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Reconstructing the palaeoenvironments of the Early Pleistocene mammal faunas from the pollen preserved on fossil bones

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ABSTRACT

We carried out a systematic investigation on the pollen content of sediment adhering to skeletal elements of large mammals which originate from the long lacustrine record of Leffe (Early Pleistocene of the Italian Alps). Three local faunas were discovered during mining activities along the intermediate part (spanning from 1.5 to 0.95 Ma) of the basin succession. The excellent pollen preservation allowed testing the reproducibility of the pollen signal from single skeletons. A clear palaeoenvironmental patterning, consistent with the ecological preferences of the considered mammal species, emerged from the canonical correspondence analysis of pollen types diagnostic for vegetation communities. Edaphic factors related to seasonal river activity changes and to the development of swamp forests in the riverbanks are significantly associated to the occurrences of *Hippopotamus cf. antiquus*, whereas finds of *Mammuthus meridionalis* belong to fully forested landscapes dominated by conifer or mixed forests of oceanic, warm to cool-temperate climate. Rhinoceros habitats include variable forest cover under different climate states. Distinct cool-temperate, partially open vegetation could be recognized for large deer included *Cervalces cf. carnutorum*.

A palynostratigraphic correlation between individual spectra and a reference palynostratigraphic record allowed assignment of many fossil remains to a precise stratigraphic position. This procedure also shown that the Leffe local faunas include specimens accumulated under different environmental and climate states, as a consequence of high-frequency climate changes characterizing the Late Villafranchian Early Pleistocene.

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1. Introduction

Reconstructing the palaeoecological setting where past mammals lived and died is an interesting challenge. Palaeoecological inferences may be derived from several independent approaches, such as whole faunal assemblage (DeGusta and Vrba, 2003, 2005), the functional morphology of the postcranial skeleton (DeGusta and Vrba, 2003, 2005) and of the cranial features (e.g. Gordon and Illius, 1988; Pérez-Barbería and Gordon, 1999; Solounias and Moelleken, 1993; Solounias et al., 1995), teeth scar topography (Walker, 1978), and skeleton isotopic analysis (Cerling et al., 1999). Recently, the analysis of dietary patterns has been implemented by new tools, such as the multiproxy analysis of coprolites and gut contents (Larkin et al., 2000; Van Geel et al., 2008), the meso-wear of the tooth crowns (Fortelius and Solounias, 2000; Kaiser and Solounias, 2003), the microwear of tooth

enamel (Boisserie et al., 2005; Green et al., 2005) and its carbon isotope composition (e.g. Palmqvist et al., 2003).

Deciphering the interaction of mammals communities with their past landscape requires proxies both for species ecology and for landscape evolution. Pollen, non-pollen palynomorphs and macroscopic plant remains (Ollz and Kapp, 1963; Gorlova, 1982) and beetles (Coope, 2007) associated to mammal finds provide palaeoenvironmental information. This is an independent, and complementary, issue addressed to the reconstruction of the sedimentary environment and of the vegetation and climate pattern at a broad (regional) scale, feasible by a multiproxy study of the sediments embedding the fossil animals. Unfortunately, many specimens stored in Museums miss stratigraphic and taphonomical information. This problem may be partially overcome by analyzing microscopic features (palynology, lithology and biochemistry) of fine sediments preserved adhering to fossil bones or in their small cavities, a method still providing factual indications of the vegetation coeval with the fossil animals, even decades after discovery (Stuart, 1986; Breda et al., 2005).

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In this paper, the pollen content of sediment adhering to mammal bones has been systematically analyzed in the case of the mammal fauna of Lefte, a well-known Early Pleistocene lacustrine site in northern Italy (Ravazzi and Rossignol Strick, 1995). The mammal fauna of Lefte has been recently revised and its bio-chronological setting discussed in the light of the magneto- and palynostratigraphic record of the complete lacustrine succession (Breda and Marchetti, 2007; Muttoni et al., 2007). The aims of this study are therefore:

- (1) To assess the quality of the pollen signal and to test its reproducibility from different elements belonging to a single skeleton. This test will allow for further statistical treatment (canonical correspondence analysis) of the collected data.
- (2) To reconstruct the vegetation developed in the catchment of the Lefte Basin at the time of deposition of sediments embedding each of the individuals analyzed. It is known that deposits embedding fossil remains may not reflect the living habitat, e.g. in case of flotation or fluvial redeposition after erosion (Kidwell and Flessa, 1996; Kaakinen, 2005; Kahlke and Gaudzinski, 2005). Lacustrine and palustrine environments isolated from main rivers offer the advantage of reducing this taphonomical bias (Spencer et al., 2003; Breda et al., 2005). This is also the case of the Lefte lake. Burial mechanisms of mammal carcasses within palustrine traps in the Lefte basin will be shortly discussed in relation to their potential of vegetation reconstruction.
- (3) To compare the obtained palaeoenvironmental record of each species represented in the Lefte fauna with available information on single species ecology. It is well-known that mammals can adapt to a wide range of environmental conditions. The presence of a taxon in a fossil assemblage may reflect its environmental optimum but it might also be the result of competition with other taxa and of the availability or not of particular items of its diet. Coupling landscape reconstructions with species palaeodiet helps clarifying the complex interaction of ecological, evolutionary and taphonomical factors.
- (4) To link the palaeoenvironmental information obtained on single individuals with the long record available from the same site. This correlation is helped by historical reference on the stratigraphical position enregistered at the time of specimen collection. Although the quality of the historical information may not be appropriate for a detailed stratigraphic reassessment, it helps identifying a rough stratigraphic interval of provenance, hence refined by palynostratigraphic correlation between pollen spectra obtained from mammal remains with the long pollen record. This procedure may allow to set single remains in the long time perspective, i.e. to compare the species occurrence with the environmental and climate record.
- (5) Finally, to test the environmental stability and uniformity commonly attached to the recognition of a local mammal fauna (sensu De Giuli et al., 1983) during the Early Pleistocene, in spite of high-frequency climate changes characterizing this time span.

2. The Lefte Basin

2.1. Stratigraphy, chronology and studies on vegetation history

The Lefte Basin, 45° 49' N, 9° 51' E, 390–550 m a.s.l., is located in the Pre-Alps of Lombardy (Northern Italy, Fig. 1). The catchment of the former lake largely corresponds to the Gandino Valley (ca. 39 km², see black spot in Fig. 1), framed by highplains nowadays at an altitude of 1300–1500 m a.s.l., but probably some 200 m

lower during Early Pleistocene time (Scardia et al., 2006). The lake reached a maximum size of ca 4.2 km² (Ravazzi, 2003). The Lefte Basin contains one of the longest continuous archive of the continental realm of environmental and climate changes occurred during almost 1 million years, from the Late Pliocene to the late Early Pleistocene (Muttoni et al., 2007). A long record was obtained from a master core (acronym FM core) drilled in the centre of the Basin (Cremaschi and Ravazzi, 1995). The mammal faunas originate from an intermediate portion of the sedimentary sequence, belonging to the uppermost Lefte Formation, i.e. the biogenic unit (lacustrine–palustrine brown coals and shell marls), and the upper unit (terrigenous palustrine clay and brown coals) (Fig. 2). A detailed lithostratigraphic subdivision within the biogenic and upper units distinguishing each of the main alternating phases of palustrine/lacustrine sedimentation is given by acronyms from #2 to #9 (Fig. 2).

Magneto- and pollen-stratigraphical analysis, integrated with mammal fauna biochronology, provide a robust chronological frame. Lacustrine deposition began during the late Olduvai Subchron at about 1.85 Ma (unit #2) and lasted up to Marine Isotopic Stage 22 (Gandino Formation) at about 0.87 Ma (Muttoni et al., 2007). The deposition of the biogenic unit lasted 700 ka, from 1.8 to 1.1 Ma.

An outline of vegetation history and its cyclic patterns is given in Ravazzi and Rossignol Strick (1995), Ravazzi and Moscarriello (1998), Ravazzi (2003). Between 1.8 and 1.1 Ma, the regional vegetation varied cyclically from mixed-oak forests dominated by deciduous *Quercus*, *Corylus*, *Ulmus*, *Tilia*, *Carpinus*, *Fraxinus* to Juglandaceae forests with *Carya*, *Pterocarya* and *Juglans* sect. *Cardiocaryon* to conifer forests (*Tsuga*, *Picea*, *Abies*, *Cedrus*). Short episodes (at millennial scale) of partial forest opening and development of xerophytic communities occur at the end of some forest cycles. This basic forest cycle, indicated by an alphabet letter, is triggered by climate forcing, and is repeated at least 18 times in the studied portion of the Lefte sequence (Ravazzi et al., 2004). A rich perilacustrine vegetation, including riparian forest, swamp forest, wet meadows, helophytic and aquatic communities developed as a belt surrounding the lake, but often floating mats of sedges, reeds, bog mosses and even conifers occupied the entire lake surface. Further wetlands extended along the valley floor of the Serio river towards the coast of the Po sea gulf. The coastal line ran close to the Alpine foothills, 20–25 km south of the Lefte lake (Pini, 2005, Fig. 1).

2.2. The mammal fauna

Vertebrate and plants remains were brought to light by mining exploitation of brown coals, which started at the beginning of XIX century. The first records of rhino teeth date back to 1840 (Balsamo Crivelli, 1840, 1842). Discoveries continued till 1956 (Cornalia, 1865–1871; Forsyth Major, 1873, 1874; Rüttimeyer, 1876; Sordelli, 1873, 1882; Portis, 1887, 1898; Airaghi, 1914; Stehlin, 1930; Venzo, 1950; Vialli, 1956). Recently, a complete revision of the mammal fauna has been carried out (Breda and Marchetti, 2007). In most cases no detailed indication on the stratigraphic provenance was reported at time of discovery. Most of these specimens originate from the so-called “main brown coal seam” within the biogenic unit of the Lefte Formation (subunit #5 of the biogenic unit in Fig. 2). The most recent finds, recovered during the 50s in the uppermost “biogenic unit” of the Lefte Formation and in the overlying “upper unit” (subunits #5–#9 in Fig. 2), are provided with more stratigraphic information. Even so, lithostratigraphic information alone doesn't allow to set the single finds in the fine-resolution record obtained from core. Collected specimens were stored mainly at the Civic Natural History Museum of Milano

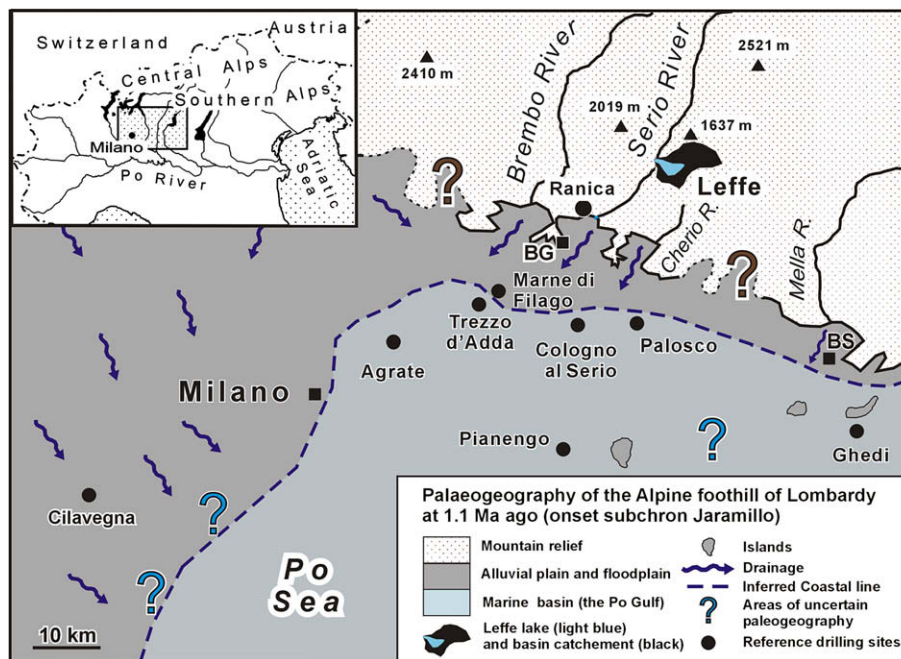


Fig. 1. Palaeogeographic map of the fringe of the Lombardy sector of the Italian Alps at about 1.1 Ma, showing the location of the Leffe Basin, the basin catchment, the development of the coastal plain and the coastal line of the Po Sea inferred from stratigraphically studied boreholes (Pini, 2005; Scardia et al., 2006).

(hereafter MCSNMI) and at the Civic Museum of Natural Sciences of Bergamo (hereafter MCSNBG) (Table 1).

2.3. Mammal biochronology

Three subsequent mammal associations have been recognized along the succession preserved in the Leffe basin (Breda and Marchetti, 2007) and correlated with the Italian biochronological scale (Masini and Sala, 2007):

2.3.1. Mammal association 1

The main brown coal seam (subunit #5) yielded a mammal association of Late Villafranchian age, made up of *Miomys savini*, *Castor fiber*, *Mammuthus meridionalis* (possibly both *M. meridionalis meridionalis* and *M. meridionalis vestinus*), *Stephanorhinus ex gr. etruscus*, *Leptobos cf. vallisarni*, *Cervalces cf. carnutorum*, *?Capreolus sp.*, *Pseudodama sp.*, *?Eucladoceros gr. ctenoides-dicranios* and *?Megaloceros cf. obscurus*. An age straddling the end of the Tasso and the beginning of the Farneta Faunal Units (FUs) of the Italian biochronological scale has been suggested for subunit #5 (details in Breda and Marchetti, 2007).

2.3.2. Mammal association 2

The fauna from the subunit #6, consisting of *Pachycrocuta brevirostris*, *S. ex gr. etruscus* and *Pseudodama eurygonos*, and the fauna from the subunit #7, represented only by *S. ex gr. etruscus*, do not provide precise biochronological information. The age of this fauna could span the time interval between the latest part of the Farneta FU and the beginning of the Colle Curti FU (Breda and Marchetti, 2005), which is between 1.4 and 1.1 Ma BP (Masini and Sala, 2007).

2.3.3. Mammal association 3

The fauna from the subunit #9 consists of *M. meridionalis vestinus* and *Megaloceros gr. verticornis-plotarandoides*. In the Italian fossil record these species occur together both in the Colle Curti FU and the Slivia FU (Ambrosetti and Cremaschi, 1976; Ficcarelli et al., 1996;

Mazzini et al., 2000). Subunit #9 recorded the Jaramillo normal polarity interval (Muttoni et al., 2007), and the subsequent Subchron 1r.1r, in agreement with the succession of Colle Curti FU and Slivia FU, which also span the Jaramillo and the subsequent 1r.1r subchrons (Gliozzi et al., 1997; Coltorti et al., 1998).

3. Materials and methods

Fossil pollen was extracted from 23 samples of sediment found on mammal bones or inside small bone cavities. The complete list of samples, of investigated skeletal elements and respective individuals is shown in Table 1a. The outer part of each sediment sample was removed using glass paper to avoid contamination from recent pollen, then the sample was weighted and the volume estimated after immersion in a known volume of distilled water. Samples quantity varying from 0.15 to 3 g (0.2–3 cm³) were treated at the Laboratory of Palynology and Palaeoecology of C.N.R. – IDPA (Milano) using the following procedure: HCl, HF, KOH, sieving at 10 μm, and acetolysis. *Lycopodium* tablets were used for calculation of pollen concentration (Stockmarr, 1971). Samples were analyzed at ×400, ×630 and ×1000 magnifications using a light microscope. The reference collection of C.N.R. – IDPA, as well as articles, pollen floras and atlases (Huang, 1972; Stone and Broome, 1975; Punt and Blackmore, 1976–1995; Reille, 1992–1998; Beug, 2004), and specific works on Plio-Pleistocene pollen types of Europe (Menke, 1976; Suc, 1978) were used for pollen identification. A mean pollen sum of 570 grains was reached for most samples; for those displaying low pollen concentration (<500 grains/g), at least 100 grains were identified. Along with pollen grains, the identification of non-pollen palynomorphs (NPP) and count of charcoal particles were carried out. Pollen % are based on a pollen sum which includes trees, shrubs and upland herbs; pollen of aquatic and wetland species, as well as spores and non-pollen palynomorphs, are excluded from the basic pollen sum and their % are calculated separately, as they mainly record a local signal. Analytical pollen data are presented in Tables 3–6 (see Supplementary material). The reproducibility of the pollen record was tested by comparing the similarity between the pollen

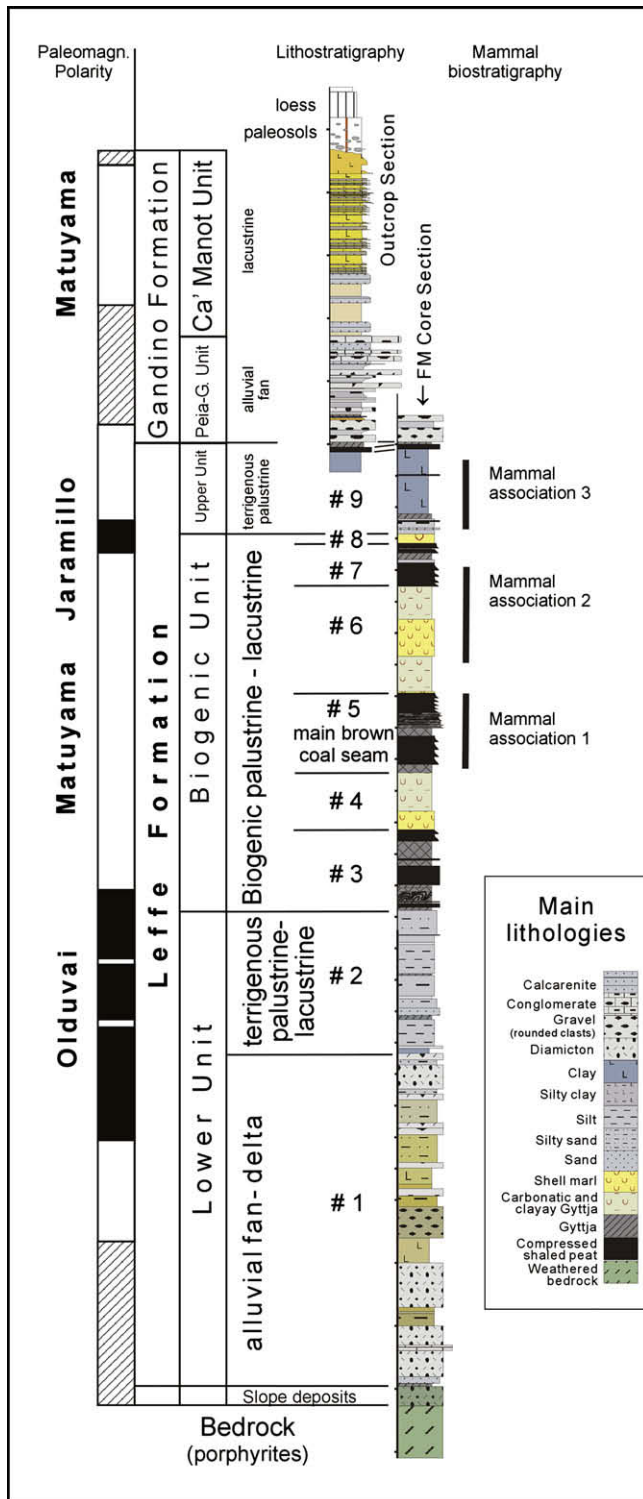


Fig. 2. Log and lithostratigraphical subdivision of the Biogenic Unit of the Leffe Formation. The recognized mammal associations (from Breda and Marchetti, 2007) and the chronostratigraphic position (Muttoni et al., 2007) are also shown.

spectrum from each skeletal element with those belonging to a single skeleton through the Fisher's exact test. Testing the reproducibility of the pollen signal from a single skeleton was done in two cases – one elephant and one hippopotamus. Here we deliberately multiplied the number of samples taken from the same individual. This is possible with material stored after decades in museums,

provided that original documentation allows to refer skeleton parts to the same individual, and that specimens were not totally cleaned or heavily restored.

The reconstructed vegetation communities refer to the classification shown in Table 2, which is based on modern analogues from N-America and Asian vegetation (Wang, 1961; Hou, 1983; Walter and Breckle, 1986; Barbour and Billings, 1988; Franklin and Dyrness, 1988), biomization procedures (Takahara et al., 2000; Yu et al., 2000) and existing reconstructions of Early Pleistocene vegetation in Europe based on lacustrine pollen and macrofossil assemblages (Buzek et al., 1985; Ravazzi and Rossignol Strick, 1995; Leroy and Roiron, 1996; Leroy, 2008). Each vegetation community is qualified by clearly recognizable diagnostic pollen types. The percentage sum of pollen types diagnostic for each vegetation community has been plotted in Fig. 3. To extract the dominant patterns of variation in community compositions, an ordination technique was applied (canonical correspondence analysis: Ter Braak, 1986) on pollen data diagnostic for different vegetation communities. It must be noticed that the pollen sums used for statistical treatment do not include all the potential pollen producers in a vegetation community, neither do they account for differences in pollen production and dispersal among plants. Therefore quantitative inferences on the development of vegetation types should be taken with care. Summary data on reconstructed regional vegetation (i.e. developed in the relevant pollen source area, sensu Sugita, 1994) and local vegetation (i.e. growing within the sedimentary basin) are given in Table 1b.

4. Results

Preservation of pollen assemblages recovered in the analyzed samples is good to excellent. Two out of the 25 collected samples turned out to be sterile. Pollen concentration varies according to lithology, i.e. higher concentration occur in samples of peat and gyttja (up to 30–50,000 grains/g of sediment) and lower ones in organic-poor terrigenous sediments (down to less than 300 grains/g); however, there are no badly preserved samples.

Summary results about the pollen record of single species and a qualitative vegetation reconstruction are presented here below (Tables 3–6; see Supplementary material and Appendix B for rare pollen types).

4.1. *Mammuthus meridionalis* (Table 3)

Seven pollen spectra were obtained from elephants related to different stratigraphical levels within the sedimentary succession (Table 1). Five of them, which were sampled from different bones belonging to the same individual (individual D), provided similar values of Arboreal Pollen ($AP = 82 \pm 10\%$), xerophytes ($1.6 \pm 1.1\%$) and of the main forest taxa, i.e. *Pinus*, *Picea*, *Abies* and *Tsuga* (Fig. 3 and Table 3). The environment reconstructed for individual D consists of dense oceanic-temperate mixed forests (conifer-dominated, with subbordered deciduous broad-leaved) accompanied by herbs growing in wetlands, riversides (Cyperaceae, *Thalictrum*, *Ranunculus acris* type, *Polygonum persicaria*) and ponds (*Myriophyllum*). Xerophyte pollen, characterizing upland open vegetation, is very reduced (2%). It is concluded that landscape was forested, with open areas limited to wetlands.

Sample Ma-6 differs for a reduced forest cover ($AP = 51.4\%$), formed by *Alnus glutinosa* type and deciduous *Quercus*. Upland herbs are abundant (47.5%), but xerophytes are low. These data indicates the development of temperate upland grasslands and deciduous forests, including alder swamps. High values of charcoal particles in Ma-6 (15,600 particles/g) may be interpreted as the result of local fires conveying charred fragments into the lake deposits. Sample Ma-7 is characterized by higher AP values (81.4%),

Table 1

(a) List of skeletal elements and individuals analyzed for pollen, including (b) a summary of main pollen results and vegetation reconstructions.

Species	Name of the individual	Acronym	Lithostratigraphy	Skeletal element	Lithology	Spectrum ⁽⁶⁾	AP %	Xero-%	Reconstructed regional vegetation	Reconstructed local vegetation
<i>Mammuthus meridionalis</i>	Indiv. D ⁽¹⁾	ST-5	Subunit #9 ⁽⁴⁾	Fragment of a right tusk	Clay	Ma-1	76.8	1.5	<i>Pinus–Picea–Tsuga</i> forests and patches of deciduous trees	Cyperaceae wetlands, <i>Sparganium–Myriophyllum</i> ponds
		V33		Right hand	Clayey gyttja	Ma-2	90.3	0.6	<i>Pinus–Picea–Tsuga</i> forests	Cyperaceae wetlands
	?	ST-8		Right tibia	Clay	Ma-3	91.8	3.4	<i>Picea–Pinus–Abies</i> forests	Meadows
		V33		Bone remains		Ma-4	66.7	1.1	open <i>Pinus–Picea</i> forests, grass meadows	Cyperaceae wetlands, <i>Thalictrum</i>
				Unidentified remains		Ma-5	84.7	1.7	<i>Pinus–Picea–Tsuga</i> forests	Cyperaceae wetlands
				Mean values and standard deviations			82	1.6	<i>Pinus–Picea</i> forests	Cyperaceae wetlands
				Femur	Clay	Ma-6	51.4	4.8	Open deciduous forests, open areas with xerophytic communities and grasses	Alder swamp, grass meadows with <i>Ranunculus</i> and <i>P. persicaria</i>
		ST-4		Pelvis	Clay	Ma-7	81.4	3.9	Open <i>Pinus–Betula</i> forests	Cyperaceae wetlands with <i>Thalictrum</i> and <i>Potentilla</i>
<i>Stephanorhinus ex. gr. etruscus</i>	Unnamed ⁽²⁾	V28	2nd bcs ⁽²⁾	Palate with first molars					<i>Sterile</i>	
	Unnamed ⁽¹⁾	81-1b	2 m below 1st bcs ⁽¹⁾	Mandible of a young specimen	Shell marl	St-1	66.9	27.4	Xerophytic scrubs with <i>Betula</i> and <i>Pinus</i>	Grass meadows
	Indiv. A ⁽¹⁾		Subunit #5 ⁽⁴⁾	Upper tooth row	Brown coal	St-2	95.6	1.1	<i>Picea–Pinus</i> forests with <i>Carya</i> stands	Wet meadows, ferns and <i>Osmunda</i>
	Indiv. C ⁽¹⁾		Subunit #5 ⁽⁴⁾	Mandible	Brown coal	St-3	96.2	0	<i>Tsuga–Picea</i> forests, Juglandaceae stands	Grass meadows
	Indiv. G ⁽¹⁾	65dx 5-8	Subunit #7 ⁽⁴⁾	Bones	Carbonatic gyttja	St-4	97.3	1.4	<i>Pinus–Picea–Abies</i> forests with <i>Carya</i>	Ponds with <i>Nymphaea</i> , <i>Myriophyllum</i> and <i>Sparganium</i>
<i>Hippopotamus cf. antiquus</i>	Possibly same individual (ST-6) ⁽³⁾	65dx 5-7		Upper teeth					<i>Sterile</i>	
		ST-6a	Unknown level of the Leffe Formation ⁽⁵⁾	Radius fragment	Clay	Hi-1	68	2	Open deciduous <i>Quercus</i> forest	Alder swamps and meadows
		ST-7		Left femur fragm.	Clay	Hi-3	78.3	0.9	Open deciduous <i>Quercus</i> forest	Alder swamps and meadows
			Mean values and standard deviations				68.1	4.3	Open deciduous <i>Quercus</i> forest	Alder swamps and meadows
	ST-7 ⁽³⁾	ST-6b		Left humerus	Clay	Hi-4	82.3	4.1	Deciduous <i>Quercus–Ulmus</i> forests	Grass meadows with Cichorioideae
<i>Cervalces cf. carmutorum</i>			Subunit #5 ⁽⁴⁾	Postcranial bone	Greyish clay	Cc-1	68.4	6.4	<i>Pinus–Picea–Abies</i> forests	Cyperaceae wetlands, meadows
<i>Pseudodama eurygonos</i>			Clay above 2nd bcs ⁽²⁾	Frontal bone with antler basis	Shell marls	Ps-1	97.6	1.2	<i>Picea–Pinus</i> forests with <i>Carya</i> stands	Ponds with <i>Myriophyllum</i>
<i>Pseudodama</i> sp.		MCSNBG 1212	Subunit #6 ⁽⁴⁾	Antler fragments	Shell marls	Ps-2	97.6	0.7	<i>Carya–Pterocarya</i> forests	Meadows
? <i>Eucladoceros</i> ex gr. <i>ctenoides-dicranios</i>		MCSNBG 1185b	Subunit #5 ⁽⁴⁾	Right metacarpal		Eu-1	98.4	1	<i>Picea–Pinus</i> boreal forests	Cyperaceae wetlands, <i>Thalictrum</i>
Large deer				Leg parts	Clay	Ld-1	83.4	9.5	<i>Picea–Pinus</i> boreal forests	<i>Nymphaea</i> and <i>Sparganium</i> ponds
<i>Leptobos</i> (small)		MCSNBG 1185		Radius		Le-1	89.2	2.1	<i>Pinus–Picea–Betula</i> forests	Cyperaceae wetlands, <i>Thalictrum</i> , wet meadows with <i>Osmunda</i>
Order Artiodactyla				Metapodial diaphysis		Ar-1	95	1	<i>Picea–Pinus–Tsuga</i> forests	Cyperaceae wetlands, <i>Nuphar Myriophyllum</i> , <i>Sparganium</i> ponds
Order Artiodactyla				Tibia fragment		Ar-2	85.5	10.4	<i>Picea–Pinus</i> boreal forests	Ponds with <i>Nymphaea</i>

Skeletal elements referred to the same individual were checked by comparing published reports with the Museum records. (1) = Vialli, 1956; (2) = Venzo, 1950; (3) = This paper, Appendix A; (4) = Muttoni et al., 2007; (5) Breda and Marchetti, 2007; (6) pollen spectra are presented in Tables 3–6. bcs = brown coal seam.

Table 2
Vegetation communities distinguished by diagnostic pollen types in the Early Pleistocene record of the Leffe Basin (see Section 2 for details).

<p>1. Steppe and xerophytic scrubs <i>Artemisia</i>, Chenopodiaceae, Ephedraceae, <i>Centaurea scabiosa</i>, <i>Hippophæ</i>, <i>Helianthemum</i>, Gramineae, Ranunculaceae p.p., Fabaceae p.p., Umbelliferae p.p. Diagnostic: <i>Artemisia</i>, Chenopodiaceae, Ephedraceae, <i>Centaurea scabiosa</i>, <i>Hippophæ</i></p> <p>2. Cold-temperate (boreal-type), open mixed forest <i>Pinus</i> p.p., <i>Picea</i> p.p., <i>Betula</i>, <i>Larix</i>, <i>Artemisia</i> Diagnostic: <i>Betula</i>, <i>Larix</i></p> <p>3. Cool-temperate conifer forest <i>Picea</i>, <i>Abies</i>, <i>Tsuga diversifolia</i> type p.p., <i>Cedrus</i>, <i>Pinus</i> p.p. Diagnostic: <i>Picea</i></p> <p>4. Mesophytic warm-temperate broad-leaved forest <i>Quercus</i> p.p., <i>Carya</i> p.p., <i>Carpinus</i>, <i>Ostrya</i>, <i>Ulmus</i>, <i>Tilia</i>, <i>Fraxinus</i>, <i>Corylus</i> Diagnostic: <i>Quercus</i>, <i>Ostrya</i>, <i>Carpinus</i>, <i>Ulmus</i>, <i>Tilia</i>, <i>Corylus</i>, <i>Fraxinus</i></p> <p>5. Oceanic-temperate mixed forest <i>Tsuga</i>, <i>Abies</i>, <i>Quercus</i>, <i>Carya</i>, <i>Pterocarya</i>, <i>Juglans</i>, <i>Fagus</i> Diagnostic: <i>Tsuga</i>, <i>Abies</i>, <i>Fagus</i></p> <p>6. Warm-temperate floodplain, riparian and swamp forest <i>Alnus</i>, <i>Pterocarya</i>, <i>Glyptostrobus</i>, <i>Chamaecyparis</i>, <i>Liquidambar</i>, <i>Eucommia</i>, <i>Vitis</i>, <i>Parthenocissus</i>, Cyperaceae, <i>Osmunda</i> Diagnostic: <i>Alnus</i>, <i>Pterocarya</i>, <i>Glyptostrobus</i>, <i>Chamaecyparis</i></p> <p>7. Wet meadows, helophyte mire and peat fen Cyperaceae, <i>Typha</i>, <i>Osmunda</i>, <i>Filipendula</i> Diagnostic: <i>Filipendula</i>, <i>Typha</i>, Cyperaceae</p> <p>8. Sphagnum-bogs <i>Sphagnum</i>, <i>Andromeda</i>, <i>Pinus</i> p.p., Cyperaceae p.p. Diagnostic: <i>Sphagnum</i>, <i>Andromeda</i></p> <p>9. Open water <i>Nymphaea</i>, <i>Nuphar</i>, <i>Potamogeton</i>, <i>Myriophyllum</i>, <i>Ranunculus</i> subgen. <i>Batrachium</i>, <i>Sparganium</i> Diagnostic: <i>Nymphaea</i>, <i>Nuphar</i>, <i>Potamogeton</i>, <i>Myriophyllum</i></p>

largely contributed by *Pinus sylvestris/mugo* and *Betula*. Herbaceous species, both terrestrial and aquatic, are well represented. Reconstructed regional vegetation is an open pine-birch forest.

4.2. *Stephanorhinus ex. gr. etruscus* (Table 4)

Four samples were picked up from fossil tooth and mandibles of rhinos of four individuals related to different stratigraphical level within the succession of the Leffe Basin (first and second brown coal seam).

The pollen spectra obtained from skeletal elements of individuals A, C, G show a similar pattern of forest-dominated environment, though there are marked differences in composition revealing climate differences. Mixed conifer forest including warm-temperate broad-leaved (*Carya*) are reconstructed for individuals A and G, whereas individual C is characterized by still mixed forests with abundant *Tsuga* (43%), probably the most important tree in the vegetation surrounding the site of skeleton burial, suggesting still temperate, but wetter climates. Wetland herbs (*Osmunda* and other ferns including *Thelypteris*) and hydrophytes of ponds (*Nymphaea*, *Myriophyllum*, *Sparganium*) also occur.

On the other hand, the pollen record of shell marl including the mandible of a young individual (Sample St-1, see specimen picture in Fig. 6) yielded high values of pollen of xerophytes (up to 27%) and *Betula* (25.3%), lower values of conifers and broad-leaved species. This composition reflects a partially open landscape, with wide-spread xerophytes and birch. Pollen of conifers and broad-leaved trees can be interpreted as deriving from scattered tree grooves or from long-distance transport.

4.3. *Hippopotamus cf. antiquus* (Table 5)

Four samples were picked up from a radius (two samples originating spectra Hi-1 and 2), a femur (Hi-3), and a humerus

(Hi-4). Samples from the same bone and from the femur (see Table 1) provided similar pollen spectra ($AP\ 68.1 \pm 10.1\%$, xerophytes = $4.3 \pm 5\%$, pollen concentration lower than 500 grains/g of sediment, charcoal concentrations lower than 110 particles/g of sediment) and similar pollen composition, i.e. trees of floodplain, riparian and swamp forest dominate the assemblage (*Alnus glutinosa* type), but also xerophytes of dry, open land are represented. This composition points to local alder swamp and meadows; conifers are missing. Sample Hi-4 shows dominance of warm-temperate broad-leaved forest, with still important floodplain forest (*Alnus*).

4.4. *Cervalces cf. carnutorum* (sample Cc-1, Table 6)

A fragment of greyish clay picked up from the surface of a frontal bone provided a very low pollen concentration (48 grains/g of sediment), thus only 101 pollen grains were identified. More than 50% of pollen grains are conifers (*Pinus* + *Picea* > 40%, *Abies* + *Tsuga* > 13%), accompanied by *Betula* (>5%) and several herbs, i.e. Cichorioideae (10.5%), Gramineae (>6%). Warm-temperate broad-leaved trees are absent. This composition indicates cold-temperate open conifer forests, wide areas of shrubs and open vegetation including meadows and patches of dry herbs. Contrary to a previous report (Ravazzi, 2003), this specimen is not burnt, as also shown by extremely low charcoal particles concentration (1 particle/g of sediment).

4.5. *Pseudodama eurygonos* (sample Ps-1, Table 6)

The shell marls embedding this skull contain a high amount of pollen of conifers (more than 75%, mainly *Pinus* and *Picea*, but also *Abies* and *Tsuga*), up to 13% of Juglandaceae and lower values of other pollen types. The inferred dominant vegetation is a dense conifer forest with patches of broad-leaved trees (*Carya* and *Pterocarya*) possibly along the border of the lake. There are no evidences of open areas ($AP = 97.5\%$).

4.6. *?Eucladoceros ex gr. ctenoides/dicranios* (sample Eu-1, Table 6)

A single pollen spectrum shows conifer (*Pinus*–*Picea*) pollen dominance with high afforestation index ($AP = 98.4\%$), pointing to a dense forest cover by cold-temperate conifer forests.

4.7. Large deer (sample Ld-1, Table 6)

A single pollen spectrum obtained from clay adhering to leg parts is dominated by conifers (*Pinus*–*Picea*–*Abies*), and xerophytes (*Artemisia*, chenopods), suggesting a mosaic of conifer forest and open steppe of cool/cold-temperate climate.

5. Discussion

The discussion is addressed to the following main topics: first of all we examine the quality of the pollen record (Section 5.1) and the taphonomy (Section 5.2) of the site. Then we address the questions related to the habitat of single species (Section 5.3), that is, palaeoenvironments reconstructed based on pollen data are here compared with the information available in literature on the ecology of the taxa considered. In a further step (Section 5.4), we evaluate the palaeoenvironmental and the mammal record as a function of time and considering the climate change.

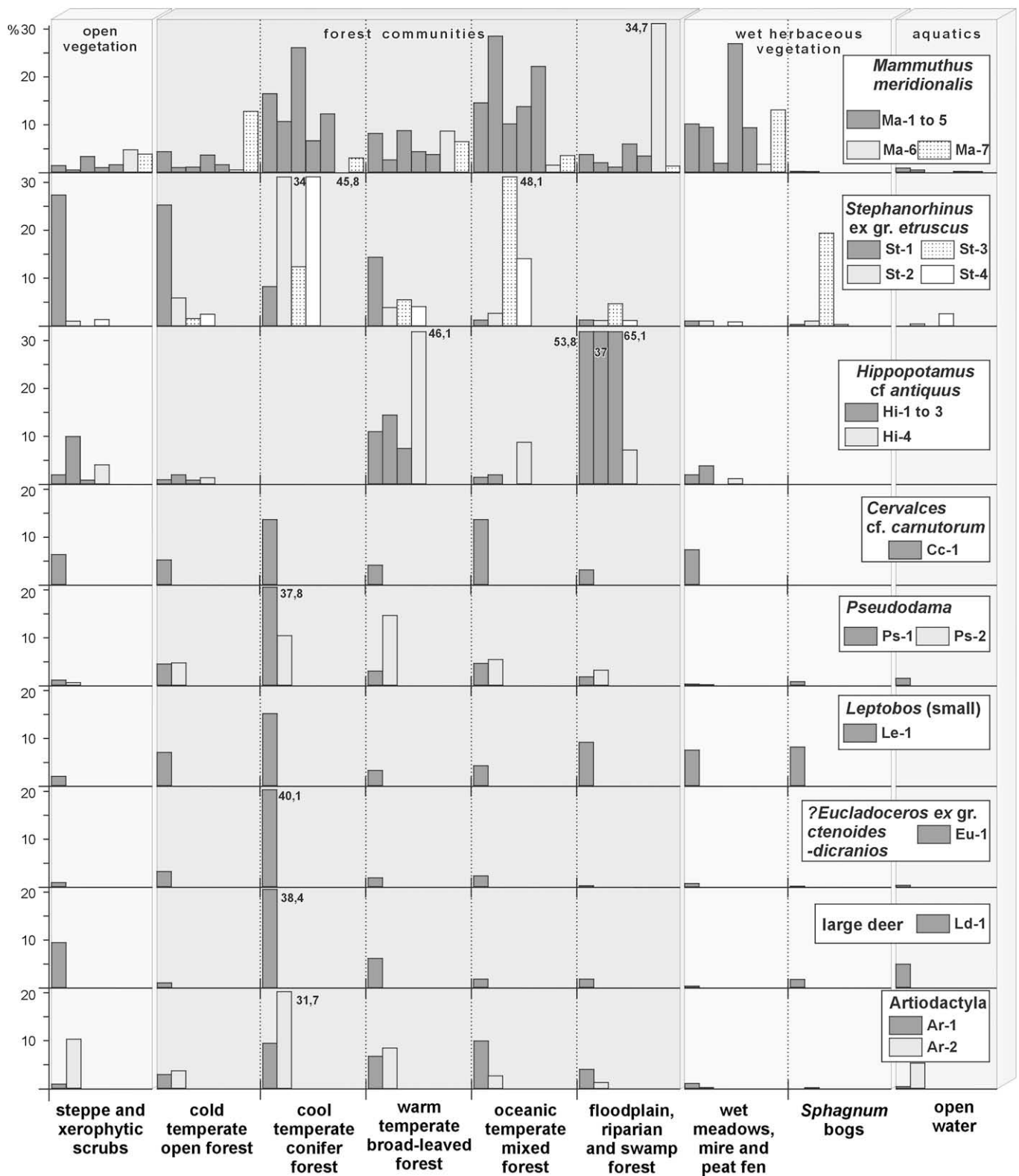


Fig. 3. Histogram plot of percentage sum of pollen types diagnostic of vegetation communities (see Section 2 and Table 2) derived from all the studied specimens. Pollen types for open vegetation of dry sites (steppe and xerophytic scrubs) are represented in the first left column; forest communities in columns 2–6 (background in green); wet herbaceous vegetation in columns 7 and 8 (background in pale yellow); open water macrophytic vegetation in column 9 (background in pale blue). The grey scale of histograms distinguishes individuals, hence more histograms filled with same grey tone refer to several specimens taken from one individual.

5.1. Quality of the pollen record and reproducibility of the pollen signal from single skeletons

With a few exceptions, the pollen sum is over the requested threshold for a statistically significant treatment of quantitative data of major components (>400 identified grains, Birks and Birks, 1980; Birks and Gordon, 1985). Given the lacustrine sedimentary environment isolated from main river, the pollen assemblage is mostly composed by airborne pollen, representing the image of the vegetation in a mountain catchment of about 40 km².

We tested the consistency of the pollen spectra by comparing the similarity between the pollen spectrum from each skeletal element with those belonging to a single skeleton, using the Fisher's exact test, a non-parametric test for the significance of the deviation from null hypothesis (=all specimens belonging to the same individual). For *Mammuthus meridionalis*, the consistency of the obtained results from single skeleton pollen spectra (Ma-1–Ma-5) is shown by overlapping statistical distributions (see Table 1b and Fig. 4) and is verified by *P*-values much higher than the 0.002 threshold, thus indicating that the null hypothesis (spectra Ma-1–Ma-5 belonging to the same individual) cannot be rejected (see Table 7). Conversely, *P*-values are much lower when comparing spectra Ma-6 and Ma-7 (originating from different individuals) with Ma-1–Ma-5. In this case the null hypothesis is to be rejected (Table 7). These results ensure that statistically significant differences in the composition of pollen spectra actually reflect different pollen sedimentation events. It is worth noting that the right hand of *Mammuthus meridionalis* (specimen V33 from individual D, pollen spectrum Ma-2 of this paper) was already analyzed for pollen by Prof. Fausto Lona in year 1954. His results fit well with our data from the same specimen (a summary was included in Vialli, 1956, see caption Table 3). This eliminates possible bias due to pollen degradation following subaerial exposure.

As for the *Hippopotamus* remains, despite the lack of information about stratigraphical provenance, the possibility that the radius and the femur belong to the same individual (indicated as ST-6 in Table 1)

Table 7
P-values after Fisher's exact test.

Taxon	Variable 1	Variable 2	<i>P</i> -value after Fisher's exact test	Interpretation
<i>Mammuthus meridionalis</i>	Ma-1	Ma-2	0.15	Spectra Ma-1–Ma-5 come from skeletal elements belonging to the same individual (ind. D)
	Ma-1	Ma-3	0.28	
	Ma-1	Ma-4	0.58	
	Ma-1	Ma-5	0.68	
	Ma-2	Ma-3	0.0048	
	Ma-2	Ma-4	0.17	
	Ma-2	Ma-5	0.89	
	Ma-3	Ma-4	0.0093	
	Ma-3	Ma-5	0.16	
	Ma-4	Ma-5	0.72	
<i>Mammuthus meridionalis</i>	Individual D (Ma-1–Ma-5), mean values	Unknown individual (Ma-6)	4.3×10^{-14}	Spectrum Ma-6 comes from a skeletal element not belonging to individual D
	Individual D (Ma-1–Ma-5), mean values	Unknown individual (Ma-7)	1.4×10^{-4}	Spectrum Ma-7 comes from a skeletal element not belonging to individual D
<i>Hippopotamus cf. antiquus</i>	Hi-1	Hi-2	0.035	Spectra Hi-1–Hi-3 come from the same individual, named ST-6 (see Table 1)
	Hi-1	Hi-3	0.50	
	Hi-2	Hi-3	0.002	
	Individual ST-6 (Hi-1–Hi-3), mean values	Unknown individual (Hi-4)	4.8×10^{-14}	

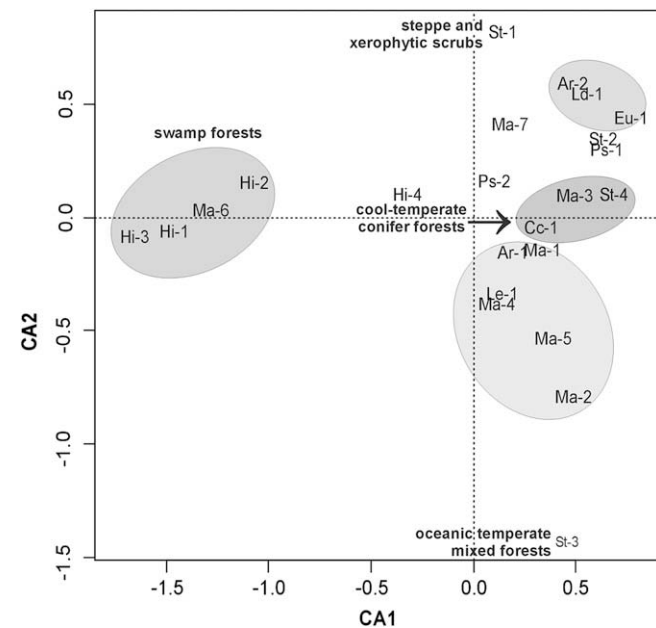


Fig. 4. Ordination diagram of the recognized vegetation communities obtained through canonical correspondence analysis. The axis 1 accounts for the 57% of total variability, whereas axis 2 accounts for 23%.

is founded on their very similar state of preservation. *P*-values from sediment pollen spectra (Hi-1–3) support this assignment (Table 7).

To our knowledge, the reproducibility of the pollen signal from single skeletons of fossil mammals has never been tested so far. Consistent results from multiple pollen spectra originating from sediment adhering to a single braincase of *Cervalces latifrons* have recently been obtained at another Early Pleistocene lacustrine site in the Italian Alps (Breda et al., 2005).

5.2. Floating meadows and the death of large mammals in the Leffe Basin

The sedimentary record from the Leffe Basin testifies to several phases of development of palustrine vegetation, leading to peat deposition. Macrofossil analysis reveals that peat layers are mainly composed by *Carex* and *Sphagnum* (Zanni, 1999). They possibly formed a layer floating over some meters of muddy water, but resembling a solid surface, occasionally interrupted by bog pools. Examples of this phenomenon, called “floating meadows” or “quaking bogs” are well-known especially from boreal countries (Skeels, 1962; Dorr and Eschman, 1970; Grünig, 1994). The sediment accumulating below such floating carpets is a gyttja, sometimes a detritus gyttja (Kowalewski and Milecka, 2003). Heavy animals venturing out on such unstable material may have broken through, became mired, and died.

Most of the remains originating from units #5 to #9 were found in anatomical connection; they do not bear signs of abrasion and are usually well-preserved, despite recovery was often inadequate

(Venzo, 1950; Lona, 1950; Vialli, 1956). Many skeletons originating from unit #5 were included in compressed (shaled) gyttja within the “main brown coal bank” (second brown coal seam). Sordelli (1896) describes the position in which some elephant remains were found in the old mines, “with the fore quarts higher than the back as if the animals, till the last moments of their life, were trying to escape ...”. This picture suggests the hypothesis that the large mammals approached the water to drink and then were trapped in these meadows, which acted as mortal pitfalls.

5.3. Pollen data, palaeoenvironmental reconstructions and the ecology of Early Pleistocene fossil mammals in the Alps

5.3.1. Palaeoenvironmental setting and feeding behaviour of the southern mammoth

The reconstructed regional vegetation for southern mammoth includes both dense temperate conifer forest and open forest with grasslands. In the first scenario, open land was limited to wetlands. This is in agreement with the ecology suggested by morpho-functional analysis. Lister (2005) suggests that *M. meridionalis* was a woodland browser. In fact, its molars, each composed by several transverse enamel plates with a dentine core and kept together by cement, are a specialised grinding surface, adapted to process coarse twigs, tender shoots, leaves of trees and shrubs. Palmqvist et al. (2003) suggest that *M. meridionalis* was a browser or mixed feeder like African elephant, although grass was probably a more significant component of its diet. We remark that, even in a fully forested landscape, sedges, ferns, reeds, forbs and many helophytes could be preferentially selected by this species along riversides and mires, thus justifying a mixed feeder dietary profile and suggesting that it preferred wetlands habitat in the valley floor instead of dense forest cover in the mountains of the Italian Alps. As living elephants which, thanks to their large body size, are able to create paths and clearings, thinning out forest vegetation, it is possible that also the southern mammoth shaped open pathways connecting reference sites for refreshing, feeding, salt seeking, and mating. As observed in recent populations, elephant behaviour promotes specific vegetation types (Haynes, 1991). A concentration of carcasses in the sediments of the Lefte and in other intermountain lakes during the pre-Jaramillo Early Pleistocene (e.g. Pietrafitta, Petronio et al., 2005) may not be only the effect of the trap produced by a floating mat to an occasional visitor to the lake. Actually, the Lefte lake was one of the most relevant pool of fresh water in the Lombardy Pre-Alpine region, given that no glacial lakes were already formed at a time which predate major alpine glaciations (Muttoni et al., 2007). The Lefte lake was surrounded by springs of water rich in magnesium and potassium dissolved from surrounding dolomite rocks, which could be relevant to the seasonal dietary needs (Haynes, 1991). The lake was connected to the coast through a floodplain mosaic of ponds and wetlands. According to paleobotanical data, these wetlands were rich in forbs, reeds and riverside Juglandaceae forests producing large nuts (notably *Pterocarya*, *Carya* and the extinct *Juglans bergomensis*) eaten by high-level browsers, such as elephants (Green et al., 2005). Therefore, in the Pre-Jaramillo fluvially-shaped and persistently forested landscape of the Alps, we speculate that a long-standing fresh water basin, coupled with the phytogeographical setting of the connecting valley to the Po Sea, promoted seasonal migrations of the elephant populations settling the Alpine border.

5.3.2. The hippopotamus and the environment of river banks

The pollen record of *H. antiquus* suggests that hippopotamus settled the Lefte basin during warm-temperate intervals, but the sample is not large enough (probably only two individuals) to allow detailed evaluations. However, the observed abundance of *Alnus*

glutinosa type (*A. glutinosa* is the main component of warm-temperate floodplain forest), accompanied by many herbs, is considered significant as it does not appear in any of the 21 samples examined from the other mammal species (Fig. 4). According to the pollen record of the Lefte lacustrine sequence, *Alnus* peaks occur in different palaeoecological settings: (i) *Alnus* mixed to *Pterocarya* and other Juglandaceae formed extensive riverside forest during wetter and warm phases with prevailing oceanic-temperate mixed forest (Ravazzi and Rossignol Strick, 1995; Ravazzi et al., 2004 and unpublished data); and (ii) limited *Alnus* grooves occurring during drier phases with mesophytic warm-temperate broad-leaved forest (*Quercus*, *Ulmus* and others) characterized by openness of the river banks, and missing a riverside Juglandaceae forest. One of these latter phases is shown by Pollen Zone Na2 (Ravazzi and Rossignol Strick, 1995) remarked by *Eucommia* and *Celtis*, acting as trees pioneering alkaline riversides (Wang, 1961; Ying et al., 1993) together with herbs of open (or frequently flooded) sites such as *Artemisia*, chenopods, Asteraceae, Gramineae. A landscape occupied by warm-temperate dry broad-leaved, with reduced walnut riverside forest and open riverbanks matches the pollen spectra obtained from hippopotamus bones. River banks features are of importance in the habitat preferences of the modern hippopotamus, spending its days in water or near water courses and selecting locations close to preferred grazing meadows (Martin, 2005). Grazing sites are often controlled by periodic fire (Olivier and Laurie, 1974). However, a definition of “savannah grazer” is not justified by fecal analysis of plant contents of hippopotamus populations living in open landscapes (Scotcher et al., 1978) which point to a diet fairly entirely composed by short-tailed, tender, mostly C₄ grass and sedges typical for floodplain (i.e. a “wetland grazer”), instead of tall grass characterizing the savannah in a proper sense (Cole, 1986; Archibold, 1995). Foraging on woodland and on aquatic vegetation has also been observed (Mugangu and Hunter, 1992). Hippopotamus may indeed populate forest regions, provided with sufficient grazing available close to water pools and rivers (Lock, 1972; Martin, 2005), which are also associated to Pre-Quaternary and Pleistocene hippopotamus within and outside tropical regions (Boisserie et al., 2005). This was probably the case of *H. antiquus* at the valley floor close to the Early Pleistocene Lefte basin, during phases of open river banks related to disturbance by river activity, commonly related to a contrasted seasonal climate and important changes in river discharge.

5.3.3. Evidence of variable forest cover for the rhinoceros habitats

Pollen data (Table 4, Fig. 3) indicate that rhinoceros populated the Lefte lake under different, and contrasting paleoenvironmental conditions, ranging from warm-temperate dense mixed forest to conifer forest, to open xerophytic communities and steppe with tree birch (*Betula* sp., *B. nana* excluded) and with sparse woodland patches. The latter scenario characterises phases of cold-temperate, continental climate (see Ravazzi and Rossignol Strick, 1995, Pollen zone Mb2). On a biochronological ground, both *S. etruscus* and early small forms of *S. hundsheimensis* may occur in the faunas of Lefte (Breda and Marchetti, 2007). The brachyodont dentition and the slender, subcursorially structured limbs let Fortelius et al. (1993) and Lacomat (2003) suppose that both species were browsers of open scrub woodlands and at the margins of small woods, mainly feeding on leaves, shrubs and twigs, therefore on plants at an intermediate level above the ground. The same diet is suggested by Mazza (1993) on the base of cranial morphology, i.e. the presence of a prehensil upper lip and an uplifted head as in living black rhino. The observed variable forest cover in the habitat of living species is fully consistent with the variable habitat reconstructed for fossil rhinos at Lefte. Furthermore, the Lefte record documents the occurrence of *Stephanorhinus* ex gr. *etruscus* in cold-temperate,

partially open environments, which is, the coldest extreme of Early Pleistocene climate cycles enregistered in the Biogenic Unit of the Leffe Formation (Ravazzi and Moscarriello, 1998). This allows precisions about the climatic limits of this species.

5.3.4. Forest habitats, forest line and Early Pleistocene cervids in the Alps

Two specimens studied suggest that *Pseudodama eurygonos* lived in the region of Leffe during a phase dominated by cool-temperate, dense forest (AP = 97.6%), either mixed or conifer-dominated. Significant open spaces occurred only along the valley floor wetlands. Additionally, alpine grasslands over the treeline may have occupied wide surfaces. An estimation of treeline positions in the Alps during the Early Pleistocene was attempted by Lona (1950), who pointed to large shifts (more than thousand meters!) linked to climate change. The pollen spectrum Ps-1 is consistent with a forested environment extending upland to the entire relevant source area for pollen (Sugita, 1994), i.e. the entire basin catchments, including highplains at an Early Pleistocene altitude of about 1100–1300 m a.s.l. (see Section 2 and Fig. 1). Small-sized deer usually live in forested habitat, avoiding predation by hiding, rather than by escaping in open ground as larger species do. However, Croitor (2001) suggests that *Pseudodama eurygonos* was adapted to open and dry habitats – like dry savanna and tree-savanna – for the proportions and morphology of its phalanxes and fore limb elements suggesting a cursorial locomotion. Its shortened premolar row and molarised P₄ would suggest an adaptation to a coarse food, but its shallow and slender mandibular ramus would suggest classifying it as a mixed feeder (Croitor, 2001) and, consequently, considering the presence of trees and/or shrubs in its environment. How can we handle conflicting paleobotanical and morpho-functional evidence? Given that the fossil specimen of *Pseudodama eurygonos* is included in a consistent slab, from which the sediment was collected, the sample analyzed is considered representative of the pollen rain coeval to or shortly postdating the animal's death. On the other hand, as stated by Masini and Sala (2007), large mammals are able to move and disperse quickly. The evolution of small runner deer may have taken place in dry districts of Asia and Eastern and Southern Mediterranean, which hosted steppes and bushlands during the Early Pleistocene (Tzedakis et al., 2006; Leroy, 2008). These deer may have then migrated to specialized habitats in forested regions of the Alps through coastal and fluvial corridors. There is no paleobotanical evidence of tropical vegetation in Europe during the Early Pleistocene, such as savannah or savannah parkland. Instead wetlands, river banks and coastal regions may have offered azonal habitat to grazers and cursorial runners, at any warm to cool-temperate climate.

It is interesting to explore the importance of alpine vegetation above the forest line as a suitable habitat for Early Pleistocene cervids. In the case of the large deer, pollen data (spectrum Ld-1 in Table 6) suggest an open conifer forest and steppe of cool-/cold-temperate. Both the vegetation composition and the inferred climate are in agreement with a depression of the forest line within the Leffe basin catchment to altitudes below 1500 m a.s.l. Consequently, altitudinal steppes and alpine grasslands could expand in the lower belts. A detailed evaluation of treeline positions is not possible, however. Experimental studies on relationships between treeline and pollen rain in the Alps and in the region of boreal treeline suggest that only Pollen Accumulation Rates are sensible to enregister tree limit positions (Seppä and Hicks, 2006; Sjögren et al., 2008).

Pollen data obtained from a specimen of *Cervalces cf. carnutorum* are also indicative of a cool-temperate, open conifer forest rich in forbs and meadows. This is in agreement with the ecological requirements of moose. Moose is a typical browser (Fortelius and

Solunias, 2000), feeding on tender bark, leaves, and green shoots of trees and shrubs (willow, aspen, pine, mountain ash, birch, larch, oak), telmatic vegetation, and high perennial forbs. Aquatic vegetation constitutes a large part of its diet for their high sodium content and digestibility (Peek, 1999). The fossil genus *Cervalces* is usually considered a dweller of open environments because the wide span of its antlers would hamper its movements in the forest. A mosaic of forest and steppe, tundra or wetlands is equally consistent with this reconstruction (Sher, 1987; Breda et al., 2005) and with the osteomorphological characters of *Cervalces* (Breda, 2008). The record of *C. cf. carnutorum* here discussed supports the presence of the alceini tribe in the cool-temperate conifer forest ecosystem that occupied wide altitudinal belts during late phases of Early Pleistocene climate cycles in the Alps (Ravazzi and Moscarriello, 1998; Ravazzi, 2003).

5.3.5. Early Pleistocene mammal life palaeoenvironments in the Alps: overview

A clear patterning of palaeoenvironmental conditions emerged from this study, which is consistent with ecological differences between the considered mammal species. Palaeoecological relationships between vegetation and mammal habitats are summarized in the ordination diagram shown in Fig. 4. Here, the first ordination axis represents the decreasing percentage of the *Alnus* swamp forest, with the two studied *Hippopotamus* individuals. *Alnus* forest is anticorrelated to the development of conifer forests, and this gradient accounts for 57% of total variation. The second axis shows a gradient of decreasing climatic wetness, from oceanic-temperate mixed forests to partially open vegetation with steppe and xerophytic scrubs. Large deer rank in this latter environmental gradient. The distribution of mammal species in this diagram therefore reflects specific habitat preferences related either to climatic or to edaphic features. But, regardless to the species-specific niches, the prevalent zonal vegetation reconstructed for warm-temperate mammal species such as *Mammuthus meridionalis* and *Stephanorhinus ex. gr. etruscus* is dominated by a dense forest with conifer dominance (*Pinus*, *Picea*, *Abies*, *Tsuga*, *Cedrus*) or mixed (conifer plus deciduous broad-leaved). While modern analogues for these Early Pleistocene forests do not exist in Europe, they can be traced in modern zonal ecosystems of North America and South-eastern Asia. The adopted classification of vegetation types, which relies on N-American and Asian analogues (Table 2), recognizes the abundance of conifers in cool, but also in warm-temperate ecosystems of the Alpine Early Pleistocene, which provided habitat and food to these large mammals. Browsing on temperate conifers (especially on tender shoots of less sclerophyll species, such as *Abies*, *Picea*, and *Tsuga*) has not been considered yet in dietary profiles (e.g. Semprebon et al., 2004). Very high Silica biomineralization, resulting in high phytolith accumulation in needles, has been observed in *Picea* and *Larix*, whereas in *Tsuga* silica concentration is observed in the extreme needle tip, a process increasing with needle age and strongly influenced by soil and parent material geochemistry (Sangster et al., 2009). These studies are still preliminary but they suggest that browsing on conifer cannot be neglected for a proper interpretation of tooth microwear analysis.

5.4. Reconstructing the stratigraphic provenance of mammal remains

The co-occurrence of mammals of either warm-temperate or cool-temperate climate in the Leffe sedimentary succession may be explained by the high-frequency climate change that affected the Alps during the Early Pleistocene. Cyclic climate changes are indeed documented in the long pollen record obtained from the basin

centre (i.e. the FM master core). Furthermore, it has been shown that the pollen signal of the regional vegetation (i.e. local pollen zones) can be traced throughout the lateral extent of the basin filling (Ravazzi and Moscariello, 1998). We therefore assume that palynostratigraphical correlation between sediment adhering to bones and the FM master core, supplemented by stratigraphic information collected at time of fossil discovery (see Table 1), may allow to infer the possible biozone(s), i.e. pollen zone(s) to which these fossil remains belong, and thus to set the mammal occurrence as a spike in the long record. This procedure is also helped by the lithostratigraphical information which was recorded at the time of discovery of mammal remains, during mining activities. Indeed most finds were provided with a preliminary stratigraphical assignment to lithostratigraphic units (#2–#9, see Venzo, 1950, and Appendix A for details on historical stratigraphic record of the studied specimens).

The palynostratigraphical correlation so far described lead to the stratigraphic assessments presented in Figs. 5 and 6. Precise assignments were possible in most cases, seldom it was impossible to distinguish between two alternative stratigraphic positions. It appears that each mammal association (local fauna)

includes specimens accumulated under different environmental and climate states. The second brown coal (unit #5) is chosen here as an example. The long pollen record (FM core) shows that four forest cycles occur within unit #5 (i.e. cycles H–I–J–K, Figs. 5 and 6). The mammal remains originating from unit #5 forms a single mammal association (Lefte m.a. 1), assigned to Tasso/Farneta Faunal Units of Late Villafranchian age (Breda and Marchetti, 2007). In only one case two fossil finds, belonging to the same mammal association, could be associated to the same regional pollen zone. This suggests that the components of a local mammal fauna of Villafranchian age, even if belonging to a single lithostratigraphic unit, may not be coeval and may not represent a uniform environmental state. Actually, the deposition of the second brown coal of the Lefte Formation (unit #5), formed by compressed gyttja and peat, 8–12 m thick, required some 100 ka (Ravazzi and Moscariello, 1998). A situation similar to Lefte m.a. 1 is given by the local fauna contained in the brown coal of Pietrafitta (Central Italy), belonging to the Farneta Faunal Unit. The components of the local fauna of the brown coal bank of Pietrafitta are considered “fairly coeval” (Petronio et al., 2005). Actually, the pollen record of this brown coal bank documents

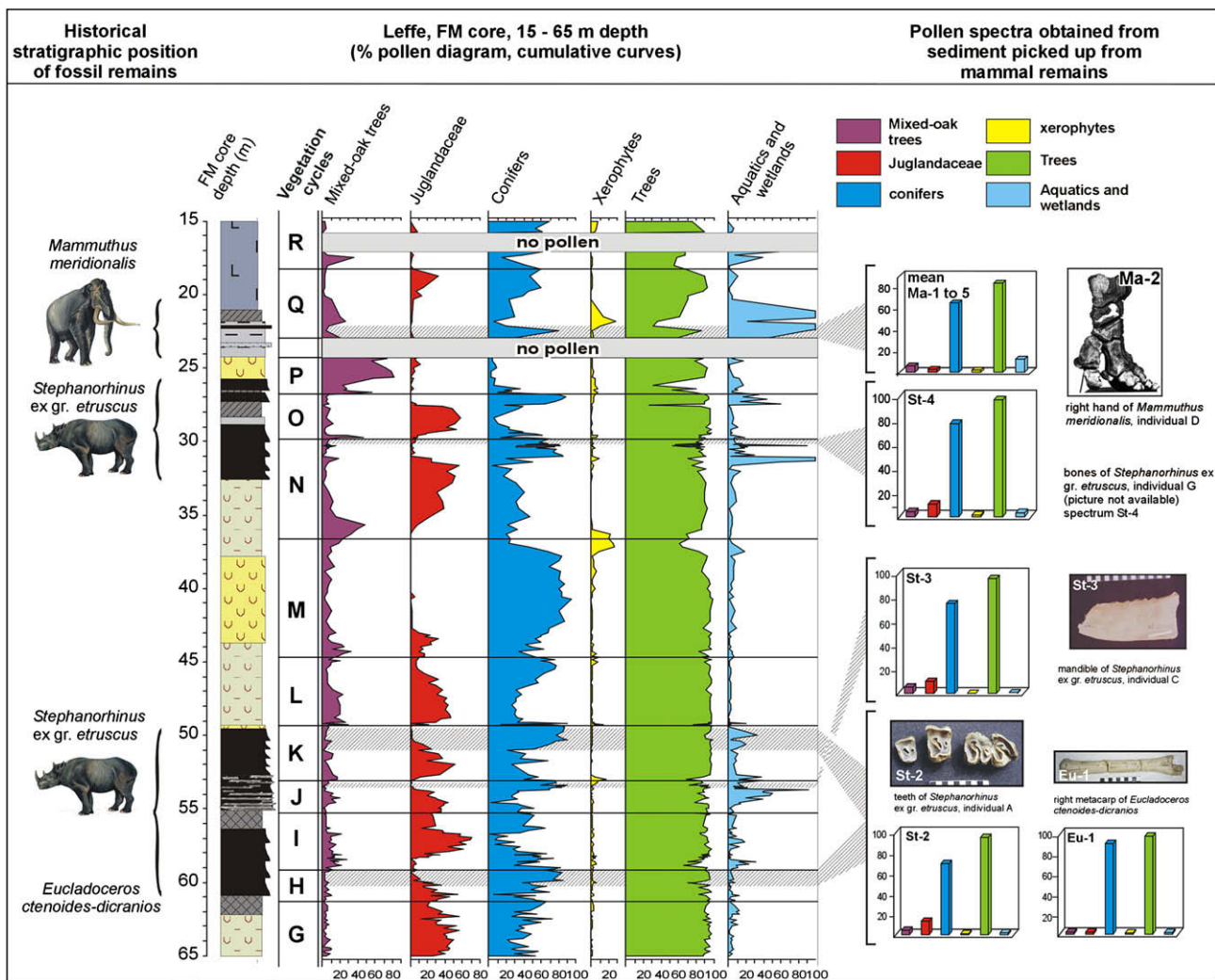


Fig. 5. Stratigraphic frame, summary pollen record and inferred stratigraphic positions for the mammals found in the Biogenic Unit of the Lefte Formation: I. Spectra indicating closed forest and wetlands (remains of *Mammuthus meridionalis*, *Stephanorhinus* ex gr. *etruscus*, ?*Eucladoceros* ex gr. *ctenoides-dicranios*). Vegetation cycles in the Lefte pollen record are from Ravazzi and Rossignol Strick (1995), Ravazzi and Moscariello (1998), Muttoni et al. (2007) and unpublished data. The palynostratigraphical correspondence between sediment samples from fossil mammals and the FM core is shown by horizontal bands.

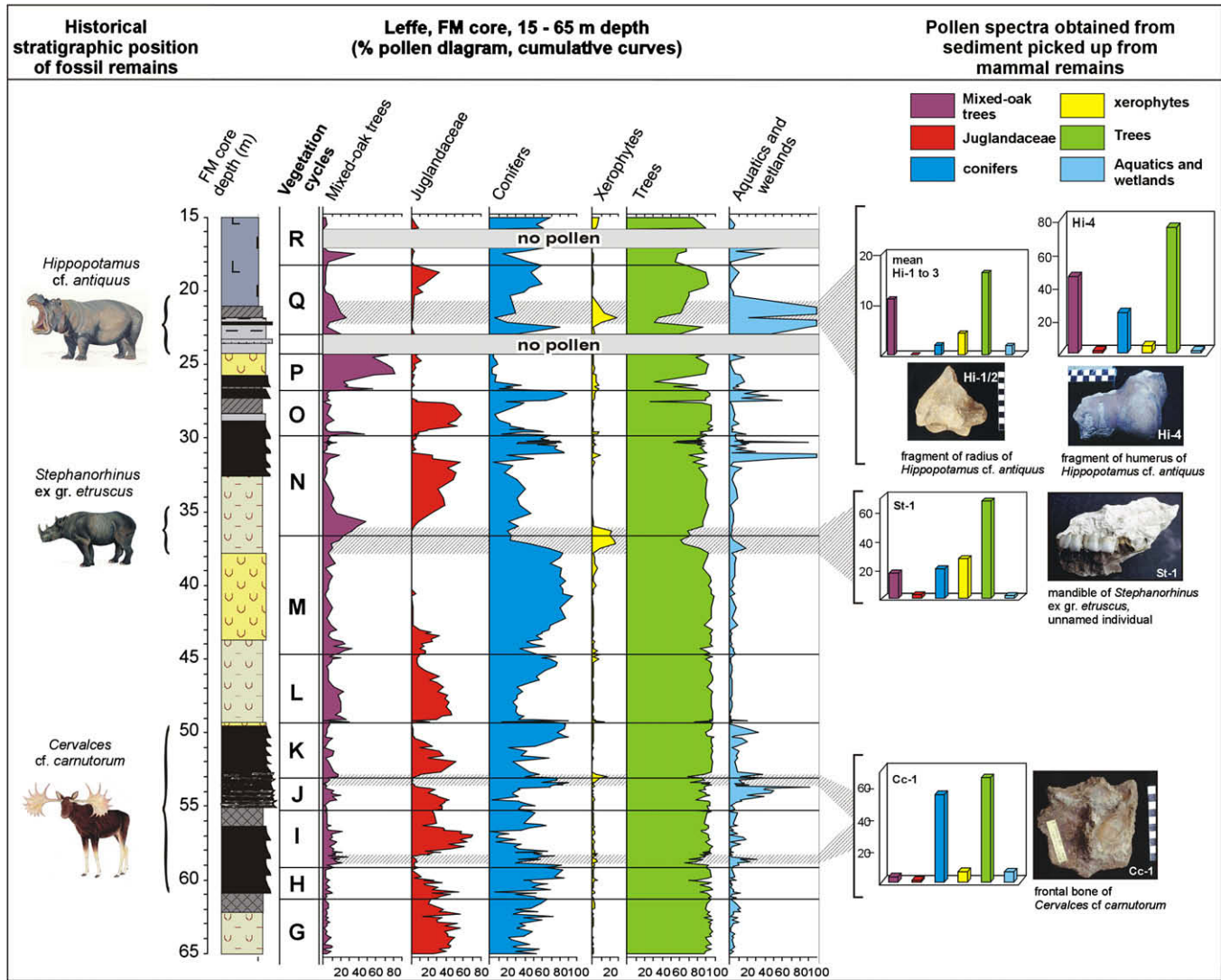


Fig. 6. Stratigraphic frame, summary pollen record and inferred stratigraphic positions for the mammals found in the Biogenic Unit of the Leffe Formation: II. Spectra indicating open vegetation of dry climate signature (remains of *Hippopotamus* sp., *Stephanorhinus ex gr. etruscus*, *Cervalces cf. carnutorum*). See Fig. 5.

several vegetation and climate changes (Ricciardi, 1969; Lona and Bertoldi, 1973).

The complexity of the lacustrine stratigraphic records suggest that specific palynological records on each sedimentary bed containing a fossil are useful when driving ecological relationships among the components of a local fauna, especially while contained in sediments of very low accumulation rate, such as compressed peat, lignite, and lacustrine marls.

6. Conclusions

We carried out a systematic investigation on pollen content of sediment adhering to skeletal elements of large mammals collected from the Leffe Basin and stored in Museums since decades or even more than a century. The excellent pollen preservation encourages further research on individuals preserved in lacustrine, palustrine and coastal (lagoonal or marshy) environments. The paleobotanical documentation collected in the present work concerns a single sedimentary succession, but deals with several mammal species belonging to different mammal faunas, a situation unprecedented in the European literature.

Given the scarcity of available paleobotanical records directly linked to Pleistocene faunas in Europe, the potential offered by long lacustrine successions may substantially improve the documentation about the habitat of past mammal life.

Some species (*Mammuthus meridionalis*, *Hippopotamus cf. antiquus*) could be provided with multiple pollen spectra from single individuals, allowing to test the reproducibility of the pollen signal from single skeletons.

A clear patterning of palaeoenvironmental conditions emerged from this study, which is consistent with ecological differences between considered mammal species. Conversely, the possibility to correlate individual spectra with a reference palynostratigraphic record, previously obtained from a master core in the same sedimentary basin, allowed each fossil remain to be associated to a single stratigraphic position within the palaeoenvironmental sequence. This procedure also demonstrated that one mammal association (local fauna), preserved in a brown coal seam or in a lacustrine deposit and spanning several thousand years, includes specimens accumulated under different environmental and climate states. The high-frequency climate variability which characterized the Villafranchian age requires careful consideration in drawing

palaeoecological inferences from whole-mammal assemblages. High-resolution pollen sampling proved to be useful to check the palaeoenvironmental setting of single faunal specimens. This approach can be applied as well to material stored since decades, as documented in the present paper. Obviously, it may be even more fruitful when it is possible to plan a sampling strategy during a palaeontological excavation.

In a further step, combining pollen spectra with tooth micro-wear analysis and elemental and isotopic determinations from the same skeletal specimen would allow more insight on regional palaeoenvironment, habitat preferences, and diet. Mammal remains stored in Museums are a potential archive for multidisciplinary palaeoenvironmental reconstructions.

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Appendix A. Palynostratigraphical correlation between sediment adhering to bones and the master core from the basin centre

Mammuthus meridionalis spectra Ma-1–Ma-5 (individual D in Vialli, 1956) originates from organic clay just above unit #8. The high percentage of conifers (*Pinus* + *Picea* > 45%, *Abies* + *Tsuga* > 25%) suggests correlation to the declining part of the cycle P/beginning of cycle Q.

Stephanorhinus ex gr. etruscus spectrum St-4, testifying open landscape, with widespread xerophytes and birch, originates from shell marls located 2 m below brown coals of unit #7 (Vialli, 1956), thus fitting the open phase ending vegetation cycle M (Fig. 6).

Stephanorhinus ex gr. etruscus spectrum St-2 (individual A in Vialli, 1956) originates from the brown coal seam of unit #5 (Vialli, 1956). The pollen spectrum yields high % of *Picea* and *Pinus*, rare grains of *Cedrus*, up to 10% of Juglandaceae and ca 5% of *Betula*. This composition occurs in the pollen spectra of cycles K and H within the second brown coal seam (Fig. 5).

Stephanorhinus ex gr. etruscus spectrum St-3 (individual C in Vialli, 1956) comes from the second brown coal seam of subunit #5 (Vialli, 1956). The pollen spectrum, dominated by *Tsuga* (up to 43%), accompanied by pine and Juglandaceae, fit with the composition of late vegetation cycle J.

Stephanorhinus ex gr. etruscus spectrum St-5 (individual G in Vialli, 1956) originates from the first brown coal seam of subunit #7 (Muttoni et al., 2007). The pollen spectrum, dominated by conifer pollen (up to 45% of *Picea*) and 10% of Juglandaceae, may be set within cycle N.

?*Eucladoceros gr. ctenoides-dicranios* (spectrum Eu-1) was found in 1877 in brown coals of unit #5 (Stehlin, 1930). The abundance of conifer pollen (>90%) and very low % values of all other taxa

resemble the composition of pollen spectrum St-2 from *S. ex gr. etruscus* (see above), suggesting a correspondence with cycles K and H of the Lefte pollen record.

Hippopotamus cf. antiquus Spectra Hi-1–Hi-4 originates from an unknown level of the Lefte formation (Breda and Marchetti, 2007). Despite the lack of information about stratigraphical provenance, the possibility that the radius and the femur belong to the same individual (indicated as ST-6 in Table 1) is founded on their very similar state of preservation. Limited content of conifer pollen and abundance of broad-leaved trees suggest a possible correspondence with forest phases within cycle Q.

Cervalces cf. carnutorum spectrum Cc-1, previously assigned to the first brown coal seam, is here attributed to the second brown coal seam of subunit #5 due to a revision of stratigraphic informations. In the pollen spectrum obtained from a poor sediment sample conifer pollen sum up to 55%, herbs to 32% and negligible amounts of broad-leaved trees pollen. This composition may fit vegetation phases within cycles I and J of the Lefte pollen record.

Pseudodama eurygonos spectrum Ps-1 was found in 1947 in a clay level above the second brown coal seam. The pollen spectrum yields a high amount of conifers (mainly *Pinus* and *Picea*), up to 10% of Juglandaceae and lower values of all other pollen types. This composition reflects those at the base of the shell marls level.

Appendix B. Rare pollen types not listed in analytical Tables 3, 4 and 6

Spectrum Ma-1. *Sorbus*, Campanulaceae, *Scabiosa*, Fabaceae, Labiatae, *Equisetum*, *Sphagnum*. **Spectrum Ma-2.** *Ostrya*, Campanulaceae, *Knautia*, *Pinguicula*, *Selaginella*, *Sphagnum*. **Spectrum Ma-3.** *Hedera*, *Olea*, *Sorbus*. **Spectrum Ma-4.** *Fraxinus excelsior*, *Lonicera xylosteum* type, *Ostrya*, *Armeria*, *Helianthemum*, *Selaginella*. **Spectrum Ma-5.** *Hedera*, *Olea*, *Ostrya*, *Polygonum*. **Spectrum Ma-6.** *Vicia* type, *Trifolium pratense* type, Labiatae, Liliaceae, *Verbena*, *Geranium*, *Glomus*. **Spectrum St-1.** *Cirsium*, Cichorioideae, Caryophyllaceae, *Polygonum bistorta* type, *Athyrium*. **Spectrum St-2.** *Carpinus orientalis/Ostrya*, *Ilex*, Caryophyllaceae, *Spirogyra*, *Pteridium*. **Spectrum St-3.** Cichorioideae, Cruciferae. **Spectrum St-4.** *Ostrya*. **Spectrum Cc-1.** *Sambucus*. **Spectrum Ps-2.** *Carpinus orientalis/Ostrya*, *Castanea*. **Spectrum Le-1.** Caryophyllaceae, Cruciferae. **Spectrum Ld-1.** *Castanea*, *Salix*, *Centaurea*, Caryophyllaceae, *Plantago*. **Spectrum Ar-1.** *Hedera*, *Anagallis*, Fabaceae. **Spectrum Ar-2.** *Eucommia*, *Salix*, Caryophyllaceae, *Lythrum*, *Plantago*.

Appendix. Supplementary information

Supplementary information associated with this article can be found, in the online version, at doi:10.1016/j.quascirev.2009.07.022

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