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# Dental wear analyses of Middle Pleistocene site of Lunel-Viel (Hérault, France): did *Equus* and *Bos* live in a wetland?

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## Abstract

This study presents comparison of dental meso and micro wear analyses on Middle Pleistocene equids and bovids from Lunel-Viel I (Hérault, France) with their extant counterpart from Camargue. Previous paleoenvironmental observations hypothesize a great proximity between the Camargue wetland and Lunel-Viel environment. Teeth wear analyses provides an innovative approach to describe eco-ethological parameters, such as diet and biotope.

Camargue's horses and cattle diets are closed and characterized by a mixed feeding. Lunel-Viel I's *Equus* had a grass-dominated mixed feeding diet while *Bos* had a browsing diet. The differences in the feeding habits and resource partitioning between the two taxa in the two locations suggest two different biotopes. While the extant sample still need to be completed, preliminary observations indicate that it is very unlikely bovids and equids from Lunel-Viel inhabited a biotope like nowadays Camargue.

This study highlights the contributions of a combined comparative approach and adds new data to analyse the paleodietary patterns of extinct ungulates.

## Keywords

Microwear; Mesowear; Equidae; Bovidae; Pleistocene; Wetland; Uniformitarianism

## 1. Introduction

Lunel-Viel I (Hérault, France) is an important site for the understanding of Human behaviour in the South of France as well as the evolution and adaption of the fauna. Discovered in 1800, the first excavation occurred between 1824 and 1827 lead by M. Mouquin-Taudon and M. de Serres (Serres (de), 1839). The site was, at first, known for its rich accumulation of fauna and later, lithic artefacts were described by E. Lartet (Garrigou, 1865). Between 1962 and 1983, new excavations took place led by E. Bonifay which permitted several aspects of the site: geology (Bonnet, 1967), human activities (Bonifay E., 1981; Guilhaumon, 1982; Le Grand, 1994a, 1994b), taphonomy (Fosse, 1994a, 1994b; Fourvel, 2012; Fourvel et al., 2012) and fauna (Bonifay M.-F., 1971, 1980; Brugal, 1983, 1984; Noury, 2005; Croitor et al., 2008; Boudadi-Maligne, 2010; Uzunidis-Boutillier, 2017) to be studied.

Several new species or sub-species were described through Lunel-Viel I fossils, among them, one of the main species represented in the site, *Equus mosbachensis palustris* Bonifay, 1980. Several morphometric criteria justify this attribution, and in particular, the significant recurrence of archaic characters, reminiscent of the oldest *Equus mosbachensis* (Bonifay, 1980). Nevertheless, M.-F. Bonifay named this subspecies from another characteristic of its skeleton. She noted the important

robustness of the horse's limbs, in particular the metapodials that she interprets as a marker of a humid climate. Given the location of the site, near the current Camargue, an important wetland, she hypothesizes that the Lunel-Viel horse occupied a biotope similar to that of the present-day Camargue (Bonifay, 1980). Indeed, *Equus* from the caballine lineage is known to be a sensitive species which inhabited a large range of biotopes during the Pleistocene. Several ecomorphological studies also suggest that this species is a good indicator to discuss some aspect of the local climate and environment such as the temperature, the humidity or the character of the substrate for example (e.g. Gromova, 1949; Eisenmann, 1984; Lindstedt and Boyce, 1985; Foronova, 2006; Bro-Jørgensen, 2008; van Asperen, 2010, 2012; Uzunidis-Boutillier, 2017; Boulbes and van Asperen, 2019). Nevertheless, this hypothesis has never been tested and the paleoenvironment around Lunel-Viel is still poorly known. In this study, this hypothesis was tested with the help of tooth wear analyses. Dental wear studies are regularly used to reconstruct the diet of an individual. For Herbivores, it can determine the plant composition of the diet and the vegetation structure is linked with habitat conditions and local climate (Frey and Lösch, 2010). Many studies use these approaches to identify past environmental parameters and the ecological behaviour of the species that inhabited them (eg. Merceron et al., 2004a; Merceron and Madelaine, 2006; Rivals et al., 2017; Rivals et al., 2019; Dumouchel and Bobe, 2019). Both meso- and micro-wear methods are based on the study of extant taxa (Fortelius and Solounias, 2000; Solounias and Semprebon, 2002; Sembrebon et al., 2004) and since the development of the method, several studies have been carried out to extend our knowledge, in particular of some taxa such as cervids, hippopotamuses, giraffes (eg. Merceron et al., 2004b; Boisserie et al., 2005; Rivals and Semprebon, 2017; Merceron et al., 2018). Studies show that there is no linear correlation between habitat parameters and mesowear scores (Kaiser et al. 2013; Schulz and Kaiser 2013) since both the vegetal composition of the diet and the presence of exogenous grit are involved in the mesowear signature (Kaiser et al., 2009). Moreover, in some case, the feeding behaviour could shift the mesowear signals (Wronski and Schulz-Kornas, 2015). Thus, mesowear signal can reflect local habitat and climate conditions but need to be compared to a database. Bovid and equid dietary behaviour were already investigated and studies indicate that their dietary traits are more diverse than previously known (Schulz and Kaiser 2007; Schulz and Kaiser 2013; Rivals et al., 2015; Marín-Leyva et al., 2016; Rivals and Ziegler, 2018; Saarinen et al., 2018) however, no dental wear studies about *Equus* and *Bos* feeding in wetland has yet been published.

The objective of this study is to describe Middle Pleistocene equid and bovid specimens from Lunel-Viel in comparison with their modern day counterparts from Camargue. *Equus* from Camargue focus mainly on monocots while *Bos* diet is more diverse (Duncan, 1983; Duncan, 1992; Menard et al., 2002). However, the grazing traits were expected to be less expressed on both meso- and microwear scale compared to grass eaters in a drier environment due to the presence of water (Kaiser and Schulz, 2006; Kaiser and Rössner, 2007; Winkler et al., 2019).

## 2. Material and method

### 2.1 Lunel-Viel

Lunel-Viel I (Fig. 1) is a cave site located in the South-East of France in the Hérault region. The cave is a long corridor 180 meters long and 1 to 4 meters wide dug into a Miocene limestone (Bonifay, 1980; Guilhaumon, 1982). Fourteen layers were identified according to sediment macroscopic criteria (Bonifay, 1968) and divided into two “ensembles” (ensemble 1: layers. 1 to 5; ensemble 2: layers 6 to 14). The first one refers to sediment that has slipped inside the cave. The second would result from natural and

anthropogenic inputs and is considered to be undisturbed (Bonifay, 1981; Le Grand, 1994b). Refitting and taphonomic studies carried out on lithic (Le Grand, 1994a) and fauna (Fosse, 1994a) materials challenge the integrity of the layers, which have been greatly altered by gravity and runoff phenomena. On the other hand, very few refitting could be done between the two large units. Thus, the two major groups can be considered as distinct archaeo-paleontological units (Fosse, 1996).

The site has not yet been directly dated and its age has been estimated through the evolutionary stage of the present taxa. For now, specialists agreed to situate the accumulation at the end of the Middle Pleistocene during an interglacial period between MIS 11 and MIS 7 (Bonifay, 1975; Lacombat, 2005; Boudadi-Maligne, 2010; Van Asperen, 2013; Uzunidis-Boutillier, 2017).

The Lunel-Viel faunal assemblage is varied with at least 9 species of herbivores and 14 species of carnivores excluding the small mammals, birds and reptiles. Among herbivores, equids (*Equus mosbachensis palustris*), bovids (*Bos primigenius trochoceros*) and cervids (*Cervus elaphus*) are the most abundant, while among carnivores, hyenas (*Crocuta spelaea intermedia*) dominate.

Very few data are available to describe the paleoenvironment around the site and the current hypotheses are based on the faunal associations. Thus, it is assumed that the environment was open for the upper “ensemble” and more closed for the lower “ensemble” (Fosse, 1994a). In addition, the robustness of the horses' limbs would indicate a very humid climate for the two ensembles (Bonifay, 1980).

The material is currently stored at the National Museum of Prehistory (Les Eyzies-de-Tayac, Dordogne, France). The focus was put on the two Lunel-Viel taxa that are the most similar to the current species present in Camargue and available for study: *Equus* and *Bos*. The diets of *Equus mosbachensis palustris* and *Bos primigenius trochoceros* were investigated through both meso- and micro-wear analyses which provide information on two timescales. Mesowear averages the diet over a few months or years (Fortelius and Solounias, 2000; Ackermans et al., 2018) and microwear indicate the diet for the last days of an animal's life (Grine, 1986). For the mesowear study, 20 equid teeth from the upper “ensemble” and 26 from the lower “ensemble” were selected, likewise 20 bovids teeth from the upper “ensemble” and 62 for the lower “ensemble”. For microwear study, 13 equids teeth from the upper “ensemble” and 14 from the lower “ensemble” were selected and 16 bovids teeth from the upper “ensemble” and 7 for the lower “ensemble”. The raw data have been published in Zenodo (Uzunidis, 2020) and are available at: <https://doi.org/10.5281/zenodo.3711415>.

## 2.2 Tour-du-Valat

The Tour-du-Valat (Fig. 1) research institute is located in the Camargue wetland near Arles (Bouches-du-Rhône, France). The park covers an area of approximately 2600 hectares in which there are various types of biotopes, such as temporary, semi-permanent and permanent marshes, salt meadows or wooded areas. Populations of horses and cattle live in the park in semi-captivity under surveillance but never artificially fed.

Many biological, ecological and ethological studies have been carried out in this research institute. Thus, the plant composition of biotopes (Rogers, 1981) and the feeding behaviour of current horses and cattle is already described and known (Duncan, 1983; Duncan, 1992; Menard et al., 2002).

The material gathered in the Tour-du-Valat wetland is currently stored at the MMSH (Aix-en-Provence, Bouches-du-Rhône, France) for the bovids and at the local archaeological association of Marignane (Bouches-du-Rhône, France) for the equids. Information about the period of death were available and, therefore, taken in consideration for the bovids. Unfortunately, it was not the case for the equids.

In total for mesowear study, 4 equids teeth and 19 bovids teeth were selected (Spring: 3, Summer: 6, Autumn: 5, Winter: 1). For microwear study, 10 equids teeth and 20 bovids teeth were selected (Spring: 3, Summer: 7, Autumn: 5, Winter: 1).

### 2.3 Tooth mesowear

Mesowear analysis is a method based on the observation of wear patterns on ungulate molar cusps that indicate the diet of an individual animal (Fortelius and Solounias, 2000, Rivals et al., 2007). The sharpness and the morphology of cusp apices are correlated with relative attritive and abrasive dental wear. Thus, a diet with low abrasion (and high attrition) shows very sharp molar buccal cusps and, on the contrary, a diet with high abrasion will result in rounded and blunted cusps. The relation between the diet and the shape of the cusp is reinforced by recent works which show that high level of abrasion is more likely due to the consumption of siliceous grass than the ingestion of soil or dust (Kaiser et al., 2013; Saarinen and Lister, 2016).

The broken and unworn (or marginally worn, corresponding to very young adults) teeth as well as extremely worn ones were excluded from the analysis following Fortelius and Solounias, 2000; Rivals et al., 2007; 2009. The paracone of the second upper molar was preferably selected as recommended by Fortelius and Solounias (2000).

In this study, the standardised method proposed by Mihlbachler et al. (2011) and modified by Rivals et al. (2013) was employed, already used in other works (e. g. Rivals et al., 2017; Uzunidis et al., 2017). This method categorizes tooth wear into seven groups (numbered from 0 to 6), according to their shape (0 = high and sharp; 6 = blunt with no relief). The average value of mesowear data from a single sample corresponds to the “mesowear score” noted here “MWS” (Mihlbachler et al., 2011).

### 2.4 Tooth microwear

The microwear analysis study follows the protocol established by Solounias and Semprebon, 2002 and Semprebon et al. (2004). The occlusal surface of each tooth was cleaned using acetone and then 96% alcohol. Then the surface was moulded with a high-resolution silicone (vinylpolysiloxane) and casts were made using clear epoxy resin. The transparent casts were then observed with a stereomicroscope at magnifications of x35. Observations were restricted to a standard surface of 0.16 mm<sup>2</sup> (using an ocular reticule), localised preferably on the upper tooth paracone and the lower tooth protoconid.

Adult molars and premolars (excluding P2) were selected as it was shown there both provide consistent data for dietary studies in Artiodactyla and Perissodactyla and because the intertooth variation in microwear pattern is not significant (Xafis et al., 2017). The specimens with badly preserved enamel or taphonomic defects were excluded from the analysis (King et al., 1999).

The observed micro-traces, scratches and pits in particular are left on the occlusal surfaces during mastication (Walker et al., 1978). The variability of the density of these traces due to the presence of phytoliths into the plants since dust appear to impact less the enamel surface (Merceron et al., 2016) is indicative of various diets: grazer, mixed-feeder and browser. Various features following the classification of Solounias and Semprebon (2002) and Semprebon et al. (2004) were observed: pits (small and large), scratches (fine, coarse and hypercoarse), and gouges. The scratch width score (SWS) is also calculated with a score of ‘0’ for teeth with predominantly fine scratches per tooth surface, ‘1’ for those with mixed fine and coarse scratches on the tooth surface, and ‘2’ for those with predominantly coarse scratches.

In order to fully investigate the specificities of the diet of the Lunel-Viel and the Tour-du-Valat bovids and equids as many variables as possible that can be observed through the study of dental microwear were analysed by principal component analysis (PCA). It was realised with the software Xlstat v.

2014.5.03. The principal component analysis is build thanks to Spearman rank correlation coefficients based on the rank of the selected data (the numbers of pits and scratches, the SWS, and the presence or absence of large pits), data were normalized using standard deviation. PCA on ranking data are recommended when the distribution of the set of data is not normal or when, like in this case, the set of data is very small. In addition, the dataset analysed shows a high degree of dispersion since some of the variables correspond to indices (coded between 0 and 1) while others are true quantitative data. Thus, the PCA of Spearman rank correlation is more robust for this kind of dataset (Vásquez Correa and Laniado Rodas, 2019).

### 3. Results

The mesowear analysis displays (Fig. 2) the *Equus mosbachensis palustris* from Lunel-Viel I among the present-days grazers with an index of 4.85 from the upper part of the sequence and 4.35 for the lower part. The *Bos primigenius* individuals are located with the extent mixed-feeders with an index of 2.05 for the upper part of the sequence and 2.08 for the lower part.

At the Tour-du-Valat research institute, there are very few differences between *Equus caballus* (MWS= 3.25) and *Bos taurus* (which plot between the nowadays grazers and mixed-feeder taxa (Fig. 2). Moreover, there are very few differences among the *B. taurus* individuals between the periods of the year: for spring, summer and winter (which is known only from one tooth), the MWS is equal to 3. Only the specimens that died in autumn differ with an index of 2.2 closest to the Lunel-Viel I bovids.

The microwear analysis indicates that *E. m. palustris* from the two assemblages of Lunel-Viel I plot close to the present-days grazers indicating a grass-dominated mixed feeding diet (Fig. 3). With the meso-wear results, it would suggest that those horses have eaten a majority of monocots during the year prior to their death. On the contrary, the *B. primigenius* from the two assemblages of Lunel-Viel I display with the present-day browsers.

According to the micro-wear analysis, the diets of the bovids and the equids from the Tour-du-Valat correspond to the present-day mixed-feeders (Fig. 3). The horses and the bovids that died during spring display more scratches than the other period of death for the bovids which suggest more feeding on dicots. The tooth from the *B. taurus* dead in winter display very few scratches corresponding to a browser diet comparable to the bovid from Lunel-Viel I. Nevertheless, it illustrates the feeding habit of one individual and cannot be extrapolate to a whole group.

The Principal Component Analysis allows us to compare the populations thought more microwear variables. In this case, the mean number of pits, the mean number of scratches, the presence of large pit and the SWS index were used. The variables “presence of gouges” and “presence of coarse scratches” were excluded since there were absent in all the studied populations (Tabl. 1). On the PCA (Fig. 4), the equids from Lunel-Viel I are located on the bottom left of the graph meaning there are characterized by the high number of scratches and large pits compare to the other populations. The bovids from Lunel-Viel I are located on the bottom right of the graph showing a low number of scratches, an absence of large pits and a high SW score. All the Tour-du-Valat samples are located in the higher part of the PCA because of the large amount of pits observed on the teeth (Tabl. 1). The Tour-du-Valat equid population is characterized by the high number of pits but also by their important SW score (0.5). The Tour-du-Valat spring bovid population display a bit more scratches than the three other bovid groups. Also, the Tour-du-Valat spring, summer and autumn bovids got few large pits and a low SW score. The characteristic of the specimen dead during the winter are very close to the bovids from Lunel-Viel with a low number of scratches and large pit and a high number of pits and SW score.

## 4. Discussion

### 4.1 Feeding habits of extant *Equus* and *Bos* in Camargue and fossil *Equus* and *Bos* from Lunel-Viel

The Tour-du-Valat *Bos taurus* is principally mixed-feeder according to both ecological and meso-wear data but it varies a little according to the seasons. During summer and autumn, cattle selected in particular old-field marshes biotopes rich in monocots like *Paspalum paspalodes*, *Phragmites australis*, *Alisma plantago-aquatica* can be found (Rogers, 1981). It appears to select herb-rich swards and clover (Menard et al., 2002), and so, eat both monocots and dicots in a same period.

In spring, the Tour-du-Valat cattle display the highest number of scratches among the Tour-du-Valat bovid population with a mean of 22.8 (Tabl. 1) which is consistent with the ecological observations (Menard et al., 2002). *Bos taurus* focus more on dicots such as *Bolboschoenus maritimus*, *Paspalum paspaloides*, *Juncus gerardii*, *Alopecurus bulbosus*, *Phragmites australis*, *Typha angustifolia* and *Alisma plantago-aquatica*. Very few species of monocots are present in the Camargue swamp at this season with the exception of *Halimione portulacoides* which is also part of the *Bos taurus* diet.

For winter, cattle focus mostly on monocots like coarse grasses and *Paspalum paspaloides* with a few dicots like *Halimione portulacoides* or *Phillyrea angustifolia* (Menard et al., 2002). These observations don't match with micro-wear analysis data which shows that the cow was a browser. However our observation is only based on one individual that cannot be considered representative of an entire population.

Unfortunately, the information about the period of death was not available for the Tour-du-Valat horses. Thus for this species, the tooth-wear signal must average the annual diet since they could have died all along the year. Ecological studies indicate that in the Tour-du-Valat research institute, horses had a less varied diet than cattle and select preferably monocots (Duncan, 1983; Duncan, 1992; Menard et al., 2002). These observations are consistent with both meso- and micro-wear analysis. The horse mesowear score is the highest for the Tour-du-Valat ungulates (MWS = 3.25) and a high number of scratches were observed on the enamel (mean = 21.5). Only the cattle population that died in spring which focuses on monocots exceed them.

The Tour-du-Valat mesowear values match with the mixed-feeder category but also with the grazer variability. Studies suggest that the abundance of water in the diet can affect plant abrasiveness. Meso- (Kaiser and Schulz, 2006; Kaiser and Rössner, 2007) and micro- (Winkler et al., 2019) wear dietary pattern in humid environment show less abrasiveness than in drier. In the Tour-du-Valat, the mesowear values are relatively low, especially for the horses which, however, focus on monocots. In most of the case, micro wear pattern on *Bos* and *Equus* are consistent with their diet in the wetland. The sample for *Equus* is very small but with this data configuration, it could suggest that 1) on this scale, the information were preserved, 2) the grazing characteristics (such as the number of scratches) are less expressed compare to what it could be in a drier environment.

Compare to the extant Camargue data, the Lunel-Viel I mesowear values of *Bos* are lower and *Equus*, higher; bovid were mixed-feeder with a browsing tendency while horses, were grazers.

As for meso-wear analysis, the micro-wear analysis also displays different results for Lunel-Viel I *Bos* and *Equus*. *Equus* is characterized by a large amount of scratches and the presence of large pit show a grazing diet. *Bos* is characterized by a low amount of scratches, absence of large pit and an important SW score show a more browsing diet.

The diet parameters of the two assemblages of Lunel-Viel I are very similar for both species but it differ a lot from each Tour-du-Valat populations (Tabl. 1, Fig. 4).

#### 4.2 Resource partitioning of extant *Equus* and *Bos* in Camargue and fossil *Equus* and *Bos* from Lunel-Viel

Important differences in *Equus* and *Bos* diet were noted at Lunel-Viel I and not at the Tour-du-Valat. It could suggest several hypotheses: 1) *Bos* and *Equus* were hunt in two different biotopes and later, bring into Lunel-Viel I cave. 2) both species had access to a biotope where both dicots and monocots were well represented. In this case, it would suggest that the diet niches of *Bos* and *Equus* were partitioned while the overlap is quite strong in Camargue wetland (Menard et al., 2002).

The main accumulator in Lunel-Viel cave is hyena (Fosse, 1994b; 1996). While this predator can get a pretty huge territory (up to 1,776 km<sup>2</sup> for some *Crocota* populations, Fourvel, 2012), they carry their prey (or part of it) to their den on a much smaller distance. Extant *Hyaena* carries carcasses on an average of 6.4 km (with a maximum of 15 km on one occurrence) (Mills, 1990). These distances are similar for extant *Crocota* (Brain, 1981). Thus, the specific content of a hyena's den correspond to prey living at relatively close distance. It is very unlikely that two very different biotopes could develop in this context which discards the first hypothesis.

In a European current artificial grazing wetland system such as Camargue but also Oostvaardersplassen (Netherlands), the rate of population increase is significantly higher in the horse population than in the cattle population (Vulink and Van Eerden 1998; Menard et al., 2002). It is predicted that when the cattle and horse populations come to equilibrium with the vegetation, the horses will outcompete the cattle. The coexistence of the two species should persist in a natural system if there are enough broadleaved plants neglected by horses or/and if it exists a high predation on horses which limits their number (Grange et al., 2004).

In Lunel-Viel, *Bos* and *Equus* avoided competition by preferably selecting dicots for the first species and monocots for the second one. Nevertheless, it should not be forgotten that the faunal assemblage of Lunel-Viel is rich in herbivorous taxa such as *Haploidoceros mediterraneus*, *Cervus elaphus*, *Stephanorhinus hemitoechus*, *Capreolus* cf. *Süßenbornensis* or *Equus hydruntinus*. It will be interesting to describe their role within the rich and complex environment of Lunel-Viel. The study of varied ecosystems rich in large herbivorous species such as that of African parks shows that, depending on the species and the context, competitive or, on the contrary, symbiotic behaviour can be observed (De Boer and Prins, 1990). In Lunel-Viel, the presence of other herbivore species may have been a factor that influenced the strong dietary segregation of horses and aurochs between monocots and dicots. This partition can be either seasonal either permitted by a mosaic biotope. Although the accumulations of horses and cattle occurred during a single season, it is not possible to specify which one and whether it is the same for both species (Uzunidis, 2020). Nevertheless, the succession of plant species over the seasons in the Camargue does not drastically reverse the trends and this biotope remains dominated by monocots throughout the year. Thus, the study of dental wear pattern show that, although changing slightly, the diet and the tooth wear of the cattle of the Tour-du-Valat remain fairly similar throughout the year.

The characteristics of the biotope that *Equus* and *Bos* from Lunel-Viel must have occupied do not correspond to those of today's Camargue in the light of our preliminary data. These two species cohabited in the same environment thanks to a strong partitioning of resources. It was made possible

thanks to the succession of marked seasons (which is already suggest by previous studies: Fosse, 1996) or through the development of a mosaic biotope rich in monocots and dicots.

This study underlines many differences between Lunel-Viel and nowadays Camargue from differences between the diet behaviour of present and fossil species to differences in the partitioning of resources and competitive relationships between taxa. Nevertheless, this study remains preliminary and the comparative database has yet to be completed with new specimens.

## 5. Conclusions

The aim of this study was to test the hypothesis Marie-Françoise Bonifay stated in 1980 based on a morphological study of the horse of Lunel-Viel I and the location of the site.

This study presents teeth use-wear results for extant cattle and horse from Camargue wetland. The results were confronted with ecological data gathered in the same location than the teeth: the Tour-du-Valat research institute. Tooth-wear results were consistent with the already known diet parameters and provide a comparative database in relation to a season for *Bos*, in general for *Equus*.

These observations were confronted with Lunel-Viel I *Bos* and *Equus* tooth wear analysis in order to determine if they already inhabited a wetland environment like the extent Camargue. This paper underlines important meso- and microwear differences between the Tour-du-Valat and the Lunel-Viel I ungulates. Also the diet partitioning between the two species was observed to be weak at the Tour-du-Valat and very strong at Lunel-Viel which reinforce the previous conclusions.

Those strong differences would indicate that neither the horse nor the aurochs from Lunel-Viel I fed in a wetland like the Camargue in the light of our preliminary data. Despite several features on the skeleton showing an adaptation to a humid environment and the location of the site, the horses' ecological niche must have been different from the extant Camargue equids.

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## Table and Figures

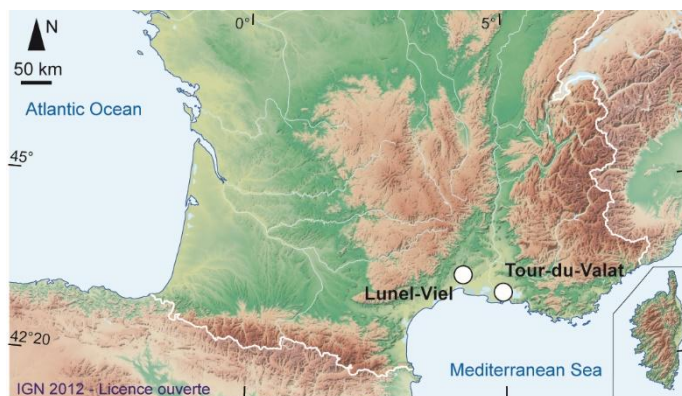


Fig. 1. Geographical location of Lunel-Viel I and the Tour-du-Valat research institute.

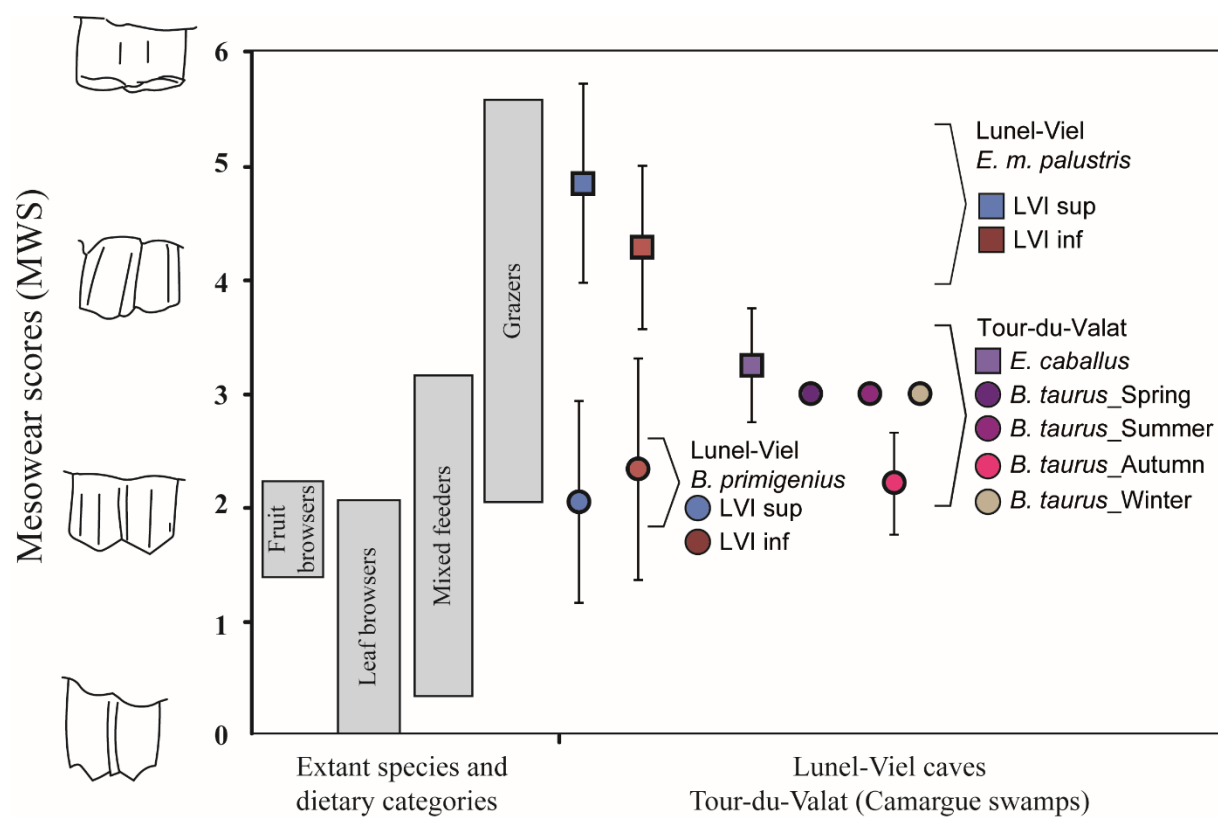


Fig. 2 . Mesowear (A)) results for the bovids and equids from Lunel-Viel I and the Tour-du-Valat research institute (this study) and extant ungulates (from Fortelius and Solounias (2000), Solounias and Semperebon (2002), Rivals et al. (2010, 2014)).

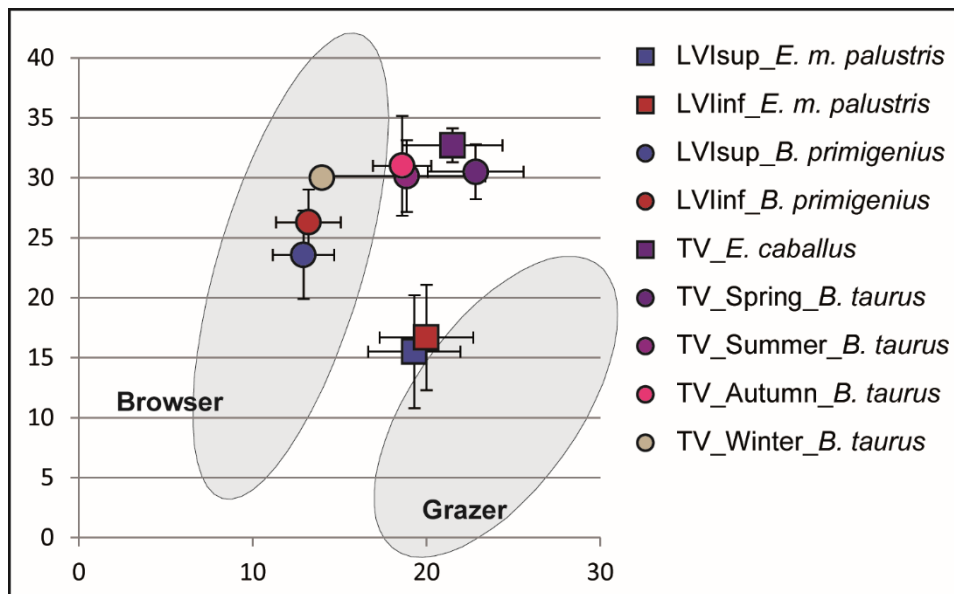


Fig. 3. Bivariate plot of the average numbers of pits and scratches in the equids and bovids from Lunel-Viel I and the Tour-du-Valat research institute. Error bars correspond to standard deviation ( $\pm 1$  SD). Plain ellipses correspond to the Gaussian confidence ellipses ( $p = .95$ ) on the centroid for the extant leaf browsers and grazers from Solounias and Semperebon (2002).

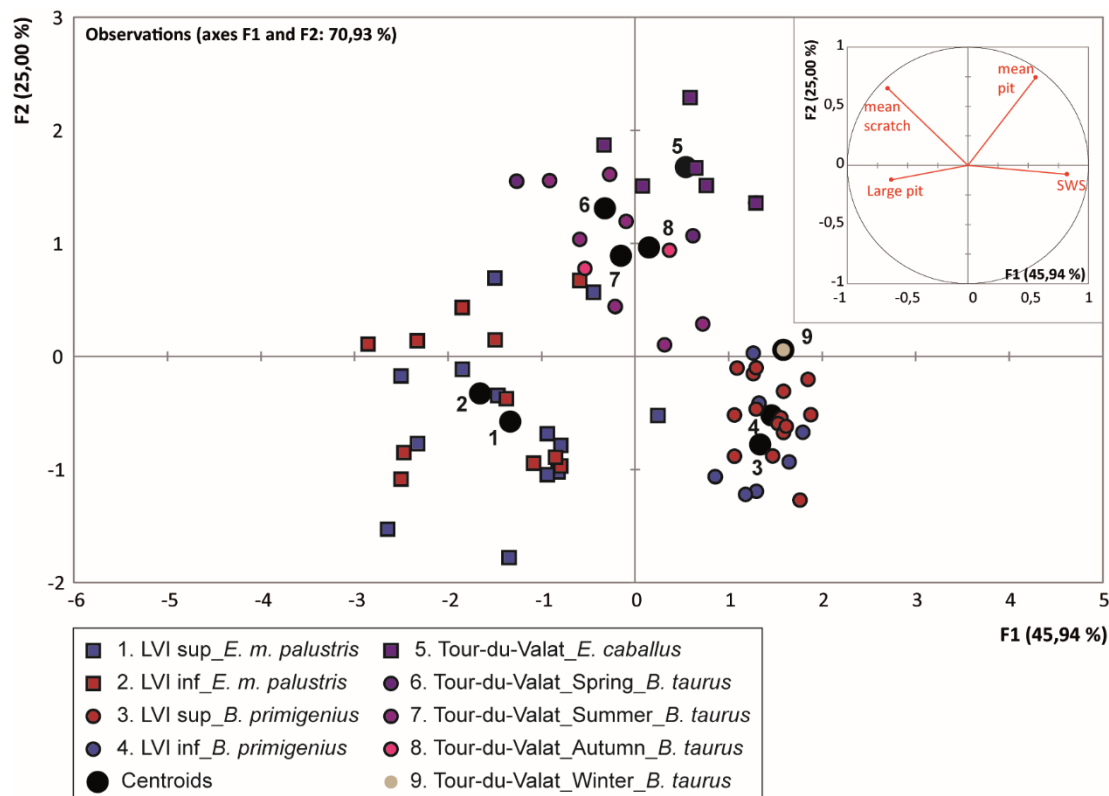


Fig. 4. Principal Component Analysis (PCA) with the microwear variables defining the diet of Lunel-Viel I and the Tour-du-Valat research institute bovids and equids. The variables used are the mean of pits and scratches for each population, the SWS index and the percentage of specimen with large pit for each population. The black dots correspond to the centroid of each population.

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Site		Mesowear		Microwear							
		N	MWS	N	NP	NS	%LP	%G	SWS	%HC	%XS
<i>Equus m. palustris</i>	M	20	4.85	13	15.5	19.30	25	0	0.07	0	100
Lunel-Viel I upper ens.	SD		0.87		4.72	2.65					
<i>Equus m. palustris</i>	M	26	4.35	14	16.68	20	42.85	21.42	0	7.14	100
Lunel-Viel I lower ens.	SD		0.8		4.39	2.69					
<i>Bos p. trochoceros</i>	M	20	2.05	7	23.57	12.93	0	0	1	0	100
Lunel-Viel I upper ens.	SD		0.69		3.69	1.77					
<i>Bos p. trochoceros</i>	M	62	2.08	16	26.28	13.22	0	0	0.94	0	100
Lunel-Viel I lower ens.	SD		0.83		2.74	1.86					
<i>Equus caballus</i>	M	4	3.25	10	32.7	21.5	0	10	0.5	0	50
Tour-du-Valat	SD		0.5		1.41	2.88					
<i>Bos taurus</i> _Spring	M	3	3	3	30.5	22.83	50	0	0.66	0	100
Tour-du-Valat	SD				2.29	2.75					
<i>Bos taurus</i> _Summer	M	6	3	7	30.14	18.85	0	14.28	0	0	100
Tour-du-Valat	SD				2.98	4.53					
<i>Bos taurus</i> _Autumn	M	5	2.2	5	31	18.6	0	0	0.2	0	80
Tour-du-Valat	SD		0.45		4.17	1.67					
<i>Bos taurus</i> _Winter	M	1	3	1	30	14	0	0	1	0	100
Tour-du-Valat											

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647 Tabl. 1. Summary of mesowear and microwear data for equids and bovids from Lunel-Viel I and  
648 Tour-du-Valat. Abbreviations: N = Number of specimens; MWS = Mesowear score; NP = Average  
649 number of pits; NS = Average number of scratches; %LP = Percentage of specimens with large pits;  
650 %G = Percentage of specimens with gouges; SWS = Scratch width score; %XS = Percentage of  
651 specimens with cross scratches; M = Mean; SD = standard deviation. The raw data have been  
652 published in Zenodo (Uzunidis, 2020) and are available at: <https://doi.org/10.5281/zenodo.3711415>.