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ABSTRACT

Alongside horses, donkeys and their first-generation hybrids represent members of the Equidae family known for their social, economic and symbolic importance in protohistoric and historical France. However, their relative importance and their respective roles in different regions and time periods are difficult to assess based on textual, iconographic and archaeological evidence. This is both due to incomplete, partial and scattered historical sources and difficulties to accurately assign fragmentary archaeological remains at the proper taxonomic level. DNA-based methods, however, allow for a robust identification of the taxonomic status of ancient equine osseous material from minimal sequence data. Here, we leveraged shallow ancient DNA sequencing and the dedicated Zonkey computational pipeline to obtain the first baseline distribution for horses, mules and donkeys in France from the Iron Age to the Modern period. Our collection includes a total of 873 ancient specimens spanning 128

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sites and comprising 717 horses, 100 donkeys, 55 mules and a single hinny individual. While horses were ubiquitous and the most dominant species identified, our dataset reveals the importance of mule breeding during Roman times, especially between the 1st and 3rd centuries CE (Common Era), where they represented between 20.0% and 34.2% of equine assemblages. In contrast, donkeys were almost absent from northern France assemblages during the whole Roman period, but replaced mules in rural and urban commercial and economic centers from the early Middle Ages. Our work also identified donkeys of exceptional size during Late Antiquity, which calls for a deep reassessment of the true morphological space of past equine species. This study confirmed the general preference toward horses throughout all time periods investigated but revealed dynamic management strategies leveraging the whole breadth of equine resources in various social, geographic and temporal contexts.

1. Introduction

Several members of the horse family (Equidae) are known for their major social and economic impact on proto-historical and historical France. Extensive textual and artistic evidence indeed describe horses, donkeys and their hybrids in a wide breadth of contexts, including not only the battlefield, castles, military and trade roads, but also in cities, villages and farmlands (e.g., Vigneron, 1968; Bautier & Bautier, 1978; Digard, 2007; Roche, 2008–2015; Mitchell, 2018). Horses (*Equus caballus*) undoubtedly represent the equine species that is the most accounted for. This is not surprising given their high symbolic status and their suitability for a broad range of equestrian activities, spanning from horseback riding to chariot pulling and plowing. Donkeys (*Equus asinus*) and mules (the offspring of a horse mare and a donkey jack) are considerably less documented, but are also known to have played important roles.

While they are completely absent from the artistic record during the Iron Age, donkeys appear in various and multiple historical sources during Antiquity, including agronomic treaties of the *scriptores rei rusticae* (Cato, Varro, Columella and Palladius) where they are acknowledged for their contribution to farming (Bodson, 1986). In the 1st century CE, Pliny also reported that donkeys were mainly used for breeding mules (*H.N. 8, 68, 1)*, an animal familiar to all authors and for which ample information is provided about breeding techniques and situations in which they can outperform other equids (Columella, 6, 36; Columella, 7, 1–3; Moulé, 1919; Johnstone, 2004; Chuang, 2016). Mules appear in various mosaics and reliefs, e.g. turning the grinding wheel, or pulling Roman military chariots or the so-called *vallus* used at the time for harvesting (Toynbee, 1973; Raepsaet, 2002). Hinnies (the offspring of a donkey jenny and a horse stallion) remain, however, more rarely mentioned and somewhat discordantly. They are for instance described as equal to donkeys for Varro (2, 8) but lazier and more impulsive for Pliny (8, 69).

While such sources provide invaluable information on equine management during Roman times, they leave many questions unanswered regarding the respective role and relative importance of each animal type in both rural and urban contexts. This is especially true for those regions such as the western provinces outside the Mediterranean range that are less documented. The situation is similar for the Medieval Period, due to abundant, yet ambiguous, textual evidence and iconography. Equine silhouettes, especially in miniatures, indeed often remain too imprecise to recognize mules and donkeys based on their morphology. Texts using words such as *summarius* (literally, '*beasts of burden*') are uninformative regarding the exact species designated. Combined, available sources nonetheless portray a highly heterogenous society, with strong regional and temporal specificities. For example, mules are more frequently mentioned than horses in the Conques Abbey charters (Aveyron, Southwestern France) and those of Cluny (Burgundy), where counter-gifts concern twice as often mules than horses (Bautier, 1981). Both mules and donkeys seem common in Central Poitou or Limousin, while horses seem to have largely dominated the Northern part of the country. This is indeed in this region that donkeys, but no mules, are mentioned as peasant auxiliaries in the 11th–12th centuries CE (Brunel, 1999) and by the 13th–14th centuries CE around the Abbeys from Bur forests (Normandy) (Delisle, 1903). Likewise, while the acts of the ecclesiastical province of Reims (Champagne) abundantly refer to horses, mules are not mentioned before the mid-13th century CE (Bautier, 1981).

Overall, available sources depict a global medieval Northern France centered on horses and a global medieval Southern France where donkeys and mules were more common. This regional polarity may even have strengthened during the 14th–15th centuries CE as mule trading intensified along the Pyrenean range and the Massif Central (Pinto, 2005) and mules were depicted as central to the rural economies of the Alps (Mouthon, 2007). Mules may also have become more widespread at the time given their increasing textual occurrence in Paris or Normandy (for examples, see Contamine, 2008).

Archaeological data hold the potential to fill the gaps in knowledge on past equine management resulting from textual and iconographic evidence. For example, skeletal remains can inform on micro-regional patterns of horse, donkey and mule production (e.g. Putelat et al., 2017), as well as on the animal individual life history (e.g. Lignereux et al., 1998) and more. In France, no site reports indicate the presence of mules during the Iron Age. In contrast, donkeys are known along the Mediterranean coast at Béziers (Columeau, 2000; Ugolini et al., 1991) from the 5th century BCE (Before Common Era), at Ambrussum (Columeau, 2002) and Pech Maho (Boulbes and Gardeisen, 2014) from the 3rd century BCE, and further North only during the Roman Period. They apparently remained relatively rare there (Lepetz and Yvinec, 2002), representing ~4.7% and ~6.7% of equine assemblages in Gaul and Rhineland, respectively (Johnstone, 2004), and they only represented sporadic identifications in Eastern regions during Antiquity (Lepetz and Morand, 2017). Mules are believed to have been more common then, reaching up to ~30% and over 40% of equine bone assemblages in Gaul and Rhineland, respectively (Johnstone, 2004). Such an apparent ubiquity of mules contrasts with the scarcity of donkeys and raises the possibility of import from other provinces, especially as isotopic analyses have identified non-local mules in Bavarian sites at the time (Berger et al., 2010). Both the existence and the location of underlying production centers remain, however, elusive and the evolution of the status of mules into the Medieval Period is largely unknown. The medieval donkey has received more archaeozoological attention, and is generally considered to have become common, and possibly even dominant, from the 6th–8th century CE (Lepetz and Yvinec, 2002). No data are, however, available across the full temporal transect, from the 2nd Middle Ages (12th–15th centuries CE) into the Modern Period.

In addition to being lacunar, equine archaeozoological data suffer from important limitations, as the morphological identification of horses, donkeys and hybrids from fragmentary material remains problematic (Peters, 1998; Uerpmann and Uerpmann, 1994; Johnstone, 2004, 2006; Chuang, 2016; Hanot et al., 2017). Although some recent applications of geometric morphometrics to whole tooth rows (Cucchi et al., 2017) or the bony labyrinth (Clavel et al., 2021) have shown great performance, including in hybrids, mule identification based on standard morphological criteria can still be unreliable (Chuang, 2016). In fact, recent DNA work has provided striking examples of species misspecification in Roman Swiss bone assemblages (Granado et al., 2020). DNA also identified donkeys in Chalcolithic Portugal, contradicting

archaeological models associating the first arrival of the animal in Iberia with Phoenician trade, some 1500 years later (Cardoso et al., 2013). Combined, these studies raise important concerns on the robustness of previous equine identifications, and consequently, challenge the overall validity of our current understanding of past equine management both in France, and more generally around the world.

In order to start to remediate this, we have gathered the largest collection of equine archaeological remains in France, representing a total of 873 specimens from 128 sites spread across the country, and have applied state-of-the-art DNA-based taxonomical tools (Schubert et al., 2017; Fages et al., 2020). The methodology relies on the Zonkey pipeline that we previously developed, which can accurately identify all equid members and their hybrids from minimal amounts of high-throughput DNA sequencing data (Schubert et al., 2017). Our approach provides the first in-depth characterization of temporal and social changes in equine management for a single country, from the Iron Age to the Modern Period. While horses remained the most prevalent equine species across the whole period investigated, our dataset reveals the importance of mule breeding in Northern France during the Roman Period, especially between the 1st and the 3rd centuries CE. It also unveils their near disappearance from the early Medieval Period in favour of donkeys, which became closely associated with important rural and urban commercial and economical centers. Finally, our work uncovers donkeys of exceptionally large sizes, which calls for a reconsideration of the true morphospace of past equine species, even in the most recent time periods.

2. Material and methods

2.1. Archaeological samples

A total of 873 archaeological remains were sampled for ancient DNA analysis. Those remains originate from 128 excavation sites and 96 municipalities spread across modern France (Fig. 1). Sampling was originally focused on petrosal bones to increase the chances of ancient DNA preservation (Pinhasi et al., 2015) but was successfully extended to teeth and post-cranial skeletal elements, including e.g., phalanges, metapodials, tarsal bones, tibia, radius and humerus, to maximize the number of sites investigated. At sites characterized by extensive numbers of equine remains, as whole skeletons were deposited (e.g. Boinville-en-Woëvre) and/or large amounts of bones were accumulated (e.g. Chartres (Rue de la Courtille), Longueil-Sainte-Marie (L'Orméon)), we systematically selected one specific anatomical element located on the same body side so as to ensure that a given individual was sampled only once.

The assemblages represented in our final dataset cover a range of cultural, socio-economical and temporal contexts. The archaeological information available for medieval sites allowed us to identify rural civil, rural elite (i.e. seigneurial or monastic), and urban elite (civil or religious) contexts. This admittedly only represents a subset of the socio-economical spectrum and may reflect a different local social experience from site to site and even within sites, as the complexity of individual social statuses cannot be fully appreciated. The temporal range indicated for each site merges various contextual data, including from ceramics, as provided by archaeologists and radiocarbon dates when available (Supplemental Table 1).

The material analyzed spans the whole temporal range between the Hallstatt and the Modern period, with Gallo-Roman and Contemporary sites representing the two time periods the most (271/873 ~ 31.0% samples) and the least (19/873 ~ 2.2% samples) sampled, respectively (Fig. 2B). Additionally, the material shows a clear over-representation of sites located in the Northern/Northeastern part of France (100/128 ~ 78/1% sites, 703/873 ~ 80.5% samples). Three other regions were also investigated, including Charente-Maritime (7/128 ~ 5.5% sites, 73/873 ~ 8.4% samples), Auvergne (2/128 ~ 1.6% sites, 44/873 ~ 5.0% samples) and the Mediterranean coast (10/128 ~ 7.8% sites, 41/873 ~ 4.7% samples). Finally, a total of 12 samples originated from nine sites spread across the country (Fig. 2A).

Our sample set encompasses different archaeological contexts, including both rural and urban settings (Fig. 2C). Nearly half (424/873 ~ 48.6%, from 82/128 ~ 64.1% sites) consist of domestic dumps and occupation refills, with diverse elements indicative of food waste, craftwork, and garbage of all kinds. In this type of dump, Iron Age samples were obtained from parts of the body that were consumed, while those from the Roman, Medieval and Ancien Régime periods were generally not. Around ~18.9% of the samples (165/873, 17/128 ~ 13.3% sites) were collected from city relegation zones where animals were gathered as they died, and carcasses were accumulated, and sometimes even exploited for their skin, hair, tendons and bones. During the Roman Period, such sites were located nearby cities and close to necropolises (Lepetz et al., 2013), e.g. at Evreux (Clos-au-Duc) and Louvres (ZAC du Parc). In the Medieval Period, these sites could be located within non-constructed city sections (e.g. at Beauvais (44 rue des Jacobins), or at Reims (Rue des capucins)) or close to the city walls (e.g. at Beauvais (Le Jeu de Paume)). At Chartres (Rue de la Courtille, 77/873 ~ 8.8% samples) and Beauvais (Abord du Théâtre, 18/873 ~ 2.1% samples), the animal bones collected were used as part of constructions for draining humid zones, while they provided the raw material for craftwork at Lille (Rue de Tournai) and Vermand (Rue Charles de Gaulle), representing a total of 7/873 ~ 0.8% samples for both sites. Ritual sites also provided around 13.5% of the samples (118/873, 10/128 ~ 7.8% sites), including animals associated within human sepultures (Woippy and Offin (Le-Bois-Monclair)), or sacrificed and concentrated within sanctuaries ritual deposits (Gondole, Orcet, Saint-Just-en-Chaussée (site 94–95), Vertault, Longueil-Sainte-Marie). In our dataset, the latter are restricted to the La Tène and Roman Periods. Finally, the last site category includes animals that died from natural death and were buried in gardens or near rural habitats (35/873 ~ 4.0% samples, 18/128 ~ 14.1% sites), within single, e.g. at Longueil-Annel (Le Village), Noyon (Rue d'Orroire), Brachaud or collective burials (Boinville-en-Woëvre).

2.2. Ancient DNA methods

A total number of 68 samples were studied in previous work (Gaunitz et al., 2018, Fages et al., 2019, Clavel et al., 2021) using methodologies similar to those applied to the 805 remaining samples that were analyzed here for the first time. Ancient DNA analyses were carried out in the clean lab facilities of the Centre for Anthropobiology and Genomics of Toulouse (CAGT), following the methodology fully described by Clavel and collaborators (2021). In brief, 40–1110 mg of powder is first partially digested within a 3.85 mL solution consisting of EDTA (0.45 M), N-lauryl Sarcosine (0,5%) and proteinase K (0,25 mg/mL) for 1 h at 37 °C. The remaining undigested pellets are then collected following 2 min centrifugation at 3000 rpm and fully digested overnight at 42 °C and adding 3.85 mL of a fresh extraction buffer. Some of the samples were subjected to bleach pretreatment as described by Boessenkool and collaborators (2017) before being processed for DNA extraction. DNA libraries were constructed from double stranded DNA templates that were treated with USER enzymes (New England Biolab), following Fages et al. (2019), and included two 7-bp internal indices (Rohland et al. 2015) as well as one 6-bp external index (Fages et al. 2019) so as to allow sequence demultiplexing robust to index hopping (van der Valk et al., 2020). DNA libraries amplification were carried out for 4–15 cycles in 25uL reactions of the 3 μL of DNA in solution with EB-Tween 0.05%, 2.5 μL of 10X AccuPrime Pfx Reaction Mix (Thermo Fisher Scientific) supplemented with 1U of AccuPrime Pfx DNA polymerase (Thermo Fisher Scientific), 0.8 mg/mL of BSA, and 200 nM of each PCR primer (inPE1 and one custom primer including a 6-bp Illumina index). Amplified DNA libraries were then purified through MinElute columns (QIAgen) or Agencourt AMPure XP beads (Beckman Coulter), with a 1.4 beads/DNA solution volume ratio and eluted in 25 μL EB buffer supplemented with

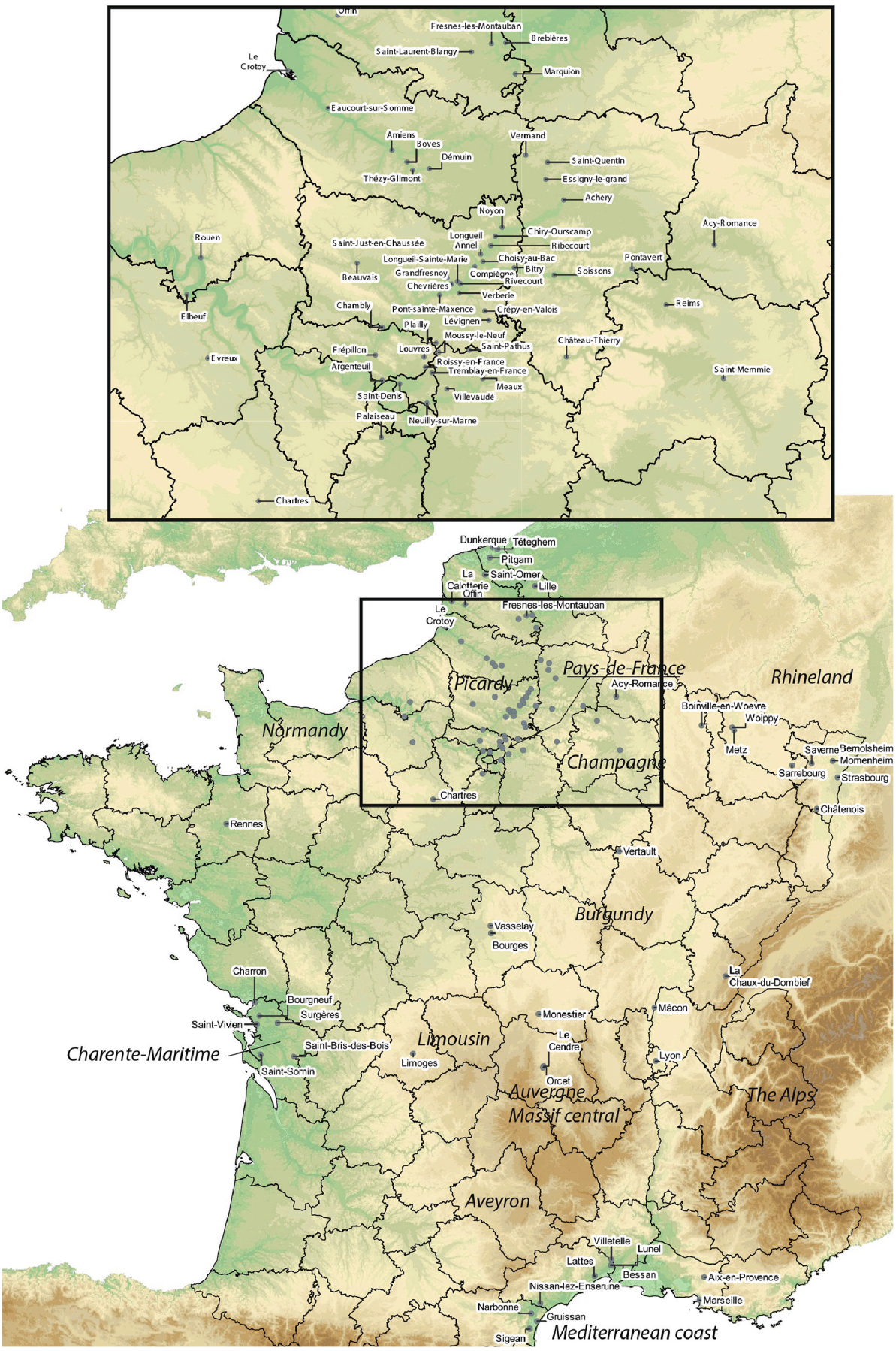

Fig. 1. Sample dataset. Geographical distribution of archaeological sites. Those main geographic regions referred to in the text are indicated in italics.

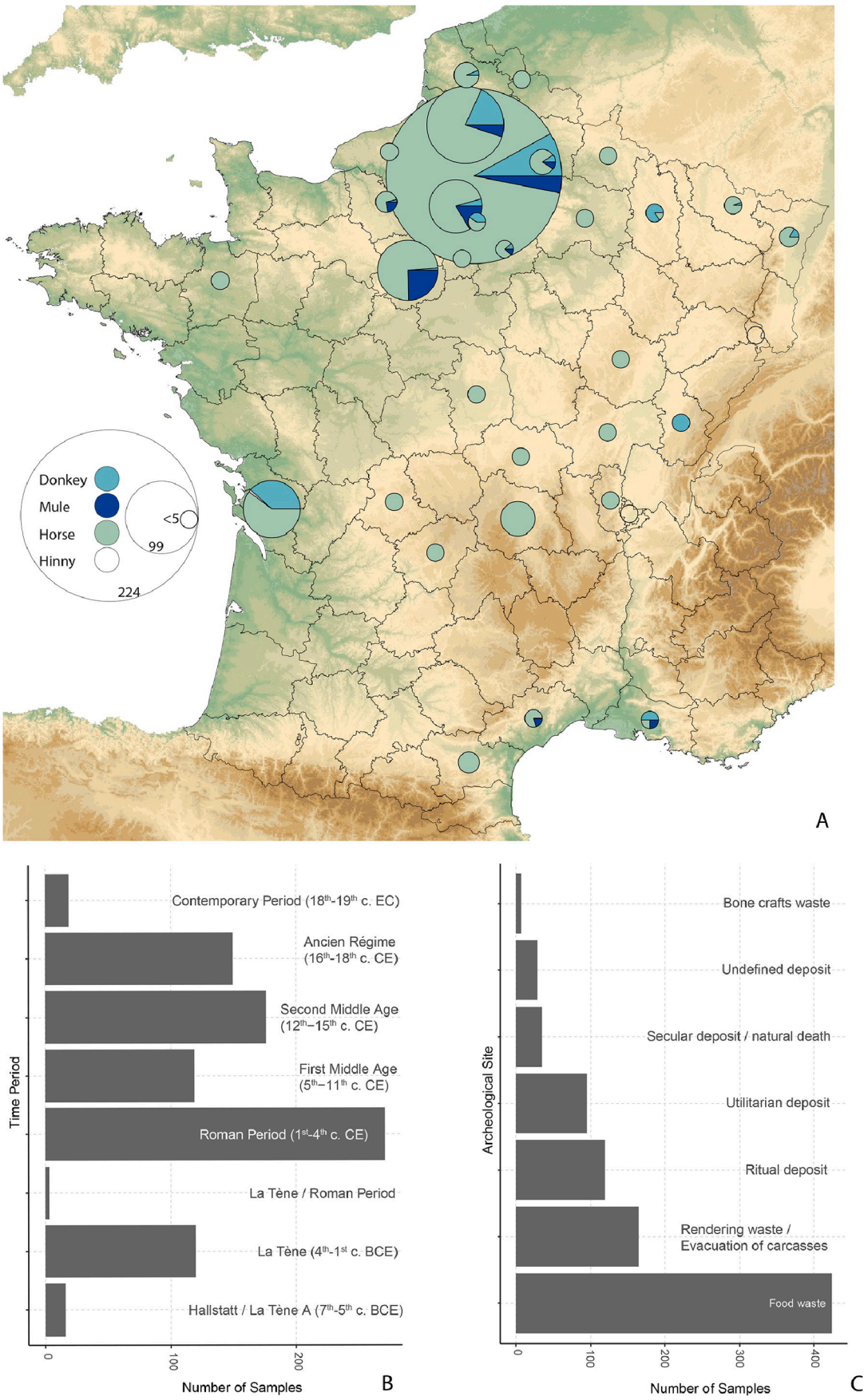

Fig. 2. Sample dataset. A: Geographic sample distribution. The size of the different piecharts is proportionate to the number of samples analyzed locally (717 horses, 100 donkeys, 55 mules, and; 1 hinny). B: Temporal distribution of samples (N = 873). C: Sample distribution across the various archaeological contexts (N = 873).

0.05% Tween. Purified DNA libraries were quantified using the TapeStation 4200 instrument (High Sensitivity D1000 Assay; Agilent) or BioAnalyzer 2100 instrument (High Sensitivity DNA Labchip Kit; Agilent) and on a QuBit HS dsDNA assay (Invitrogen), before being pooled together with 30–50 other libraries for sequencing on the MiniSeq Illumina platform (80 Paired-End mode) at CAGT, or on the HiSeq4000 Illumina platform (150 Paired-End mode) at Genoscope, Evry.

Both those sequences previously published and those generated here were subjected to the same downstream analyses. Fastq sequences were demultiplexed, trimmed for low-quality ends and collapsed if showing sufficient overlap using AdapterRemoval2 (Schubert et al., 2016) with default parameters, except that at best one sequence mismatch was tolerated in each internal index. Sequences were further processed for mapping against the EquCab2 horse reference genome (Wade et al., 2009), to match the Zonkey pipeline expectations (Schubert et al., 2017), supplemented with the Y-chromosome contigs from Wallner et al. (2017) and the horse mitochondrial reference genome (NC_001640, Xu and Arnason, 1994) using Paleomix v1.2.13.2 together with the Bowtie2 aligner (Langmead and Salzberg, 2012) and the parameters recommended by Poullet and Orlando (2020). Sequence alignments were filtered for minimal mapping quality of 25 and PCR duplicates, and assessed for signatures of post-mortem DNA damage, including nucleotide mis-incorporation and base compositional patterns, using mapDamage2 (Jónsson et al., 2013). Such patterns conformed to what expected considering the USER-treatment of DNA extracts and the type of DNA library constructed. More precisely, the genomic position preceding the first alignment position was enriched in Cytosine residues, as a result of USER treatment cleaving DNA at those Cytosine residues that were deaminated after death (Briggs et al., 2010). The magnitude of C → T mis-incorporation rates was limited due to USER treatment but decreased consistently from read starts, as expected (Briggs et al., 2007). Finally, taxonomic and sex identification were carried out by subjecting BAM alignments files to the Zonkey pipeline (Schubert et al., 2017), and considering a minimal of 1018 alignments in order to achieve full specificity (median = 115,469, maximum = 959,339). Final assignments are provided as Supplemental Table 1.

3. Results

3.1. Shifting temporal preferences in equine management

The collection of samples available for this study was largely dominated by horses (717/873 ~ 82.1%) but also led to the identification of 100 (~11.4%) donkeys, 55 (~6.3%) mules and a single hinny, dated to the 16th–17th centuries CE (Fontdouce Abbey (Saint-Bris-des-Bois)). Interestingly, the different taxa identified are not distributed evenly through space and time, but showed striking differences between proto-historic, Roman and Medieval periods (Fig. 3). More specifically, no hybrids were identified during the proto-historic period, which was only represented by horses. Hybrids were almost exclusively restricted to the Roman Period (53/55 ~ 96.4%) while the vast majority of donkeys were associated with medieval and modern contexts (85/100 ~ 85.0%). Therefore, our data indicate shifting temporal preferences in the management of donkey and mule resources, with horses remaining dominant and essential throughout the whole period investigated and hinnies exceptional.

3.2. Donkey management

The earliest donkey identified in our dataset was found in the urban context of Chartres (Boulevard de la Courtille), which is dated to 100–110 CE. Donkeys were no longer detected in the following two centuries until they reappeared again at Boinville-en-Woëvre. This late Antiquity site (3rd–6th centuries CE) was characterized by the presence of 22 (almost) complete skeletons in over a dozen of burials, both single and multiple, located in the *Pars Rustica* of a *villa* (Fig. 4A). Thirteen such

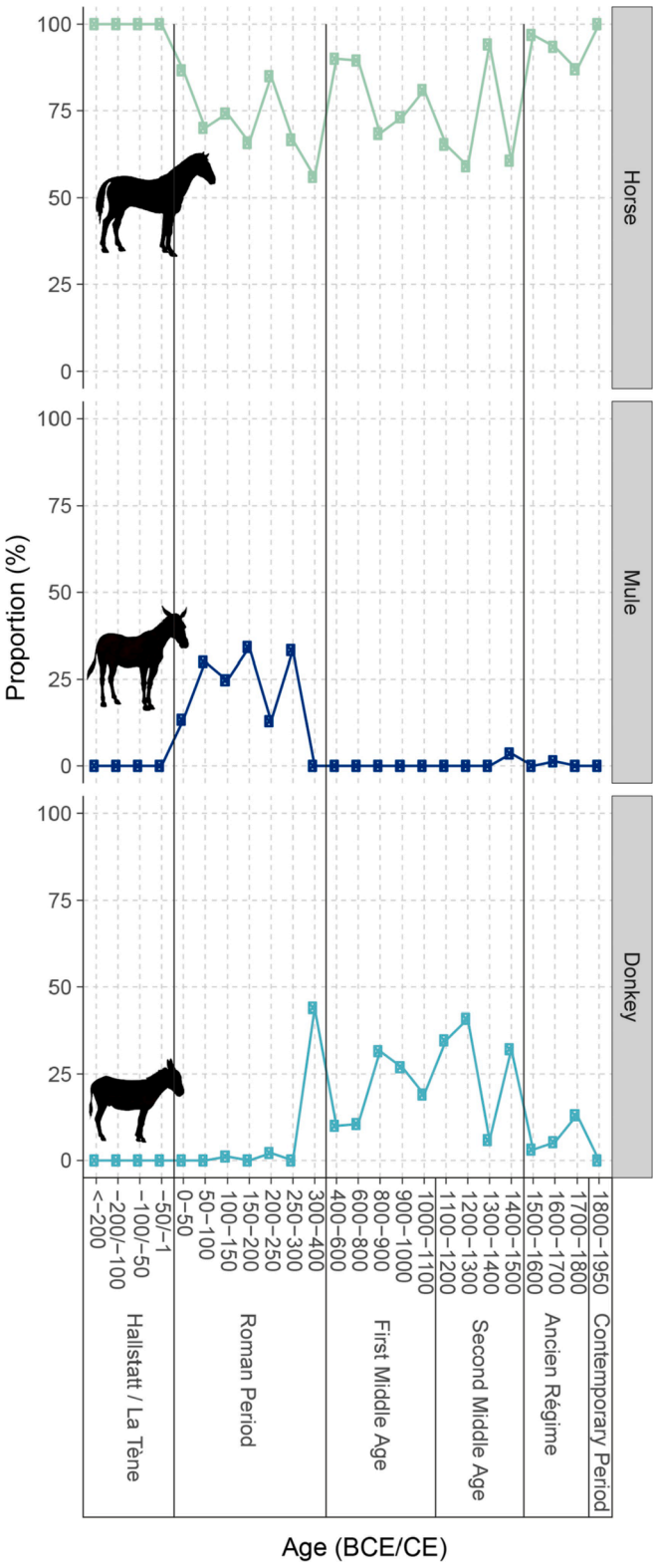

Fig. 3. Temporal patterns of horse, donkey, and mule representation within our collection of equine remains.

animals were tested positive for DNA and included two horses and eleven donkeys (eight males, three females). Three additional donkeys showing poor DNA preservation were also suggested (data not shown). Such a predominance of donkeys is unprecedented and indicates management strategies largely focused on this species. Furthermore, those donkey specimens identified genetically at Boinville-en-Woëvre showed

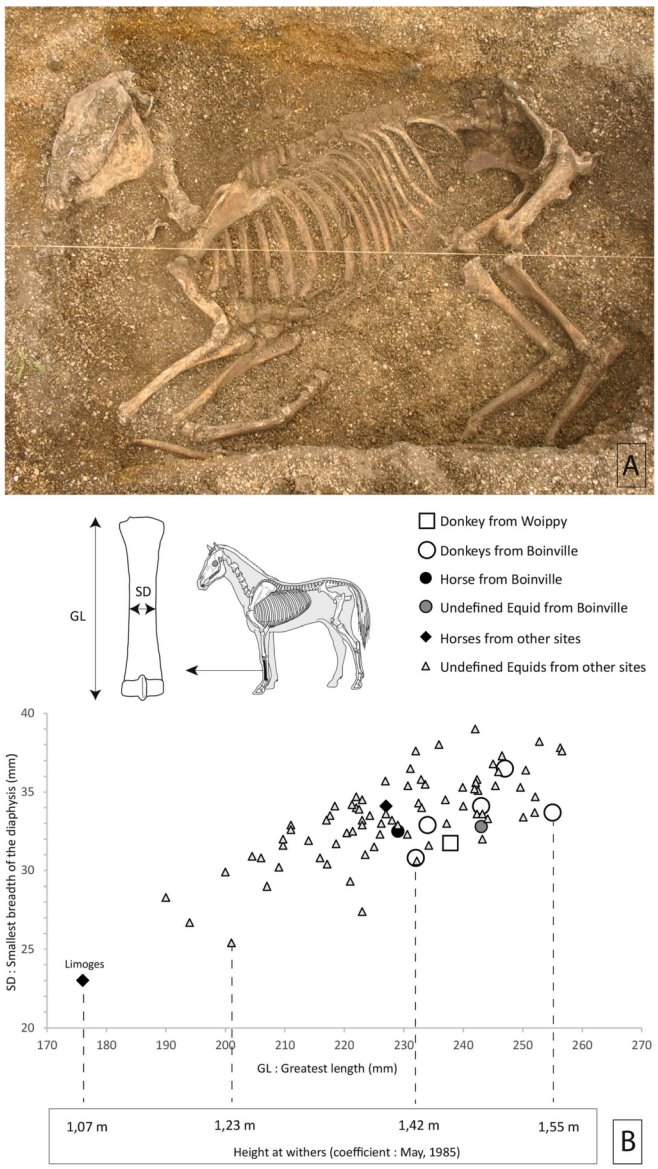

Fig. 4. Donkey identification and morphological characteristics. A: *In situ* photograph of the donkey identified along Structure 3144 at Boinville-en-Woëvre. B: Distribution of measurements (greatest length and smallest breadth of the diaphysis) of equid metacarpals from the Roman period (1st–5th centuries CE; Lepetz, 1996 and unpublished data). Estimates of height at the withers are proposed for 4 individuals for illustration purpsose (following (May 1985); the function for metacarpal bones is Gl × 0.6102). The specimens genetically identified as donkeys at Boinville appear amongst the largest equids measured, and are closely followed by the donkey characterized at Woippy. Conversely, a very small horse was also identified in Limoges (Villa Brachaud) during the Roman period.

exceptional osteological characteristics that are suggestive of particularly high stature, ranging 141–155 cm at the withers (Fig. 4B). The only other site in our dataset that delivered donkey remains in Northern France in the Roman Period was Woippy and was located 35 km east of Boinville-en-Woëvre. It comprised a complete skeleton deposited next to a human burial dated to the 5th century CE. In the South, only two donkeys were identified in the late Antiquity context of La Bourse in Marseille. Overall, our results portray a picture of limited donkey presence across the northern country, with the exception of Late Antiquity sites such as Boinville-en-Woëvre, where donkeys appear locally, at exceptionally elevated percentages.

The situation changed drastically from the beginning of the Medieval Period. Donkeys were found within limited proportions (two bones at Moussy-le-Neuf) in the natural region of 'Pays de France' (North of Paris) during the Merovingian Period (6th–8th centuries CE) but became more common thereafter. They represented ~28.2% (20/71) of the remains analyzed, during the Carolingian Period (8th–10th century CE) and until the 11th century CE (Fig. 5A). It reached maximal proportions (43/135 ~ 31.8%) between the 11th and the 13th centuries CE, and decreased to ~17.7% (11/62) in the 14th-15th centuries CE to only represent 5.5% (9/163) of the remains analyzed in the next three centuries.

The temporal changes in the relative prominence of donkeys in our dataset were not uniform across the different socio-economical contexts (Fig. 5B). They reflected contrasted patterns of resource management in which the animal was most common in rural elite contexts during the 7th and 10th century CE (Chi-squared test, p-value = 0.044), but in urban elite contexts between the 11th and 13th centuries CE (Chi-squared test, p-value = 0.010). The relative importance of donkeys found in rural civil contexts remained secondary across the whole Medieval Period.

3.3. Mule management

The earliest mule identified in our dataset (G'VA-219) was excavated at the site Saint-Just-en-Chaussée (Plainval). It was found within a ditch connected to the borders of an Iron Age Celtic sanctuary and was revised to the Augustean Period, between the late 1st century BCE and the early 1st century CE, since its original report by Fages et al. (2019) in the terminal La Tène period. Another remarkable mule belonging to the 1st century CE (G'VA-1057) was identified at Meaux (Rue Alfred Maury) and consisted of a complete fetus found in an urban dump deposit. In fact, while the size of our dataset is limited for the 1st century CE (N = 25), mules represented ~20.0% of the taxonomic assignments (5/25). Their relative importance significantly increased to ~24.7% (22/89) in the first half of 2nd century CE and to ~34.2% (13/38) from the second half of 2nd century CE (Fig. 2), then decreased in the first half of 3rd century CE to ~12.9% (12/93) until it suddenly vanished from the mid-3rd century CE (Chi-squared test, p-value = 0.039). Sample G'VA-555, excavated from the rural context of Saint-Pathus, represents the latest Roman sample identified during the Late Antiquity. Strikingly, no mules were identified amongst the 297 medieval samples present in our dataset, apart from one individual from Aix-en-Provence, Southern France, from the 15th century CE. In fact, the number of mule identifications remained also extremely limited during the Modern Period, with only one individual (1/163 ~ 0.6%) detected at Evreux (Parking de l'Hôtel de Ville), a site from the Northern region dated to the 17th century CE. The under-representation of Southern France assemblages in our dataset prevents rigorous comparisons with the situation observed in the Northern France. However, our dataset suggests that mule management in Northern France remained only significant during Antiquity and was particularly important between the 1st and 3rd centuries CE in both rural and urban contexts.

3.4. Horse management

Horses are the only species of equids identified in Iron Age France. They have remained the most frequently used equine species across all time periods and socio-economic contexts investigated in this study (717/873 ~ 82.1%; Fig. 2). This indicates a general preference for horses in France during almost the last 2500 years.

A number of situations, however, reflect ritual rather than husbandry-related management practices. This is the case for the two sites of Gondole Les Piots and Orcet La Roche Blanche, dated between the 1st century BCE and the 1st century CE. These famous archaeological sites are located at the foothills of the Gergovia plateau and play host to a number of multiple horse burials, sometimes accompanied by humans. These are generally interpreted in connection with the battle of Gergovia

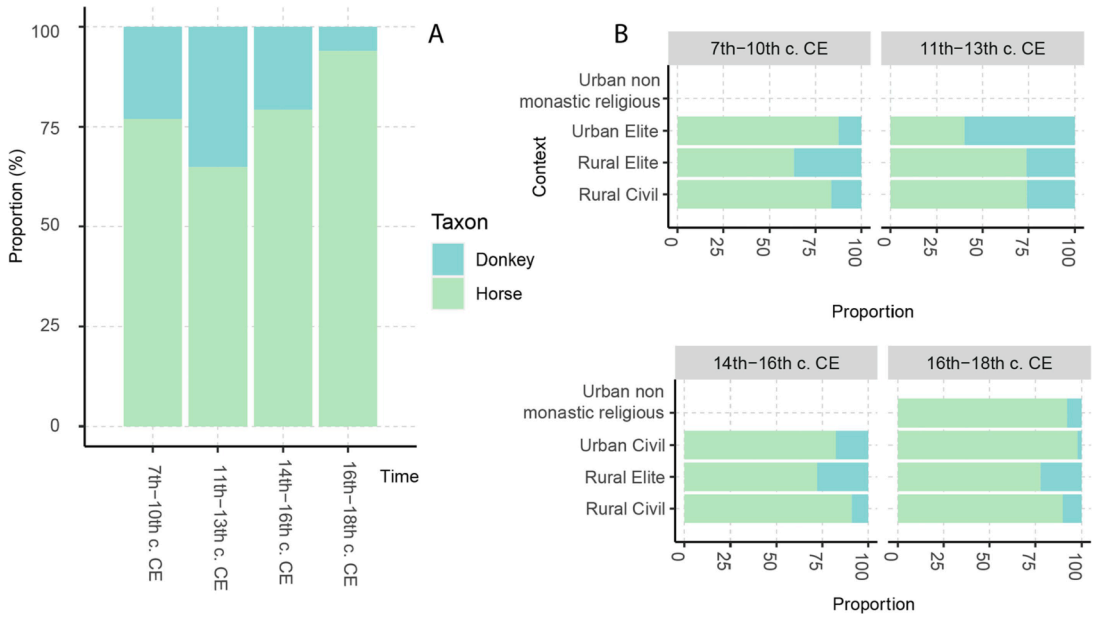

Fig. 5. Temporal proportions of horse (green) and donkey (blue) identifications. A: Overall proportions from the Middle Ages (7th century CE) to the Modern period (18th century CE). B: Temporal dynamics within four individual socio-economic contexts.

or as sacrificial rituals specific to the Arvernes political center (Foucras et al., 2019). Regardless, our work confirms that only horses were inhumated on site, even though previous morphological analyses had suggested mules (Foucras et al., 2019). The same holds true for the sanctuaries of Vertault (1st century BCE) and Saint-Just-en-Chaussée (La Tène D1-D2 – 2nd-1st century BCE), that only comprised horses. The Roman site at Longueil Sainte-Marie (L'Orméon) is also worth mentioning, as it is interpreted as a rural sanctuary dated to the 2nd-3rd centuries CE (Gaudefroy and Lepetz, 2000). While mules were most prevalent at the time in our global dataset, none of the 26 samples analyzed consisted of mules, which supports contention of intentional horse sacrifice at the site.

It is important to emphasize that our analysis only revealed the presence of horses at the Iron Age site of Pech-Maho, dated to the early 2nd century BCE, while donkeys had been identified morphologically there (Boulbes and Gardeisen, 2014, Boulbes and Gardeisen, 2018). Our sampling strategy for that site was strictly designed to exclude the latter specimens from our analyses, as our original aim was focused on the genetic characterization of horses exclusively. The apparent absence of donkeys resulting from our analysis hence only reflects this sampling bias, and shall not be taken against previous morphological reports. In fact, our analyses confirm previous morphological identification for all 25 horse specimens genetically tested. Importantly, this site is the only one of those analyzed in this study where sampling was implemented to avoid other equine species than the horse. While no other situations can be expected to reflect similar bias, the proportion of non-horse taxa may be considered as conservative.

4. Discussion

This study provides the first genetic attempt to characterize the geographic, temporal and socio-economic patterns of equine resource management in France. It confirms the prevalence of horses across all contexts and time periods, which is also reflected in textual evidence and iconography. Interestingly, this study reveals important temporal shifts that were not immediately apparent from other sources, including previous archaeozoological work. Alongside horses, mules have represented an important resource during the Roman Period in France, especially between the end of the 1st and the beginning of the 3rd centuries CE where they contributed between ~20.0% and 34.2% of the equine skeletal assemblages. They suddenly vanished almost completely from the archaeological record by the Late Antiquity and were largely absent during the Middle Ages, a time period when they were superseded by donkeys.

That our work uncovers the Roman Period as the Golden Age of mule breeding reflects the important socio-economic changes at the time. During the Roman Period, the magnitude of trade exchange indeed reached unprecedented levels (Reddé et al., 2018). The need for transportation was ubiquitous and equally fit private and public interests, both for trade, transportation and military supply (Roth, 1999; Porte. 2016), and the Imperial post service (the so-called *cursus publicus*) (Pflaum, 1940). Long-distance exchange between civitates and provinces were mainly carried out by sea and rivers. However, wherever waterways were impracticable or lacking, and for short distances, including between ports, cities and the countryside, transportation was by land (Deman, 2002). An important road network was, thus, developed across the Roman Gauls (Duval, 1989). Our work reveals that the physiological qualities of mules, which are more sure-footed and show stronger work capacities than horses (Tegetmeier and Sutherland, 1895), largely contributed to fuel this economic expansion and land transportation demands. Our findings mirror the countless numbers of Antique figured reliefs representing carriages often composed of two mules led by the *muliones,* literally the mule drivers (Raepsaet, 2002).

The large proportion of mules identified during the Roman Period contrasts with the almost absence of donkeys and opens questions about the underlying production models.

Indeed, no mules can be bred without any donkey jacks. Taken at face value, the absence of donkeys may support models assuming exogenous production, with mules representing imported commodities. Interestingly, the existence of true breeding centers specialized in mule production was reported by Varro (2, 8) in Italy and recent isotopic work suggested non-local mule breeding in Bavaria (Berger et al., 2010). However, other regions must also have developed such a production across the whole Empire since these Italian production areas are unlikely to have produced animals in sufficient numbers to supply all the northern territories of the Empire. Therefore, the near absence of donkeys revealed in this study does not necessarily imply far-away importation.

The *Gallia Belgica* overlapped the area where most Roman mules were identified in this study. This region had the agro-pastoral capacity

to develop such a large-scale production (Lepetz and Zech-Matterne, 2018). In fact, mule production does not require large donkey stocks as only a limited number of jacks can mate with many mares. More than the mules themselves, import strategies may, thus, have focused on acquiring good donkey breeders, such as those described by Varo (2, 6), which could apparently be sold for 40,000 (3, 2) and even 60,000 (2, 6) sesterces, an amount that is approximately worth 3.2–4.8 kg of gold. Interestingly, the donkeys identified at Boinville-en-Woëvre during the 3rd–5th centuries CE showed an exceptional size (Fig. 3) and may reflect such animals, or their local descent. With current evidence, this remains, however, speculative. In any case, as donkeys remained uncommon in the Northern regions at the time, their main purpose may have been to sire mules.

Now that archaeological sites characterized with large proportions of mules or donkeys have been identified, future work shall be aimed at investigating the geographic and evolutionary origins of such equine resources. This will ideally be achieved by coupling the power of strontium isotope analyses (Bendrey et al., 2009) together with high-resolution genetic data informing on local population affinities (Lawson et al., 2012). Investigating the case of the mule fetus found at Meaux (1st century CE) with such technologies will also be essential to address whether import was also oriented toward pregnant horse females carrying mules.

The Late Antique and early Medieval Periods mark the rise of the donkey in our dataset. This largely coincides with new economic systems involving a reorganization of trade and transportation (Devroey, 1992; Lebecq, 1999; Devroey and Nissen, 2015), which noticeably no longer favored the production of sterile mules. Redirecting equine management toward donkeys, which represent strong pack animals, particularly suited to farming activities and easier to produce, may, thus, reflect pragmatic decisions adapting to the new economic reality of the time. The substantial proportion of donkeys identified in this study contrasts with their relative scarcity in the textual record. This is especially true in rural elite contexts during the Carolingian Empire, a time when horses are exceedingly mentioned in textual sources from large rural establishments, such as at Saint-Bertin and Saint-Riquier (Fossier, 1968). Our work, thus, highlights the archaeological record as an essential source to reconstruct a comprehensive history of animal management.

Furthermore, our dataset reveals that donkeys were primary used in rural elite contexts between the 7th and 10th centuries CE (Fig. 5B). Such contexts most often consist of seigneurial farms or Church-controlled establishments. For example, excavations at Boves (Le Château – Picardy), a location under Bishop control, uncovered a large number of storage structures used for cereals, which indicated a site of particular economic importance. There, 14 out of the 18 equine remains analyzed were identified as donkeys (~77.8%). They may thus have been particularly useful for transporting cereals (and other farm products) between farmlands and storage facilities, which were located at places where elites, political and religious power were concentrated. This would depict donkeys as instrumental vectors linking together the different elements composing what was then a new form of territorial organization. A similar phenomenon was characteristic of the following time period (11th to 13th centuries CE), however, not in rural but urban elite contexts. This is perhaps best illustrated by Surgères (Rue Barabin), a site where skeletal elements were found close to the city castle, but this is also true for other sites accumulating economic and political power, such as Boves (Le Château) and Démuin (Le Château). During the next two centuries, donkey management appears to have shifted again to rural elite contexts, including monasteries and castles, such as at Saint Sornin (Tour de Broue), where donkeys were likely used in relation to saltworks (Périsse, 2012; Normand and Champagne, 2019). Finally, the donkey remained used in rural contexts during the Modern Period but became rather uncommon, if not exceptional, within cities.

One of the main limitations of the present study pertains to the over-representation of archaeological material from the Northern part of France. Therefore, it remains unknown whether the management of equine resources followed similar temporal and socio-economic trajectories in the southern half of the country. Future work should, thus, be aimed to extend our focal area to fill this important gap in knowledge.

Finally, our work uncovered considerable size variation amongst Gallo-Roman equine species, including miniature horses and gigantic donkeys. Therefore, size differences can no longer be used to make robust taxonomic assignments from fragmentary remains. Likewise, while hinnies never became common, mules appeared to have been only second to horses during Antiquity. Therefore, proper identification of mules is needed before the equine skeletal assemblages of that time period can be accurately characterized. This calls for future re-assessment of equine skeletal assemblages that embrace the full predictive power of the new tools now available, such as those based on DNA identification (Schubert et al., 2017), 2D geometric morphometrics applied to teeth (Cucchi et al., 2017) or 3D geometric morphometrics applied to the bony labyrinth (Clavel et al., 2021), and possibly, ancient proteins (Hendy et al. 2018).

Author contributions

SL, BC and LO designed research. SL, BC, JR, JMA, AP, OP, SF, GJ, NM, OR, SF, MS, CV, MB, JHY, AB, FD, NB, PW, AG and LO provided material and reagents. LC, SS, LTC, AF, NK, PC, ASO, CDS, CG, XL performed ancient DNA experiments. SS, LTC, ASO, JMA, AP and PW carried out and/or coordinated DNA sequencing. DA and LO performed sequence analyses. SL, BC and LO interpreted the results, with input from all co-authors. LO coordinated the study. SL and LO wrote the manuscript, with input from all co-authors.

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

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