

Review

What Does the “Elephant-*Equus*” Event Mean Today? Reflections on Mammal Dispersal Events around the Pliocene-Pleistocene Boundary and the Flexible Ambiguity of Biochronology

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Abstract: The dispersal of primitive elephantines and monodactyl equids in Eurasia has long been regarded as representative of a substantial turnover in mammal faunas, denoting the spread of open environments linked to the onset of cold and dry conditions in the Northern Hemisphere. During the 1980s, this event was named the “Elephant-*Equus* event” and it was correlated with the Gauss-Matuyama reversal, today corresponding to the Pliocene-Pleistocene transition and the beginning of the Quaternary, dated at ~2.6 Ma. Therefore, the Elephant-*Equus* event became a concept of prominent biochronological and paleoecological significance, especially in western Europe. Yet, uncertainties surrounding the taxonomy and chronology of early “elephant” and “*Equus*”, as well as conceptual differences in adopting (or understanding) the Elephant-*Equus* event as an intercontinental dispersal event or as a stratigraphic datum, engendered ambiguity and debate. Here, we provide a succinct review of the Elephant-*Equus* event, considering separately the available evidence on the “elephant” and the “*Equus*”. Elephantines dispersed out of Africa during the Pliocene (Piacenzian). Their earliest calibrated occurrences from eastern Europe date at ~3.2 Ma and they are usually referred to *Mammuthus rumanus*, although the allocation of several samples to this species is tentative. Available dating constraints for other localities do not resolve whether the dispersal of *Mammuthus* was synchronous across Eurasia, but this possibility cannot be ruled out. The spread of *Mammuthus* was part of an intercontinental faunal exchange between Africa and Eurasia that occurred during the Piacenzian, but in this scenario, *Mammuthus* is quite unique in being the only genus of African origin dispersing to western Eurasia. The arrival of monodactyl equids from North America coincides with the Pliocene-Pleistocene transition, with several occurrences dated or calibrated at ~2.6 Ma and no compelling evidence prior to this age. In Europe, early monodactyl equids are often aligned to *Equus livenzovensis*, but the material from the type locality of this species is chronologically time-averaged and taxonomically heterogeneous, and western European samples are seldom abundant or informative. Regardless, this does not diminish the biochronological significance of the “*Equus* event”. Indeed, while the term “Elephant-*Equus* event” should no longer be used, as the appearance of elephantines in the European fossil record markedly precedes that of monodactyl equids, we endorse the use of the “*Equus* event” as a valid alternative to refer to the intercontinental dispersal event that characterizes the middle Villafranchian faunal turnover, epitomized by but not limited to monodactyl equids.

Keywords: biochronology; bioevent; dispersal event; *Equus* Datum; Gauss-Matuyama reversal; faunal turnover; land mammal ages; large mammals; Pleistocene; Villafranchian



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1. Introduction

The beginning of the Quaternary Period is formally tied to 2.58 Ma, the age of the GSSP for the Gelasian Stage in the Monte San Nicola section in Italy, corresponding to the Gauss-Matuyama paleomagnetic reversal [1,2]. Around 2.7–2.6 Ma, the glacial activity of the Northern Hemisphere increased, and major climatic changes took place, basically resulting in a transition from long-term warm–humid conditions to large amplitude alternations between cool–arid and warm–humid environments [2–5]. The long-lasting trend of increasing cold and aridity observed during most of the Cenozoic and especially after the Mid-Miocene Climatic Optimum—of which the more humid and warmer conditions of the Early Pliocene were a small countertrend [6]—was now accompanied by oscillations between glacial and interglacial periods and, at a finer scale, by a more marked seasonality [7,8].

The important biotic response to these environmental changes has long been recognized and correlated to a transition from the early Villafranchian to the middle Villafranchian, in terms of mammal biochronology [9–12]. During the 1960s and the 1970s, the concept of biochronology was coming to age as a crucial approach for relating biological events to the geological time scale [13–16], alongside efforts aimed at identifying consistent subdivisions in the Villafranchian in western Europe (e.g., [9,10,17–21]).

Lindsay et al. [22] undertook paleomagnetic investigations of two stratigraphic sections in Italy yielding the Triversa (early Villafranchian, MN 16a) and Montopoli (middle Villafranchian, MN 16b) classic faunas. The results of this study allowed the authors to correlate what is now identified as the early Villafranchian to middle Villafranchian transition—and the concurrent appearance of *Equus* Linnaeus, 1758 [23], and *Mammuthus* Brookes, 1828 [24]—with the Gauss-Matuyama reversal (today dated at ~2.6 Ma). To clarify the appearance of *Equus* and *Mammuthus* in Europe, Lindsay et al. [22] already recognized the necessity of more data on the 3.0–2.6 Ma timespan, and they further noted that “Biochronological-palaeomagnetic sequence studies [25] of the Ponto-Caspian Basin show the beginning of the *Archidiskodon* Superzone (equivalent to the appearance of *Mammuthus*, and possibly *Equus*) at the Mammoth event (about 3.1 Myr) in that area” [22] (p. 137). *Archidiskodon* Pohlig, 1888 [26], is a genus to which early European *Mammuthus* have long been referred, although it is seldom adopted as valid today [27]. Basically, the important point here is that while Lindsay et al. [22] stressed the correlation of the faunal datum with the Gauss-Matuyama reversal, there was also room for an earlier chronology.

Azzaroli [28] summarized the available data on—and popularized—the major mammal dispersal events that occurred during the Quaternary of Europe, including the “Elephant-*Equus* event”. Since then, the term (sometimes also referred to as the *Equus*-Elephant event, *Equus*/Elephant turnover, *Mammuthus*-*Equus* event, or similar expressions) has widely been used in the literature (e.g., [8,12,29–45]). It is worth noting that Lindsay et al. [22] and Azzaroli [28] used the term “dispersal events” to refer to short periods of intercontinental dispersals and faunal replacement (basically following the concept elaborated by Repenning [46,47]), epitomized by, but not limited to the taxa after which each event was named. Moreover, these dispersal events were also directly associated and thus intrinsically linked (in their interpretation at least) to salient climatic and environmental changes [29]. In other terms, the Elephant-*Equus* event was envisioned as a period of marked faunal renewal, witnessing the disappearance of a “warm forest assemblage” and the arrival of species of a “more open, parkland or savannah landscape”, most notably, primitive elephantid and monodactyl equid [28] (p. 118). Azzaroli [28] suggested a possible chronological range for the Elephant-*Equus* event between 3.0 and 2.5 Ma, but later Azzaroli et al. [29] favored approximating it at 2.6–2.5 Ma.

In the years following the introduction of the term in the literature, that is, between the 1990s and the early 2000s, further discoveries and reinterpretations of old collections have engendered doubts on the correlation of the Elephant-*Equus* event with the Gauss-Matuyama reversal, and on its synchronicity across Eurasia [48–51]. On the other hand, growing evidence was piling up testifying to abiotic [3–5,7] and the possibly related bi-

otic changes in the environment (e.g., [52,53]). Eventually, in 2009, the Quaternary Period/System was formally ratified, and the base of the Pleistocene Epoch/Series was revised, officially resolving a long-lasting debate [54–56]. The agreed Pliocene-Pleistocene boundary, corresponding to the beginning of the Quaternary, was set in correspondence to MIS 103 and the Gauss-Matuyama boundary, hence at ~2.6 Ma. Indirectly, this provision enhanced the importance of the Elephant-*Equus* event, owing to its correlation with the beginning of the Quaternary.

Basically, despite representing an important biochronological concept evoked numerous times, the Elephant-*Equus* event has been, and it is still, invested by different meanings, spanning from it being used in a chronostratigraphic sense for denoting the beginning of the Quaternary [37,57], to considering it “a misleading term depicting a diachronous biochronological event” [45] (p. 23). Here, we show that both arguments have some points, and we offer a succinct review of the Elephant-*Equus* event, considering separately its two constituents bioevents, that is, the spread of primitive elephantids possibly related to *Mammuthus* (the elephant) and that of monodactyl equids (the *Equus*).

2. Quaternary Large Mammal Biochronology

Before addressing the Elephant-*Equus* event in particular, it is appropriate to provide an overview of large mammal biochronology in general or, at least, to schematize the context within which the concept developed and might be used today.

Biochronological correlations based on terrestrial large mammals offer many conceptual and practical challenges. For a start, continental sedimentary deposits are generally discontinuous in comparison to those of the marine realm, resulting in an imperfect representation of taxa (species is the most common category, but genus and subspecies are also considered) in the fossil record. Biases can be temporal, geographic, or both, and can influence species representation in different ways. In the most common case, a taxon can be considered absent from a certain area only due to the lack of adequate deposits. At the same time, it is also possible that documentation is only missing for a certain timespan, but a taxon is present before and after the gap. If such records are misunderstood (e.g., if an absence of occurrence due to inadequate sampling is taken as a biochronological argument), they can generate erroneous paleobiogeographic interpretations [36,58–60]. Basically, the stratigraphic datum of a taxon does not necessarily correspond to the “true” underlying bioevent (also referred to as paleontological event, fossil event, paleobiological event . . .), for instance, the dispersal of that taxon into the investigated geographic area. Of course, species that are genuinely rare in nature might be disproportionately affected by all the aforementioned factors. On the other hand, “rarity” in the fossil record does not necessarily imply a low demographic density, rather it can result from a taphonomic bias, which in turn can relate to several factors, for instance body size or environmental preferences [58,61–66]. These biases can affect the representation of a taxon within a specific geographic area due to its biological and ecological characteristics, but also between areas that hosted different ecosystems. A striking example is the paucity of the fossil record concerning the evolution of African great apes (chimpanzees and gorillas) in comparison to that of East African hominins [67]. During the Quaternary, interpreting the impact all these entwined factors is further complicated by the evolution of large mammal species in a context of enhanced climatic instability, which promoted the evolution of species prone to react to environmental changes by shifting their range [68].

Even so, the large mammal fossil record attracted extensive interest and generated a huge body of research that greatly counterbalances all the cons. It might also be argued that large mammals are a close approximation to our own “scale” of experiencing and understanding the environment. This means, for instance, that investigating the large mammal fossil record offers implications for inferring the dynamics of hominin dispersal outside Africa, which would be difficult to reconstruct exclusively by means of the scanty remains of our own clade. At the same time, and arguably as importantly, it likely facilitates the formulation of conceivable working hypotheses and the interpretation of the available

evidence, scale being a prominent aspect to understand how species perceive and respond to the environment (e.g., [69]).

In any case, subdividing the Quaternary on the basis of the mammal fossil record is a challenging and yet fundamental task. The “Italian” approach, which is mainly rooted in the work of Azzaroli (e.g., [9,10,28])—within which dispersal events such as the Elephant-*Equus* event were introduced and discussed—starts from local faunas, i.e., lists of taxa recovered from a locality. Ideally, local faunas should be representative of species living in certain area at a certain time (i.e., from a single fossiliferous horizon); however, for historical and practical reasons, this is not always the case. Local faunas are then grouped into faunal units (FUs), which are named after one representative local fauna (e.g., the Montopoli FU). The emphasis is on the faunal content and the boundaries between FUs are, by definition, not defined [11,36]. FUs in biochronology basically corresponds to coenozones in biostratigraphy, being characterized by a typical association of taxa. FUs are further grouped into higher ranking biochronological units, Land Mammal Ages (LMAs) (see Palombo and Sardella [36] for further discussion). We noticed that in recent years, probably since the last ten years or so, there has been a tendency to refer to them as European Land Mammal Ages (ELMAs), to which we also adhered, for consistency and stability, in recent studies (e.g., [68,70–74]). This approach is not harmful and probably manifests the necessity for the scientific community of a cohesive terminology both in time (e.g., for the Neogene and the Quaternary) and between different geographic areas (i.e., similar for Europe, Asia, etc.). However, it is worth noting that unlike other cases, most of the Pliocene–Pleistocene, and especially, the Quaternary biochronological subdivisions based on terrestrial mammals, have not been the subject of collective discussions of a “European dimension”, and hence their reference as ELMAs merely attaches a different designation to what has been previously simply known as Mammal Ages or Land Mammal Ages [11,36]. We anticipate that this could become a further confounding terminological factor, especially should different overlapping “local” Land Mammal Ages or biochronological units that are alternatively used for small mammals or large mammals be contemporary elevated as ELMAs.

Several other aspects of the biochronological methodology are often a cause of misunderstandings. First and foremost, biochronology is not the subject of formal provisions discussed in a stratigraphical code. In other terms, this means that nowhere is “formally defined” what a biochronological unit is or how it is subdivided, and that applies to any biochronological term. Of course, common sense and, indeed, common practice keeps authors within certain customs. However, what happens when there are long-established divergent approaches? Additionally, when is it necessary to use biochronological terms and concepts outside strictly biochronological studies? Basically, either if perceived as a flexibility or simply tolerated in the absence of strict formal guidelines, the variety of approaches and application of biochronological terms and concepts might be misleading for most. Early endeavors in this field for the Plio-Pleistocene of western Europe were the result of a single or few researchers with a wide background who were capable of offering pioneering syntheses of conceptual and practical value (e.g., [9,19]). However, we think that today, in the absence of ratified formal provisions, the best way to minimize inconsistent approaches are collective efforts aimed at reaching a general consensus, which are, however, seldom carried on (e.g., [11]). It would be, in any case, a good practice to provide more information on the biochronological terminology adopted in a study, in the same way, for instance, morphological nomenclature and measurement protocols are customarily detailed even when they are well-established and presumably understood by most specialists of a specific topic.

Additionally, counterintuitively but linked to the aim of promoting consistency and stability is the fact that the subdivisions and rankings of biochronological units do not necessarily or precisely reflect taxonomic (and hence eco-functional) differences. A good example is the early Villafranchian, which is often stressed to share a more similar “warm forest assemblage” [22] (p. 118) with the preceding Ruscian than with the middle Villafranchian

(e.g., [11]). Basically, Villafranchian faunas are still referred as such for historical reasons, despite the fact that the term is currently not biochronologically informative without the addition of early, middle, or late epithets.

Another concept that is often misinterpreted is that of FU and its relationship with its type local fauna. Basically, the age of a FU is of course linked to that of its representative local fauna, but the latter, as aforementioned, should be ideally a “snapshot” of the fauna inhabiting a certain area at a certain time, and necessarily, it cannot cover all the FU. To clarify, for instance, the Middle Pleistocene site of Fontana Ranuccio yielded an important archeological and paleontological record, including hominin remains (e.g., [66,75–78]) and its mammal fauna is representative of the Fontana Ranuccio FU. This fauna has long been referred to MIS 12 (e.g., [79]), following the $^{40}\text{K}/^{39}\text{Ar}$ age of 458 ± 12 ka obtained by Biddittu et al. [80]. Recently, Pereira et al. [81] redated the same horizon with the $^{40}\text{Ar}/^{39}\text{Ar}$ technique and obtained a younger age, specifically 408 ± 10 ka (hence MIS 11). However, the rejuvenation of the local fauna of Fontana Ranuccio does not imply that the homonymous FU has similarly be redated, rather, local faunas referred to the Fontana Ranuccio FU spans in age from MIS 13 to MIS 11 (e.g., [82–84]), and the type fauna is simply one of those correlated to MIS 11.

This introductory panegyric on large mammal biochronology should have given some perspective and partly explains why even widespread concepts such as the Elephant-*Equus* event have been used in different and contradictory ways over the years. Besides conceptual differences in the approaches, data are however crucial, and in the following, a brief updated review on the early occurrences of primitive elephantids and monodactyl equids in Europe is provided.

3. The “Elephant Event”

The first fossil representatives of the Elephantini *Elephas* and *Mammuthus* are known from the latest Miocene to Early Pliocene of Africa [85–87]. During the Late Pliocene, primitive elephantines dispersed across Eurasia (Figure 1). *Elephas planifrons* Falconer & Cautley, 1845 [88], reached the Upper Siwaliks of the Indian Subcontinent ~3.6–3.2 Ma [89,90], while the material assigned to *Mammuthus rumanus* (Stefanescu, 1924) [91] is known from the upper part of the Mazegou Formation (~3.7–2.8 Ma [92,93]) in China [94]. As pointed out by Böhme et al. [90], paleomagnetic calibrations [95] support an age close to 3.2 Ma for the elephantine occurrences at Cernătești and Tuluțești (the latter being the type locality of *Mammuthus romanus*).

Outside Africa and along the plausible dispersal route of elephantines to Eurasia, the site of Bethlehem (tentatively referred to the Late Pliocene, early Villafranchian), in the Levantine corridor, yielded intriguing elephantine remains [96–98]. Rabinovich and Lister [98] described the material and concluded to referring most of it to *Mammuthus*, with the possible presence also of *Elephas* Linnaeus, 1758. Another Levantine site of even more uncertain chronology but also yielding remains likely belonging to an early mammoth is Erq el Ahmar [99].

Further north, the Turkish sample of Kale Tepe-3, also of the Late Pliocene age, was referred to a primitive elephantid, most likely *Elephas* [100]. On the other hand, the Greek site of Tsotylio, inferred to be dated at around 3.5–3.0 Ma, yielded a maxilla best fitting with an attribution to an early *Mammuthus* [101]. Collectively, the records from Bethlehem, Kale Tepe-3, and Tsotylio support the view of the presence of two primitive elephantines in the Late Pliocene of the eastern Mediterranean, respectively, belonging to *Elephas* and *Mammuthus*. Although the uncertainty in the estimated ages of these findings and the overall conservative dental morphology of early representatives of *Elephas* and *Mammuthus* leave room for different taxonomic and paleobiogeographic interpretations—pending the discovery and description of further material [97,98,100,101]—the available evidence of primitive elephantines out of Africa corroborates the scenario of a mid-Piacenzian bi-directional faunal exchange from Africa and Eurasia, after a period almost devoid of dispersals (~5.6–3.3 Ma) regulated by the Arabian hyperaridity [90,102]. In this scenario,

Mammuthus is quite unique in being the only genus dispersing from Africa to western Eurasia during this mid-Piacenzian faunal exchange.

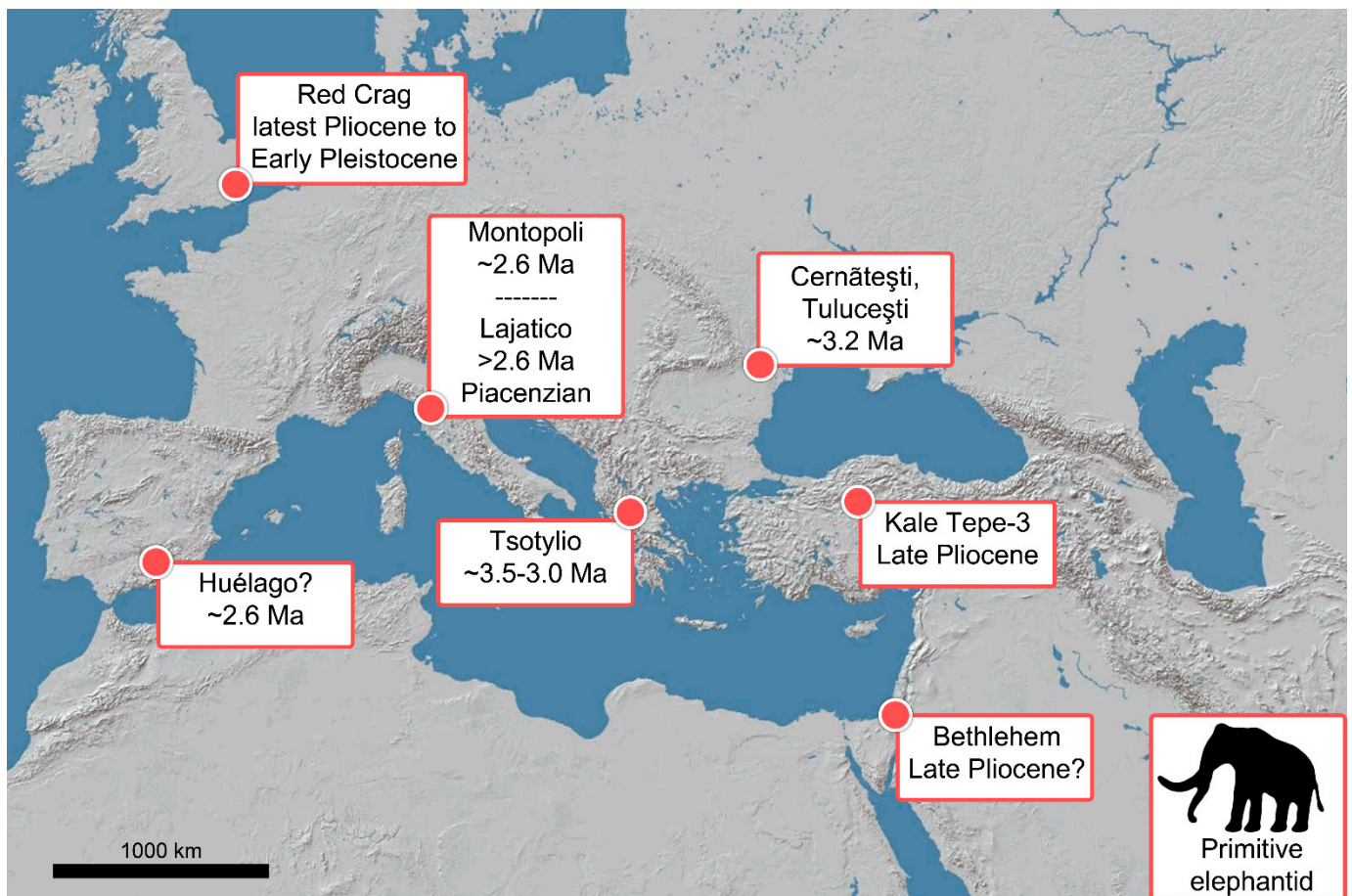


Figure 1. Selected localities mentioned in the text showing the occurrence of primitive elephantid in western Eurasia.

As mentioned above, the earliest calibrated occurrences of early mammoths outside Africa are from eastern Europe at ~3.2 Ma, and they are usually assigned to *M. rumanus* [90,97]. For comprehensive information on the application of the name of *M. rumanus* and the diverging opinions expressed around the related early mammoth material between the 1990s and the early 2000s (e.g., [103,104]), we refer the reader to Lister et al. [50] and Markov [97]. In brief, originally introduced as a subspecies of *Elephas antiquus* Falconer & Cautley, 1847 [105], (today referred to the genus *Palaeoloxodon* Matsumoto, 1924 [106]) by Stefanescu [91], *M. rumanus* was then taken as a representative of the early and primitive mammoth recorded in Eurasia [50,97,107]. On the other hand, it has been argued that given the paucity of the material and the overall plesiomorphic dental morphology of early elephantines, most early Eurasian samples should rather be left in open taxonomy, i.e., as *Mammuthus* sp. [101,108].

This taxonomic opinion has been advocated, for instance, for the Italian samples of Montopoli and Lajatico (modern correct spelling of the toponym often referred to as Laiatico in the literature) [108]. The abundant and diverse fauna of Montopoli has been taken as representative of the first FU of the middle Villafranchian, and the locality is correlated with the Gauss-Matuyama reversal at 2.6 Ma, arguably representing a fundamental sample for the development of the concept of the Elephant-*Equus* event [10,11,22,28,32,108–110].

The record of Lajatico is often treated together and is basically overshadowed by the geographically close locality of Montopoli, but it is of key importance and hence, more information is provided herein. The finding of an elephantid skeleton at La Vallata,

1 km north of Lajatico, was first briefly communicated and then discussed in detail by Ramaccioni [111,112]. The first elephantid remains were discovered by chance in the summer of 1933, promoting a systematic excavation of the area during the following year that lasted for around two months, from September to November 1934. This excavation revealed a good portion of the rest of the skeleton of a single old individual (with the third molar in use), whose bones laid disarticulated on a surface of ~ 360 m². Apart from the material initially exposed by agricultural works, Ramaccioni [112] described the elephantid bones as coming from a level of clays rich in gypsum crystals, which in terms of the national geological cartography, corresponds to the lower part of Villamagna Formation (Formazione di Villamagna), which is of the Piacenzian age [113,114]. Montopoli is also referred to the Villamagna Formation, but its fauna was recovered from sand deposits near the top of the formation [10,28,111]. Basically, Montopoli is correlated with the Gauss-Matuyama reversal at ~ 2.6 Ma, but the record of Lajatico is stratigraphically lower than that of Montopoli, and hence, 2.6 Ma is only the minimum age of the Lajatico elephantid skeleton. The difference in age between the two localities is often believed to be little [29,108], but we think this mainly reflects the now superseded assumption of a short chronology for the dispersal of primitive elephantid in Europe (i.e., close to 2.6 Ma), rather than being based on geological evidence, the latter only allowing a generic reference to the Piacenzian [113]. Azzaroli [28] (pp. 118–119) already remarked this point, clearly stating that “The immigration of the elephant is in any case older than the Montopoli local fauna: the skeleton from Lajatico was found interbedded in marine and brackish clays underlying the sands that cap the local Pliocene sequence and which represent the level of the Montopoli local fauna.”

Another elephantid record from western Europe usually considered to be from ~ 2.6 – 2.4 Ma is that of the Red Crag Formation, from which few dental remains referred to *Mammuthus* cf. *rumanus* are known [50]. Prior to the revalidation of *M. rumanus* [50,97,107], Lister [115] regarded the material from the Red Crag as possibly representing the earliest mammoth in Eurasia, with an estimated age of ~ 3.0 – 2.5 Ma, following Zalasiewicz et al. [116]. Then, Lister and Van Essen [107] (p. 48) reasoning on the Red Crag, stated that “The majority of surface exposures are of Pre-Ludhamian age, so it is likely that the bulk of the collected mammalian fauna is of this age”, which they correlated to 2.6–2.5 Ma based on the works by Head [117,118] and Funnell [119]. Approximately the same reasoning and estimated age have been reproposed in subsequent studies [120]. Yet, as summarized by Davies et al. [121] the precise age of the Red Crag Formation remains contentious, with general agreement only in recognizing that its deposition spanned from the latest Pliocene (Piacenzian) to the earliest Pleistocene (Gelasian) and lasted for around 800–600 ka. Therefore, the fossil record from this locality should be considered with caution when hypothesizing biochronological correlations.

Finally, remains referred to cf. *Mammuthus meridionalis* (Nesti, 1825) [122] were also reported from Huélago, in Spain [123,124] as coming from sediments of normal polarity referred to the upper part of the Gauss [125]. This sample was, however, neither considered in subsequent works discussing early European elephantines (e.g., [50,97,126]), nor mentioned in a recent overview of the mammal recoveries from the basin, where the earliest *Mammuthus* reported from the area of Huélago is referred to MN 17 [127]. We tentatively included this occurrence in Figure 1, pending further studies aimed at clarifying the taxonomic status and chronology of the elephantid record from Huélago, which would be very welcome given its geographic position.

4. The “*Equus* Event”

Monodactyl equids dispersed from North America into Eurasia around the Pliocene-Pleistocene boundary, being almost instantaneously (in a geological sense) documented across the continent, with different occurrences from China to western Eurasia [41,128–135] (Figure 2).

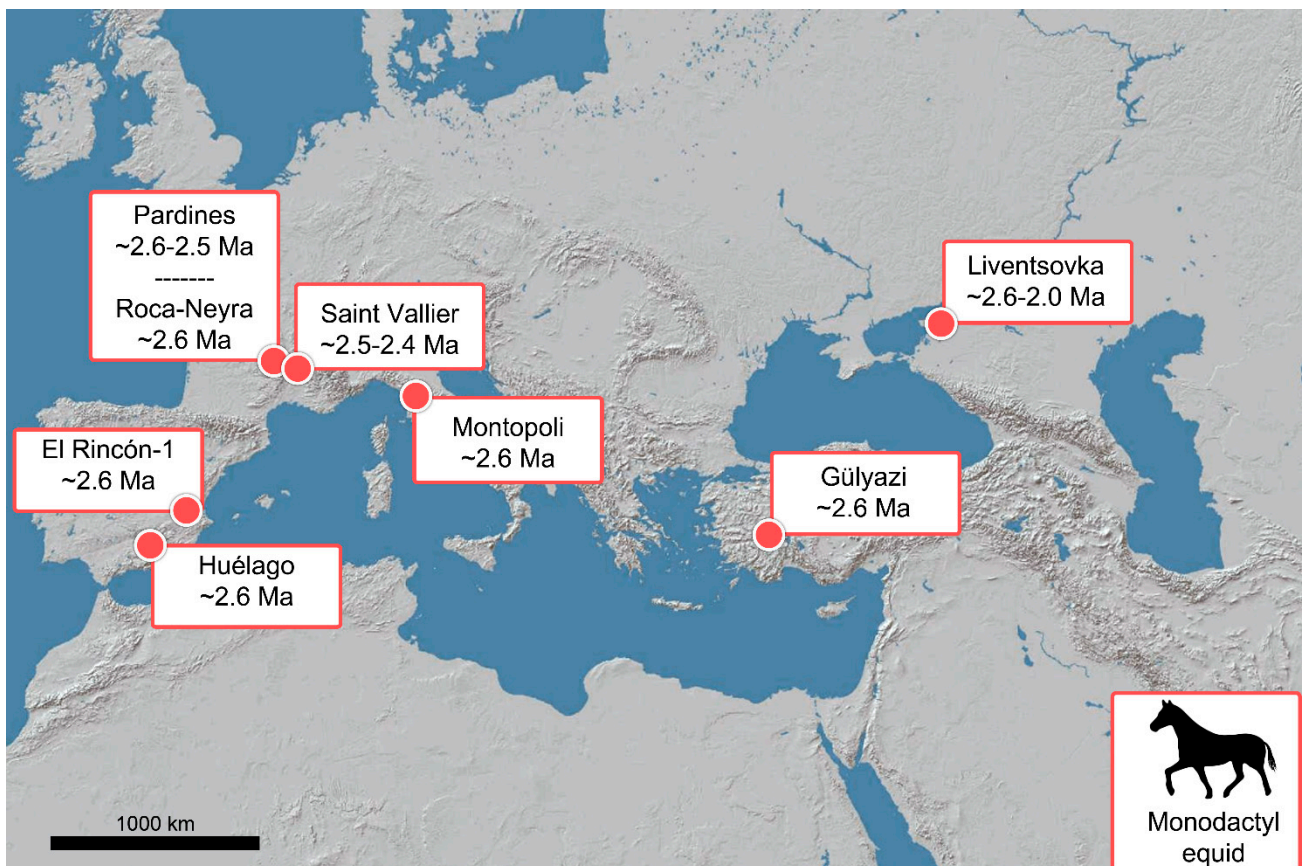


Figure 2. Selected localities mentioned in the text showing the occurrence of early monodactyl equid in western Eurasia.

Early European monodactyl equids are generally referred to as stenoroid or stenoroid horses, that is, species related to *Equus stenonis* Cocchi, 1867 [136], forming a monophyletic group and having its earliest representatives in *Equus livenzovensis* Baigusheva, 1978 [137], from Liventsovka, to which further occurrences from Italy, Spain, and France have also been aligned [129,132,134,138]. However, this is not universally accepted, partly because the remains recovered from several localities are not abundant or informative, and partly due to the uncertainties surrounding the consistency of the material of the type locality of *E. livenzovensis*, Liventsovka [41]. Recently, Eisenmann [135] reexamined the material from Liventsovka, vindicating Forsten's [139] realization of taxonomic and chronological heterogeneity in the sample from this locality. Indeed, the fact that the faunal assemblage from this site is not chronologically homogeneous has been remarked by several authors [139–142]. Titov [143] estimated a time-averaged deposition spanning ~2.6–2.2 Ma at Liventsovka. On the other hand, the occurrence of the giant hyena *Pachycrocuta brevirostris* (Gervais, 1850) [144], not documented elsewhere in Europe prior to ~2.0 Ma, points to an even somewhat younger upper chronological limit [142]. Considering that the sediments at Liventsovka show a negative magnetic polarity [143], a pre-Olduvai age is likely, suggesting that their deposition is bracketed at ~2.6–2.0 Ma. Basically, it is neither certain that *E. livenzovensis* is the earliest stenoroid horse in Europe, nor that western samples (e.g., Montopoli and El-Rincón-1) belong to this species. The latter point has been especially stressed by Forsten [139] and Eisenmann [135].

It has also been questioned whether the aforementioned early European monodactyl equids (stenoroid horses) should be ascribed to *Equus* or rather to a separate genus, namely *Allohippus* Gromova, 1949 [135,145–148]. This mainly rests on certain differences in cranial proportions between stenoroid horses and *Equus* s.s., which following this taxonomic opinion, would have its earliest European representative in the Early Pleistocene *E. vekuae*

Eisenmann, 2022, from Dmanisi [148]. On the other hand, Dmanisi equids were previously referred to as *E. altidens* von Reichenau, 1915 [72,149]. In general, cranial remains of early stenorid horses that allow to check features diagnostic of *Allohippus* (following Eisenmann [148]) are scanty, and some authors use *Allohippus* as a subgenus of *Equus* including the stenorid horses [41]. For the ease of reference, here we pragmatically continue to use “*Equus*” in a broader sense, while acknowledging the existence of radically divergent taxonomic opinions between specialists of the group. In any case, these alternative opinions do not diminish the biochronological value of the spread of monodactyl equids in Europe.

Another point that pushes exercising caution in referring early stenorid horses from western Europe to *E. livezovensis*, is the presence of other species as early as ~2.5–2.4 Ma, the best example being the abundant sample from Saint Vallier [150], with further material reported from Pardines (dated between Roca-Neyra and Saint Vallier, i.e., ~2.6–2.5 Ma [40]) [132]. Further studies are also needed to clarify the status of the stenorid horse from Gülyazi [151,152], also considered to be dated at ~2.6 Ma [134].

Indeed, the material from western Europe aligned by many authors to *E. livezovensis* is generally not abundant and placed in open taxonomy (i.e., as *Equus* cf. *livezovensis*). For instance, although of great significance for the development of the concept of the Elephant-*Equus* event [10,22,28,29], the *Equus* record of Montopoli is limited to a few phalanges described and assigned to *Equus* cf. *livezovensis* by Bernor et al. [153]. Similarly, the site of Roca-Neyra yielded only three teeth referred to *Equus* cf. *livezovensis*, which were likely belonging to a single individual [134]. More abundant is instead the Spanish record and in particular the sample of El-Rincón-1, assigned to *E. livezovensis* by Alberdi et al. [154].

A purported occurrence of *Equus* earlier than ~2.6 Ma based on some isolated postcranial elements, namely, a second phalanx, a pyramidal, and a lunatum, was reported from Vialette, considered to be dated at 3.14 Ma [51]. It is mainly on this basis that the synchronicity in the spread of monodactyl equids in Eurasia has been sometimes doubted in subsequent studies [12,39]. However, Palombo and Alberdi [132] argued that the taxonomic attribution to *Equus* of the material from Viallette is not substantiated by the morphology of the remains. Most importantly, the proposed age of the site is not reliable, or at least, it cannot be applied to all the material labelled as from Viallette in the same collection (Musée Crozatier, Le Puy-en-Velay) [132,155]. The problem has been already discussed in detail by Van der Made et al. [155] and Palombo and Alberdi [132], see also Guérin [156]. In brief, the collection of “Vialette” is made up of historical material whose provenance is not certain, and that even includes some undeniably Miocene taxa. For instance, some suids remains have been referred to as *Listriodon* von Meyer, 1846 [157], and cf. “*Microstonyx*” *major* (Kaup, 1833) [158–160], the latter species being more commonly placed in *Hippopotamodon* Lydekker, 1877 [161], in the recent literature [162]. For completeness, it is worth mentioning that another notable alleged earliest European occurrence based on the material from Vialette, that of *Canis* Linnaeus, 1758 [51], which played a significant role in the decline of the use of Azzaroli’s “Wolf event” [28,29], has also been recently questioned by Böhme et al. [90], who regarded it as *Eucyon* Tedford & Qiu, 1996 [163].

5. Discussion and Conclusions

The Elephant-*Equus* event has long been an important biochronological concept, but today it is used with different meanings, resulting in misleading and ambiguous applications. Apart from conceptual and semantic differences, the available data indicate that the dispersal of the “elephant” across Eurasia definitely predates that of the “*Equus*” (Figure 3).

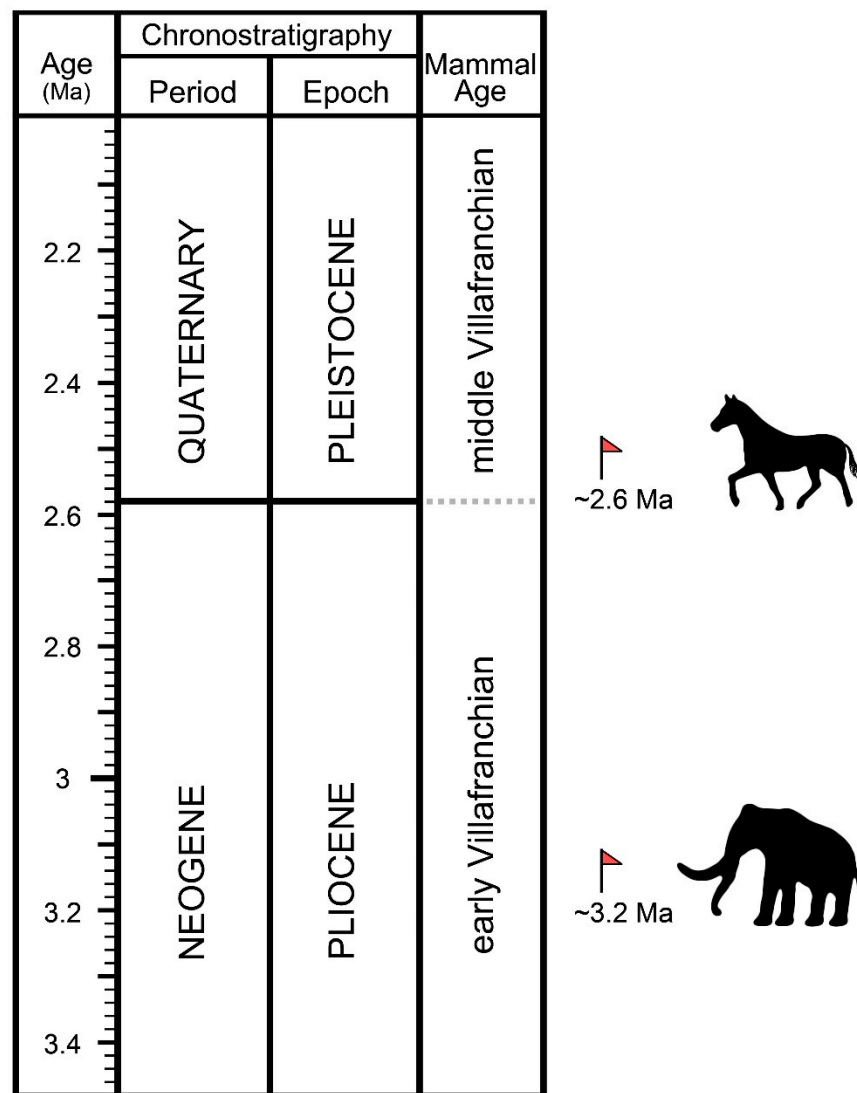


Figure 3. Chronological chart showing the first appearance of primitive elephantid (*Mammuthus*) and early monodactyl equid (*Equus*) in western Eurasia. In the region, the arrival of *Mammuthus* is an isolated bioevent calibrated at ~3.2 Ma, while the “*Equus* event” testifies to a marked faunal renewal ~2.6 Ma.

The earliest calibrated occurrences of primitive elephantines in Eurasia referred to *Mammuthus* are dated at ~3.2 Ma, markedly prior to the Pliocene-Pleistocene transition. The fossil record of this contingent is sparsely but widely represented across Eurasia, and we concur with Palombo [68] in considering this evidence to be the likely result of a fast (geologically speaking) dispersal. In this regard, it is not certain whether the early chronology of the eastern findings is an indication of a diachronous spread of early mammoths to the western part of Europe. Indeed, it is worth noting that the available age constraints for some of the western localities do not allow to rule out the possibility of a roughly synchronous dispersal. In particular, the elephantid skeleton from Lajatico is stratigraphically lower than the record of Montopoli, hence older than 2.6 Ma, only generically tied to a Piacenzian age [113]. The elephantid record of the Red Crag is similarly often considered ~2.6–2.4 Ma [107,120]. However, the precise age of the Red Crag Formation is debated, and its deposition is considered to have lasted for around 800–600 ka, thus encompassing the Pliocene-Pleistocene boundary [121]. Most importantly, the large mammal assemblage recovered from this locality also yielded evidence of faunal heterogeneity. For example, it includes both remains assigned to *M. rumanus* and to its purported descendent, *M. meridion-*

alis [50,120]. Even more significant is the cooccurrence of middle Villafranchian and some Ruscinian to early Villafranchian “holdovers”, such as the suid *Sus arvernensis* (Croizet & Jobert, 1828) [164], which is not firmly recorded elsewhere in Europe from localities successive to MN 16a (equivalent to the Triversa FU) [165].

The latter point calls for a succinct comment on the $^{40}\text{Ar}/^{39}\text{Ar}$ age of 2.78 ± 0.01 Ma reported by Nomade et al. [40] for Perrier-Les Etouaires, which includes both early Villafranchian and middle Villafranchian species (e.g., [166]). Indeed, while Nomade et al. [40] provided this age for pumices of la Côte d’Ardé, which they considered stratigraphically close to the Perrier-Les Etouaires “classical site”, they also recognized, as did many previous studies (e.g., [166,167]), that the fauna originated from several layers of different ages. Basically, we argue that the Perrier-Les Etouaires fauna cannot be altogether dated at 2.78 ± 0.01 Ma and careful historiographic and curatorial studies should be carried out to clarify (or infer) the stratigraphic position of each taxon with respect to the level dated at 2.78 ± 0.01 Ma. Only such an effort, if successful, would eventually allow us to refine the “boundary” (see Sardella and Palombo [168]) between the early and the middle Villafranchian (MN 16a–MN 16b; Triversa FU–Montopoli FU). Following the $^{40}\text{Ar}/^{39}\text{Ar}$ ages and stratigraphic correlations provided by Nomade et al. [40], the fauna of Perrier-Les Etouaires as a whole is only constrained between a Plinian fall dated at 3.11 ± 0.01 Ma and an overlying debris avalanche, whose intercalated pumices have been dated at 2.60 ± 0.02 Ma. The latter debris avalanche is contemporary to the fauna of Roca-Neyra, therefore implying that the appearance of middle Villafranchian elements occurring in Perrier-Les Etouaires fauna indeed predates that represented in the fauna of Roca-Neyra. However, it remains to be answered how much older these occurrences really are.

The earlier (than formerly assumed) appearance of *Mammuthus* in western Eurasia also pushes a critical reconsideration of the paleoecological significance of this event. Indeed, if the previously estimated age for the “elephant” dispersal in Eurasia allowed the hypothesis of a relationship with the Pliocene–Pleistocene changes towards cooler and drier conditions [22,28], the revised chronology reveals instead that it was part of a major period of faunal exchange, between Africa and Eurasia, which was linked to the mid-Piacenzian climatic warmth [90]. Of course, this is not to say that all the species that took part in this intercontinental dispersal were indicative of warm–humid environments. Rather, the retreat of the deserts allowed a bi-directional dispersal of ecologically diverse species. In this scenario, *Mammuthus* is quite unique in being the only genus dispersing from Africa to western Eurasia during this mid-Piacenzian faunal exchange [90]. Palombo [68] suggested that *Mammuthus* dispersal was linked to the development of a thermic seasonality in the Mediterranean terrestrial domain at ~ 3.3 – 3.2 Ma [169]. Direct paleoecological evidence on early European mammoths is somewhat limited. Microwear analyses performed on two teeth of *M. rumanus* from the Red Crag suggested this early mammoth inhabited more open environments than *Anancus arvernensis* (Croizet & Jobert, 1828) [120], but this evidence is not conclusive, given the very small sample size.

Most of the positive aspects of the “Elephant–*Equus* event” concept as traditionally conceived can still be used, but referring only to the spread of monodactyl equids, i.e., to an “*Equus* event”. Based on the available evidence, the appearance of monodactyl equids is virtually synchronous across Eurasia and corresponds to the Gauss–Matuyama reversal, at ~ 2.6 Ma. Therefore, the *Equus* event would excellently serve those who wish to use it primarily in a chronological sense (and indeed, it is already sometimes used in this way (e.g., [170])). The term “*Equus* Datum”, which conceptually emphasizes this aspect [15], is also used in many studies (e.g., [133]), and could be favored when a distinction or an emphasis on the stratigraphic datum is needed. Additionally, the *Equus* event is also consistent with its interpretation as a major large mammal dispersal event (*sensu* Azzaroli [28]), corresponding to the early Villafranchian to the middle Villafranchian faunal turnover. It is of course predictable that further discoveries will refine our knowledge and push for a reconsideration of the chronology of the arrival of some of the species involved. Intriguingly is, for instance, the possibility that the spread of wolf-like canids is

also coincident with the *Equus* event, as suggested by the identification of related material from Perrier-Les Etouaires (somewhat older than 2.6 Ma, see discussion above), reported by Böhme et al. [90]. If confirmed, this would basically render Azzaroli's "Wolf event" [28] representative taxon appearance as approximately coincident with the *Equus* Datum, and hence would push a reconsideration of the arrival of monodactyl equids and wolf-like canids as part of the same dispersal event (*sensu* Azzaroli [28]).

The potential allocation of early European monodactyl equids to a species other than *E. livenzovensis*, or even to a genus other than *Equus*, namely *Allohippus* (e.g., [135,148]), would not diminish the biochronological significance of the *Equus* event, similarly to the case of the "Hipparion" Datum [171]

Biochronology is a flexible and yet potentially ambiguous tool, especially when applied to Quaternary large mammals of western Europe, for which terms and approaches have long and sometimes conflicting traditions. The case of the Elephant-*Equus* event is emblematic of the problematics but also of the opportunities of relating large mammal evolution with the geological time.

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