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Pleistocene mammal faunas from the Leffe Basin (Bergamo, Northern Italy): revision and new data

With 7 figs, 1 pl., 2 tabs

Marzia Breda & Marco Marchetti

Abstract

In this study, the mammal remains collected from the second half of the 19th century until the late 1950's in the brown coal mine of Leffe (Bergamo, Northern Italy) are re-evaluated. We studied both the material preserved in the collections and the remains now lost but nonetheless well described in the literature. Along with *Mammuthus meridionalis* and *Stephanorhinus* ex gr. *etruscus*, several species not previously recorded from Leffe have been found in the collections (*Pachycrocuta brevirostris, Hippopotamus* cf. *antiquus, Cervalces* cf. *carnutorum,* and *Megaloceros* ex gr. *verticornis-pliotarandoides*). Furthermore, *Mimomys savini*, ?*Capreolus* s.l. sp. and ?*Megaloceros* cf. *obscurus* are recorded thanks to the descriptions and measurements given in the literature of specimens now lost. Also, the previous specific identifications of *Leptobos etruscus* and of a *Dama*-like cervid have been modified into *Leptobos vallisarni* and *Axis eurygonos*, respectively.

Three Early Pleistocene mammal groups are represented: one from the main brown coal level (subunit #5, Biogenic Unit), spanning the end of the Tasso FU (FU = Faunal Unit) to the beginning of the Farneta FU, one from subunit #6 and #7 (again Biogenic Unit), ranging from the latest part of the Farneta FU to the beginning of the Colle Curti FU, and one from the Upper Unit (subunit #9), which is attributed to the Colle Curti FU.

A *Palaeoloxodon antiquus* upper palate, which was found in the collections of the Civic Museum of Milan, belongs to a more recent period. In fact, its light coloured surfaces and adhered red clay sediment imply that it comes from the red palaeosoils overlying the Leffe Formation.

Key words: Northern Italy, Early Pleistocene, mammals, systematics, biochronology

Introduction

The Plio-Pleistocene Leffe Basin (45°49'N, 9°51'E) is located in Valgandino, a tributary valley of the Serio River in the Southern Alps north of Bergamo, Northern Italy (fig. 1). The brown coal mine of Leffe has been well known since the 19th century for its numerous fossil materials, consisting of large mammals, turtles, molluscs and plant remains. In 1991, an 189 m long core was drilled [Fornace Martinelli core (acronym FM core), (Muttoni et al. 2007)], which provided the most complete stratigraphical record of the sedimentary sequence of the Leffe Basin.

Among the rich fossil material, it was primarily the mammalian fossils which captured the interest of many students. The first records date back to 1840, with descriptions by Balsamo Crivelli (1840, 1842) of rhino teeth, which were then gathered in the collection of the "Gabinetto di Minerali e Fossili di Santa Teresa" in Milan. Later on these samples were transferred to the newly founded Civic Museum of Natural History in Milan. Soon afterwards, the mammal fauna from Leffe had a prominent position in the monograph by Cornalia (1858–71) on the "Mammifères fossiles de Lombardie", which was enriched by wonderful hand drawings accurately depicting the osteological details.

Several publications dealt with the fauna from Leffe (Sordelli 1872, 1882, Major 1873, 1874, Rütimeyer 1876, Portis 1887, 1898, Venzo 1950), but two deserve particular mention for the precision of their descriptions, measurements, and pictures, which enabled the identification of the specimens. These are the detailed work on the elephant remains by Airaghi (1914) and the paper by Stehlin (1930), which gave the state of the art of the mammal findings up to that year.

As with many important sites of the 19th century, the fossil material was scattered throughout numerous muse-

Authors' addresses: M. Breda, Dipartimento di Geologia, Paleontologia e Geofisica, University of Padova, Via Giotto 1, 35137 Padova, Italy, <marziabreda@hotmail.com>; M. Marchetti, Dipartimento delle Risorse Naturali e Culturali, University of Ferrara, Corso Porta Mare 2, 44100 Ferrara, Italy, <marcopaleo@hotmail.com>

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Fig. 1: Geographic position of the Leffe Basin in Valgandino, Southern Alps, north of Bergamo, Italy.

ums, such as Bergamo, Berna, Parma, and Torino. However, the richest collection was undoubtedly in the Civic Museum of Natural History of Milan. Unfortunately, the Leffe collection of the Milan Museum, gathered in more than a century of research, was partly destroyed, along with other important collections, by a fire that broke out in 1944 after a bombing raid during the Second World War. In the following years, new fossil remains were collected up to the late 50's, when the brown coal mining finally ended.

Since then, the Leffe fauna has been known only through the literature and had never been revised. An updated list of the specimens still preserved in the Museum of Milan was needed.

Materials and Methods

The revision of the mammal fauna began in 2002, by verifying if the specimens from Leffe cited in the literature were still housed in the different museums. It was determined that a minor part of the collections had gone lost (or, at least, thery do not figure in the museums' records), but fortunately the Civic Museum of Natural History of Milan (henceforth M-MI) and the Museum "E. Caffi" of Bergamo (henceforth M-BG) still preserve material from Leffe.

The material stored in Bergamo corresponds well to that described by Airaghi (1914) and Stehlin (1930). In addition, there were several unexpected findings, which are described below. The material stored in Milan is mostly from excavations accomplished after the Second World War, which confirms that the oldest collections had been largely destroyed by the 1944 fire. Fortunately, good and reliable casts of some of the best elephant specimens are kept in Bergamo. Other specimens (e.g. *Mimomys*, *Castor*, *Leptobos*, *Dama* and still others) have gone lost, but detailed descriptions, measurements, and pictures of these specimens had been fortunately given by many early authors, mainly Cornalia (1858–71) and Stehlin (1930).

The material still kept at Milan consists primarily of partial skeletons of *Mammuthus meridionalis* and *Stephanorhinus etruscus*, which had been described by Vialli (1956). Additional undescribed remains, recovered in the same years, enrich the faunal list of new species, which had never been recorded before from Leffe.

The major difficulty we were confronted with in studying the Leffe fauna was establishing the stratigraphic provenance of the material, which could in part be inferred from the labels or the museum records.

Through a detailed study of the literature, we concluded that all companies mining for brown coal in the 19th and early 20th century extracted the lignite only from the so-called "main brown coal bank", which corresponds to "subunit #5 – Biogenic Unit" in the present work and in Muttoni et al. (2007). So, all the specimens collected up to the 40's are considered to come from this bank unless otherwise stated.

Over the next few years new excavations unearthed other fossil remains from the entire "Biogenic Unit" of the Leffe Formation as well as from the overlying "Upper Unit" (fig. 2). Vialli (1956) was the first author to record the stratigraphic position of these new finds. When present, the levels of provenance of the specimens collected in the 50's reported on the labels as well as in the catalogue of the M-MI follow Vialli's numbering system.

Indeed, these inferences on the level of origin of the material are sometimes rather weak. However, in order to avoid influencing the results, they were conducted independently from the identification of the material. If the initial evidence is very scarce, it is surprising how all the identified remains, independently assigned to the same stratigraphic level, gather in reliable mammal associations (see the biochronological discussion below). A further independent confirm of the consistency of the levels inferred for each species comes from the palynological study of the sediment associated to several mammal remains (preliminary data in Pini & Ravazzi 2006.). This pollen analysis enabled positioning the involved specimens on the detailed palyno-stratigraphical column of the Leffe section and its results are consistent with the inferences here suggested.

Lithostratigraphical succession

The sedimentary succession has been described by Cremaschi & Ravazzi (1995) and updated by Muttoni et al.

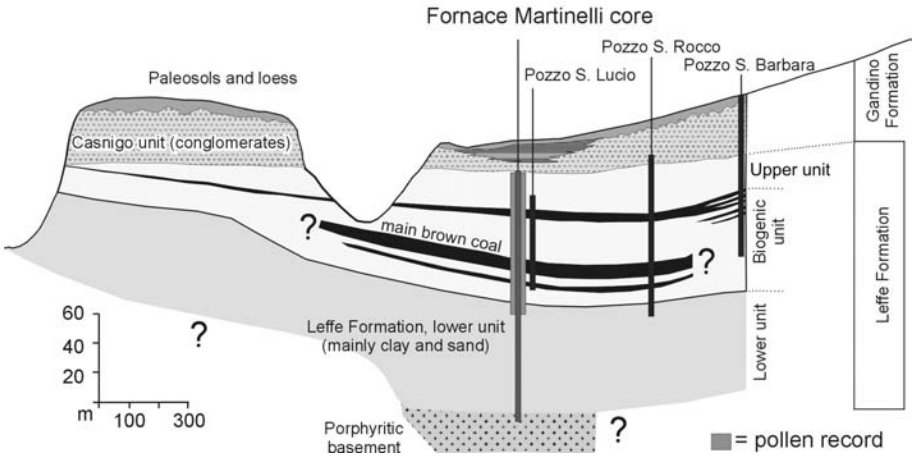

Fig. 2: W-E Section through the Leffe Basin (after Cremaschi & Ravazzi 1995).

(2007) through the stratigraphical, paleomagnetical and palynological analysis of the FM core and of outcropping sections. We refer to these works for a detailed description of each of the sedimentary units. However, the units are briefly described and numbered from the bottom to top:

– Bedrock: altered greenish andesite dykes.
– Leffe Formation, Lower Unit composed of:
  subunit #1: gravel, sand, and clay;
  subunit #2: finer-grained sand and silt, compressed peat, and gyttja (i.e., organic mud).
– Leffe Formation, Biogenic Unit composed of:
  subunit #3: gyttja and brown coal known as the "third lignite bank";
  subunit #4: shell marls with very low organic matter content, calcareous gyttja, and gyttja;
  subunit #5: brown coal and gyttja of the "second lignite bank" (level 5 in Vialli 1956);
  subunit #6: carbonatic gyttja and shell marls (level 6 in Vialli 1956);
  subunit #7: brown coal and gyttja forming the "first lignite bank" (levels 7, 8 and 9 in Vialli 1956);
  subunit #8: shell marls (level 10 in Vialli 1956).
– Leffe Formation, Upper Unit (subunit #9): clays, gyttja, and compressed peat (level 11 in Vialli 1956).
– Gandino Formation with:
  Peia-Gandino Unit: breccias and conglomerates;
  Cà Manot Unit and Casnigo Unit (coeval and interfingering one to the other on the eastern and western part of the Leffe Basin).
– Palaeosoils and loess, capping in this order the Leffe sequence.

The detailed stratigraphical log reconstructed by Cremaschi & Ravazzi (1995) and updated by Muttoni et al. (2007) has been correlated with Vialli's (1956) sketch of the strata in fig. 3 [note that Vialli's (1956) numbering of the strata differs from that used by Venzo (1950) and by Vialli (1967)].

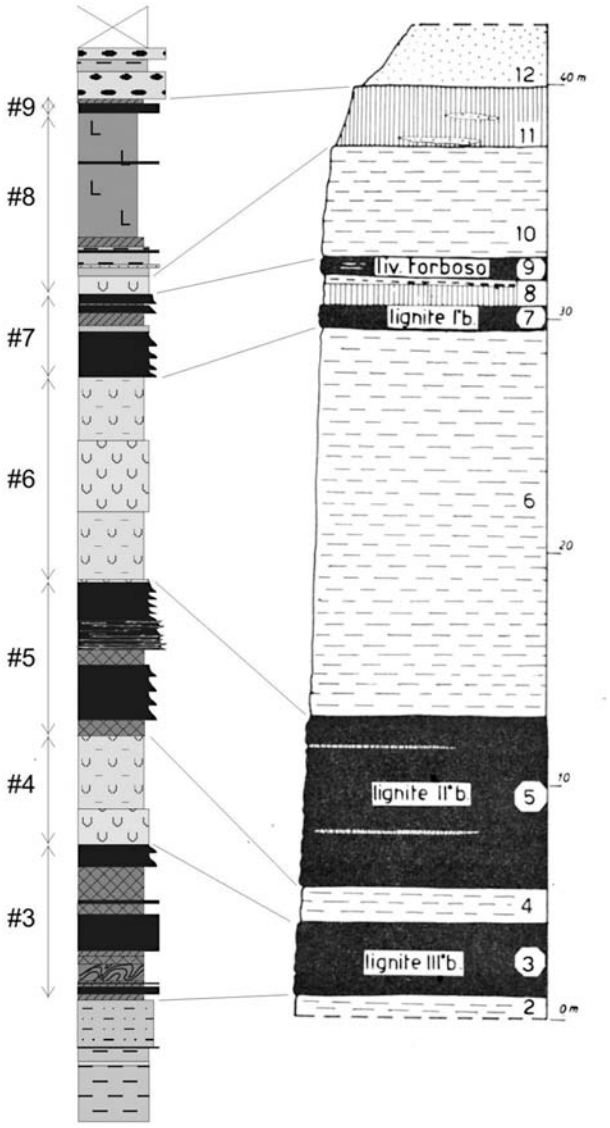

Fig. 3: Stratigraphic section of the Leffe mine with the level of origin of some mammal remains, after Vialli (1956: fig. 1), correlated to the modern stratigraphic section by Muttoni et al. (2007).

Revision of the Fauna

Leffe's Early Pleistocene fauna reported in the literature comes from the Biogenic and Upper Units. However, newly discovered taxa as well as the identification of the levels of origin of the different specimens has shown that there are three different faunas within this portion of the Leffe Formation. Our studies thus led to an improved biochronological resolution.

Order Rodentia Bowdich, 1821

Remains of rodents were recorded from Leffe by Cornalia (1858–71) and Stehlin (1930). They had gone lost during the Second World War. The identification was based on the descriptions, measurements and pictures reported in earlier literature.

Family Arvicolidae Gray, 1821
Genus ***Mimomys*** Major, 1902
Mimomys savini Hinton, 1910

Cornalia (1858–71) describes and provides pictures (pl. 14, figs 1-6) of a facial skull, a mandibular ramus with teeth, two incisors, and a humerus from a small vole, which he calls *Arvicola agrestis*. These remains had gone lost already by the 1920's (Stehlin 1930) and we agree with Stehlin (1930) that the descriptions and pictures by Cornalia are insufficient for identification, because they do not even show clearly if the teeth were rooted or not.

Stehlin (1930) was able to examine a lower first molar stored in the M-MI but, unfortunately, it was destroyed during the Second World War. Although this molar had been described by Cornalia, he failed to provide a drawing of it. This tooth had been found between the tusks of the elephant specimen, which was extracted in 1865 from the main lignite bank (subunit #5) by the Biraghi mining company. In his description of this tooth, Stehlin concludes that because of the large size (length 4 mm) and the presence of roots, it belongs to a large species of the extinct genus *Mimomys*, which is possibly an ancestor to the living *Arvicola amphibius*. Probably, Major's (1873) reference to a large *A. amphibius*-like water-vole species, but with rooted teeth, is based upon the same specimen.

The picture and measurements by Stehlin (1930: fig. 8) are suggestive of *M. savini* because of the presence of roots, the large size, the presence of cement, the absence of the enamel islet and of the *Mimomys* ridge, and the general outline of the occlusal surface (fig. 4).

Family Castoridae Hemprich, 1820
Genus ***Castor*** Linnaeus, 1758
Castor fiber Linnaeus, 1758

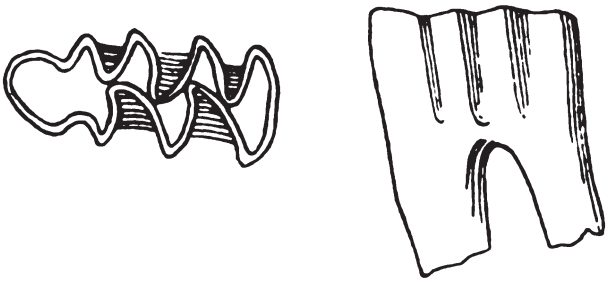

Fig. 4: *Mimomys savini*. Left M_1 from subunit #5, from Stehlin (1930: fig. 8). Stehlin drew the sketch with the help of a magnifying lens and he did not assigned a scale bar; however he states that the tooth is long 4 mm.

Cornalia (1858–71) describes and provides pictures (pl. 14, figs 10–13) of beaver remains stored in the M-MI. These remains consisted of three jugal teeth, which were subsequently destroyed during the Second World War, and of an incisor, which had already gone lost (Cornalia reports on a drawing by Balsamo Crivelli). The measurements were not reported by Cornalia. We agree with Stehlin (1930) that the morphology of the teeth fully corresponds to that of the living *Castor fiber*. The beaver remains are thought to originate from the main brown coal level (subunit #5), because they are from the earliest excavations.

Order Carnivora Bowdich, 1821
Family Hyaenidae Gray, 1869
Genus ***Pachycrocuta*** Kretzoi, 1938
Pachycrocuta brevirostris (Aymard, 1846)

An upper lateral incisor of a carnivore was found among uncatalogued material collected in the 1950's and stored in the M-MI. This represents the first and to date, the only carnivore specimen from Leffe. This tooth was stored in the same box with the lower jaw of a young rhino collected in the 1950's from the carbonatic gyttja and shell marls of subunit #6 (see below). Therefore, they are both believed to come from the same level. At first, the tooth was believed to be the lower canine of a dirk-toothed cat and assigned to the genus *Megantereon* for the lack of crenulation (Breda & Marchetti 2004). Actually, the large size excludes this genus, and the hypothesis that it could belong to the larger genus *Homotherium* and that the crenulation could have been worn out, has also to be rejected since the tooth belonged to a relatively young animal, and because it is not flattened in mediolateral direction as the lower canines of this genus are. The presence of two very strong ridges – posterior and anteromedial – and the short crown, suggest rather it is the right I^3 of a Hyaenidae (pl., fig. 4). The tooth is as-

Table 1: Dental parameters of *Mammuthus meridionalis* teeth (LF = Lamellar Frequency; ET = Enamel Thickness; PF = Plate Formula; LD = Lamellar Density = % PF/Greatest Lenght). The data on the specimen of 1877 and on the upper left molar of the specimen of 1865 are after Airaghi (1914).

Specimen	tooth	LF	ET	PF (T = talon)	LD
Specimen of 1947	M^1	5 (n = 2)	2.5–3 (n = 2)	4–8 (n = 2)	4.9 (n = 1)
Specimen of 1865 (cast)	M^1	5-6 (n = 2)	3 (n = 1)	7T-8 (n = 2)	4.6 (n = 1)
Specimen of 1865 (cast)	M_1	5+ (n = 2)	3 (n = 2)	8 T–9 (n = 2)	4.9 (n = 2)
Specimen of 1867	M^2	5.5-6 (n = 2)	3 (n = 2)	6.5–7.5 (n = 2)	5.2–5.4 (n = 2)
Specimen of 1867	M^3	6.5 (n = 1)		T14T (n = 1)	6.4 (n = 1)
Specimen of 1867	M_2	5.5-6 (n = 2)	3.5 (n = 2)	5.5–6 (n = 2)	5.0–5.6 (n = 2)
Specimen of 1877	M^3	5 (n = 2)		13 (n = 2)	
Specimen of 1877	M_3	5 (n = 2)		14 (n = 2)	

signed to *Pachycrocuta brevirostris*, based on the large size of the crown (Dt = transverse diameter 15 mm; Dap = antero-posterior diameter 20 mm; H max = maximum height 27 mm).

Order Proboscidea Illiger, 1811
Family Elephantidae Gray, 1821
Genus ***Mammuthus*** Burnett, 1830
Mammuthus meridionalis ssp. (Nesti, 1825)

Cornalia (1865), Major (1873) and Rütimeyer (1876) were the first authors to record *M. meridionalis* from Leffe. A comprehensive analysis of the elephant remains was carried out by Airaghi (1914), who itemized all of the material found up to that year in the main lignite bank (subunit #5). However, only the teeth were described in detail. Unfortunately, the material stored in the M-MI has gone completely lost. Later on, Vialli (1956) described the postcranials and tusks found after the Second World War.

The following material is now available for the study: three specimens, found in 1865, 1867, and 1877 respectively, from the main lignite bank described by Airaghi (1914); Vialli's (1956) specimen "D" from subunit #9; Venzo's (1950) palate found in 1947 in the lower part of the main lignite bank; and some unidentifiable molar and tusk fragments. Most of these specimens were almost complete but so delicate that they couldn't be extracted from the brown coal or went destroyed during the extraction and the subsequent drying (Cornalia 1865, Venzo 1950). The following portion of the skeletons could be preserved:

– Specimen found in 1865: we don't know exactly what was originally preserved because the remains were destroyed during the war but some good quality casts are stored in the M-BG. They consist of one upper first molar, the lower jaws with first molars under wear and second molars still erupting, one rib, the left tusk and the incomplete right hand.
– Specimen found in 1867, M-BG: palate with second and third molars and tusks, lower jaws with second and third molars.
– Specimen found in 1877, M-BG: lower jaw and fragment of skull with palate, teeth and base of tusks (these cranial portion are still under restoring at the M-BG and were not available for the study), atlas, first left rib, left scapula, right humerus, fragments of right ulna and radius, right hand, some sesamoid bones.
– Specimen "D" of Vialli (1956), M-MI: atlas, left femur, right tibia, distal epiphyses of right radius and ulna, right hand, part of the right foot.
– Specimen found in 1947: upper palate with incomplete and very worn first molars.

Table 2: Measurements of *Mammuthus meridionalis* atlas (in mm) (acronyms after von den Driesch 1976).

	GB	H	BFcr	BFcd
Specimen of 1877 (Subunit #5)	481	256	280	240
Specimen D of Vialli (Subunit #9)	500	275	272	244

Vialli (1956) pointed out that his specimen "D" from subunit #9 is more evolved than the specimens from the main lignite bank (both those from the earliest excavations and those collected in the 50's).

The Italian late subspecies of *M. meridionalis*, which is named *M. meridionalis vestinus*, is larger than the type subspecies *M. meridionalis meridionalis* from the Upper Valdarno. Furthermore, *M. meridionalis vestinus* has a more derived skull, although it does not differ in the dental characters. This makes discrimination between the two taxa very difficult (Ferretti 1999, Palombo & Ferretti 2005).

Actually, we found that specimen "D" and the one found in 1877 are significantly larger than the typical *M. meridionalis* from Upper Valdarno. This is evident both in the forefoot and in the atlas measurements (tab. 2), which are suggestive of *M. m. vestinus*. Unfortunately, there are no postcranial morphological features distinguishing the two sub-species so, such an attribution, cannot be confirmed due to the lack of cranial remains. The specimen recovered in 1877 is intermediate in size between those found in 1865 and 1947 (tab. 1).

Genus ***Palaeoloxodon*** Matsumoto, 1924
Palaeoloxodon antiquus (Falconer & Cautley, 1847)

Falconer (1868) described a fragmented lower molar of *Elephas antiquus* from Leffe, which was later cited by Portis (1898) and Penck & Brückner (1909). Stehlin

(1930) points out that the tooth on which Falconer based his identification (kept, at the time, in the M-MI and now destroyed) actually belongs to *E. meridionalis*, as it appears to be identical to all the other elephant tooth specimens from Leffe found up to that time.

E. antiquus is mentioned again by Vialli (1956), who suggests that the *E. meridionalis* specimens from the upper levels of the Leffe Formation are evolved toward the *E. antiquus* specimen from Viterbo (see above). At Vialli's time, *E. antiquus* was considered to be descendant from *E. meridionalis* and mistaken with the coeval *M. trogontherii*, because of their similar lamellar frequency and plate formula, which are both higher than in *M. meridionalis*. *E. antiquus* is now considered to belong to a different phyletic line and assigned by some authors to the genus *Palaeoloxodon* (e.g. Stuart 2005) and by others to the genus *Elephas*, subgenus *Palaeoloxodon* (e.g. Palombo & Ferretti 2005). Given the uncertainty on the actual descent of living *Elephas maximus* from the straight-tusked elephant (Athanassiou 2000, Shoshani & Tassy 2005), we prefer to keep the latter distinct indicating it as *Palaeoloxodon*.

The M-MI keeps an elephant upper maxilla, catalogued as V.2884, with both M^2 (pl., fig. 6). It was identified as *P. antiquus* by Ferretti (1997). The bony surfaces are light coloured and smooth and red clay-like sediment is borne inside the foramina. The label on the specimen states "Leffe, donated by T. Tomasi". In the 1940's the Engineer Tullio Tomasi was the director of the lignite mining company S. Andrea of the Val Gandino society. The red clay suggests that the specimen originated from the red palaeosoils overlying the Leffe Formation.

The tooth is morphologically referable to *Palaeoloxodon* rather than to *Mammuthus*, due to the accentuated wriggles of the enamel, the shape of the new plates (consisting of a long central ellipse and two lateral circular rings rather than of three sub-equal rings), and the tooth's overall occlusal outline. The sizes fall in the range of this species (L = length 205 mm; B = breadth 82 mm; PF = plate formula 11 or more; LF = lamellar frequency 6; ET = enamel thickness 2.5 mm).

Order Perissodactyla Owen, 1848
Family Rhinocerotidae Owen, 1845
Genus ***Stephanorhinus*** Kretzoi, 1942
Stephanorhinus ex gr. ***etruscus*** (Falconer, 1868)

Rhinoceros remains from Leffe were first described by Balsamo Crivelli (1842) as *Rhinoceros de Filippi*. Later on, they were attributed to *R. leptorhinus* Cuvier by Falconer (1868) and Major (1874), but also to *R. etruscus* by Rütimeyer (1876). Portis (1878, 1898) identified the specimens from Leffe as *R. mercki* s.l. (which included *R. etruscus*, *R. hemitoechus* and *R. leptorhinus*) and subsequently Penck & Brückner (1909), quoting Portis, called them *R. mercki* s.s. Stehlin (1930) points out that the sizes of the rhinoceros teeth from Leffe fall in the upper range of *R. etruscus*, and are somewhat smaller than those of *R. mercki*. Moreover, the premolar to molar length ratio corresponds to that of *R. etruscus* and exceeds that of *R. mercki* (Stehlin 1930). The author identifies the Leffe representative as *R.* cf. *leptorhinus*, stressing that the specimens are morphologically similar to those of *R. etruscus*, but somewhat more brachyodont. Later on Venzo (1956) and Vialli (1967) identified the rhinoceros from Leffe as *R. etruscus*.

The material now available for study consists of some fragmentary jaws and isolated teeth, collected from the main lignite bank and stored in the M-BG, and of five specimens described by Vialli (1956), collected after the Second World War from different levels of the Biogenic Unit (from subunit #5 to #7) and stored in the M-MI. The measurements of these remains are consistent (see Stehlin 1930 and Vialli 1956 for measurements) with *S. etruscus* and with the small-sized *S. hundsheimensis* recorded from some European Early Pleistocene localities among which Pietrafitta (Fortelius et al. 1993, Mazza et al. 1993, Lacombat 2003, 2006). Lacombat (2003, 2006) describes some differences between the teeth of *S. etruscus* and *S. hundsheimensis*. Fortelius et al. (1993) already noticed some of these differences but they consider them non-diagnostic. Some of these, as the constant lack of lingual cingula in the lower teeth of *S. etruscus* and, in contrast, their presence in some *S. hundsheimensis* specimens, were checked in the fossils from Leffe. All the lower teeth from Leffe lack lingual cingula: hence they cannot be assigned with certainty to any of the two species. Also other differences suggested by the quoted authors, which could help in the determination of the Leffe material, were not observed.

Order Artiodactyla Owen, 1848
Family Hippopotamidae Gray, 1821
Genus ***Hippopotamus*** Linnaeus, 1758
Hippopotamus cf. ***antiquus*** Desmarest, 1822

Hippopotamus amphibius is present in the old faunal lists from Leffe (Sordelli 1896, Portis 1898, Penck & Brückner 1909, Caffi 1930). However, Rütimeyer (1876) already considered this record dubious, suggesting that the remains ascribed to the large artiodactyl were neither hippopotamus nor from Leffe. Stehlin (1930) agreed and pointed out that the specimen mentioned by Rütimeyer was the upper maxilla of a large artiodactyl from Leffe, associated with some *Anthracotherium* molars from Majorca. This specimen, now lost to record, was labelled as "hippopotamus" and had been stored together with other Leffe specimens of the M-MI, probably because it was fossilized in a way similar to those of the other remains from the brown coal levels of Leffe (Stehlin 1930).

Nonetheless, Sordelli (1896) describes some isolated teeth from the Villa collection, attributed to the hippo-

potamus by Balsamo Crivelli and undoubtedly coming from Leffe. Stehlin (1930) informed that the Villa collection was later incorporated into the M-MI. However, there are no hippopotamus teeth in collection, but we cannot know if they went destrojed in the fire or if either Sordelli or Stehlin were wrong.

Among the material from Leffe, which was collected in the 1950's and which is now preserved in the M-MI, there are several postcranial bones attributable to the hippopotamus. These remains consist of a right astragalus, catalogued as V.40 (pl., fig. 7), and three uncatalogued distal epiphyses of left long bones: a humerus, a radius, and a femur. These bones, when compared with the European Pleistocene *Hippopotamus* described by Mazza (1995), are larger and morphogically different from *H. amphibius* and slightly smaller but morphologically consistent with *H. antiquus*. As for the astragalus, which is the most distinguishing bone, the distal ends of both lips of the troclea, in dorsal view, are not in contact with the proximal margin of the distal articular surface, as is typical of *H. antiquus* and *H. tiberinus* (which, however, is considered synonymous of *H. antiquus* by Petronio 1995). The opposite is true for *H. amphibius*. Furthermore, the proximal troclea is not inflated as in *H. tiberinus*. The measurements, in millimetres, are after the acronyms by Mazza (1995): BD 140 and BT 104 for the humerus; BDr 130, BDar 122 and DDr 71 for the radius; DD 170 for the femur; L 105, LL 95, ML 85, B 93, BP 83, BD 86, DM 67 and DL 62 for the astragalus.

Unfortunately, the stratigraphic provenance of the older specimens is unknown, while the material collected in the 1950's is from both the "Biogenic Unit" and the overlying "Upper Unit". However, the state of preservation is quite similar to that of the elephant specimen "D" described by Vialli (1956), which originated from the organic clays of subunit #9.

Family Bovidae Gray, 1821

Genus ***Leptobos*** Rütimeyer, 1877–1878

Leptobos vallisarni Merla, 1949

Many authors recorded a bovid from Leffe, identifying it as *Bos etruscus*, which is now attributed to the genus *Leptobos*.

Cornalia (1858–71) described the specimens and showed a left upper jaw as well as a right lower jaw, each with the six complete jugal teeth, in his pl. 27 (figs 1 and 2). These remains were stored together with some isolated teeth and postcranials in the M-MI and were destroyed during the Second World War. The measures given by Stehlin (1930) of the tooth row length for the upper (P^2-M^3 145 mm; M^1-M^3 82 mm) and lower (P^2-M^3 154 mm; M^1-M^3 94 mm) jaws fall in the size range of *Leptobos* given by Duvernois (1992). However, Stehlin (1930) casts doubts on the specific attribution of these specimens, because there are no cranial remains and for the constant absence of the pillar on the lingual sides of all the lower teeth from Leffe, while *L. etruscus* sometimes shows such a feature. Stehlin (1930) thus assigned the Leffe bovid to *Bos* cfr. *etruscus*.

Cornalia pictured the *Leptobos* specimens in a way that prevents the recognition of distinctive features. Furthermore, the tooth enamel is somewhat too plicated, as also noticed by Stehlin (1930). Fortunately, we could analyze some isolated upper and lower teeth from the main lignite bank preserved in the M-BG. There are four upper molars kept in Bergamo (catalogued as 1208) (pl., fig. 3) and all have a vertical groove on their mesial and distal walls, which is typical of *L. vallisarni* and which lacks instead in *L. etruscus* (Merla 1949). The measurements of these teeth are consistent with both *L. vallisarni* and *L. etruscus* (LM^1 22.0 mm; BM^1 26.2 mm; LM^2 33.0 mm; 27.4 mm; BM^2 28.5 mm; 29.2 mm; LM^3 30.0 mm; BM^3 26.0 mm). There is no pillar on the lingual wall of any of the lower teeth (catalogued as 1207, 1209, 1210), as already noticed by Stehlin (1930) on some jaws once in Milan and now destroyed. This pillar is present in the earlier representatives of *Leptobos* (e.g. *L. stenometopon*), only occasionally in *L. etruscus*, and never in the later *L. vallisarni* (Merla 1949). The measurements of the lower teeth are also consistent with both *L. vallisarni* and *L. etruscus* (e.g. measurements of the three last molars: LM_3 40.0 mm, 40.4 mm, 38.1 mm; BM_3 17.1 mm, 18.2 mm, 17.9 mm).

Our new identification of the *Leptobos* from Leffe as *L. vallisarni* was already suggested indirectly by Portis (1898), who wrote that "the ox from Leffe could be a descendant of *Bos elatus* but not the genuine *Bos elatus*" (Portis considered *Bos etruscus* Falconer as younger synonym of *Bos elatus* Croizet).

Family Cervidae Goldfuss, 1820

Early authors recorded many different species of small deer from Leffe: *Moschus* sp., *Cervus orobius, C. affinis, C. dama, C. elaphus,* and *Capreolus capreolus.* All of these species are of the size of a small fallow deer (Stehlin 1930).

Balsamo Crivelli (1842) attributed to *Moschus* sp. a very incomplete skeleton, with the molar teeth of a small ruminant and a tusk-like canine, found in the lignite by Mr. Botta. None of the successive authors included *Moschus* in their faunal lists. We know nothing about the stratigraphical location of these specimens, and we do not even have any accurate description of them.

With regards to the other species, Cornalia (1858–71) described and provided pictures of three deer of similar size: *C. orobius* (his pl. 25, figs 1–4, figured from an original by Balsamo Crivelli, because these remains were already lost in Cornalia's time), *C. affinis* (pl. 26, fig. 1) and *C. dama fossilis* (pl. 26, fig. 2). Stehlin (1930) underscores that it is ecologically unlikely that three cervids approximately the same size might have

coexisted. The author suggests that the skull remains and upper dentition, which Cornalia attributed to *C. orobius*, could actually belong to one of the other two species, both represented only by lower dentitions. Moreover, Stehlin (1930) interprets the difference in size and in crown height separating the remains attributed to *C. affinis* and *C. dama fossilis* (the former being somewhat smaller and slightly more hypsodont) as intraspecific variation. Stehlin (1930) thus assigns both to *C. affinis* Cornalia believing them the same small deer known also from the Upper Valdarno. Later on Azzaroli (1947) set *C. affinis* in the synonymy of *C. nestii*. On the contrary, Venzo (1950) and Ambrosetti et al. (1980) prefer to call the small deer from Leffe "*C. orobius*".

C. elaphus was introduced in Leffe's faunal list by Rütimeyer (1883, fide Venzo 1950), who observed that the antlers of the skull represented by Cornalia as *C. orobius* looked like the second year antlers of a red deer.

Stehlin (1930) mentions two large deer, *C. ctenoides* and *Cervus* sp.

Usually, deer systematics is based only on antler and cranial morphology, while limb bone morphology is overlooked. Postcranial remains are assigned to the species of comparable size present at any particular site. In fact, apart from the Alceini tribe, which have unmistakable osteological and dental traits, postcranial and dental elements of other large deer are of problematic determination even at a generic level due to their conservative morphology.

Only one antler from Leffe is preserved in the collections of the Museums of Milan and Bergamo, and it belongs to *M.* ex gr. *verticornis-pliotarandoides* from subunit #9 (see below for a detailed description). Assigning all the other large deer specimens from Leffe is problematical because of the extensive overlap of the size ranges of the postcranials and dentitions of the various *Eucladoceros* and *Megaloceros*.

In this paper, only a small number of postcranial and dental remains are tentatively identified from size. It is worth noting that some postcranial remains labelled in the collections or published as *Leptobos* are assigned to a large deer by the authors. The tarsal elements and incomplete long bones are proportionally comparable with those of *Leptobos*, but morphologically in line with the large-sized deer morphology described by Heintz (1970).

Genus ***Axis*** Erxleben, 1777
Axis sp. and ***Axis eurygonos*** (Azzaroli, 1947)

The size of the material described and illustrated by Cornalia (1858–71) as *C. orobius, C. affinis* and *C. dama fossilis* (see above) is compatible with di Stefano & Petronio's (2002) *Axis* sp. However, a specific identification is impossible. Also the isolated teeth and postcranials from the main lignite bank, which were recorded by Stehlin (1930) as *C. affinis*, can be ascribed to *Axis* but cannot be identified at the species level. Unfortunately, the latter specimens were partly destroyed and only fragments are now preserved in the M-BG's collections. Stehlin also describes two frontals with antler bases (M-BG 1188) together with other antler fragments (M-BG 1212) from the carbonatic gyttja and shell marls overlying the main lignite bank (subunit #6). Stehlin himself warns that these antler remains cannot be ascribed to the living fallow deer and that their precise identification is problematic.

The only specimen that may be definitively identified at the species level is the partial skull recorded by Venzo (1950) and found in 1947 in a clay level just above the main lignite bank of the Perani quarry (pl., fig. 1). This specimen, stored in the M-BG under the incorrect number 1188 (1188 is the number of other two much more incomplete pedicles with burrs already recorded by Stehlin 1930), consists of a partial skull, which was found lying upside down in a clay body. This skull consists of the frontals, part of the nasals and maxillaries (still preserved in the clayey matrix), and the antler bases. The burrs are well preserved and very developed. The antler portion has evident groves of the blood- vessels. Just above the burrs, there are two forward directed tines, which depart from the main beam approximately at right angles. Even though both of the tines are incomplete and their exact angle to the beam cannot be measured, because of the deformation of the specimen, it is clear that it was wider than 100°. Moreover, the position of the tines is quite close to the burr (dx: distance from the burr 10 mm; sx: distance from the burr 11 mm). Therefore the specimen should be attributed to the species *Axis eurygonos* after the features described by di Stefano & Petronio (1998). The size of pedicles (dx: Dap 29 mm; Dt 29 mm; sx: Dap 28 mm; Dt 28 mm), burrs (dx: Dap 43 mm; Dt 41 mm; sx: Dap 44 mm; Dt 42 mm) and first tine (dx: Dap 22 mm; sx: Dap 11 mm) is consistent with this identification.

Genus ***Capreolus*** Frisch, 1775
?***Capreolus*** s.l. sp.

The roe deer was present in Penck & Brückner's (1909, fide Stehlin 1930) list of Leffe's fauna. Stehlin (1930) stated that there is no material that could be attributed to this animal. Yet, he described as *Cervus affinis* some postcranials, then stored in the M-MI and now destroyed, which fall within the size range of *Capreolus*. This material consists of three phalanges of the same toe (then catalogued as 926 ter; GL = greatest length I 35 mm; GL II 30 mm; GL III 30 mm) and of the proximal epiphyses of two metacarpals (then catalogued as 926 quater; Bp = proximal breadth 22.5 mm), which possibly belong to the same specimen. A more precise identification is impossible.

Genus ***Cervalces*** Scott, 1885
Cervalces cf. ***carnutorum*** (Laugel, 1862)

Among the uncatalogued material collected in the 1950's and stored in the M-MI there is a right frontal of *Cervalces* cf. *carnutorum* (pl., fig. 8). It represents the only remain of this genus from Leffe and one of the few from Northern Italy (Breda 2002, Breda & Marchetti 2005).

According to the old label, the specimen was collected in the upper lignite bank (subunit #7), near the Re creek in the 1950's. The frontal belonged to an adult male and is incomplete, missing the foremost portion toward the orbit and the pedicle extremity. The pedicle is set horizontally and perpendicular to the sagittal body plane, which is a trait that distinguishes the Alceini from any other deer. Furthermore, the pedicle is elliptical in section, being compressed in the dorso-ventral plane (the diameters are 77 x 56 mm). This is typical of the genus *Cervalces*, in contrast to *Alces*. The size of this frontal (113 mm from the sagittal suture surface to the postorbital restriction) is consistent with the species *C. carnutorum*. However, because of the wide overlapping measurements of the different species of the genus *Cervalces*, and of the absence of measurements of sure *C. carnutorum* skulls, we prefer identifying this specimen as *C.* cf. *carnutorum*.

Genus ***Eucladoceros*** Falconer, 1868
?***Eucladoceros*** ex gr. ***ctenoides-dicranios*** (Nesti, 1841)

Stehlin (1930) recorded *Cervus ctenoides* from Leffe, with reference to remains mainly stored in the M-BG. Unfortunately, in the present revision, we were unable to find the antler fragments (catalogue number 1186), on which Stehlin based his identification. However, nowadays *C. ctenoides* is included in the genus *Eucladoceros* and without antlers *E. ctenoides* is indistinguishable from *E. dicranios*.

With regards to the other remains, we were only able to suggest the identification of a right metacarpal of a large deer (catalogued as 1185 bis), which was collected in 1877 by the Biraghi mining company, presumably from the main lignite bank (subunit #5) (pl., fig. 5). This specimen is quite well preserved, even though it is broken into three pieces and is missing the disto-medial trochlea. We tentatively ascribe this specimen to *E.* ex gr. *ctenoides-dicranios*, because of its size (GL 289 mm; Bp 49 mm; Dp = proximal depth 35 mm; Bd = distal breadth 49 mm; SD = smallest depth of the diaphysis 25 mm; SB = smallest breadth of the diaphysis 30 mm), which is smaller than all the Megalocerines but also than the more recent *Eucladoceros giulii* (*Arvernoceros giulii* according to Croitor & Kostopoulos 2004) (fig. 5).

Genus ***Megaloceros*** Brookes, 1828

In the last decades, the name *Megaloceros* has been used in Italian publications (Azzaroli & Mazza 1992, 1993, Azzaroli 1994, Abbazzi 1995, Abbazzi & Masini 1997) to indicate *M. savini* and *M. giganteus* whilst the other Megalocerines were assigned to *Megaceroides* Joleaud, 1914 on the basis of a supposed different structure of the forehead and first tine. Recently Abbazzi (2004), Croitor & Kostopoulos (2004) and Croitor (2006) supported the utilization of the name *Praemegaceros* Portis, 1920 for the European species formerly attributed to *Megaceroides*, keeping in the latter genus only its nominal species *M. algericus*. However, different evolutionary trends have been proposed, both within the giant deer lineage as well as between it and *Eucladoceros*, without reaching a sufficiently wide consensus. Thus, in this paper, we prefer following Lister (1993, 1994, 1996) and Pfeiffer (2002, 2005) grouping up all the giant deer species in the single genus *Megaloceros*, because the systematics of these cervids go beyond the scope of our investigation.

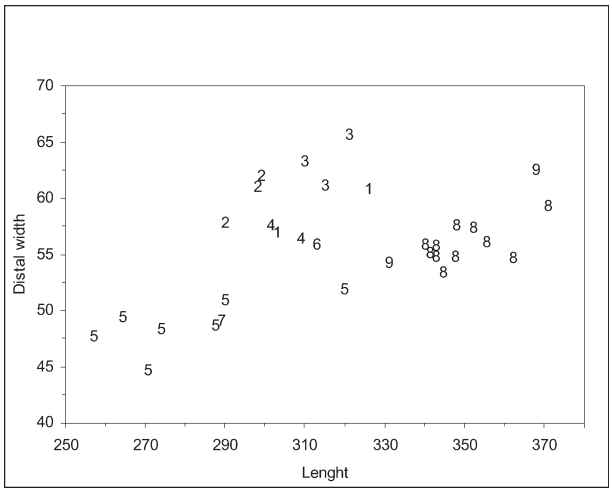

Fig. 5: Dispersion graph of the distal width of the metacarpus plotted against the total length of the same bone of the European fossil Eucladocerini and Megalocerini. *M. obscurus* from Selvella (1), *M. verticornis* from Petralona (2), Süssenborn (3), and Upper Valdarno (4), *Eucladoceros dicranios* from Upper Valdarno (5) and Olivola (6), ?*Eucladoceros* ex gr. *ctenoides-dicranios* from Leffe (7), *E. giulii* from Untermassfeld (8), and *M.* aff. *solilhacus* from Venta Micena (9). Data on *E. giulii* after Kahlke (1997), all other data after Abbazzi (1991).

?***Megaloceros*** cf. ***obscurus*** (Azzaroli, 1953)

Stehlin (1930: fig. 7) describes and provides pictures of a right metatarsus of a large deer from the main lignite bank (subunit #5), at that time stored in the M-MI. The author points out that this metatarsal is somewhat smaller than those of *Cervus giganteus* and suggests that it could belong to a Megalocerine. Nonetheless, the author identifies it as *Cervus* sp. Unfortunately, this specimen has gone lost. However, the measurements given by Stehlin (GL 33 mm; Bp 60 mm; SB 33 mm; Bd 71 mm)

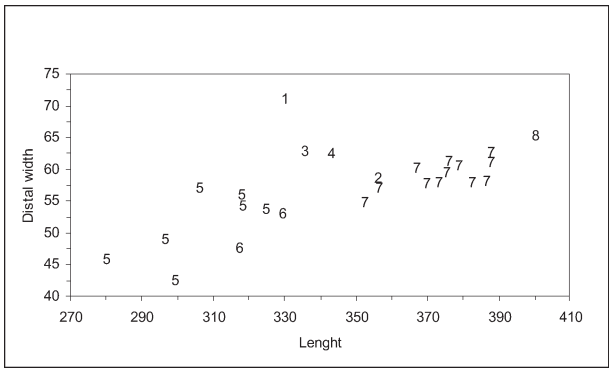

Fig. 6: Dispersion graph of the distal width of the metatarsus, plotted against the total length of the same bone of the European fossil Eucladocerini and Megalocerini. ?*M.* cf. *obscurus* from Leffe (1), *M. obscurus* from Selvella (2), *M. verticornis* from Voigtstedt (3) and Colle Curti (4), *Eucladoceros dicranios* from Upper Valdarno (5) and Olivola (6), *E. giulii* from Untermassfeld (7), and *M.* aff. *solilhacus* from Venta Micena (8). Data on *E. giulii* after Kahlke (1997), all other data after Abbazzi (1991).

fall within the size range of *Megaloceros* (*M. giganteus* excluded) (fig. 6). Therefore, we tentatively identify this specimen as *M.* cf. *obscurus*, the only species of this genus recorded in the Italian Villafranchian faunal assemblages to date.

Stehlin (1930) identifies as *C. ctenoides* a right lower tooth row (P_3-M_3 in his fig. 6a), some left lower teeth (P_3-P_4 and M_1 in his fig. 6b), and a left upper molar, which were all numbered 1215 in the M-BG. These specimens are most likely from the main lignite bank (subunit #5). The size of these teeth (first specimen: LP_3 19.8 mm; BP_3 10.7 mm; LP_4 21.1 mm; BP_4 13.6 mm; LM_1 25.9 mm; BaM_1 16.1 mm; LM_2 28.7 mm; BaM_2 16.9 mm; BbM_2 17.6 mm; BbM_3 16.4 mm; second specimen LP_3 19.9 mm; BP_3 11.1 mm; LP_4 22.1 mm; BP_4 13.0 mm; LM_3 38.3 mm; BaM_3 18.2 mm; BbM_3 17.6 mm; with Ba = anterior breadth; Bb = posterior breadth) is larger than the size range of *E. ctenoides-dicranios* and within the size range of *M. obscurus*. Consequently, we tentatively identify these remains as *M.* cf. *obscurus*.

Megaloceros ex gr. ***verticornis*** (Dawkins, 1872) – ***pliotarandoides*** (de Alessandri, 1903)

In the collections of the M-BG, there is a right frontal with the base of the antler of a large deer, which was found in 1940 and is numbered 1423 [note that this discovery occurred after Stehlin's (1930) paper]. It was found in the red clays over the first lignite bank on the west slope of the Casnigo terrace, which correlates with the Upper Unit (subunit #9). This specimen is very badly preserved (pl., fig. 2). The frontal retains only a small part of the sagittal suture surface, so the angle between the pedicle-proximal beam axis and the sagittal body plane is hard to establish. The burr is almost abraded and on the dorsal surface of the beam, at 27 mm from the burr, there is a bulge, or vestigial knob, which is broken and abraded. In place of this bulge, *M. obscurus* has a well-developed spurious tine (Abbazzi 1995) (= subbasal tine in Croitor 2006), so the attribution to this species has to be ruled out. The outer tine (= dorsal tine in Croitor 2006) starts on the caudal side of the beam, 50 mm from the burr, and bends upward, but it is broken off a little after the bending. The beam is compressed on the dorso-ventral plane (Dap 50 mm; Dt 72 mm) and bends forward from there on, although it is broken a little after this tine. The size of the specimen (pedicle diameters are respectively Dap 69 mm and Dt 55 mm), the presence of the bulge, the shape of the tine and the bending of the beam itself suggest either *M. verticornis* or *M. pliotarandoides*, following Croitor's (2006) criteria. Nonetheless, the early age of the sediments that yielded the beam (see below) suggests an assignation to *M. pliotarandoides*.

Biochronological discussion

The tentative stratigraphic re-attribution of the different specimens, on the basis of information drawn from the literature as well as from the museum labels, leads to a suitable overall biochronological picture. Three mammal associations can be identified (fig. 7):

The fauna from the main brown coal level (subunit #5) consists of a mammal association of Late Villafranchian age, consisting of *Mimomys savini*, *Castor fiber*, *Mammuthus meridionalis* (possibly both *M. meridionalis meridionalis* and *M. meridionalis vestinus*), *Stephanorhinus* ex gr. *etruscus*, *Leptobos* cf. *vallisarni*, ?*Capreolus* s.l. sp., *Axis* sp., ?*Eucladoceros* ex gr. *ctenoides-dicranios* and ?*Megaloceros* cf. *obscurus*.

The presence of ?*E.* ex gr. *ctenoides-dicranios*, ?*M.* cf. *obscurus*, and possibly both *M. m. meridionalis* and *M. m. vestinus*, suggests tentatively an age straddling the end of the Tasso and the beginning of the Farneta Faunal Units (FUs) of the Italian biochronological scale, that, following the biochronological scheme proposed by Breda & Marchetti (2005), should range from about 1.55 to 1.45 Ma BP. In fact, in Italy, *Eucladoceros* and *Mammuthus m. meridionalis* disappear at the end of the Tasso FU, whereas *Megaloceros obscurus* and *Mammuthus m. vestinus* appear at the beginning of the following Farneta FU. Actually, *M. obscurus* appears earlier in the rest of Europe [in the older levels of the Cromer Forest-bed Formation in England (Azzaroli 1953) and in the X Terrace of Dniester River in Moldova and Ukraine (Abbazzi et al. 1999)], as its coexistence with *M. m. meridionalis* and *Eucladoceros* (Lister 1996, Abbazzi et al. 1999), both typical of the Tasso and earlier FUs, suggests. Thus, an earlier appearence of *M. obscurus* in northern Italy cannot be excluded, given the

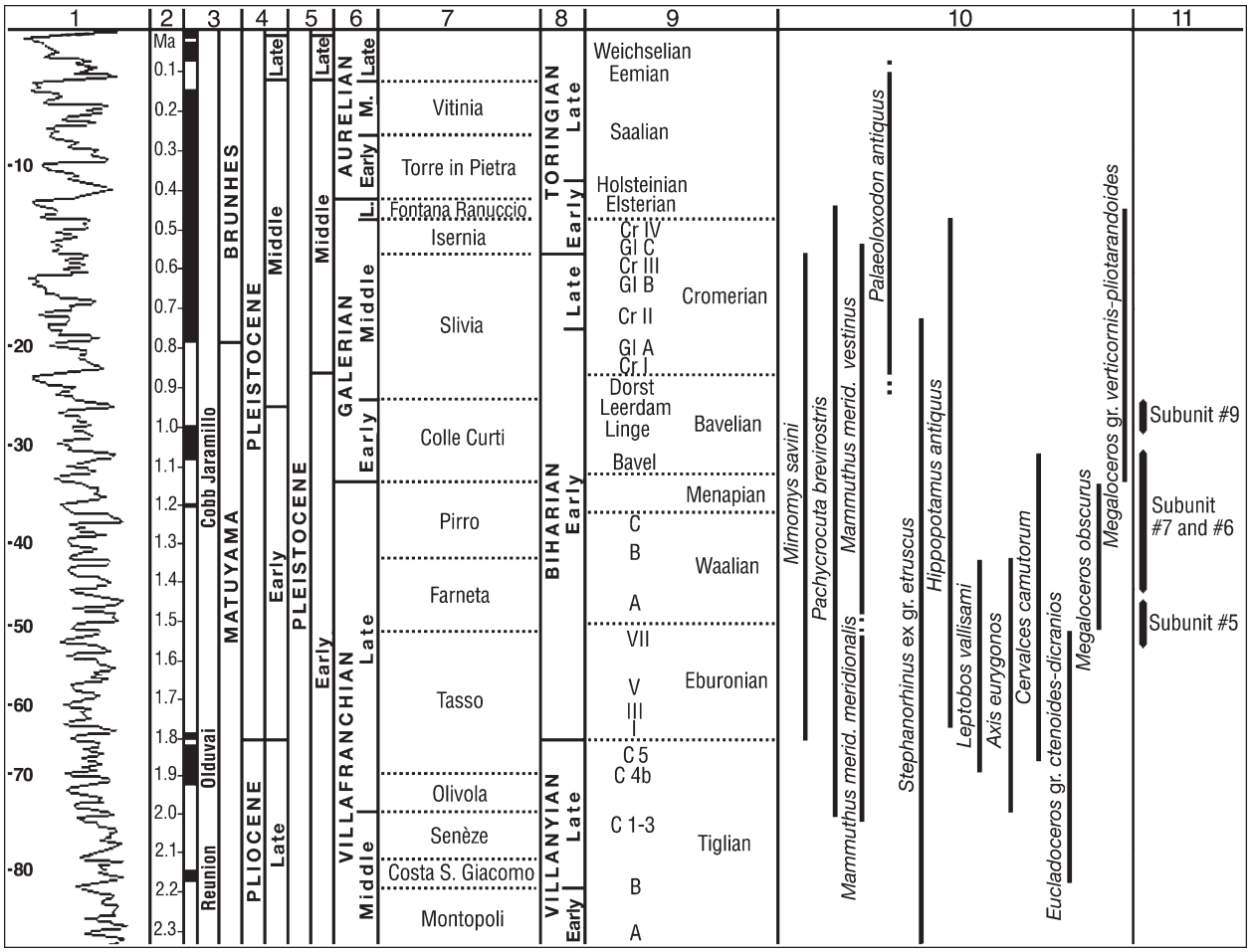

Fig. 7: Biochronological range in Italy of the mammal taxa found at Leffe (10) and hypothetical correlation of the faunal associations from Leffe (11) to $\delta^{18}O$ curve (Shackleton 1995) (1), absolute ages (2), magnetostratigraphy (3), geochronology adopted in Italy (Gliozzi et al. 1997) (4), geochronology adopted in North-Western Europe (Gibbard et al. 1991) (5), Italian Large Mammal Ages (Gliozzi et al. 1997, modified) (6), Italian Faunal Units (Gliozzi et al. 1997) (7), Small Mammal Ages of West and Central Europe (Fejfar et al. 1998) (8), and Floristic Complexes of Northern Europe (Gibbard et al. 1991) (9).

fact that the Italian local faunas with *M. obscurus* and assigned to the Farneta FU are located in central and southern Italy. However, the co-occurrence, in the main lignite bank, of mammals belonging to two different biochronological units might not be surprising, because the sedimentation of brown coal is estimated to span a time period of no less than 100,000 years (extrapolated from Muttoni et al. 2007). Therefore, evolution of the fauna within it is plausible.

The fauna from the subunit #6, consisting of *Pachycrocuta brevirostris*, *Stephanorhinus* ex gr. *etruscus* and *Axis eurygonos*, and the fauna from the subunit #7, consisting of *Stephanorhinus* ex gr. *etruscus* and *Cervalces* cf. *carnutorum*, 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, which is between 1.4 and 1.1 Ma BP as suggested in the biochronological scheme by Breda & Marchetti (2005).

The fauna from the subunit #9 consists of *Mammuthus meridionalis* cf. *vestinus* and *Megaloceros* ex gr. *verticornis-pliotarandoides*. In the fossil record these species coexist throughout the Colle Curti FU and following Slivia FU. Subunit #9 sediments show a normal polarity followed by a reverse one (Muttoni et al. 2007), which are correlated with the Jaramillo Subchron and with the latest negative episode of the Matuyama Chron. Hence, the fauna from this subunit could be assigned to the Colle Curti FU, in that this FU roughly correlates with the Jaramillo (Gliozzi et al. 1997, Coltorti et al. 1998).

The hippopotamus remains might belong to this fauna since they are tentatively assumed to originate from subunit #9 based on their degree of preservation.

Palaeoloxodon antiquus from the red palaeosoils overlying the Leffe Formation belongs to a generic time interval, which spans the early Middle Galerian – Late Aurelian Mammal Ages, i.e., from the Slivia FU to the Last Interglacial. The red palaeosoils are younger than the Gandino Formation, which straddles the Jaramillo Subchron/Brunhes Chron transition (Muttoni et al. 2007). The elephant remains are therefore younger than 0.85 Ma BP and older than 0.1 Ma BP.

Conclusions

Several species previously unrecorded from Leffe were found in the M-MI. They are:

– *Pachycrocuta brevirostris* from the Biogenic Unit (subunit #6), carbonatic gyttja and shell marls;
– *Palaeoloxodon antiquus* from the red palaeosoils overlaying the Leffe Succession;
– *Hippopotamus* cf. *antiquus* from an unknown level, possibly from the Upper Unit (subunit #9), compressed shaled peat with gravels;
– *Cervalces* cf. *carnutorum* from the Biogenic Unit (subunit #7), upper brown coal level;
– *Megaloceros* ex gr. *verticornis-pliotarandoides* (this last kept in the M-BG) from the red clays over the first lignite bank in the Casnigo terrace.

Moreover, thanks to the descriptions and measurements by Stehlin (1930) of the specimens which are now lost, three other species from Leffe (main brown coal level – subunit #5) are identified here for the first time:

– *Mimomys savini*, described by Stehlin as *Mimomys* sp.;
– ?*Capreolus* s.l. sp., part of the remains described by Stehlin as *Cervus affinis*;
– ?*Megaloceros* cf. *obscurus*, described by Stehlin as *Cervus* sp.

The previous identifications of *Leptobos etruscus* and *Cervus affinis* (*Pseudodama nestii*) (Cornalia 1858–71, Caffi 1930, Stehlin 1930, Vialli 1967, Ambrosetti et al. 1980) have been modified here, respectively, into *L. vallisarni* and *A. eurygonos*.

The fauna from the main brown coal level (subunit #5 - brown coal and gyttja) spans the end of the Tasso FU to the beginning of the Farneta FU.

The fauna from the subunit #6 (carbonatic gyttja and shell marls) and from the subunit #7 (brown coal and gyttja forming the "first lignite bank") could range from the latest part of the Farneta FU to the beginning of the Colle Curti FU.

The fauna from the subunit #9 (clays, gyttja, and compressed peat) belongs to the Colle Curti FU.

P. antiquus from the red palaeosoils overlying the Leffe Formation could belong to any time from the Slivia FU to the Last Interglacial.

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Plate 1

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Fig. 1: *Axis eurygonos* (partial skull: right ventral and left lateral view; metrical bar 10 cm).

Fig. 2: *Megaloceros* ex gr. *verticornis-pliotarandoides* (right frontal and antler in dorsal view; metrical bar 10 cm).

Fig. 3: *Leptobos vallisarni* (upper molars in occlusal view; metrical bar 2 cm).

Fig. 4: *Pachycrocuta brevirostris* (right I^3: left labio-distal and right linguo-mesial view; metrical bar 2 cm).

Fig. 5: ?*Eucladoceros* ex gr. *ctenoides-dicranios* (right metacarpal III–IV in dorsal view; metrical bar 10 cm).

Fig. 6: *Palaeoloxodon antiquus* (upper maxilla with M^2 in occlusal view; metrical bar 10 cm).

Fig. 7: *Hippopotamus antiquus* (right astragalus in dorsal view; metrical bar 5 cm).

Fig. 8: *Cervalces* cf. *carnutorum* (right frontal in dorsal view; metrical bar 5 cm).


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