

Mesopithecus (Primates: Cercopithecoidea) from Villafranca d’Asti (Early Villafranchian; NW Italy) and palaeoecological context of its extinction

CHIARA PRADELLA & LORENZO ROOK*

Key words: *Mesopithecus*, Cercopithecidae, Early Villafranchian, Villafranca d’Asti, Palaeoecology, extinction

ABSTRACT

Remains of the cercopithecoid *Mesopithecus monspessulanus* are relatively rare. Two previously unpublished mandibles of *M. monspessulanus* (housed in the Basel Naturhistorisches Museum), from the Italian locality of Villafranca d’Asti are described. These remains belong to the assemblage of the Triversa Faunal Unit, dated to the Early Villafranchian, that is to the unit MN16a (Middle Pliocene) of the European mammal biochronology. According to this recently revised biochronological attribution, Villafranca d’Asti records the last *Mesopithecus* occurrence in Europe.

The NOW (Neogene Old World) database has been used as a basis to evaluate both the mammalian faunal and the palaeoenvironmental context at the time surrounding this last occurrence of *Mesopithecus*. The comparison (taxonomical composition and ungulate hypsodonty), between the Villafranca d’Asti assemblage and other Plio-Pleistocene mammal communities of Europe, shows that the extinction of *Mesopithecus* is related to a faunal turnover and a change toward more open landscapes during the Early–Middle Villafranchian transition. This is consistent with the “Elephant–*Equus* event”, that occurred in Europe at 2.5 Ma. Furthermore, the co-occurring but more terrestrial cercopithecoid *Macaca* crossed this faunal turnover. This strengthens the assumption that the latest *Mesopithecus* species, *M. monspessulanus*, had woodland-oriented adaptations.

RIASSUNTO

Resti di *Mesopithecus monspessulanus* sono relativamente rari nel record fossile. In questo lavoro vengono descritte due mandibole inedite di *Mesopithecus monspessulanus* provenienti dal Villafranca d’Asti (conservate nelle collezioni del Museo di Storia Naturale di Basilea). I reperti provengono dall’associazione faunistica appartenente alla Unità Faunistica Triversa del Villafranchiano inferiore, corrispondente alla Unità MN 16a della scala biochronologica a mammiferi dell’Europa continentale (Pliocene medio). Questi resti rappresentano l’ultima documentazione del genere *Mesopithecus* in Europa.

Al fine di valutare il contesto paleoecologico e l’entità del rinnovamento faunistico nell’intervallo di tempo che abbraccia questa ultima segnalazione, è stata utilizzata la base di dati NOW (Neogene Old World). I confronti effettuati (composizione tassonomica, indice di ipsodontia degli ungulati) tra Villafranca d’Asti e altre associazioni del Plio-Pleistocene mostrano che l’estinzione del genere *Mesopithecus* in Europa è da mettere in relazione al rinnovamento faunistico e alle modificazioni ambientali avvenute alla transizione tra Villafranchiano inferiore e medio. Questo momento corrisponde al cosiddetto «Elephant–*Equus* event», che è registrato in Europa occidentale a circa 2.5 Ma. È significativo notare che il genere cercopithecide *Macaca* (compresente a Villafranca d’Asti insieme a *Mesopithecus*) attraversa lo stesso rinnovamento faunistico e sopravvive, in Europa, almeno sino al Pleistocene Medio.

Introduction

Mesopithecus is a small to medium-sized “colobine” monkey, known from the Late Miocene to the Early and Middle Pliocene deposits in Europe. A distinction is currently drawn between two species, which differ in their chronological range and body size (Jablonski 2002): the Late Miocene *Mesopithecus pentelicus* WAGNER 1839, larger than the Pliocene *Mesopithecus monspessulanus* GERVAIS 1849. In addition, *M. monspessulanus* differs from *M. pentelicus* by its narrower molars and less terrestrial adaptations. A third species, *Mesopithecus delsoni*, has been described on some larger remains from the

Late Miocene of Greece (de Bonis et al. 1990). Although the taxonomic status of this latter has been questioned (Zapfe 1991; Delson 1994; Andrews et al. 1996; Rook 1999), a recent study by Koufos et al. (2003), based on new fossils from Bulgaria, provides further evidences in favour of a specific distinction for this larger species.

The last known occurrence of the genus *Mesopithecus* is from the Early Villafranchian faunal assemblage of Villafranca d’Asti (Hürzeler 1967; Gentili et al. 1998), in northwestern Italy. In this locality, *Mesopithecus* is associated with other cercopithecoid remains, belonging to the genus *Macaca* (Rook et

Dipartimento di Scienze della Terra, Università di Firenze, via G. La Pira 4, I-50121, Italy.

* Corresponding author: L. Rook. E-mail: lorenzo.rook@unifi.it

Tab. 1. Systematics, localities, ages and data origin of the *Mesopithecus* material used in this study. See text for abbreviations of the collections.

Systematics	Locality	Country	Age	Collection	Data from			References
					Original	Cast	Literature	
<i>Mesopithecus monspessulanus</i>	Villafranchia d'Asti	Italy	MN16a	NHMB	x			
<i>Mesopithecus monspessulanus</i>	Montpellier	France	MN14	MNHN UCBL	x	x		
<i>Mesopithecus pentelicus</i>	Casino	Italy	MN13	BMNH MSNC	x			
<i>Mesopithecus pentelicus</i>	Baltavar	Hungary	MN13	MAFI		x		
<i>Mesopithecus cf. pentelicus</i>	Dytiko 2	Greece	MN13	LGPU			x	de Bonis et al. (1990)
<i>Mesopithecus pentelicus</i>	Dytiko 1,3	Greece	MN13	LGPU			x	de Bonis et al. (1990)
<i>Mesopithecus pentelicus</i>	Hadjidimovo	Bulgaria	MN12	PMA			x	Koufos et al. (2003)
<i>Mesopithecus pentelicus</i>	Kalimanci	Bulgaria	MN12	NMNHS PMA			x	Koufos et al. (2003)
<i>Mesopithecus pentelicus</i>	Ravin des Zouaves 5	Greece	MN12	LGPU			x	de Bonis et al. (1990)
<i>Mesopithecus pentelicus</i>	Pikermi	Greece	MN12	PMUA MNHN BSPM BMNH NHMW MRSTNT NMHU	x	x	x	Zapfe (1991)
<i>Mesopithecus pentelicus</i>	Vathylakkos 2	Greece	MN11	LGPU			x	de Bonis et al. (1997)
<i>Mesopithecus pentelicus</i>	Maragha	Iran	MN11	MNHN			x	de Bonis et al. (1990)

al. 2001). The *Mesopithecus* specimens (housed in the Basel Naturhistorisches Museum) from Villafranca d'Asti have never been described in detail. We provide here the first full description and illustration of the specimens and examine the faunal and palaeoenvironmental context of its extinction, at the Early–Middle Villafranchian transition.

Institutional abbreviations

BMNH: Natural History Museum, London (UK); BSPM: Bayerische Staatssammlung für Paläontologie und historische Geologie, München (Germany); UCBL: Université Claude Bernard Lyon I, Lyon (France); IGF: Museo di Storia Naturale, Sezione Geologia e Paleontologia, Firenze University (Italy); LGPUT: Laboratory of Geology and Paleontology, University of Thessaloniki (Greece); MAFI: Museum of the Hungarian Geological Institute, Budapest (Hungary); MNHN: Muséum national d'Histoire naturelle, Paris (France); MRSNT: Museo Regionale di Storia Naturale, Torino (Italy); MSNC: Museo di Storia Naturale di Calci, Pisa (Italy); NHMB: Naturhistorisches Museum, Basel (Switzerland); NHMW: Naturhistorisches Museum, Wien (Austria); NMHU: Naturkunde Museum der Humboldt Universität, Berlin (Germany); NMNHS: National Museum of Natural History, Sofia (Bulgaria); PMA: Paleontological Museum of Assenovgrad (Bulgaria); PMUA: Paleontological Museum, University of Athens (Greece).

The *Mesopithecus* material used in the present study is reported in Table 1.

Geological setting and origin of the specimens

The sedimentary basin of Villafranca d'Asti (Piedmont, north-western Italy) is well known since the last century for its abundance of fossil mammals. Pareto (1865) first used the term “Villafranchian”, with reference to the fossil material collected in the vicinity of the hamlet of Villafranca d'Asti; today, it is widely used as a biochronological unit (e.g. Gliozzi et al. 1997). For an updated faunal list of the Villafranchian assemblages from the area of Villafranca d'Asti, see Campanino et al. (1994), Carraro (1996) and Gentili et al. (1998).

The palaeoenvironmental facies in the lower Villafranchian section, as outcropping in the so-called RDB quarry section (cf. Basilici 1996), corresponds to a deltaic woodland landscape, under temperate/warm to subtropical seasonal climate, with lithofacies indicating a patchy development of more or less immature (waterlogged) soils (Basilici 1996; Bertoldi 1996; Martinetto & Mai 1996). Gentili et al. (1998) and Boano et al. (1999) reported on a new *Mesopithecus* mandibular remain, which came from a major soil at the top of the lower Villafranchian deltaic deposition (Rook et al. 2001).

The two reported *Mesopithecus* mandibles (V.J. 87 and V.J. 130) have been collected in the RDB quarry and belong to the Masoero collection of the Basel Naturhistorisches Museum (Hürzeler 1967). Under the number V.J. 130, there is actually more than one specimen in the Basel Masoero collection: in addition to the *Mesopithecus* mandible, twenty *Macaca* postcranial bones (Rook et al. 2001) are labelled under the same number, as “Villafranca d'Asti – 1954” (originally labelled as “Cynomorph”). The recent geological and sedimentological revision of the Villafranca d'Asti area (Carraro 1996), showed

that all lithologies progressively exploited until now by the RDB quarry, lie exclusively in the so-called “Cascina San Martino” (litho)unit, that is within the lower sedimentary complex of the Villafranca d’Asti succession (Boano & Forno 1996). This allows us to confirm that all Villafranca fossil remains stored at the Basel Naturhistorisches Museum and labelled as “Fornace”, belong to the Early Villafranchian Triversa Faunal Unit. In spite of the fact that the site name “Fornace” for the RDB quarry is a common place-name in the vicinity of Villafranca d’Asti, there is no doubt (Francavilla et al. 1970; Azaroli 1977 and pers. comm.) that Masoero’s finds (among which are both *Mesopithecus* and *Macaca*) were recovered only from the major RDB quarry exploitation (see also Rook et al. 2001). Evidence from the hand-written original labels, as well as similarities in fossilization features (fossil colouring and appearance of the bone), indicate that the *Mesopithecus* mandibles most likely came from the lower sedimentary complex of the RDB quarry (cf. Rook et al. 2001 for details).

Systematic Palaeontology

Order Primates LINNAEUS 1758
 Suborder Anthrooidea MIVART 1864
 Infraorder Catarrhini GEOFFROY SAINT-HILAIRE 1812
 Superfamily Cercopithecoidea GRAY 1821
 Family Cercopithecidae GRAY 1821
 Subfamily Colobinae BLYTH 1875

Genus *Mesopithecus* WAGNER 1839

The genus *Mesopithecus*, erected for the species *M. pentelicus* WAGNER 1839, on material from Pikermi (MN12, Greece), is well known since the study of Gaudry (1862) and has been revised in detail by Delson (1973, 1975), Heintz et al. (1981), de Bonis et al. (1990, 1997), Hohenegger & Zapfe (1990), Kullmer & Doukas (1995) and Koufos et al. (2003). In addition, Zapfe (1991) published a monograph on the *M. pentelicus* specimens from Pikermi. Most authors recognized that the representatives of the genus present typical cercopithecoid and colobine characters. Several specimens retain ancestral features (moderate molar flare, only slightly reduced thumb, and the shallow medial groove for the *flexor tibialis* muscle on the astragalus), suggesting that *Mesopithecus* is among the most conservative members of the subfamily Colobinae, so it was assigned at the tribe level to either Colobini or Presbytini (Szalay & Delson 1979; Strasser & Delson 1987; Andrews et al. 1996).

Temporal and geographical ranges of *Mesopithecus* span from the Late Vallesian to the Early Villafranchian in Southern and central Eastern Europe, and the Turolian in Iran and Afghanistan. The type species *M. pentelicus* WAGNER 1839 (Late Vallesian–Late Turolian) is the best representative of the genus. It is a medium-sized species, well known from the large sample collected at Pikermi, the type locality, since the 1830s. All teeth (except anterior deciduous ones) and most el-

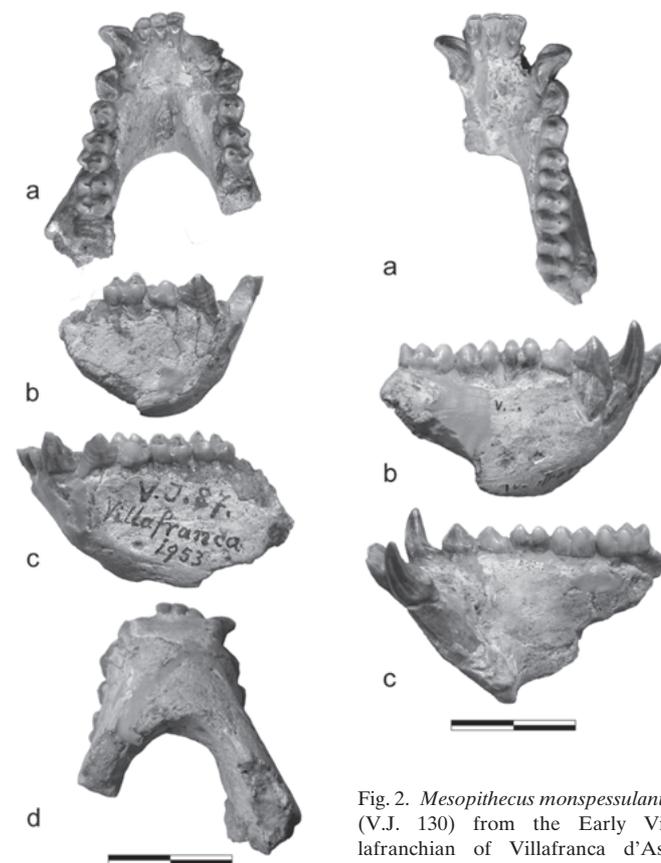


Fig. 1. *Mesopithecus monspessulanus* (V.J. 87) from the Early Villafranchian of Villafranca d’Asti (RDB Quarry), northwestern Italy. Mandible in occlusal (a), labial (right) (b) and lingual (left) (c) and inferior (d) views. Scale bar: 2 cm.

Fig. 2. *Mesopithecus monspessulanus* (V.J. 130) from the Early Villafranchian of Villafranca d’Asti (RDB Quarry), northwestern Italy. Mandible in occlusal (a), labial (right) (b) and lingual (right) (c) views. Scale bar: 2 cm.

ements of the postcranial skeleton are represented in the collections of several European museums (see Zapfe 1991). The mandibular ramus is shallow, presents a steeply inclined planum alveolare and a weak inferior torus. The p3 has a well developed and short metalophid, there is a well marked fovea on the premolars, and the m3 hypoconulid, though variable in size, is usually small (Zapfe 1991).

Mesopithecus monspessulanus is mainly distinguishable from *M. pentelicus* and *M. delsoni* by its smaller size and narrower molars. In comparison with both *M. pentelicus* and *M. delsoni*, few partial limb bones (elbow joint) suggest that this later form had somewhat less terrestrial adaptations (cf. Delson 1975; Ciochon 1993). *Mesopithecus monspessulanus* was formerly ascribed to the genus *Semnopithecus* (cf. Szalay & Delson 1979). Current opinion is that *M. monspessulanus* shows sufficient similarity with *M. pentelicus* to validate their congeneric relationships (cf. Szalay & Delson 1979; Jablonski 2002).

Tab. 2. Teeth measurements (in mm) of the *Mesopithecus* mandibles from Villafranca d’Asti (Early Villafranchian, northwestern Italy). Abbreviations: L, length; B, breadth; H, height; m, molar; p, premolar; r, right; l, left.

Specimen	side	p3		p4		m1			m2			m3			H mand. at p4
		L	B	L	B	L	anterior B	posterior B	L	anterior B	posterior B	L	anterior B	posterior B	
V.J. 87	r	5.80	4.19	4.70	4.30	7.00	5.30	5.40							19.30
	l	5.60	4.30	5.50	4.40	6.90	5.00	5.30	7.00	6.10	6.40				
V.J. 130	r	8.20	4.30	5.20	4.40	6.30	4.90	5.30	7.20	5.80	5.90	8.90	6.10	5.90	19.75
	l			5.20	4.30	6.70	4.80	5.00	7.10	5.70	6.00				

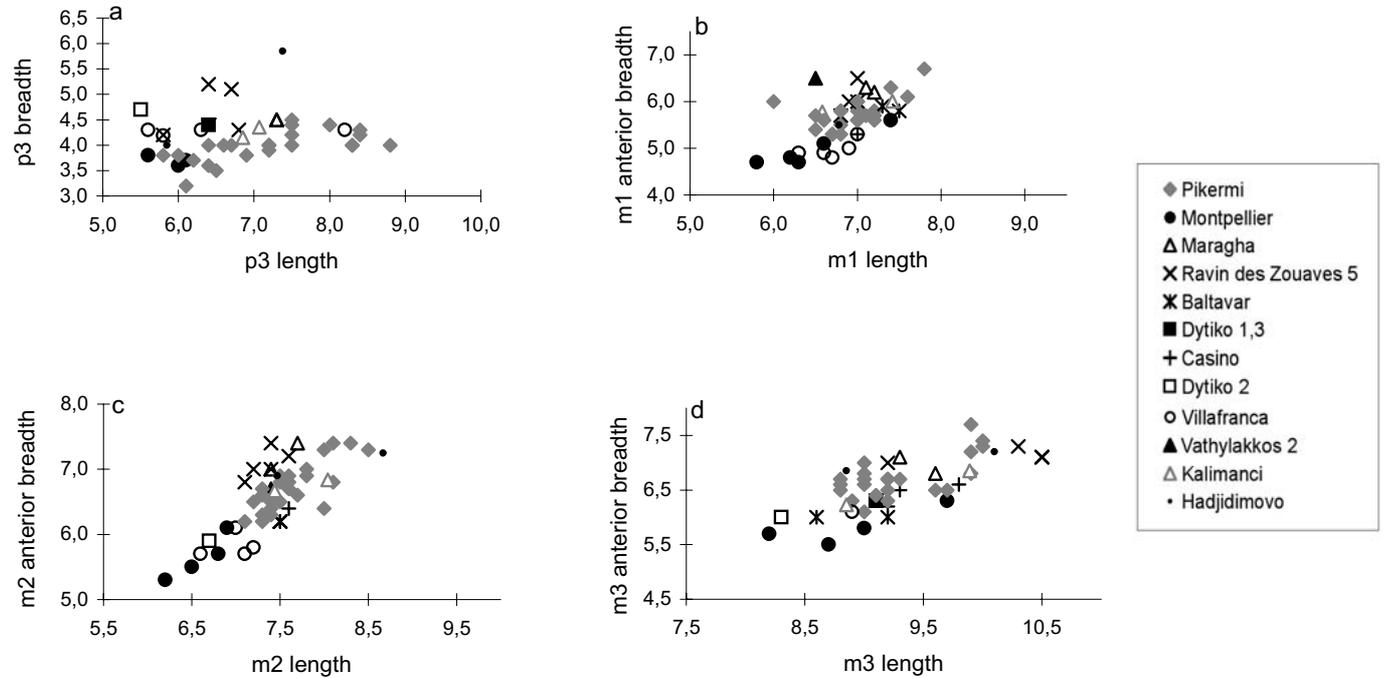


Fig. 3. Scatter diagrams showing a dimensional comparison (length versus breadth) of the lower dentition of *Mesopithecus*, from Villafranca d’Asti and other Miocene and Pliocene European localities. Abbreviations: m, molar; p, premolar. Measurements are in mm. See Table 1 for the analysed material and data source.

The *Mesopithecus* remains from Villafranca d’Asti

V.J. 87 (Figs. 1a–d; Table 2) – The mandible preserves on the right side the teeth i1, p3–p4, m1 and, on the left side the teeth i1–i2, c, p3–m2. The small size of the canine and the narrow diastema between the c and the p3 suggests that this specimen was a female individual. The thickness of the mandibular body below the m1 is 6.5 mm, the height under the same tooth is 19.6 mm. On both sides, the p3 and the p4 have a similar height from the occlusal plane. The p3 is almost unworn. The left p4 appears to be less worn than the right one. An advanced wear stage is indicated by extensive dentine exposure, especially on both m1.

V.J. 130 (Figs. 2a–c; Table 2) – A much more complete specimen, preserving on the right side the teeth i1, c, p3–m3 and on the left side only the teeth i1–i2 and c. The thickness of the mandibular body below the m1 is 7.1 mm, while the height under the same tooth is 20.4 mm. This specimen, apart from a

very large canine, has a p3 (definitely unworn) with a well inflated enamel mesially, above the root, and they protrude above the occlusal plane a little more than the p4. All these features are controlled by sexual dimorphism (cf. Szalay & Delson 1979), and, especially in their association, clearly indicate that it was a male individual.

All molars are at early stage of wear, with dentine just exposed on the tips of the main cusps. The teeth are bilophodont, with moderate high cusp relief. Their dimensions compare well with *M. monspessulanus*. The scatterplots (Figs. 3a–d), show that the teeth measurements (p3, m1–3) of the specimens from Villafranca d’Asti appear as very close to those of the *M. monspessulanus* from Montpellier (MN14, France), which is the holotype, notably for p3 and m2 (Figs. 3a, c). It is noteworthy, as suggested by de Bonis et al. (1990), that the overall size of individuals belonging to the Dytiko sample (especially Dytiko-2; Latest Miocene, Macedonia) is quite similar to that of *M. monspessulanus*, but is different from that of the Miocene *M. pentelicus*.

Tab. 3. Comparison of the mammalian family composition between Villafranca d'Asti (MN16a) and three other European localities ranging from MN15 to MN17. Localities: Perpignan (France), Villafranca d'Asti (Italy), Kislàng (Hungary) and Saint Vallier (France).

Order	Family	Perpignan	Villafranca	Kislàng	Saint	
		MN15	d'Asti MN16a	MN16b	Vallier MN17	
Insectivora	Erinaceidae	2.2%				
	Petauristidae	2.2%				
	Soricidae	2.2%	12.1%			
	Talpidae	6.1%	2.8%	5.2%		
Primates	Cercopithecidae	4.4%	6.2%		2.8%	
Rodentia	Cricetidae			1.8%		
	Sciuridae			2.2%		
	Gliridae	4.2%	9.3%			
	Castoridae	2.2%	2.8%	2.2%	3.1%	
	Hystriidae	6.3%			3.1%	
	Anomalidae			2.2%		
	Muridae	15.1%	5.8%	7.2%		
	Arvicolidae	4.5%	12.0%	9.0%	3.1%	
Lagomorpha	Ochotonidae	2.2%	6.0%	1.9%	3.1%	
	Leporidae	2.2%	2.8%	4.5%	3.1%	
Carnivora	Viverridae	2.2%	2.8%			
	Mustelidae			7.3%	12.5%	
	Canidae	5.9%		6.8%	6.2%	
	Ursidae	2.2%	2.8%	5.3%	3.1%	
	Felidae	6.1%	9.0%	14.5%	16.2%	
	Hyaenidae	4.2%	2.8%	2.1%	5.8%	
	Proboscidea	Gomphoteridae	2.2%	2.8%	1.8%	3.1%
		Mammutidae	2.2%	2.8%	2.0%	
Elephantidae				→ 2.1%	3.1%	
Perissodactyla	Equidae	2.2%		→ 9.0%	3.1%	
	Tapiridae	2.0%	2.8% ←			
	Rhinocerotidae	4.4%	2.8%	2.0%	2.8%	
Artiodactyla	Suidae	2.2%	6.0%			
	Cervidae	6.0%	2.8%	7.3%	12.9%	
	Bovidae	4.4%	2.8%	1.8%	12.9%	
	Camelidae			1.8%		

Palaeoecological analyses

Given that the last occurrence of the *Mesopithecus* genus is recorded within the fossil assemblage of Villafranca d'Asti, we have analysed its impending extinction with reference to middle Pliocene European mammalian palaeoecology. For this purpose, we used the Neogene Old World Database (NOW; www.helsinki.fi/science/now/). This database has been released to the public in 1996, since then the number and geographical range of localities has been substantially improved, and ecomorphological information has been added (Fortlious 2005). We have selected 32 European faunas across the Pliocene and used the information from the NOW database in order to perform three analyses: 1) Mammalian family composition; 2) Genus rank faunal resemblance indices; 3) Relative ungulate hypsodonty.

Mammalian family composition

The mammalian family composition is related to different habitats, abrupt changes in composition may reveal ecological and/or climate changes. The Early–Middle Villafranchian transition (the MN16a–MN16b transition) was characterized by the arrival in Western Europe of typical open-environment

taxa (the first true elephant, a primitive form of *Mammuthus romanus-gromovi*, as well as the first horse of the *Equus* genus), and the extinction of numerous woodland dwellers (like *Mammut borsonii*, *Tapirus arvernensis*, *Sus minor* and *Ursus minimus*) (Azzaroli 1983; Azzaroli et al. 1986; Torre et al. 1992, 2001; Eronen & Rook 2004).

Such a faunal turnover is clear also at the family level (Table 3), as indicated by the occurrence in the Perpignan (MN15) and Villafranca d'Asti (MN16a) assemblages of the Tapiridae family, which then disappears during MN16b. On the contrary, the first occurrence of the Elephantidae family is at Kislàng (MN16b). The environmental trend toward more open areas is maintained in the youngest selected unit (MN17, Saint Vallier), with a strong increase in the percentage of Bovidae (up to 13%). Finally, there is a persistence (at MN17) of the Elephantidae, Equidae, Rhinocerotidae and Cercopithecidae (*Macaca*), despite the cooling and the increased seasonality (Azzaroli et al. 1988; Suc et al. 1995).

Genus Faunal Resemblance Index (GFRI)

According to the procedure followed by Bernor et al. (2001, 2004), we calculated both the Dice and Simpson faunal similarity indices, at the genus level. Dice's index is a commonly used

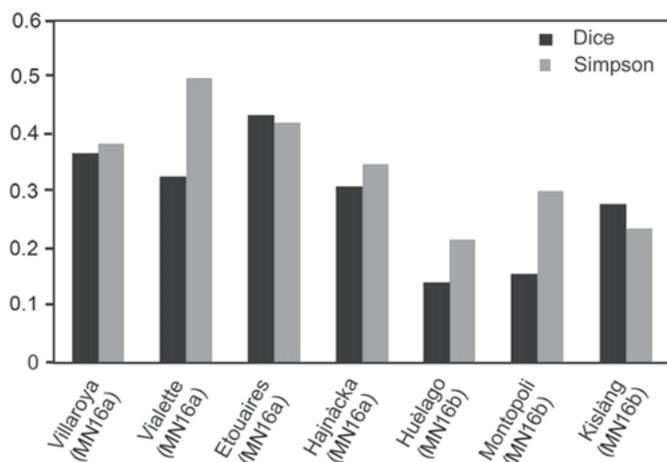


Fig. 4. Genus faunal resemblance index (GFRI), between the assemblage of Villafranca d’Asti and seven other European faunas from MN16a and MN16b. Localities: Villaroya (Spain); Viallette (France); Etouaires (France); Hajnacka (Hungary); Huèlago (Spain); Montopoli (Italy); Kislàng (Hungary). Data from the NOW database (www.helsinki.fi/science/now/). See text for the calculation of the Dice and Simpson faunal similarity indices.

faunal resemblance index, especially by zoologists, while palaeontologists have long used Simpson’s index. Furthermore, this latter similarity index adjusts for differences in sample sizes, what is useful for the present analysis. Dice’s index is calculated as follow: $2A/(2A+B+C)$. A is the common genus number between the two assemblages; B is the genus number present in the fauna 1 (here Villafranca d’Asti) but absent in the fauna 2 (the different terms of comparison); C is the genus number present in the fauna 2 but absent in the fauna 1. Simpson’s index is calculated by the formula: $A/(A+E)$, where E is smaller between B and C. A result of 1 would represent 100% of similarity between two assemblages.

In Figure 4, the Genus Faunal Resemblance Index (GFRI) shows high values of resemblance for the selected faunas in the MN16a unit (Villaroya, Viallette, Les Etouaires and Hajnàc-

ka), with Simpson index values of 0.35 or more, reaching a maximum of about 0.50 at Viallette. The GFRI for MN16b localities (Huèlago, Montopoli and Kislàng) is lower than in the previous set of assemblages, with values of the Simpson index of 0.30 (Montopoli) or less than 0.25. The comparison of the GFRI clearly indicates a faunal turnover, at the genus level, during the MN16a–MN16b transition.

Hypsodonty index

It has been shown that overall hypsodonty increased progressively through the Neogene and that such a trend in ungulate faunas co-occurs with increased percentages of tougher (mostly graze) foods in diets (Damuth & Fortelius 2001; Fortelius et al. 2002).

As final analysis, we compared some localities from the standpoint of ungulate dental crown height (Fig. 5). The 3-part subdivision is derived from the field “TCRWNHT” (crown height) of the NOW database, expressing the hypsodonty degree: brachydont, where the m2 crown length is greater than its crown height; mesodont, where the m2 crown length is roughly the same as the crown height; hypsodont, where the m2 crown height is higher than the crown length.

This analysis reveals that during MN15, the percentage of brachydont taxa was dominating, with more than 70% (here for the assemblage of Perpignan). For MN16a, the brachydont percentage remains very high, as seen at Villafranca d’Asti, where they reach almost 80% of the total assemblage. MN16b is characterized by a dramatic contraction of brachydont forms and by a noticeable increase of hypsodontic taxa. These latter represent 11–21% in MN15–MN16a assemblages, whereas they reach 50% at MN16b (here at Kislàng). Quite similar percentages of hypsodontic taxa are also found in MN17 (here at Saint Vallier).

The comparison of the composition of ungulate crown heights clearly shows a change during the MN16a–MN16b transition.

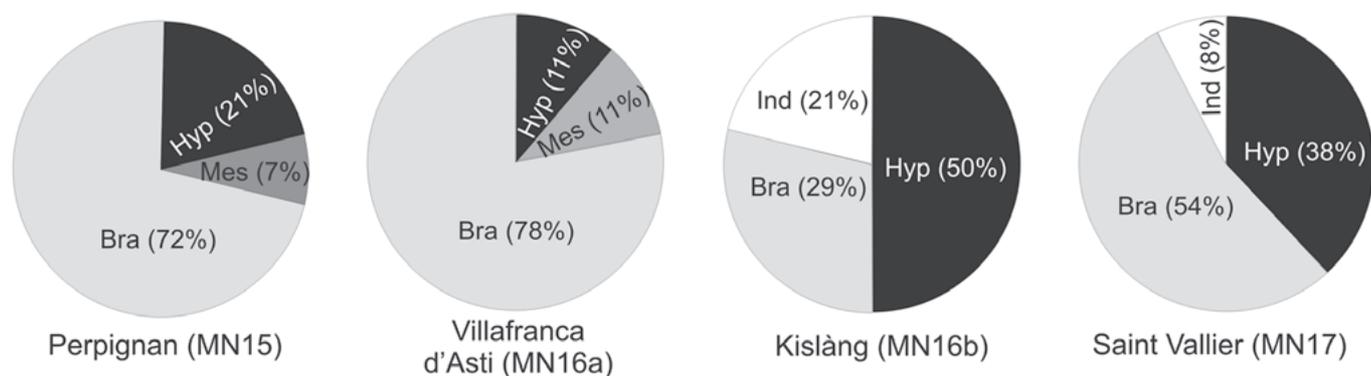


Fig. 5. Diagrams of the composition of the ungulate crown heights, between Villafranca d’Asti (MN16a) and three other European localities ranging from MN15 to MN17. Localities: Perpignan (France), Villafranca d’Asti (Italy), Kislàng (Hungary) and Saint Vallier (France). Abbreviations: Bra, brachydont; Hyp, hypsodont; Ind, Indeterminate; Mes, mesodont.

Conclusions

The *Mesopithecus* remains reported here are included into the RDB quarry (Villafranca d'Asti) historical collection, come from Middle Pliocene sediments and belong to an Early Villafranchian large mammal assemblage. They record the last occurrence of *Mesopithecus* in Europe. The description and the inter-specific comparisons reveal that the two specimens have dimensional/dimorphic ranges that best fit (among the genus) with *M. monspessulanus*, but the only available specimen for comparison is the holotype.

Palaeoecological data, from the comparison of the Villafranca d'Asti fauna with other Plio-Pleistocene mammal assemblages of Europe, show that the extinction of the genus *Mesopithecus* is related to a faunal turnover and a change of the palaeoenvironment at the Early–Middle Villafranchian transition. The analyses stress a trend toward more open environments, both in terms of taxonomical composition (at family and genus levels) and ungulate hypsodonty. This is consistent with the faunal turnover known as “Elephant-*Equus* event” (Azzaroli 1983), that occurred at 2.5 Ma in Europe. Furthermore, it coincides with one of the major shifts among the $\delta^{18}\text{O}$ isotopic oscillations (cf. Miller et al. 2005).

Mesopithecus became extinct during that time, this fact may support the suggestion that it had woodland-oriented adaptations, particularly in association with the locomotory patterns inferred for the latest species *M. monspessulanus* (Ciochon 1993). In this respect, the co-occurring but more terrestrial cercopithecoid species *Macaca sylvana* (*M. s. cf. prisca*), crossed the same faunal turnover and survived in Europe until at least Middle Pleistocene.

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REFERENCES

Andrews, P., Harrison, T., Delson, E., Bernor, R.L. & Martin, L. 1996: Distribution and biochronology of European and Southwest Asian Miocene Catarrhines. In Bernor, R.L. et al. (Eds.): *The Evolution of Western Eurasian Mammal Faunas*, Columbia University Press, New York, 168–207.

Azzaroli, A. 1977: The Villafranchian stage in Italy and the Plio-Pleistocene boundary. *Giornale di Geologia* 41, 61–67.

Azzaroli, A. 1983: Quaternary mammals and the “end-Villafranchian” dispersal event – a turning point in the history of Eurasia. *Palaeogeography Palaeoclimatology Palaeoecology* 44, 117–139.

Azzaroli, A., De Giuli, C., Ficarelli, G. & Torre, D. 1986: Mammal succession of the Plio-Pleistocene of Italy. *Memorie della Società Geologica Italiana* 31, 213–218.

Azzaroli, A., De Giuli, C., Ficarelli, G. & Torre, D. 1988: Late Pliocene to early Mid-Pleistocene mammals in Eurasia: faunal succession and dispersal events. *Palaeogeography Palaeoclimatology Palaeoecology* 66, 77–100.

Basilici, G. 1996: Sedimentologia. In: Carraro, F. (Ed.): *Revisione del Villafranchiano nell'area-tipo di Villafranca d'Asti*. *Il Quaternario* 9, 42–46.

Bernor, R.L., Fortelius, M. & Rook, L. 2001: Evolutionary Biogeography and Paleogeology of the “*Oreopithecus bambolii* Faunal Zone” (late Miocene, Tusco-Sardinian Province). *Bollettino della Società Paleontologica Italiana* 40, 139–148.

Bernor, R.L., Kordos, L., Rook, L., Agusti, J., Andrews, P., Armour-Chelou, M., Begun, D., Cameron, D., Daxner-Höck, G., Bonis, L. de, Ekart, G., Fejfar, O., Fessah, N., Fortelius, M., Franzen, J., Gasparik, M., Gentry, A., Heissig, K., Herniak, G., Kaiser, T., Koufos, G.D., Krolopp, E., Janossy, D., Llenas, M., Meszáros, I., Muller, P., Renne, P., Roek, Z., Sen, S., Scott, R., Szindlar, Z., Theobald, G., Topal, G., Werdelin, L., Ungar, P. & Ziegler, R. 2004: Recent Advances on Multidisciplinary Research at Rudabánya Late Miocene (MN9), Hungary: a compendium. *Palaeontographia Italica* 89, 3–36.

Bertoldi, R. 1996: Pollini: il Complesso Inferiore. In: Carraro, F. (Ed.): *Revisione del Villafranchiano nell'area-tipo di Villafranca d'Asti*. *Il Quaternario* 9, 79–85.

Boano, P. & Forno, M. G. 1996: La successione-tipo Villafranchiana. In: Carraro, F. (Ed.): *Revisione del Villafranchiano nell'area-tipo di Villafranca d'Asti*. *Il Quaternario* 9, 38–62.

Boano, P., Boero, W., Forno, M.G. & Mottura, A. 1999: Significato di concentrazioni di resti fossili associati a un suolo e a prodotti colluviali entro la successione – tipo villafranchiana. *GEOITALIA: 2° Forum Federazione Italiana di Scienze della Terra, 20-23/9/1999 Bellaria (RN)* 1, 203–206 (abstracts).

Bonis, L. de, Bouvraïn, G., Geraads, D. & Koufos, G. 1990: New remains of *Mesopithecus* (Primates, Cercopithecoidea) from the Late Miocene of Macedonia (Greece), with the description of a new species. *Journal of Vertebrate Paleontology* 10, 473–483.

Bonis, L. de, Bouvraïn, G., Geraads, D. & Koufos, G. 1997: New material of *Mesopithecus* (Mammalia, Cercopithecoidea) from the late Miocene of Macedonia, Greece. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1997, 255–265.

Campanino, F., Forno, M.G., Mottura, A., Ormezzano, D. & Sala, B. 1994: *Stephanorhinus jeanvireti* (Guerin) 1972 (Rhinocerotidae, Mammalia) from Roatto near Villafranca d'Asti, NW Italy. Revision of the specimen from Dusino. *Bollettino del Museo Regionale di Scienze Naturali di Torino* 12, 439–499.

Carraro, F. (Ed.) 1996: *Revisione del Villafranchiano nell'area-tipo di Villafranca d'Asti*. *Il Quaternario* 9, 5–119.

Ciochon, R.L. 1993: Evolution of the cercopithecoid forelimb: phylogenetic and functional implications from morphometric analyses. *University of California publications in Geological Sciences* 138, 1–251.

Damuth, J. & Fortelius, M. 2001: Reconstructing mean annual precipitation, based on mammalian dental morphology and local species richness. In: Agusti, J. & Oms, O. (Eds.): *EEDEN Plenary Workshop on Late Miocene to early Pliocene Environments and Ecosystems*. EEDEN Programme, European Science Foundation, Sabadell, 23–24 (abstracts).

Delson, E. 1973: Fossil Colobine Monkeys of the Circum-Mediterranean Region and the Evolutionary History of the Cercopithecoidea (Primates, Mammalia). Unpublished PhD Thesis, Columbia University, New York, 856 pp.

Delson, E. 1975: Evolutionary history of the cercopithecoidea. *Contributions to Primatology* 5, 167–217.

Delson, E. 1994: Evolutionary history of the colobine monkeys in palaeoenvironmental perspective. In: Davies, G. & Oates, J. F. (Eds.): *Colobine Monkeys: Their Ecology, Behaviour and Evolution*, Cambridge University Press, Cambridge, 11–43.

Eronen, J. & Rook, L. 2004: The Mio-Pliocene European primate fossil record: dynamics and habitat tracking. *Journal of Human Evolution* 47, 323–341.

Fortelius, M. (coordinator 2005): *Neogene of the Old World Database of Fossil Mammals (NOW)*. University of Helsinki. <http://www.helsinki.fi/science/now/>. Public release 030717.

- Fortelius, M., Eronen, J., Jernvall, J., Liu, L., Pushkina, D., Rinne, J., Tesakov, A., Vislobokova, I., Zhang, Z. & Zhou, L. 2002: Fossil mammals resolve regional patterns of Eurasian climate change during 20 million years. *Evolutionary Ecology Research* 4, 1005–1016.
- Francavilla, F., Bertolani Marchetti, D. & Tomadin, L. 1970: Ricerche stratigrafiche, sedimentologiche e palinologiche sul Villafranchiano tipo. *Giornale di Geologia ser. 2*, 36, 701–741.
- Gaudry, A. 1862: Animaux fossiles et Géologie de l'Attique. Savy, Paris, 476 pp.
- Gentili, S., Mottura, A. & Rook, L. 1998: Fossil Primates in Italy: recent finds and their geological context. *Geobios* 31, 675–686.
- Gliozzi, E., Abbazzi, L., Argenti, P., Azzaroli, A., Caloi, L., Capasso Barbato, L., Di Stefano, G., Esu, D., Ficarelli, G., Girotti, O., Kotsakis, T., Masini, F., Mazza, P., Mezzabotta, C., Palombo, M.R., Petronio, C., Rook, L., Sala, B., Sardella, R., Zanalda, E. & Torre, D. 1997: Biochronology of selected mammals, molluscs and ostracods from the middle Pliocene to the late Pleistocene in Italy. The state of the art. *Rivista Italiana di Paleontologia e Stratigrafia* 103, 369–388.
- Heintz, E., Brunet, M. & Battail, B. 1981: A Cercopithecoid Primate from the Late Miocene of Molayan, Afghanistan, with remarks on “*Mesopithecus*”. *International Journal of Primatology* 2, 273–284.
- Hohenecker, J. & Zapfe, H. 1990: Craniometric investigations on *Mesopithecus* in comparison with two recent colobines. *Beiträge zur Paläontologie von Österreich* 16, 111–143.
- Hürzeler, J. 1967: Nouvelles découvertes de mammifères dans les sédiments fluviolacustres de Villafranca d’Asti. Problèmes actuels de paléontologie. Évolution des vertébrés. Colloques Internationaux du Centre National pour la Recherche Scientifique, Paris 163, 633–636.
- Jablonski, N.G. 2002: Fossil Old World monkeys: The late Neogene radiation. In: Hartwig, W.C. (Ed.): *The primate fossil record*, Cambridge University Press, Cambridge, 255–299.
- Koufos, G.D., Spassov, N. & Kovatchev, D. 2003: Study of *Mesopithecus* (Primates, Cercopithecidae) from the late Miocene of Bulgaria. *Palaeontographica, Abt. A* 269, 39–91.
- Kullmer, O. & Doukas, C. 1995: The vertebrate locality of Maramena (Macedonia, Greece) at the Turolian-Ruscian Boundary (Neogene). 6 – The deciduous dentition of *Mesopithecus pentelicus* Wagner (Primates, Mammalia). *Münchner Geowiss. Abh.* 28, 65–74.
- Martinetto, E. & Mai, D. 1996: Macrofossili vegetali. In: Carraro, F. (Ed.): *Revisione del Villafranchiano nell’area-tipo di Villafranca d’Asti. Il Quaternario* 9, 73–79.
- Miller K.G., Komazin, M.A., Browning, J.V., Wright, J.D., Mountain, G.S., Katz, M.E., Sugarman, P.J., Cramer, B.S., Christie-Blick, N. & Pekar, S.F. 2005: The Phanerozoic Record of Global Sea-Level Change. *Science* 310, 1293–1298.
- Pareto, M. 1865: Sur la subdivision que l’on pourrait établir dans les terrains de l’Apennin Septentrional. *Bulletin de la Société Géologique de France* 22, 210–277.
- Rook, L. 1999: Late Turolian *Mesopithecus* (Mammalia, Primates, Colobinae) from Italy. *Journal of Human Evolution* 36, 535–547.
- Rook, L., Mottura, A. & Gentili, S. 2001: *Macaca* remains from RDB quarry (Villafranca d’Asti, Italy): new data and overview. *Journal of Human Evolution* 40, 187–202.
- Strasser, E. & Delson, E. 1987: Cladistic analysis of cercopithecoid relationships. *Journal of Human Evolution* 16, 81–99.
- Suc, J.-P., Bertini, A., Combourieu-Nebut, N., Diniz, F., Leroy, S. Russo Ermolli, E., Zheng, Z., Bessais, E. & Ferrier, J. 1995: Structure of west Mediterranean vegetation and climate since 5.3 ma. *Acta zoologica cracoviense* 38: 3–16.
- Szalay, F. & Delson, E. 1979: *Evolutionary History of the Primates*. Academic Press New York, 580 pp.
- Torre, D., Ficarelli, G., Masini, F., Mazza, P., Rook, L. & Sala, B. 1992: Mammal dispersal events in the early Pleistocene of western Europe. *Courier Forsch.-Institut Senckenberg* 153, 51–58.
- Torre, D., Abbazzi, L., Bertini, A., Fanfani, F., Ficarelli, G., Masini, F., Mazza, P. & Rook, L. 2001: Structural changes in Italian Late Pliocene – Pleistocene large mammal assemblages. *Bollettino della Società Paleontologica Italiana* 40, 303–306.
- Zapfe, H. 1991: *Mesopithecus pentelicus* Wagner aus dem Turolien von Pikermi bei Athen, Odontologie und Osteologie. *Neue Denk-Schriften Naturhistorisches Museum Wien* 5, 1–203.

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