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BEWARE OF THE "WOLF EVENT" - REMARKS ON LARGE MAMMAL DISPERSALS IN EUROPE AND THE LATE VILLAFRANCHIAN FAUNAL TURNOVER

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ABSTRACT: The "Wolf event" is a prominent concept in large mammal biochronology of western Europe. It was defined in the 1980s as an intercontinental "dispersal event", best represented by the arrival of a "primitive wolf", *Canis etruscus*, but also involving other species. The Wolf event denoted the late Villafranchian faunal turnover, first expressed in Italy in the Olivola Faunal Unit. This event was also considered approximately coincident with the Pliocene-Pleistocene boundary adopted prior to 2009 (~1.8 Ma, Gelasian-Calabrian transition), hence indicating important environmental changes and representing a relevant tool for correlation. Whilst it became soon clear that sporadic finds of modern canids (and, to some extent, other species) pre-dated the age assumed for the Wolf event, several authors continued to use the term and to associate it to the late Villafranchian, referring to the "massive expansion" of the species involved, rather than their first appearance in the European fossil record. Several bioevents traditionally included in the Wolf event and others that have been considered to occur later are today already documented in middle Villafranchian faunas. The "*Pachycrocuta brevirostris* event", proposed as a replacement term for the Wolf event, based on current evidence would be characterized by the arrival in Europe of the giant hyena *P. brevirostris* and *Panthera gombaszoegensis*, and the increase in the documentation of other species traditionally included in the Wolf event. However, this does not correspond to a sharp faunal turnover as traditionally envisioned for the Wolf event and it is possibly heralded in faunas slightly older than Olivola at ~2.0 Ma. In other terms, available evidence highlights the rather diachronic nature of large mammal dispersal occurred in the late middle and early late Villafranchian (late Gelasian, ~2.2–1.8 Ma), pushing to critically evaluate the biochronological, paleoecological, and paleobiogeographical significance of each bioevent. For instance, the arrival of *Hippopotamus* in Europe is now attested since ~2.2 Ma, documenting an African dispersal of a species linked to humid conditions in a context that is generally deemed to denote the spread of open-adapted faunal elements of mainly Asian affinities.

Keywords**:** Biochronology, bioevent, faunal renewal, Pleistocene, Villafranchian.

1. INTRODUCTION

During the Quaternary, marked climatic and environmental changes took place at a global scale, most notably affecting meteorological and oceanographic circulations, the intensity of the glacial activity in the Northern Hemisphere, and the frequency and amplitude of oscillations between cool-arid and warm-humid conditions (Shackleton, 1995; Flesche Kleiven et al., 2002; Gibbard et al., 2005; Ehlers & Gibbard, 2007; Etourneau et al., 2010; Gibbard & Head, 2020). In turn, these changes promoted substantial reorganizations of the large mammal fauna. Forty years ago, Azzaroli (1983) recognized and named three major "dispersal events" (Repenning, 1967, 1980), referring to them as "short periods of rapid intercontinental migrations and faunal replacements" (Azzaroli, 1983, p. 117), namely the "Elephant-*Equus* event" (between 3.0 and 2.5 Ma), the "Wolf event" (~1.7 Ma), and the "end-Villafranchian dispersal event" (~1.0-0.9 Ma). In the following years, the proposed timing of these events was further discussed and refined (Azzaroli et al., 1988; Azzaroli, 1995; Gliozzi et al., 1997), eventually correlating the Elephant-*Equus* event with what is currently recognized as the Pliocene-Pleistocene transition (~2.6 Ma), the Wolf event with the Gelasian-Calabrian transition (~1.8 Ma; the Pliocene-Pleistocene boundary prior to 2009), and the end-Villafranchian event with the Early-Middle Pleistocene transition (~0.8 Ma).

Whilst Azzaroli (1983) regarded the aforementioned dispersal events as moments of marked faunal renewals and recognized in some cases the gradual character of the associated turnover, the approximate synchronicity between dispersal events and relevant geological transitions exacerbated their geochronological importance. This resulted in a widespread use of the appearance of the "representative" species after which the events were named (e.g., the genus *Equus* for the Elephant-*Equus* event) as a stratigraphic datum (see Iannucci & Sardella, 2023, for discussion). Essentially, there are at least two aspects of Azzaroli's dispersal events that resulted in ambiguous applications. First,

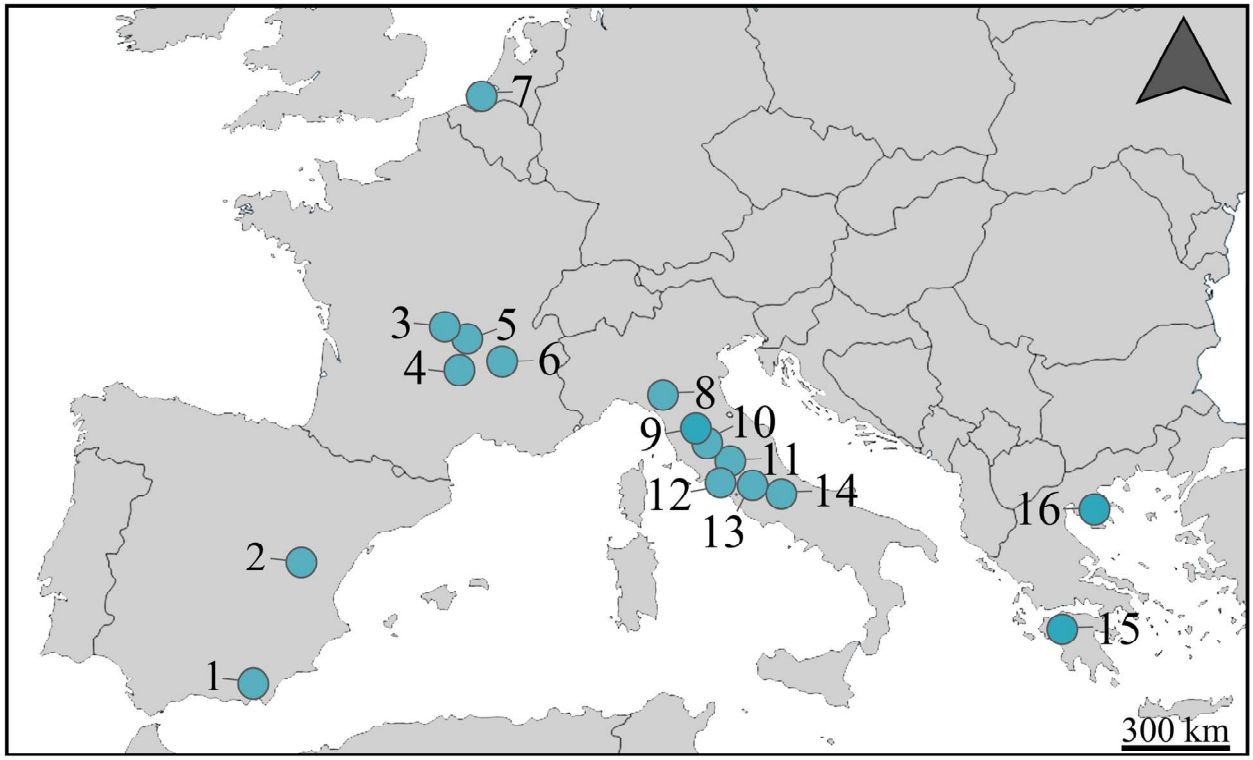

Fig. 1 - Main fossiliferous localities mentioned in this work: 1 - Fonelas P-1; 2 - La Puebla de Valverde; 3 - Perrier-Les Etouaires, Roca-Neyra; 4 - Senèze; 5 - Vialette; 6 - Saint Vallier; 7 - Oosterschelde; 8 - Olivola, Quercia; 9 - Valdarno Superiore (several localities); 10 - Montagnola Senese; 11 - Vigna Nuova, Chiusi Basin, Torre Picchio; 12 - Monte Riccio; 13 - Bocchignano, Castel San Pietro; 14 - Coste San Giacomo, Fontana Acetosa; 15 - Elis, Aetorráchi, Hághios Demétrios, 16 - Gerakarou 1.

although named after one or few taxa, these periods of faunal turnover involved, by definition, many species. Second, they were envisioned as "short", but not properly geologically instantaneous intervals. To this list can be added that Azzaroli (1983) emphasized the link between faunal and environmental changes, or, in other terms, he inherently included a paleoecological component in the biochronological event.

Of course, this is not to say that implementations of the dispersal event concept with a meaning that deviate from that used by Azzaroli (1983) are necessarily wrong. Indeed, as in general for other biochronological terms, concepts, principles, and practices, they are not formally defined within a stratigraphic code, which means that there exist a (legit) variety of approaches among different researchers (e.g., Gradstein et al., 1985; Lindsay, 2003; Palombo & Sardella, 2007; Palombo, 2009). However, this unavoidably leaves room for ambiguity, most notably when divergent adoptions of a dispersal event are discussed as if referring to the same thing, while different authors might have invested the same term with different meanings. Conceptual dichotomies aside, over the years several discoveries have pushed to reconsider the timing of specific bioevents (i.e., those linked to a single taxon), and thus, partly depending on the different acceptances with which Azzaroli's dispersal events have been used, authors opinions diverge as to whether reinterpret, reimagine, or abandon the use of specific dispersal events.

The Wolf event played a special role in Quaternary large mammal biochronology, especially in western Europe (Fig. 1), given the approximate coincidence between this event (in its original formulation) and the formerly adopted Pliocene-Pleistocene boundary at ~1.8 Ma (i.e., prior to the placement of the Pleistocene Epoch/Series at ~2.6 Ma, in 2009; Aguirre & Pasini, 1985; Pillans, 2004; Clague, 2006; Gibbard & Head, 2010; Gibbard et al., 2010; Head & Gibbard, 2015; Capraro & Maiorano, 2023).

Here, using the Wolf event as a case study, we offer a discussion, partly conceptual, partly factual, on the dispersal of wolf-like canids into Europe and on some other specific bioevents currently recognized to have occurred in the late middle and late Villafranchian (late Gelasian, ~2.2–1.8 Ma) that have been the subject of debate and in some instances considered in the framework of the Wolf event.

2. THE "WOLF EVENT"

Azzaroli (1983) remarked that turnover associated with the Wolf event was overemphasized in the Italian fossil record due to the lack of middle Villafranchian faunas, but he included in the Wolf event the arrivals of *Leptobos etruscus* (replacing *L. stenometopon*), *Sus strozzii*, *Pachycrocuta brevirostris*, and *Canis etruscus*. The latter is the "wolf" after which the event was named. This turnover would correspond to the beginning of the late Villafranchian, and to the Olivola Faunal Unit (FU). Other groups of *Canis* were considered to appear only in

the subsequent Tasso FU (Azzaroli, 1983). Azzaroli et al. (1988) remarked the coincident disappearance of *Nyctereutes* and *Gazella*, the appearance, possibly related to evolutionary changes, of *Eucladoceros dicranios* and *Dama nestii* (currently often referred to '*Pseudodama*', see Cherin et al., 2022, and references therein), and the arrival of another species, *Panthera toscana* (today referred to *P. gombaszoegensis*), alongside the bioevents previously recognized. Concerning the latter, however, Azzaroli et al. (1988, p. 84) referred to the "massive expansion in Europe" of the considered species, rather than their earliest appearance in the fossil record, again leaving room for divergent interpretations. Therefore, there are different aspects of Azzaroli's Wolf event that need to be critically evaluated based on the available evidence. It is worth considering: first, whether the dispersal of wolf-like canids in Europe is coincident with the beginning of the late Villafranchian in correspondence of the Olivola FU or not; second, how many of the aforementioned bioevents are indeed part of the same "dispersal event". In the following, these two points are briefly discussed.

When Azzaroli (1983) schematized the Wolf event and placed it in correspondence of the Olivola FU, remains of possibly older *Canis* were already known at least from the French site of Senèze (Martin, 1973), but the chronological consistency of the faunal assemblage recovered from this locality was often doubted (Masini & Torre, 1990; Mazza & Rustioni, 1994; Rook & Torre, 1996). Further canid remains were recovered from Coste San Giacomo (predating Olivola and now dated at ~2.2 Ma, Florindo et al., 2021; Coste San Giacomo FU) and attributed to *Canis etruscus* by Rook & Torre (1996), in line with ongoing investigation. Rook & Torre (1996) also reported the presence of a partial hemimandible of a canid recovered from Quercia (near Olivola and stratigraphically lower than it; Iannucci, 2023), accepted a middle Villafranchian age for the canids of Senèze, and concluded that the earliest dispersal of modern dogs occurred during the middle Villafranchian. Nonetheless, Rook & Torre (1996, p. 499) argued that "the meaning of the "wolf-event" for the beginning of the Late Villafranchian does not loose its value of "faunal event" in the sense of marked change in faunal assemblages". In the seminal synthesis on Italian biochronology by Gliozzi et al. (1997), the status of the Wolf event was not directly discussed, but the authors reiterated the first occurrence of wolf-like canids (*C. etruscus*) in Italy from the middle Villafranchian of Coste San Giacomo and the proper spread of the group since the beginning of the late Villafranchian.

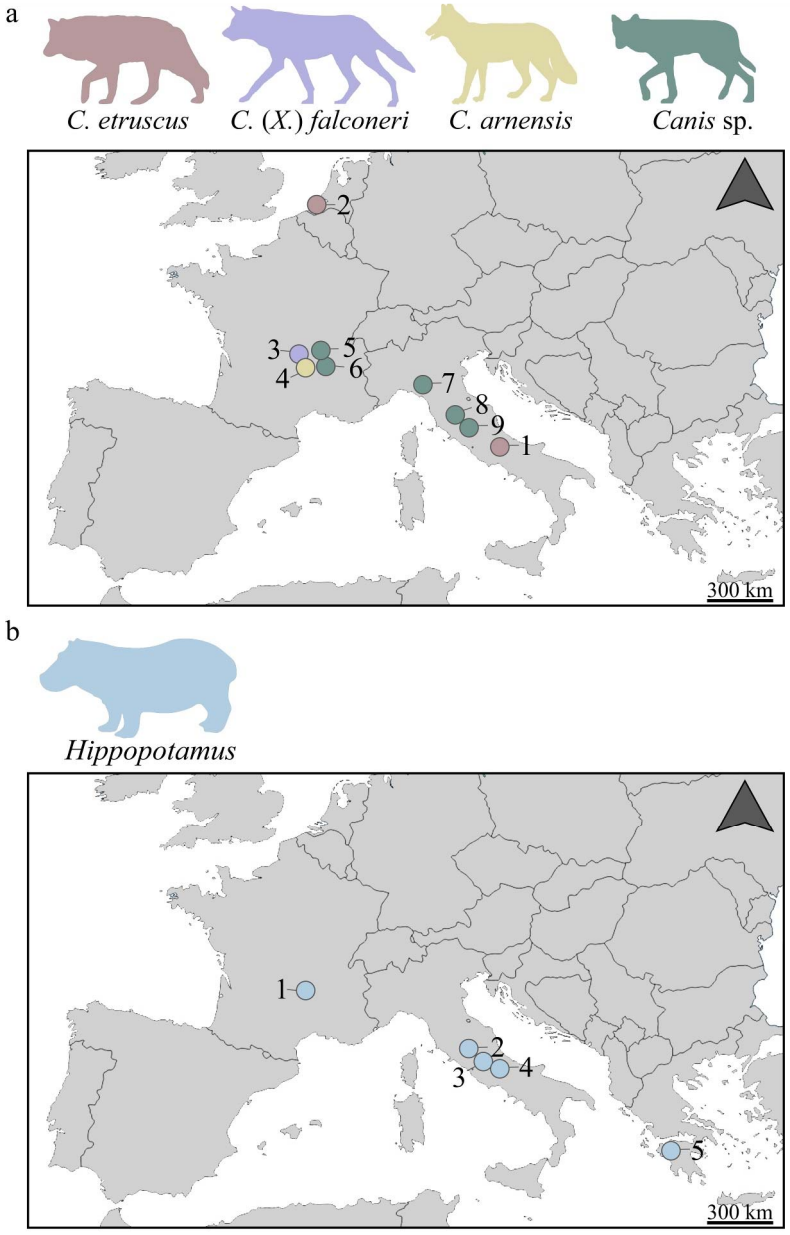

Fig. 2 - Distribution of *Canis* (a) in the middle Villafranchian of western Europe: 1 - Coste San Giacomo, Fontana Acetosa; 2 - Oosterschelde; 3 - Roca-Neyra; 4 - Senèze; 5 - Chilhac 2; 6 - Saint Vallier; 7 - Quercia; 8 - Montagnola Senese; 9 - Vigna Nuova, Torre Picchio. Silhouettes of canids modified from: Iurino et al. (2022; *Canis etruscus, Canis* sp.); Bartolini Lucenti & Spassov (2022; *Canis* (*X.*) *lycanoides*); Wikimedia Commons (https://commons.m.wikimedia.org/wiki/File:Canis_arnensis_restoration.jpg; *Canis arnensis*). Distribution of *Hippopotamus* (b) in the middle Villafranchian of western Europe: 1 - Senèze; 2 - Chiusi Basin; 3 - Castel San Pietro; 4 - Coste San Giacomo, Fontana Acetosa; 5 - Hághios Demétrios, Aetorráchi. Silhouette of hippopotamus modified from PhyloPic, by Zimices (phylopic.org/image/c2d68ebb-50ec-45f4-8cd1-6cf52ad02286).

Further evidence of middle Villafranchian *Canis* has piled up in the following decades, some of which perhaps related to wolf-like canids, either deriving from

new discoveries or reconsiderations of old collections (Fig. 2a). Two lower incisors assigned to *Canis* sp. were reported by Fondi (1972) from Montagnola Senese, whose fauna has been referred to the Coste San Giacomo FU (Bona et al., 2015). A fragmentary premolar and a portion of a distal metapodial of *Canis* sp. are known from Torre Picchio (Girotti et al., 2003), also referred to the Coste San Giacomo FU (Bona et al., 2015). During the revision of the carnivoran record of Saint Vallier, Argant (2004) identified the presence of a partial neurocranium referable to the genus *Canis*. The locality is customarily biochronologically placed between Montopoli and Coste San Giacomo FUs, with estimated ages ranging from 2.5 to 2.0 Ma (Viret, 1954; Azzaroli, 1970, 1977; Torre et al., 1992; Gliozzi et al., 1997; Guérin, 2004; Nomade et al., 2014; Brugal et al., 2020). Reumer & Piskoulis (2017) assigned to *Canis* cf. *etruscus* a mandibular fragmented recovered from the Oosterschelde estuary, whose Early Pleistocene fossil fauna, although resedimented in Late Pleistocene deposits and collected during dredging activity, is referred to the middle Villafranchian, or to ~2.4–2.1 Ma (Scager et al., 2017). Azzarà et al. (2022) described a portion of the axial skeleton of a single individual of *Canis* sp. recovered from the middle Villafranchian (Coste San Giacomo FU) site of Vigna Nuova, considering it very similar to comparable material of *C. etruscus* known from Olivola (Torre, 1967). Finally, concerning the long debate on the possibility of age heterogeneity in the faunal assemblage from Senèze (see Delson et al., 2006), Pastre et al. (2015) performed $^{40}Ar/^{39}Ar$ datings that constrain the sequence between ~2.2 and 2.09 Ma. Recently, U-Pb dating on volcanic zircons was also applied at Senéze, with results providing a mean age of of 2.100 ± 0.029 Ma (Paquette et al., 2021).

An even older record of *Canis* sp. would be that of Vialette (Heintz et al., 1974), which Lacombat et al. (2008) referred to 3.14 Ma. However, the attribution of the material and the chronology of the site have been contested. The problems concerning the chronology of the site or, more precisely, the mixing of different faunal elements among those labelled as from Vialette in the collection of the Musée Crozatier (Le Puy-en-Velay), has been commented by several authors (Guérin, 2005; Van der Made et al., 2014; Palombo & Alberdi, 2017). Perhaps the clearest example of chronological heterogeneity is represented by the identification of some remains belonging to Late Miocene suids, namely assigned to *Listriodon* and cf. "*Microstonyx*" *major* (Van der Made 2005; Van der Made & Moullé, 2005), the latter species being more commonly placed in *Hippopotamodon* in recent literature (Iannucci et al., 2021a). As for the taxonomic attribution of the canid material to *Canis*, Lacombat et al. (2008, p. 67) argued that: "The morphology, the size and the proportions of these remains allow us to exclude genera occurring in the Early Pliocene", while Böhme et al. (2021) recently suggested it could rather belong to *Eucyon*. On the other hand, Böhme et al. (2021) reported material of wolf-like canids from Perrier-Les Etouaires, referring it to 2.78 Ma following Nomade et al. (2014). This chronology calls for further discussion. Nomade et al. (2014) provided this age for pumices of la Côte d'Ardé, which they considered stratigraphically close to Perrier-Les Etouaires "classical site". However, as pointed out by Iannucci & Sardella (2023), this age cannot be accepted uncritically for all the mammal remains recovered from Perrier-Les Etouaires. Indeed, it is known that the fauna of Perrier-Les Etouaires contains early Villafranchian and middle Villafranchian species, which originated from layers of different ages (Poidevin et al., 1984; Palombo & Valli, 2004). In any case, following the dating and correlations proposed by Nomade et al. (2014) for the entire area of Perrier, the fossil findings should be constrained between ~3.1 and 2.6 Ma, an age that would be thus enough to make the record of wolf-like canids from Perrier-Les Etouaires reported by Böhme et al. (2021) the earliest (excluding Vialette) in Europe (Iannucci & Sardella, 2023), although the material has not been described. Indeed, the presence of *Canis* aff. *etruscus* from Etouaires was reported by Heintz et al. (1974) based on material part of the Bravard Collection housed in the British Museum listed by Lydekker (1885, p. 126). However, the material mentioned by Lydekker (1885) is possibly from younger deposits at Tour-de-Boulade, and indeed the author considered it undistinguishable from *C. lupus*. This view was reaffirmed by Torre (1979), who stated that these fossils were of large size, similar to that observed in wolves of the last Glaciations (which would correspond to the second part of Late Pleistocene).

Marciszak et al. (2023) also reported unpublished material of *Canis* cf. *etruscus* from Węże 2, referring it to 2.9–2.6 Ma, also listing further material from Poland potentially of middle Villafranchian age.

In sum, while the evidence for some of the aforementioned findings might not be conclusive, it has long been quite clear that the arrival of wolf-like canids in Europe is at least as early as the Coste San Giacomo FU (middle Villafranchian), and there is further putative evidence that would suggest an even older age. It is worth reiterating that the occurrence of wolf-like canids already in the middle Villafranchian did not discourage several authors to continue using the Wolf event to refer to the late Villafranchian faunal turnover as a whole, emphasizing the increase in the abundance of wolf-like canids, rather than their earliest appearance in the fossil record (e.g., Rook & Torre, 1996). This late Villafranchian "massive expansion", as it has been referred to by Azzaroli et al. (1988) and generally agreed in subsequent research (e.g., Gliozzi et al., 1997), is well documented in Italy, for instance by historical samples from Olivola and the Upper Valdarno, and by the abundant record of Pantalla (Cherin et al., 2013, 2014).

3. THE "HIPPO EVENT"

The earliest dispersal of *Hippopotamus* in Europe was not among the bioevents listed by Azzaroli (1983) as part of the Wolf event, but we consider particularly appropriate to discuss it here as there is now evidence of late middle Villafranchian (late Gelasian) hippopotamuses from several European localities, some of which also yielded early *Canis* (Fig. 2b). In particular, a fragmentary incisor of *Hippopotamus* sp. is known from Coste San Giacomo (Bellucci et al., 2012, 2014; Sardella, 2012). The age of the fossil horizon was consid-

ered around 2.1 Ma by Bellucci et al. (2014), based on magnetostratigraphy, pollen, and small mammals, and further refined at ~2.2 Ma by Florindo et al. (2021). Bellucci et al. (2012) firstly identified the specimen as belonging to a hippopotamus, although a more precise taxonomic attribution is clearly precluded by the scanty nature of the sample. Sardella et al. (2018) clarified that the hippopotamus incisor from Coste San Giacomo was not collected during systematic excavations but is part of the 1980s field collection, causing some authors to doubt the age of the finding (Marra et al., 2018; Martino & Pandolfi, 2022). However, field activities and excavations at Coste San Giacomo co-directed by one of us (RS) have pointed out that the vertebrate assemblage comes from a single fossiliferous level, from which the old collections can also be related (Bellucci et al., 2012, 2014; Bona et al., 2015; Strani et al., 2015; Palombo et al., 2017). It is worth noting that the fauna of Coste San Giacomo has long been considered a homogeneous assemblage, besides representative of the homonymous FU, the latest of the middle Villafranchian (Gliozzi et al., 1997).

The reason why the hippopotamus record of Coste San Giacomo has often been considered controversial (e.g., Martínez-Navarro et al., 2015; Pandolfi & Petronio, 2015) seems rather contingent. Traditionally, the earliest occurrence of *Hippopotamus* in Italy was placed in the Tasso FU, based on several historical findings from the Upper Valdarno (Nesti, 1820; Leonardi, 1947; Azzaroli, 1977; Gliozzi et al., 1997). Napoleone et al. (2003) suggested that the hippopotamuses might be of a younger age than that of the rest of the main Upper Valdarno fauna, considering the lack of their remains among those collected during modern excavations in the area. This possibility was also previously evoked by Faure (1985) and Mazza (1991). It is worth noting that most of the fossils from the Upper Valdarno is part of historical collections gathered at least since the nineteenth century (Rook et al., 2013). Moreover, the absence of hippopotamus remains from certain deposits might also be related to their ecological requirements, namely their sensitivity to the presence and amount of water (Mazza & Bertini, 2013). Martínez-Navarro (2004, 2010) and Rook & Martínez-Navarro (2010), following the suggestion of Napoleone et al. (2003) on the younger age of the Upper Valdarno hippopotamuses, remarked that consequently Venta Micena yielded the oldest European record of *Hippopotamus antiquus* (although other older records were known, e.g., that from Monte Riccio, Mazzini et al., 2000). Mazza & Bertini (2013, p. 195) also argued that "The first certified occurrence of *Hippopotamus antiquus* is from the Early Pleistocene locality of Venta Micena", but not excluding the occurrence of earlier findings of uncertain taxonomic status (e.g., the authors quoted Fontana Acetosa). In brief, the finding of the hippopotamus of Coste San Giacomo was published at a time when some researchers were hypothesizing a later chronology for the arrival of *Hippopotamus* into Europe (Bellucci et al., 2012; Sardella, 2012). This was, however, not universally accepted (e.g., Arribas et al., 2009).

In general, the finding of Coste San Giacomo represents the earliest occurrence of a middle Villafranchian hippopotamus in Europe (dated at ~2.2 Ma), but it is not the only. Cassoli & Segre Naldini (1984) listed *Hippopotamus* sp. among the faunal remains recovered from Fontana Acetosa, like Coste San Giacomo, another locality of the Anagni Basin in central Italy. The authors remarked the similar nature of the fossiliferous levels of Coste San Giacomo and Fontana Acetosa, yellow sands, although somewhat more clayey at Fontana Acetosa, but did not exclude the possibility of a slightly younger age for the latter site. The presence of *Hippopotamus* seemed indeed at odds with the then accepted first appearance of the species in the Tasso FU (Azzaroli, 1983). When Bellucci et al. (2012) recognized the presence of *Hippopotamus* at Coste San Giacomo, they also accepted the correlation between the two sites, although the fauna of Fontana Acetosa would be in need of a systematic study to clarify the biochronological value of the species reported.

During the revision of the fossil collection stored at Faculté des Sciences de l'Université Claude Bernard, Lyon I, a first phalange (FSL 211082), previously ascribed to *Equus* sp., was attributed to *Hippopotamus* cf. *antiquus* by Mazza & Rustioni (1994). The fossil was recovered from Domeyrat, one of the toponyms generally considered as part of Senèze locality. The presence of hippopotamuses at Senèze was previously listed by Jung (1946) and Bout (1960), but then excluded from subsequent faunal lists (e.g., Heintz et al., 1974), possibly due the supposedly later arrival of *Hippopotamus* in Europe. It seems conceivable that reports older than the work by Mazza & Rustioni (1994) were based on further undescribed material and, in any case, even after that Mazza & Rustioni (1994) reaffirmed the occurrence of hippopotamuses at Senèze, these were seldom considered in subsequent biochronologic schemes (but see Arribas et al., 2009), likely due to the uncertainty on the chronology of the locality (see previous section above). Nonetheless, as discussed in the previous section, several radiometric estimates now constrain the succession of Senèze at ~2.2–2.1 Ma (Nomade et al., 2014; Pastre et al., 2015; Paquette et al., 2021), approximately coeval with Coste San Giacomo.

Several findings of middle Villafranchian hippopotamuses are known from the area of Elis, in Greece, as recently reviewed by Athanassiou (2022). These remains include: dentognathic material described by Thenius (1955), which according to Athanassiou (2022) can be considered of earliest Pleistocene age owing to invertebrate biochronology; further osteological and dental finds mentioned by Symeonidis & Theodorou (1986) from Hághios Demétrios; a juvenile fragmented cranium from Aetorráchi (Reimann & Strauch, 2008).

Other hippopotamus remains attributed to *H. antiquus* were recovered from the Chiusi Basin (Cuscani Politi, 1966, 1971; Mazza, 1995; Pandolfi & Petronio, 2015). An accompanying faunal assemblage was also reported by Pandolfi & Petronio (2015), including *Gazella* sp., *Axis* (='*Pseudodama*') cf. *nestii* and *Eucladoceros* sp., although not described and made up of surface finds, the authors referred it to the Coste San Giacomo or Olivola FUs. The occurrence of *Gazella* would point towards the former, considering that the taxon is not recorded in Italian localities younger than the Coste San

Giacomo FU (Masini et al., 2013; Bellucci & Sardella, 2015).

The scheme proposed by Azzaroli (1983) featured the first appearance of *Hippopotamus* in the Tasso FU, which has been most influential in the biochronological correlation of several faunas. The implications for the inferred age of three localities are especially worth mentioning here, recognizing the presence of hippopotamuses in Europe already in the middle Villafranchian, namely Castel San Pietro, Bocchignano, and Monte Riccio (all in Italy). At Castel San Pietro, several fossil mammal remains were collected and partly described during the nineteenth century, as a by-product of the exploitation of a lignite mine (Tuccimei, 1889a, 1889b, 1891, 1898; Maxia 1949). The presence of hippopotamuses from the area of Castel San Pietro was reported by Meli (1882) and Tuccimei (1891). Pandolfi et al. (2017) carried out a revision of the scanty mammal remains, and further analysis based on ostracods and paleofloristic remains. Their results converged to suggest a Gelasian deposition of the lignite beds of Castel San Pietro (~2.5–1.8 Ma) in a warm-humid and forested area. Concerning the hippopotamuses, the authors casted doubt on their association with the rest of the fauna and commented that the whereabouts of the material are unknown. Marra et al. (2018) argued for the presence of two different assemblages at Castel San Pietro, the older with *Anancus arvernensis*, the younger with *H. antiquus*. Nonetheless, the cooccurrence of *A. arvernensis* and *Hippopotamus* cannot be ruled out and, if confirmed, would point to a reference to the Coste San Giacomo FU, as exemplified by the record from the reference fauna of this FU (Bellucci et al., 2014).

Bocchignano is another site whose hippopotamuses remains have been considered indicative of faunal mixing (Marra et al., 2018). The fossil remains recovered from the site were reported and described by Tuccimei (1889b, 1891, 1893). Kotsakis (1988) revised the taxonomic attribution of the arvicoline rodents, referring them to *Mimomys polonicus* or *Mimomys pliocaenicus*. Recently, Marra et al. (2018) suggested the presence of two different assemblages, the oldest with *Mimomys* (Saint Vallier to Olivola FUs), the youngest with *Hippopotamus* (Tasso FU). As in the case of Castel San Pietro, the cooccurrence of the two species is arguably conceivable (if the arvicoline belongs to *M. pliocaenicus*) and in agreement with a correlation of the fauna with the Coste San Giacomo or Olivola FUs (Bellucci et al., 2014; Bona et al., 2015).

Unlikely of middle Villafranchian age but worth of consideration here is the diverse fauna of Monte Riccio, including *Prolagus* sp., cf. *Mammuthus meridionalis, Sus strozzii, H. antiquus, Leptobos* cf. *etruscus, Procapreolus* sp., *Eucladoceros ctenoides, Axis* (= '*Pseudodama*') *nestii, Stephanorhinus* cf. *etruscus, Equus stenonis, Vulpes* cf. *alopecoides, Canis etruscus*, and *Megantereon cultridens* (Mazzini et al., 2000). Indeed, this assemblage has been referred to the Tasso FU due to the presence of *H. antiquus* (Mazzini et al., 2000; Marra et al., 2018), while Croitor (2012) suggested a correlation with the Olivola FU or even a slightly older age, based on the ruminants.

In brief, there is evidence for a middle Villafranchian dispersal of hippopotamus into Europe ~2.2–2.1 Ma, partly documented by remains collected from some of the localities that have been also important to recognize an earlier (than what proposed by Azzaroli, 1983) arrival of modern canids, namely Coste San Giacomo and Senèze. The "Hippo event" is of paleobiogeographic and paleoecological relevance, in that it testifies to the dispersal into Europe of a taxon of clear African origin and of distinct ecology. Indeed, though not necessarily limited to warm environments, remains of *Hippopotamus* are indicative of the presence of permanent water bodies and humid climatic conditions (Candy et al., 2006, 2010; Bellucci et al., 2012; Russo Ermolli et al., 2010; Mazza & Bertini, 2013; Adams et al., 2022). Moreover, morphological considerations and dietary proxies suggest that *H. antiquus* was even more adapted to an aquatic lifestyle than *H. amphibius* (Palmqvist et al., 2003, 2008; Adams et al., 2022). As mentioned previously, perhaps these ecological requirements explain the patchy distribution of middle and late Villafranchian occurrences of hippopotamuses in Europe, whereas since ~1.5 Ma *Hippopotamus* become a common element of the European terrestrial ecosystems (Caloi et al., 1980; Faure, 1985; Kahlke, 1989, 2001; Mazza, 1991, 1995; Kahlke et al., 2011; Van der Made et al., 2017; Fidalgo et al., 2021; Mecozzi et al., 2021; Adams et al., 2022; Strani et al., 2022). In this regard, it is worth mentioning that paleoenvironmental reconstruction based on ungulate dietary adaptations attest the presence of humid subtropical-like environments at Coste San Giacomo (Strani et al., 2015), whereas comparable analyses point to the occurrence of more open conditions at Olivola, where no hippopotamuses are known (Strani et al., 2018).

4. OTHER BIOEVENTS

Apart from the arrival of *C. etruscus*, several other bioevents were listed by Azzaroli (1983) and Azzaroli et al. (1988) as part of the Wolf event, and others have been proposed and discussed over the years. In particular, Azzaroli (1983) listed *L. etruscus*, *S. strozzii*, and *P. brevirostris*. The giant hyena is the only species of this contingent whose first appearance in Europe is still related to the late Villafranchian faunal turnover (see section 5). Indeed, while the "massive expansion" (Azzaroli et al., 1988) of *L. etruscus* and *S. strozzii* can still be placed in correspondence of Olivola and Tasso FUs, remains of both species are already documented in middle Villafranchian faunas (Masini & Sala, 2007; Cherin et al., 2018, 2019; Iannucci et al. 2020; Sorbelli et al., 2023).

Isolated dental remains of large-sized suids, which are generally referred to *S. strozzii*, are known from several middle Villafranchian sites, including Saint Vallier, Valdeganga II, Coste San Giacomo, Quercia, and Vigna Nuova, among others, and the locality of Senèze yielded an almost complete skeleton (Schaub, 1943; Mein et al., 1978; Azzaroli et al., 1988; Faure, 2004; Cherin et al., 2018; Iannucci et al., 2020; Azzarà et al., 2022; Iannucci, 2023).

Remains of *L. etruscus* are also known from Senèze (Masini, 1989; Cherin et al., 2019). Moreover, the

debate surrounding the taxonomy and evolutionary relationships of middle and late Villafranchian *Leptobos* spp., the presence of chronologically overlapping different lineages, and the possible appearance per-evolution (rather than per-dispersal) of the species in Europe, clearly push to exercise caution in biochronological correlations (Cherin et al., 2019; Sorbelli et al., 2023).

Objective difficulties in the attribution of isolated remains and disagreement on the taxonomy also complicate identifying and resolving the timing of species-level event of *Eucladoceros* spp. and '*Pseudodama*' spp. between the middle and late Villafranchian, as reflected by the many samples left in open taxonomy (e.g., Bellucci et al., 2014; Pandolfi & Petronio, 2015; Azzarà et al., 2022).

Apart from evolutionary changes in the aforementioned cervid lineages, Azzaroli et al. (1988) also mentioned the extinctions of *Nyctereutes* and *Gazella*. Both are still considered typical middle (or even early) middle Villafranchian taxa, but at least *Gazella* is present in some faunas that could be regarded as late Villafranchian or as transitional between the middle and the late Villafranchian (e.g., Fonelas P-1 and Gerakarou 1, see section 5).

The arrival of the Caprinae *Procamptoceras brivatense* was listed among the bioevents characterizing the late Villafranchian turnover by Gliozzi et al. (1997), based on its occurrence at Olivola (Azzaroli, 1950), but the species is already present in Senèze and tentatively listed in older faunas (Heintz et al., 1974; Palombo & Valli, 2004). In general, the record of *P. brivatense* is arguably too patchy to be stressed in a biochronological context, although this might change with further discoveries.

The arrival of *Panthera gombaszoegensis* was added by Azzaroli et al. (1988) among the bioevents characterizing the Wolf event. The first appearance of the species in the Italian fossil record is still in the Olivola FU (Ficcarelli & Torre, 1968; Gliozzi et al., 1997; Palombo, 2009). The locality of Gerakarou 1 also yielded remains of the species (Koufos, 1992, 2014). The occurrence of the species at La Puebla de Valverde, calibrated between Feni and Olduvai subchrons at ~2.12–1.92 Ma and generally considered close in age to but more progressive than Saint Vallier (Sinusía et al., 2004; Cuccu et al., 2023), was listed by Madurell-Malapeira et al. (2014), but not reported by Kurtén & Crusafont-Pairó (1977) and Cuccu et al. (2023).

When Azzaroli (1983) discussed the Wolf event, *C. etruscus* was the only modern canid whose arrival was correlated with the Olivola FU, while the first appearance of *Canis arnensis* and *Canis falconeri* was placed in the following Tasso FU. Both species are now already documented in middle Villafranchian faunas of western Europe. Recently, Bartolini Lucenti & Spassov (2022) substantially extended the chronological range of the wild dog *Canis* (*Xenocyon*) *falconeri*, referring to this taxon a mandible from Roca-Neyra (~2.6 Ma), which suggests a patchy distribution of the species in Europe since the beginning of the middle Villafranchian. The earliest record of *C. arnensis* known to date is from Senèze, based on the available dating for the site and the generally accepted synonymy between *C. arnensis* and *C. senezensis* (Brugal & Boudadi-Maligne, 2011; Bartolini Lucenti & Rook, 2016). Several early occurrences of *Canis* sp. listed previously (see section 2) might also belong to species other than *C. etruscus* (Fig. 2a).

5. THE "*PACHYCROCUTA BREVIROSTRIS* EVENT" AND THE BEGINNING OF THE LATE VILLAFRANCHIAN

The term "*Pachycrocuta brevirostris* event" or similar expressions have been sporadically used since the 1990s, e.g., by Masini & Torre (1990; "*Pliohyaena brevirostris* Event"), Torre et al. (1992; "*Pachycrocuta brevirostris* dispersal event"), Palombo et al. (2008; "*Pachycrocuta* event"), but it is only with the work of Martínez-Navarro (2010) that this concept acquired the meaning of a replacement term for Azzaroli's Wolf event. As mentioned in section 2, the evidence of middle Villafranchian remains of modern canids alone did not push other researchers to abandon the use of the Wolf event earlier, mainly emphasizing the increase in abundance of wolf-like canids, rather than their first appearance in the European fossil record (Azzaroli et al., 1988; Rook & Torre, 1996). Sardella & Palombo (2007) reviewed the concept of the Wolf event and analyzed carnivoran faunas of western Europe around the old Pliocene-Pleistocene boundary (Aguirre & Pasini, 1985; see Pillans, 2004 and Clague, 2006), i.e., prior to the provisions adopted in 2009, following which the base of the Pleistocene Epoch/Series was placed at ~2.6 Ma (Gibbard & Head, 2010; Gibbard et al., 2010; Head & Gibbard, 2015). Sardella & Palombo (2007) argued that, considering the carnivorans, the Wolf event includes several diachronic bioevents, such as the dispersals of different canids, *Panthera*, and *Pachycrocuta*. The latter, involving the giant hyena *Pachycrocuta brevirostris*, was regarded as the most representative dispersion in Europe.

According to Iannucci et al. (2021b), the earliest calibrated occurrence of *P. brevirostris* is likely from Fonelas P-1, placed between Feni and Olduvai subchrons, hence between ~2.12 and 1.92 Ma (Arribas et al., 2009). Some uncertainty persists, however, considering that the taxonomic identification is based on few elements of the deciduous dentition (Arribas & Garrido, 2008), with only one tooth actually exceeding the biometric range known for *Pliocrocuta perrieri*, a species also present in the site (Iannucci et al., 2021b). Like Fonelas P-1, the fauna of Gerakarou 1 is either referred to as middle or late Villafranchian (or as transitional), especially due to the cooccurrence of *P. brevirostris* and *Gazella* (Koufos, 1992; Konidaris et al., 2021). In Italy, *Gazella* is not recorded after the Coste San Giacomo FU (Masini et al., 2013; Bellucci & Sardella, 2015) and indeed its disappearance was listed among the bioevents characterizing the late Villafranchian faunal turnover (Azzaroli et al., 1988; Gliozzi et al., 1997). In France, it could have become locally extinct even earlier, as it is already absent in Senèze and other faunas usually considered of similar age (Heintz et al., 1974; Palombo & Valli, 2004). Assuming that this absence is not due to the paucity of the fossil record and/or biased by the environmental preferences of *Gazella*, the association of

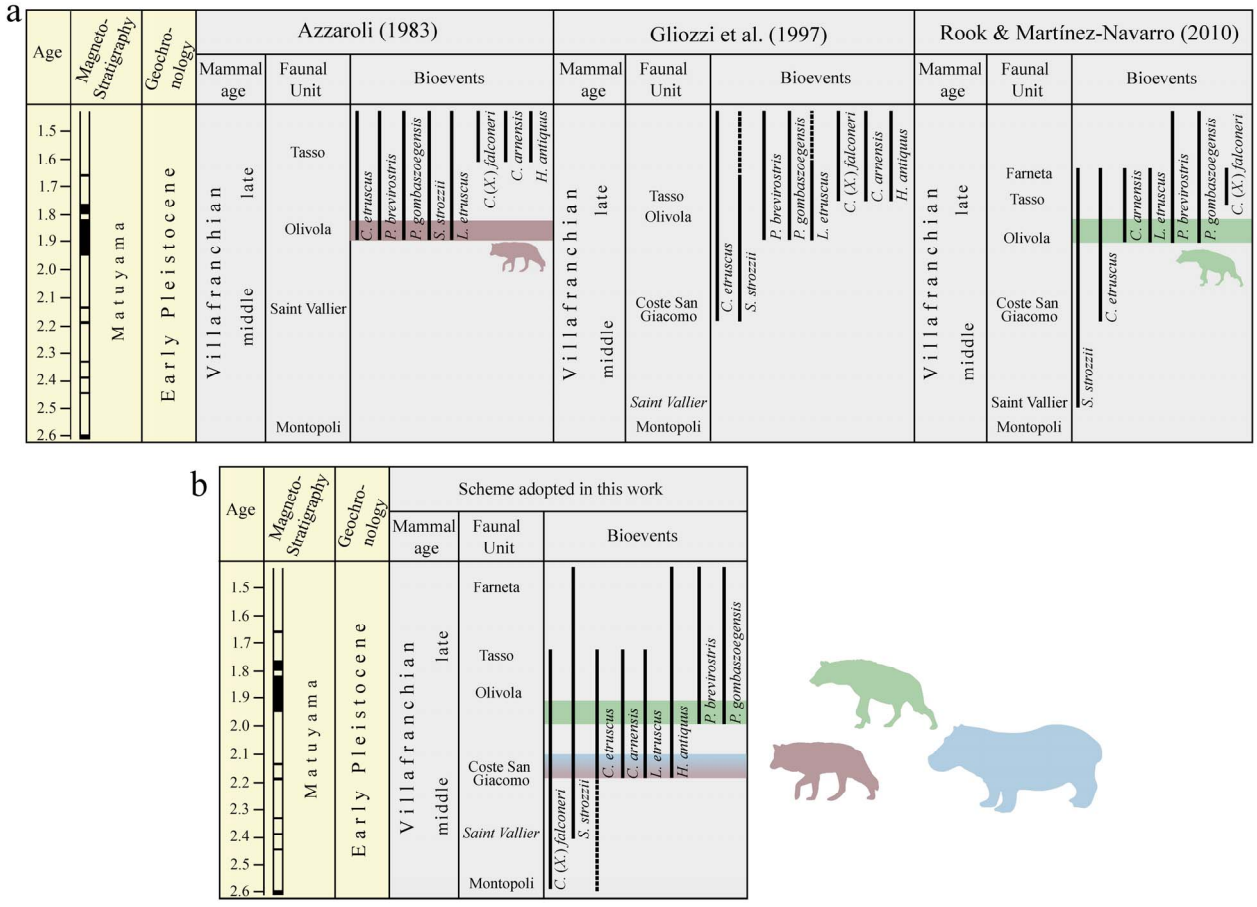

Fig. 3 - Selected biochronological schemes and mammal ranges proposed over the years (a) and the updated scheme adopted in this work (b). Saint Vallier has often been placed in italics to emphasize that it is not an Italian site. Silhouettes modified from: Iurino et al. (2022; *Canis etruscus*); Iannucci et al. (2021, *Pachycrocuta brevirostris*); PhyloPic, by Zimices (phylopic.org/image/c2d68ebb-50ec-45f4-8cd1-6cf52ad02286, hippopotamus).

Gazella and *P. brevirostris* suggests an age intermediate between Coste San Giacomo and Olivola FUs. This implies a certain degree of subjectivity in referring faunas in which such association is documented, like Fonelas P-1 and Gerakarou 1, as to middle or late Villafranchian. We argue that these faunas could simply be considered transitional between biochronological units traditionally recognized (Arribas et al., 2009; Konidaris et al., 2021). This is probably the best choice to minimize inconsistency in current research and with previous studies.

The fauna of Olivola includes *P. brevirostris* (Ficcarelli & Torre, 1970) but it is not directly dated. Paleomagnetic investigations carried out at Poggio Rosso, allowed to correlate this latter locality within the Olduvai subchron at ~1.92–1.77 Ma (Napoleone et al., 2001, 2003; Mazza et al., 2004). The fauna of Poggio Rosso has been considered transitional between Olivola and Tasso FUs (Gliozzi et al., 1997), or in other terms it cannot be unequivocally ascribed to one of the two FUs, but in any case provides indirect constraints for both.

The giant hyena *P. brevirostris* is documented by direct skeletal evidence in ~60 localities across Europe (Iannucci et al., 2021b), a number that would likely increase taking into account indirect evidence (e.g., coprolites, gnawing marks) and reports in open taxonomy. Actually, roughly coeval early occurrences are known from both sides of Eurasia at ~2.0 Ma (Arribas et al., 2009; Liu et al., 2021; Iannucci et al., 2021b). The giant hyena is a species that played an important role as a taphonomic agent and has been the subject of much research focused on investigating its potential relationships with other carnivorans and early hominins dispersing out of Africa (Turner & Antón, 1996; Palmqvist et al., 2011; Espigares et al., 2013; Madurell-Malapeira et al., 2017; Iannucci et al., 2021b). This explains why *P. brevirostris* has been considered a representative species of the late Villafranchian faunal turnover (Palombo & Sardella, 2007; Martínez-Navarro, 2010).

The earliest material referred to *Pachycrocuta* sp. is from the Pliocene of East Africa, but African remains of Pleistocene age are only known from the South of the continent, possibly indicating that *Pachycrocuta* did not survive long in East Africa (Werdelin, 1999; Werdelin & Lewis, 2008). *Pachycrocuta brevirostris* is thought to derive from a large-sized population of *Pliocrocuta perri-*

eri, most likely in Asia, where transitional samples are known (Qiu et al., 2004; Iannucci et al., 2021b). In western Eurasia, remains assigned to *Pachycrocuta brevirostris* and *Pliocrocuta perrieri* are jointly known from Fonelas P-1, Gerakarou 1, and Dmanisi (collectively ~2.1–1.8 Ma; Koufos, 1992, 2014; Vekua, 1995; Lordkipanidze et al., 2007; Arribas et al., 2009; Iannucci et al., 2021b). The two species share an overall similar morphology in many respects and, especially dealing with isolated remains, attributions often relied on biometric comparisons. As the often-evoked "giant" size of *P. brevirostris* suggests, this approach is generally accepted, but considering the close relationship between the two species and the many implications associated to the appearance of *P. brevirostris*, it should be accompanied by some reflection (see Iannucci et al., 2022b, for discussion).

6. DISCUSSION AND CONCLUSIONS

Azzaroli (1983) named "Wolf event" the faunal turnover associated to the beginning of the late Villafranchian, coinciding with the Olivola FU. This was also roughly coincident with the old (i.e., prior to 2009) Plio-Pleistocene boundary at ~1.8 Ma. Initially, this event was considered to document the first appearance in the European fossil record of *Canis etruscus* (the "wolf", hence the name) and other large mammals (*Leptobos etruscus*, *Sus strozzii*, and *Pachycrocuta brevirostris*), but soon modified to include the "massive expansion" of the considered species and other bioevents (Azzaroli et al., 1988, p. 84). The latter adjustment was a good compromise between the need not to disregard occurrences of the considered species potentially older than Olivola (but at the time of doubtful chronology or taxonomic attribution, like those from Senèze), and the intention of maintaining the reference role of the Olivola FU. However, this definition left room for different interpretations. It is now clear that several bioevents traditionally included in the Wolf event and others that have been considered to occur later are conversely already documented in middle Villafranchian faunas, most notably the arrival in Europe of modern canids, but also of *S. strozzii* and *Hippopotamus*, among others (Fig. 3).

If a single species has to be taken as representative of the late Villafranchian faunal turnover, the best candidate based on the current evidence is the giant hyena *Pachycrocuta brevirostris* (Sardella & Palombo, 2007; Palombo et al., 2008; Martínez-Navarro, 2010; Iannucci et al., 2021b). *Pachycrocuta brevirostris* is indeed the only species among those initially listed by Azzaroli (1983) as part of the Wolf event whose first appearance in the European fossil record is still coincident with the beginning of the late Villafranchian at the Olivola FU, and its occurrences are abundant across Eurasia. The first appearance in the European fossil record of *Panthera gombaszoegensis* (added in the Wolf event as an accompanying species by Azzaroli et al., 1988), is also documented at that time. However, the faunas Fonelas P-1 (Spain) and Gerakarou 1 (Greece) contains *Pachycrocuta brevirostris* in association with *Gazella*, a "typical" middle Villafranchian taxon (actually a holdover of even older faunas) that is not documented in Italy after the Coste San Giacomo FU (last FU of the middle Villafranchian, older than Olivola) (Bellucci & Sardella, 2015). Gerakarou 1 includes also *Panthera gombaszoegensis*. Therefore, even the arrival of *Pachycrocuta brevirostris* and *Panthera gombaszoegensis* somewhat anticipates the chronology previously assumed. Moreover, the beginning of the late Villafranchian does not correspond to a sharp faunal turnover as traditionally envisioned for the Wolf event. Current evidence highlights the rather diachronic nature of large mammal dispersal occurred in the late middle and early late Villafranchian (late Gelasian, ~2.2–1.8 Ma). In this regard, it would be arguably better avoiding naming this time-averaged phenomenon after a single species.

Here, we dedicated space to discuss the "Hippo event" (Section 3), as we think that this case eloquently speaks for the need of critically evaluating the biochronological, paleoecological, and paleobiogeographical significance of each bioevent. Indeed, the presence of *Hippopotamus* in Europe is now attested since ~2.2 Ma, documenting an African dispersal of a species linked to humid conditions in a context that is generally deemed to denote the spread of open-adapted faunal elements of mainly Asian affinities. However, this bioevent was once considered younger than ~1.8 Ma and placed in the Tasso FU (Azzaroli, 1983; Gliozzi et al., 1997). Consequently, the presence of *Hippopotamus* at Coste San Giacomo and Senèze was perceived at odds with a middle Villafranchian age and engendered ideas of mixing with substantially younger faunas, which are, however, not supported by available dating and field evidence (Delson et al., 2006; Bellucci et al., 2014; Palombo et al., 2017; Paquette et al., 2021). Several other faunas have been considered mixed or younger than they really are due to the presence of *Hippopotamus*, including, for instance, Castel San Pietro, Bocchignano, and to some extent Monte Riccio (e.g., Marra et al., 2018).

It might be argued that since the arrival of many species once considered to indicate the beginning of the late Villafranchian is now recognized to be older, then the passage between the middle and late Villafranchian could be moved back as well. However, such an approach would be inconsistent with a huge body of previous research in which the beginning of the late Villafranchian is typified by the Olivola FU, and hence it would be unavoidably ambiguous. Moreover, while it is true that the arrivals of many species traditionally included in the Wolf event are now already recorded in middle Villafranchian faunas, their "massive expansion" (*sensu* Azzaroli et al., 1988) can still be correlated with the Olivola FU. This is the case of *Leptobos etruscus*, *Sus strozzii*, and not least *Canis etruscus*. We argue that the earliest occurrence of *Pachycrocuta brevirostris* and *Panthera gombaszeogensis* heralds the late Villafranchian faunal turnover, which is then best expressed by the increase in the documentation of the other species. To minimize inconsistent approaches, "transitional" faunas like Fonelas P-1 and Gerakarou 1 could be simply referred to as such.

In general, resolving the exact timing of large mammal bioevents in the late Gelasian is complicated by the paucity of middle Villafranchian localities, as already

pointed out by Azzaroli (1983). Moreover, of the two most important large mammal middle Villafranchian faunas postdating the Montopoli FU listed in the synthesis of Gliozzi et al. (1997), namely those of Collepardo and Coste San Giacomo, only the correlation of the latter has been confirmed (Bellucci et al., 2012, 2014; Bona et al., 2015). Conversely, although the fauna of Collepardo was initially considered close in age to Saint Vallier (Gliozzi et al., 1997), it is now recognized as markedly older than the French site and referred to the Triversa FU (early Villafranchian; Bellucci et al., 2019; Iannucci et al., 2022a). On the other hand, a huge number of localities, more or less abundant in terms of fossil remains, including mainly either sporadic (i.e., not coming from systematic excavations) and/or historical findings, have yielded Early Pleistocene large mammal faunas. As shown by the recent case of Vigna Nuova (Azzarà et al., 2022), proper examinations of these samples might reveal further middle Villafranchian faunas simply not recognized as such.

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