperature conditions show a regionally contrasted situation in Western Europe (Lowe & N.A.S.P. Members 1995; Walker 1995; Coope *et al.* 1998; Witte *et al.* 1998). The large “Mammoth-Steppe” communities blossomed in this heterogeneous landscape, and survived successfully until the early Holocene in northern areas (Guthrie 1982, 1990; Kahlke 1999; Lister & Sher 2001). Later on, under climatic impulsions, a global biozonation modification

took place in the Eurasiatic continent where the “plaid” landscape of the Mammoth-Steppe changed into the modern “stripes” pattern (Guthrie 1982, 1990), the heterogeneous mosaic landscapes being replaced by more marked and less diversified zonations (Hopkins *et al.* 1982; Kahlke 1999).

Indeed, a complex palaeoecological transition (Guthrie, 1982, 1984) occurring during the warmer Bölling/Alleröd interstadial (12 700 – 11 000 BP) results in an increase of the number of species inside most regional communities of Western Europe (Eriksen 1996, Bridault & Chaix 2002). During this process, current glacial animal communities tend to be gradually changed, with massive extinction of some species (woolly mammoth, woolly rhinoceros, etc.) and new associations of some others (red deer, roe deer, wild boar, aurochs, etc.). But the Pleistocene-Holocene transition is not a simple shifting of elementary faunal or flora components, it is an evolutionary process that modified the coevolutionary

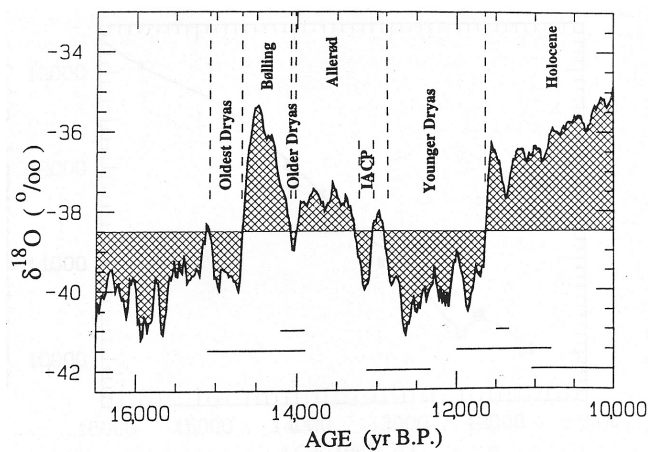


Fig. 1. Late Glacial climate variations and pollen chronozones (Stuiver et al., 1995).

inner interactions between both animal and vegetal communities (Graham & Lundelius 1984).

The subject of this study is the wild horse, *Equus caballus arcelini* (Guadelli 1991), during the very Late Glacial. The wild horse is a common component of the Mammoth-Steppe faunal communities, and moreover a key-species, in initiating the grazing process and, in this way, opening the access of other herbivores to their respective vegetation layers (Bell 1971, Guthrie 1982, Martin 1982). The study of its anatomy may give some general information on its interaction with the landscape and the evolution of the latter. In addition, evidence of its diversity could lead to a better appreciation of adaptive strategies of populations during this unstable period, namely demographic structuration and interpopulational degree of genetic flux (Bignon 2003; Bignon et al. 2005).

A multi-scale approach, inspired by biogeographical methods (Blondel 1995), is used to compare the fossils of three different regions (Fig. 2):

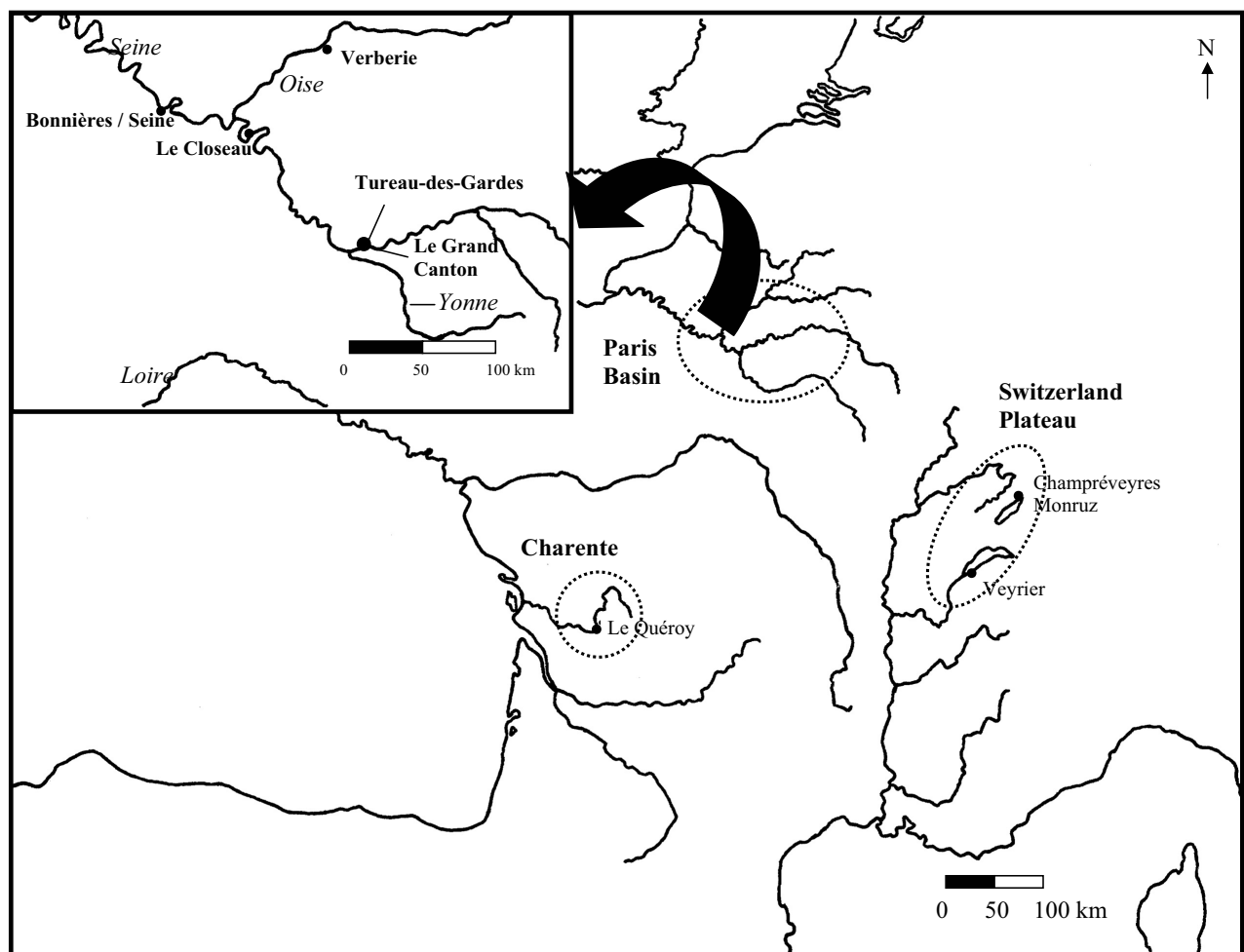


Fig. 2. Location of sites and regions.

Table 1. Chronological data per geographical areas. 1) J.-F. Tournepicche (1987); 2) D. Leesch (1997); 3) A. Bridault (2000), J. Bullinger (2002); 4) P. Bodu (1998); 5) M. Julien & J.-L. Rieu (1999); 6) A. Bridault (personal communication); 7) O. Bignon (personal communication); 8) F. Audouze (1994).

| Areas             | Sites                         | Lab code           | Radiocarbon ages BP  | Radiocarbon ages cal BP |
|-------------------|-------------------------------|--------------------|----------------------|-------------------------|
| 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         |
| 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 – 12834          |
|                   |                               | OxA-3139           | 12 650 +/- 130       | 15 128 – 14621          |
| Parisian Basin    | Tureau-des-Gardes – S.6 (6)   | Ly 6988            | 12 290 +/- 90        | 15 450 – 14 050         |
|                   | Tureau-des-Gardes – S.10 (7)  | AA44214            | 12 170 +/- 130       | 14 660 – 13 830         |
| Parisian Basin    | Verberie (Buisson Campin) (8) | Thermoluminescence | 13 300 +/- 850       | 18 011 – 13 489         |
| Parisian Basin    | Bonnières/Seine               |                    | Magdalenian industry |                         |

- Paris Basin (France, 6 archaeological sites),
- Switzerland Plateau (Switzerland, 3 archaeological sites),
- Charente (France, the palaeontological site of Le Quéroy).

All the Magdalenian or Azilian sites of the Paris Basin and the Switzerland Plateau are dated around 13 300 BP and 12 000 BP, while Le Quéroy (Charente) has yielded horses from the bottom (around 13 000 BP) to the top of its stratigraphy (around 10 000, Tab. 1). Given the

radiocarbon efficiency limitations, all the horses studied here are considered as contemporaneous. The diversity inside each region and between them is addressed at continental and regional scales. These informations are completed at a local scale by the observation of population-environment relationships, supposed to be distinct between the mountainous region of the Switzerland Plateau and the two other French regions of large valleys and lower relief.

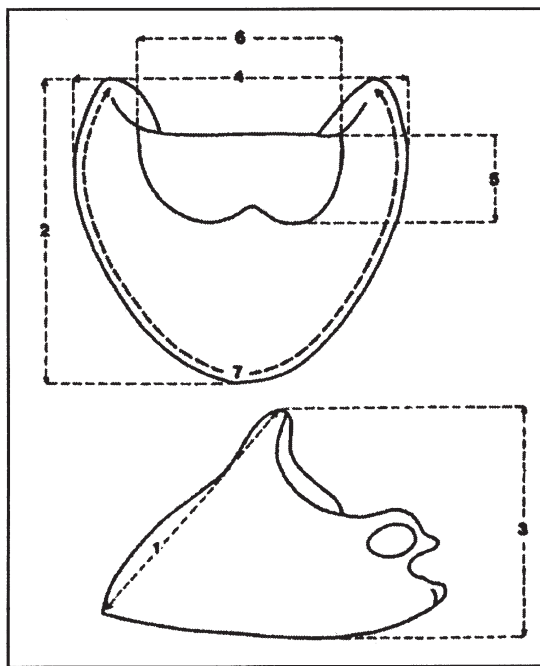


Fig. 3. Measurements of third phalanges (Eisenmann, 1986).

### Material and methods

For both the Paris Basin and the Switzerland Plateau, we studied some large horse bone collections (Le Grand Canton, Tureau-des-Gardes: Bridault 1996, 1997, Bridault *et al.* 1997, 2000, *in progress*, Bridault & Bemilli 1999, Bemilli 2000, Champréveyres, Monruz: Leesch 1997, Morel & Müller 1997) and some smaller ones (100 determined bones or less, like Verberie, Audouze 1994, Bonnières-sur-Seine: Bridault *et al. in progress*, Le Closeau: Bodu 1998, 2000, and, Veyrier: Jayet 1937, Bridault *et al.* 2000). For the Northern Aquitaine Basin, we investigated the site of Le Quéroy (Charente), which yielded numerous and well preserved horse bones (Tournepeche 1982, 1987).

The “population-environnement” relationships of Late Glacial horses is considered at the local scale by conventional morphometry of third phalanges and metapodials. Previous studies have shown that the relative width of the hoof partly depends on the nature of the ground (Fig. 3, Eisenmann 1984): in equids walking on heavy grounds, the hooves are wider, whereas they are more narrow in equids running on hard grounds or climbing rocky slopes. Table 2 gives the sample sizes.

Both regional and continental scales are analysed by the homologous landmarks method, from the geometric morphometrics approach (Bookstein 1991, Baylac 1996). This method allows to work separately on shape and isometric size of a given object; the latter is defined by landmarks that have three dimensional coordinates. Each

Table 2. Sample sizes of third phalanges.

| Areas                          | Third phalanges |
|--------------------------------|-----------------|
| <b>Charente [1]*</b>           | <b>19</b>       |
| Le Quéroy                      | 19              |
| <b>Switzerland Plateau [3]</b> | <b>18</b>       |
| Monruz                         | 15              |
| Veyrier                        | 3               |
| <b>Paris Basin [6]</b>         | <b>4</b>        |
| Le Grand Canton                | 1               |
| Tureau-des-Gardes (5-6)        | 3               |
| <i>Equus przewalskii</i>       | 27              |
| <i>Equus hemionus</i>          | 31              |
| <b>Sample size</b>             | <b>99</b>       |

group of objects is normalised and superimposed by a procrustes algorithm, and subjected to Principal Component Analyses (PCA), to Canonical Variate Analyses (CVA), and discriminant functions. A detailed explanation of this method is exposed in detail elsewhere (Bignon *et al.* 2005). Our studies focus on the distal condyle of metapodials, because conventional morphometry has shown that metapodials may be good discriminators of equid species (Eisenmann 1986, Eisenmann & Beckouche 1986). The selection of our 15 landmarks (Fig. n° 4) is inspired by the current morphometric measurements defined by V. Eisenmann (1986): some landmarks derive directly from the usual measurements, while the others complete the three dimensional definition of the distal condyle. Table 3 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.

### Local scale : the “population-environnement” relationships

From the usual measurements of third phalanx (Fig. 3, Eisenmann 1986), both the maximal width (4) and the articular surface width (6) show that (Fig. 5): 1) the measurements of all the Late Glacial horses and the extant equids have a significant correlation ( $y = 0,3763 x + 1,7713$ ,  $R^2 = 0,85$ ), 2). According to either of these parameters, Late Glacial horses of all regions had larger phalanges than extant equids. Could that be an adaptation to heavy grounds? To answer that question, we need to consider that the width of the hoof is also related to the size of the animal.

In order to evidence possible differences in relative width of the hooves, we have compared the metacarpal lengths and the maximal widths (4) of anterior third phalanges. The material consists in associated bones of

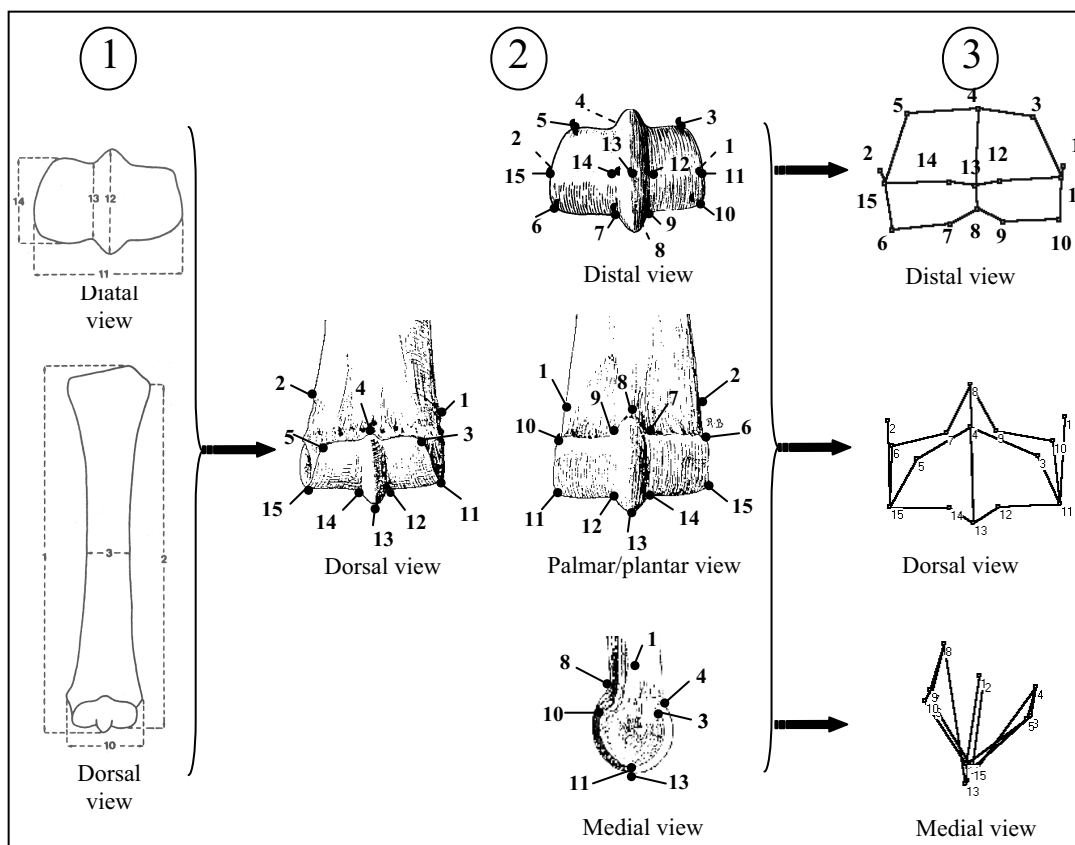


Fig. 4. Location of metapodials landmarks : (1) Traditional measurements (dotted lines) of metapodials (V. Eisenmann, 1986), (2) compared with location of landmarks (original illustration R. Barone, 1986, modified), (3) the linking of which allows the visualization of overall shapes.

Table 3. Sample sizes of metapodials. \* The number of sites per areas is indicated between brackets. \*\* In progress

| Areas                          | Metacarpals | Metatarsals |
|--------------------------------|-------------|-------------|
| <b>Charente [1]*</b>           | <b>10</b>   | <b>13</b>   |
| Le Quéroy                      | 10          | 13          |
| <b>Switzerland Plateau [3]</b> | <b>23</b>   | <b>22</b>   |
| Hauterive-Champréveyres        | 2           | 1           |
| Monruz                         | 18          | 18          |
| Veyrier                        | 3           | 3           |
| <b>Paris Basin [6]</b>         | <b>22</b>   | <b>35</b>   |
| Le Closeau                     | 0           | 1           |
| Le Grand Canton                | 3           | 9           |
| Tureau-des-Gardes (5-6)        | 7           | 7           |
| Tureau-des-Gardes (10)         | 12          | 15          |
| Verberie                       | 0           | 1           |
| Bonnières/Seine                | 0           | 2           |
| <b>Sample size</b>             | <b>55</b>   | <b>70</b>   |

three species living in semi-desertic conditions: *E. hemionus onager* (the Iranian Hemione), *E. grevyi* (the largest extant Zebra), and *E. przewalskii* (the Mongolian horse). The fossil horses range from the beginning of Würm (or possibly earlier: Binagady) to the end of the Würm, and from Azerbaidjan (Binagady) to Western France (Le Quéroy-Sondage). Because most of fossil remains are not individually associated, we plotted for each locality the average metacarpal lengths and widths of what we recognized as anterior third phalanges. The scatter diagram (Fig. 6) shows that in Onagers and Grevy's zebras, third phalanges are relatively narrower than in most Horses. Possibly the truly wild *E. przewalskii* had also narrow phalanges but we had to use many zoo specimens the third phalanges of which may have been modified by breeding in captivity. Modern Arab and Egyptian Bronze Age horses (Clutton Brock 1974) have also narrow third phalanges; because they may have been iron-shod, we did not plot them on the diagram. The horse of the Late Quaternary of San Sidero 6 (Italy) is of particular interest because it is represented by a complete skeleton of uncommonly large size and narrow third phalanges. Remains of *E. hydruntinus* were found nearby

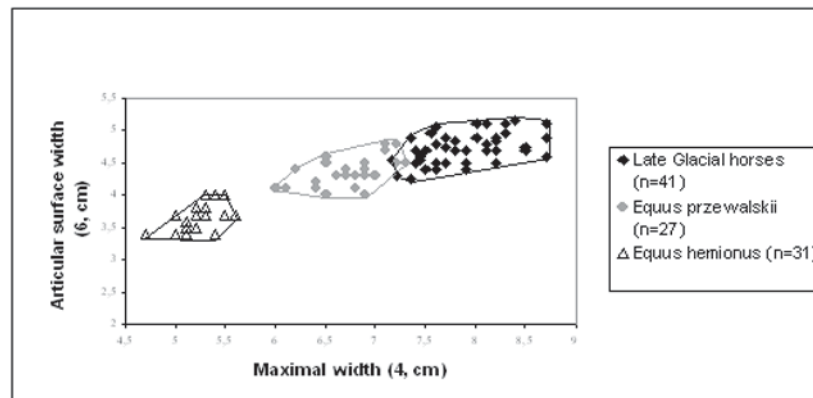


Fig. 5. Comparison between third phalanges of extant equids and Late Glacial horses: maximal width (4; see Fig. 3) and articular surface width (6).

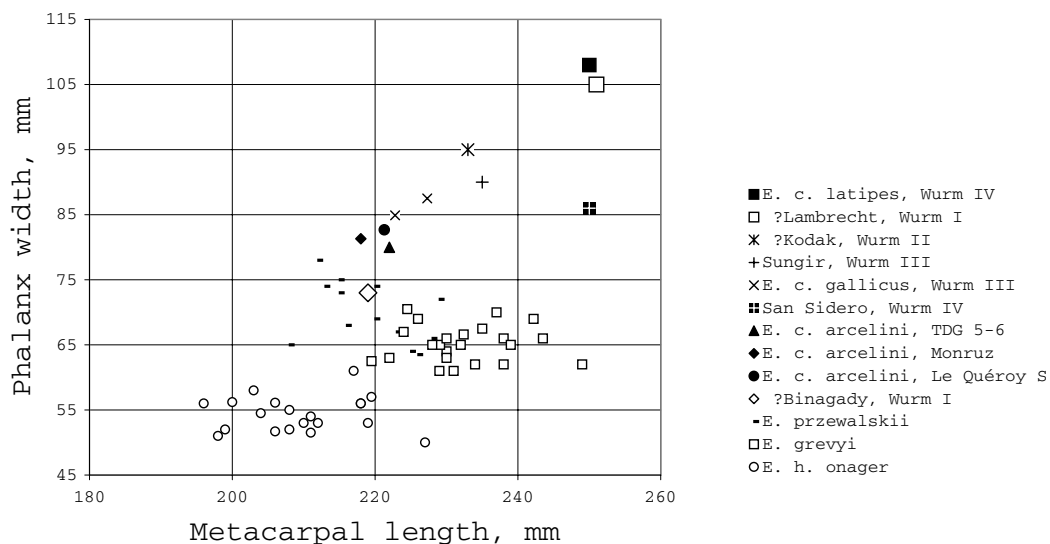


Fig. 6. Comparison between the relative width of anterior third phalanx and the length of the metacarpals.

in another sinkhole (Azzaroli, 1999). The horse of Binagady resembles more *E. przewalskii* than most Pleistocene horses (Eisenmann 1998) and seems to have also a rather narrow third phalanx. The fauna of Binagady includes remains of Hemionus and *E. hydruntinus* (Eisenmann & Mashkour 1999).

All other horses have wide third phalanges. The widest belong to the horse of Lambrecht (Hungary) probably Early Wurm (Janossy 1986) and to *E. caballus latipes* of the 'Early Magdalenian' of Kostenki IV, Russia, described on three associated anterior phalanges (Gromova 1949). Because the first phalanx resembles that of San Sidero 6, we supposed that the metacarpal length was the same. If we are right, *E. caballus latipes* had not a particularly wide third phalanx with reference to its size.

Indeed, the proportions are similar in most Wurmian horses whether smallish like *E. caballus arcelini* of Wurm IV (Tureau des Gardes, Monruz, Le Quéroy) and *E. caballus gallicus* (Siréjol and Jaurens) of Wurm III (Philippe *et al.* 1980; Mourer-Chauviré 1980) or larger like the horses of Kodak (Mousterian) and Sungir (Wurm III) measured by Gromova (1949) and Vangengeim (1966). It seems that all these horses were adapted to rather heavy grounds.

The Late Glacial horses *E. caballus arcelini*, seems to have constantly frequented heavy grounds habitats despite the different topographical features of our regional areas. A possible explanation for that common adaptation in these contrasted landscapes is the importance of two particularly developed habitats during this period (Leesch



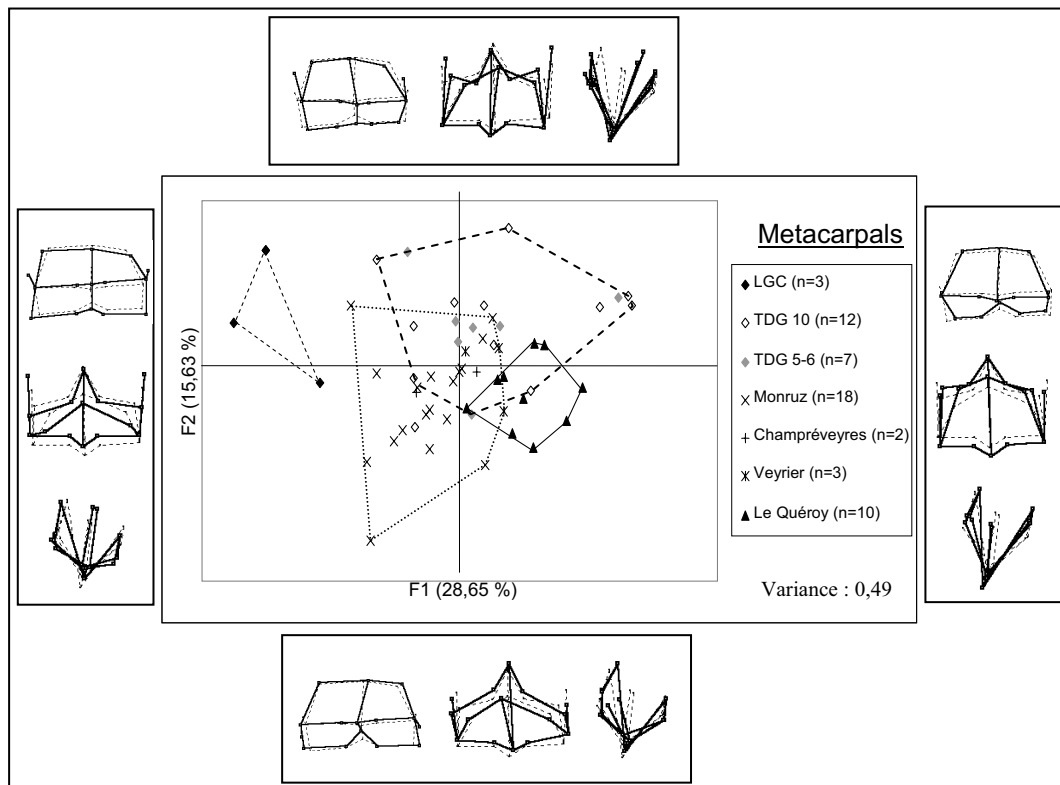


Fig. 7. Plots onto the first PCA plane for metacarpals. Symbols are for sites, while convex-hulls delineate regions. Extreme shapes are represented at both extremities of each PCA axis (left and right for the first axis, bottom and top for the second one). Extreme shapes are figured out by a solid line. Superimposed in dotted line, the consensus (or mean) shape.

1997, Antoine *et al.* 2000, Pastre *et al.* 2000): large river banks in valleys or lakes and occurrence of local marshy environments. Indeed, the most important Magdalenian butchery sites in the Paris Basin (Tureau-des-Gardes, Le Grand Canton) or on the Switzerland Plateau (Champréveyres, Monruz), were located directly on river banks with important marshes in the vicinity. These habitats appear to favour the annual maintenance of a varied vegetation suitable to horses (as in the Camargue, Duncan 1992), which should have been a crucial point in the unstable Late Glacial climate (Guthrie 1982, 1984, 1990).

#### Regional and continental scales : horse morphotypes and regional population pattern

While the low isometric size differences between sites or regions are discussed in detail elsewhere (Bignon *et al.* 2005), the results presented here focus on the shape analysis of metapodials. Preliminary PCA analyses have been realised separately for the metacarpals and metatarsals, in order to highlight the total group variability, expressed by shape trends and specimen distributions on

scatter diagrams. The two first axes express the main shape trends and add up to more than 40 % the variability (44,98 % for the metacarpals; 40,98 % for the metatarsals). The shape differences exhibit a regional grouping pattern with partial overlaps, despite a less clear distribution in the case of metatarsals. The plane of metacarpals (Fig. 7) shows the complex variability of Paris Basin specimens; this region possesses two morphotypes, one of which is characteristic of Le Grand Canton equids (and Le Closeau in the case of metatarsals). The first axis evidences that distinction and tends to separate also the horses of the Switzerland Plateau and Le Quéroy. The shape trend associated to this first axis is a more massive and rounded condyle structure (Le Grand Canton), in opposition to a distally stretched morphology (Paris Basin, Le Quéroy). The second axis of metacarpals tends to separate Paris Basin specimens from the Switzerland and Le Quéroy ones: the former have a more developed dorsal articular surface with a “V”-like border, opposed to the balanced articular surface and “W”-like dorsal border of the latter. In the case of metatarsals, the shape trend tends also to distinguish the different regional horses, but on the F2 axis (F1 registering common features of each regional sample). These PCA results suggest the

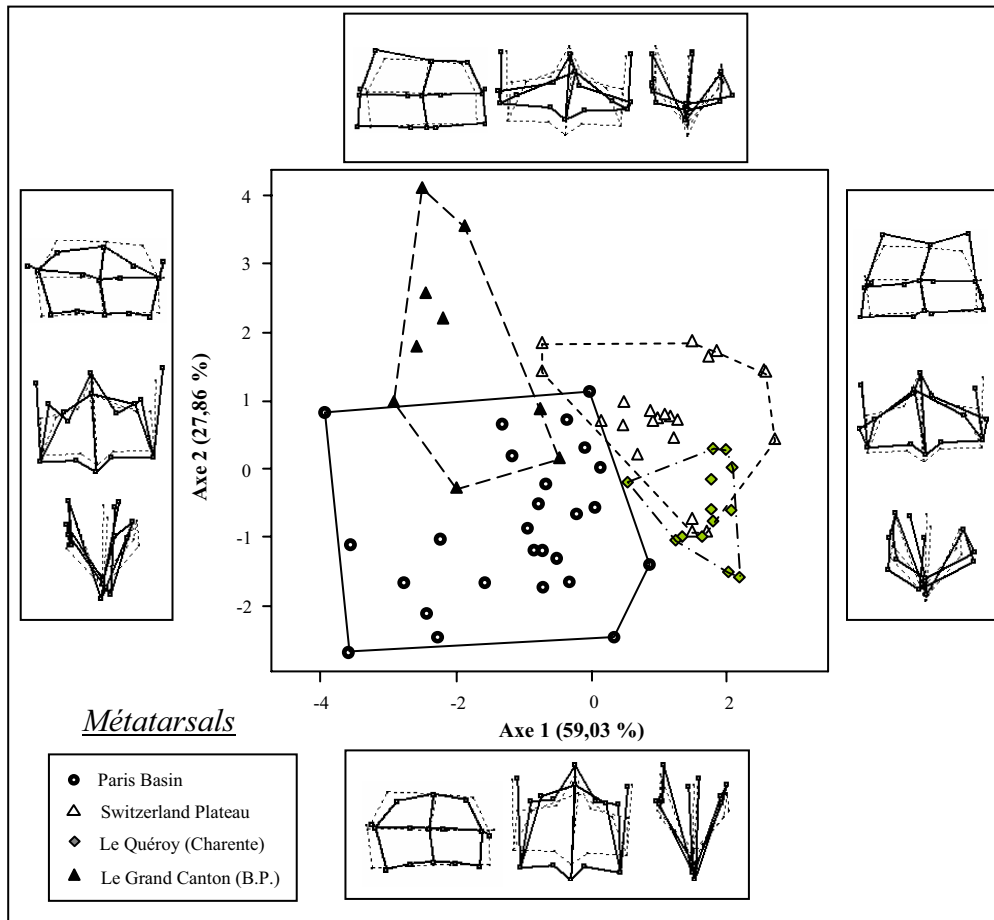


Fig. 8. Plots onto the first plane of a canonical variate analysis of metatarsi at the region level. Le Grand Canton specimens have been treated separately from the Paris Basin for reasons of shape heterogeneity (see text).

existence of regional population of horses at the very end of Late Glacial.

Subsequent CVA analyses try to characterise more precisely each of the regional shape trends. Since those trends are the same, and produce a similar distribution pattern, only the largest set of samples, i.e. the metatarsals, is presented here, (Fig. 8). Taking into account the PCA results, the Paris Basin samples have been modified: the metatarsal sample has been divided into two sub-samples, one for Le Grand Canton and one for the remaining localities. The component numbers of CVA analyses are those which maximize the correct classification percentages obtained by cross-validation (Tab. 4): first six principal components for metacarpals and first nine for metatarsals.

The metatarsal MANOVA results are highly significant: Wilks = 0.1149,  $F = 9.912$ ,  $df = 27 / 170.03$ ,  $p = 3.09 \cdot 10^{-16}$ . The total percentage of cross-validated correct classifications obtained by discriminant analyses (74.9 %) were lower than those observed for the metacarpals. Results for each region (Tab. 6) are also

lower with the single exception of Switzerland. The F1 x F2 plane explaining 86.9 % of the variance will be the only one discussed, since the third axis (13.1 %) does not increase the discrimination. The CVA for metatarsals (similar for metacarpals) shows a global grouping pattern (Fig. 10): the first canonical axis (59.8 %) opposes the groups of Paris Basin to Switzerland Plateau and Charente; the second axis (27.9 %) tends to separate on the one hand, Le Grand Canton specimens from the rest of the Paris Basin, and on the other hand, the Switzerland Plateau specimens from those of Charente. The CVA shape trends of metatarsals are remarkably close to metacarpals trends, but their order is inverted: the F1 shape features of metatarsals looks like the F2 of metacarpals and conversely. Although the CVA is less efficient for metatarsals than for metacarpals, both provide a similar clear pattern of shape trends and a coherent regional grouping.

Table 4. Cross-validated classification percentages obtained by linear discriminant analyses of metatarsal shapes. Lines = original memberships, columns = predicted memberships. Le Grand Canton has been separated out from the Parisian Basin for heterogeneity reasons (see text).

|                     | Paris Basin (France) | Le Grand Canton (B.P., France) | Le Qu erois (Charente, France) | Switzerland Plateau | Sample size |
|---------------------|----------------------|--------------------------------|--------------------------------|---------------------|-------------|
| Paris Basin         | <b>69,23</b>         | 11,54                          | 3,85                           | 15,38               | 26          |
| Le Grand Canton     | 0,00                 | <b>69,23</b>                   | 0,00                           | 30,77               | 13          |
| Le Qu erois         | 0,00                 | 0,00                           | <b>55,56</b>                   | 44,44               | 9           |
| Switzerland Plateau | 0,00                 | 4,55                           | 9,09                           | <b>86,36</b>        | 22          |

## Discussion and Conclusions

Our multi-scale biogeographic approach, with the help of conventional and geometric morphometrics, highlights some aspects of horse ways of life during the late Glacial in Western Europe. At a local scale, we observe a remarkable homogeneity in the third phalanges: their large relative width brings evidence of a rather heavy ground in all areas. It is probably related to the global climatic context and the local ecology, namely the food exploitation by horses of river banks and marshes vegetation.

At a regional scale, the homogeneity of horses within Switzerland Plateau or Le Qu erois (Charente) is evidenced by geometric morphometrics analyses of metapodials. On the contrary, the Paris Basin horses are represented by two morphotypes.

At the continent scale, the landmarks method associated to canonical and discriminant analysis shows that there were regional horse populations until the very end of Pleistocene in Western Europe (Bridault & Chaix 2002). Our study of horses confirms the results obtained on other taxa, namely by morphometric studies on reindeer (Weinstock 1997, Fontana 2000), that reached the same conclusion: regional populations did exist through Western Europe (in south of France, Paris Basin, Belgium, Germany and Switzerland). The fragmentation of Late Glacial horse populations should have depended on the existence of high demographic density (Remmert 1980, Chernov 1985) and the exchanges of genetic flux between each regional population must have been low at that time. Large scale migrations, far from being a necessity for food procurement or renewing genetic flux, seem to have been rare, at least until the end of B olling pollen chronozone (around 12 000 BP). These observations appear to confirm the persistence of a fragmented structuration of animal communities, very likely in relation with the maintaining of the mosaic pattern of vegetal communities.

The horses story scenario at the end of Late Glacial can be drawn as follow. After the maximum glacial (around 18 000 BP), the horse recolonisation of

septentrional territories has been realised during unstable climatic and ecological periods. The colonisation process produces a regional fragmentation of horse populations, while the recapture is carried out essentially by the lowlands. Within northern areas, as inside the Paris Basin, the diversity appears higher than in southern areas, supposed to be the origin territories. This higher diversity may result from superimpositions of recapture waves originating in other areas than those studied here. Two main factors could explain this phenomenon. First, the warming trend at the end of the Late Glacial increased the sea level, reducing therefore the northern and western terrestrial territories. Thus, some horse populations should have been pushing back out of the Channel area, partly to the South and Central part of France. Secondly, the sedges and graminoids, which represented the main horse's food, should have been more sensitive to climatic fluctuations in northern areas than equids themselves (Groves 1974, Duncan 1992): during this instable period, the available amount of food could have played a important role in the distribution of high density horse populations. A complementary research in different Western Europe areas should confirm the validity of these assumptions, developing the multi-scale approach and using both conventional and geometric morphometrics analyses.

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