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Mammuthus meridionalis (Nesti, 1825) from Apollonia-1 (Mygdonia Basin, Northern Greece) and its importance within the Early Pleistocene mammoth evolution in Europe

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ABSTRACT
In the present article, we study the mammoth remains from the late Villafranchian (Early Pleistocene) locality Apollonia-1 (Mygdonia Basin, Northern Greece). The material consists of a hemi-mandible with the m3, isolated m3/M3 and a maxilla fragment with DP2-DP3. The mandibular and dental features permit their attribution to the southern mammoth *Mammuthus meridionalis* (Nesti, 1825). Yet, the dental features indicate an evolutionary stage somewhat more derived than the Upper Valdarno mammoth (beginning of late Villafranchian) in terms of the higher number of plates in the DP3 and the marginally higher hypsodonty index in the M3. This is also revealed by the application of a Principal Component Analysis, where several dental features are combined. Moreover, the relatively deep mandibular corpus is a derived feature. In these aspects, the Apollonia-1 sample fits better with corresponding specimens from European localities correlated to the second part of the late Villafranchian and the Epivillafranchian. From this period, two subspecies have been proposed from Western Europe: *M. m. vestinus* (Azzaroli *in* Ambrosetti, Azzaroli, Bonadonna & Follieri, 1972) from Italian localities correlated to the Farneta Faunal Unit and *M. m. depereti* Coppens & Beden, 1982 from Saint-Prest (France). We propose that *M. m. vestinus* can be regarded a valid subspecies of the southern mammoth and that *M. m. depereti* is possibly a junior synonym. The results of this study are in agreement with the existing biochronological correlation of the Apollonia-1 fauna and further support the potential biostratigraphic significance of *M. meridionalis* within the Early Pleistocene, albeit conclusions based on limited/fragmentary sample should always be taken with caution.

KEY WORDS
Greece,
Villafranchian,
Pleistocene,
Mammuthus,
biostratigraphy.

RÉSUMÉ

Mammuthus meridionalis *(Nesti, 1825) d'Apollonia-1 (Bassin de Mygdonia, Grèce septentrionale) et son importance dans le cadre de l'évolution des mammouths du Pléistocène inférieur d'Europe.*

Dans cet article, nous étudions les restes de mammouths d'Apollonia-1 (Bassin de Mygdonia, Grèce septentrionale) du Villafranchien supérieur (Pléistocène inférieur). Le matériel étudié comprend une demi-mandibule avec la m3, une m3/M3 isolée et un fragment de maxillaire avec DP2-DP3. Les caractéristiques mandibulaires et dentaires permettent l'attribution de ces spécimens au mammouth méridional *Mammuthus meridionalis* (Nesti, 1825). Cependant, quelques caractéristiques dentaires indiquent un stade évolutif un peu plus dérivé que le mammouth méridional typique du Valdarno supérieur (début de Villafranchien tardif), de par un nombre plus élevé de lames dans le DP3 et l'indice d'hypsodontie légèrement élevé de la M3. Cela est également révélé par l'analyse en composantes principales, qui combine plusieurs caractéristiques dentaires. De plus, le corpus mandibulaire relativement profond est un caractère dérivé. Sous ces aspects, le mammouth d'Apollonia-1 s'accorde mieux avec les spécimens correspondants des localités européennes corrélées à la deuxième partie de la fin du Villafranchien et de l'Épivillafranchien. À partir de cette période, deux sous-espèces d'Europe occidentale ont été proposées : *M. m. vestinus* (Azzaroli *in* Ambrosetti, Azzaroli, Bonadonna & Follieri, 1972), de localités italiennes en corrélation avec l'unité de faune de Farneta et *M. m. depereti* Coppens & Beden, 1982, de Saint-Prest (France). Nous suggérons que *M. m. vestinus* soit une sous-espèce valide du mammouth méridional et *M. m. depereti* son synonyme. Les résultats de cette étude sont en accord avec la corrélation biochronologique connue de la faune d'Apollonia-1 et confirment la signification biostratigraphique potentielle de *M. meridionalis* dans le Pléistocène inférieur, bien que les conclusions fondées sur un échantillon limité/fragmentaire soient toujours à prendre avec prudence.

MOTS CLÉS
Grèce,
Villafranchien,
Pléistocène,
Mammuthus,
biostratigraphie.

INTRODUCTION

Mammoths originated in Africa during the late Miocene-early Pliocene and during the late Pliocene (*c.* 3.5-3.0 Ma) migrated through the Levant to Eurasia (Sanders *et al.* 2010; Markov 2012; Rabinovich & Lister 2017). Although mammoths did not prosper in Africa and survived there until the Early Pleistocene, they thrived in Eurasia until the Late Pleistocene, where they show significant morphological adaptations through time, related to the general dietary trend from browse-dominated mixed feeding towards grazing, as a response to the changing environmental conditions of the Pleistocene (Lister & Sher 2001; Rivals *et al.* 2012, 2015; Saarinen & Lister 2016). These morphological adaptations are related to biomechanical advantages for grazing and increased resistance to abrasion, and are evident in the skull and dental morphology: shortening and heightening of the cranium and mandible, increase in the height of the molar crown (hypsodonty), increase in the number and packing of enamel plates in the molars, enamel thinning, and relatively thicker middle enamel layer with occlusally oriented prisms in the enamel microstructure of the molars (Lister 1996; Lister & Sher 2001; Ferretti 2003a, b). Based mainly on these features, Eurasian mammoths are distinguished into four successive species (Lister 1996; Lister *et al.* 2005):

1) a primitive morph, commonly, but tentatively, attributed to *M. rumanus* (Stefanescu, 1924): early Villafranchian, late Pliocene, ?3.5-2.5 Ma; see Markov (2012) and references cited therein; *M. meridionalis rumanus* according to Baygusheva & Titov (2012); for the sake of simplification will be referred to as *M. rumanus* thereafter in the article, not on the basis of new data;

2) the southern mammoth *M. meridionalis* (Nesti, 1825): middle Villafranchian-Epivillafranchian, Early Pleistocene, *c.* 2.5-?0.8 Ma;

3) the steppe mammoth *M. trogontherii* (Pohlig, 1885): late Early-Middle Pleistocene; and

4) the wooly mammoth *M. primigenius* (Blumenbach, 1799): late Middle-Late Pleistocene.

Apart from *M. rumanus*, the rest of the mammoth species are properly defined. Yet, the time and mode of the transition/replacement from *M. rumanus* to *M. meridionalis*, from *M. meridionalis* to *M. trogontherii*, and from *M. trogontherii* to *M. primigenius* are still open issues, and several intermediate/mosaic morphotypes or subspecies have been proposed by various researchers. In the present article, based on the mammoth specimens from the Early Pleistocene of Apollonia-1, we focus our study on *M. meridionalis*, including its primitive, typical and advanced morphotypes, and its replacement by *M. trogontherii*.

FOSSILIFEROUS LOCALITY, MATERIAL AND METHODS

All the mammoth material described in the present article originates from the fossiliferous locality Apollonia-1 (APL) in Mygdonia Basin (Macedonia, Greece). APL is located near to the village Nea Apollonia, about 45 km east of Thessaloniki (Fig. 1A). The locality was discovered in 1990 (Koufos *et al.* 1992) and subsequently excavated until 1996, and provided a wealth of mammal fossils (Koufos 1992; Kostopoulos 1997; Koufos & Kostopoulos 1997; Koufos *et al.* 1997). A new excavation series was conducted from 2012 to 2014, which further

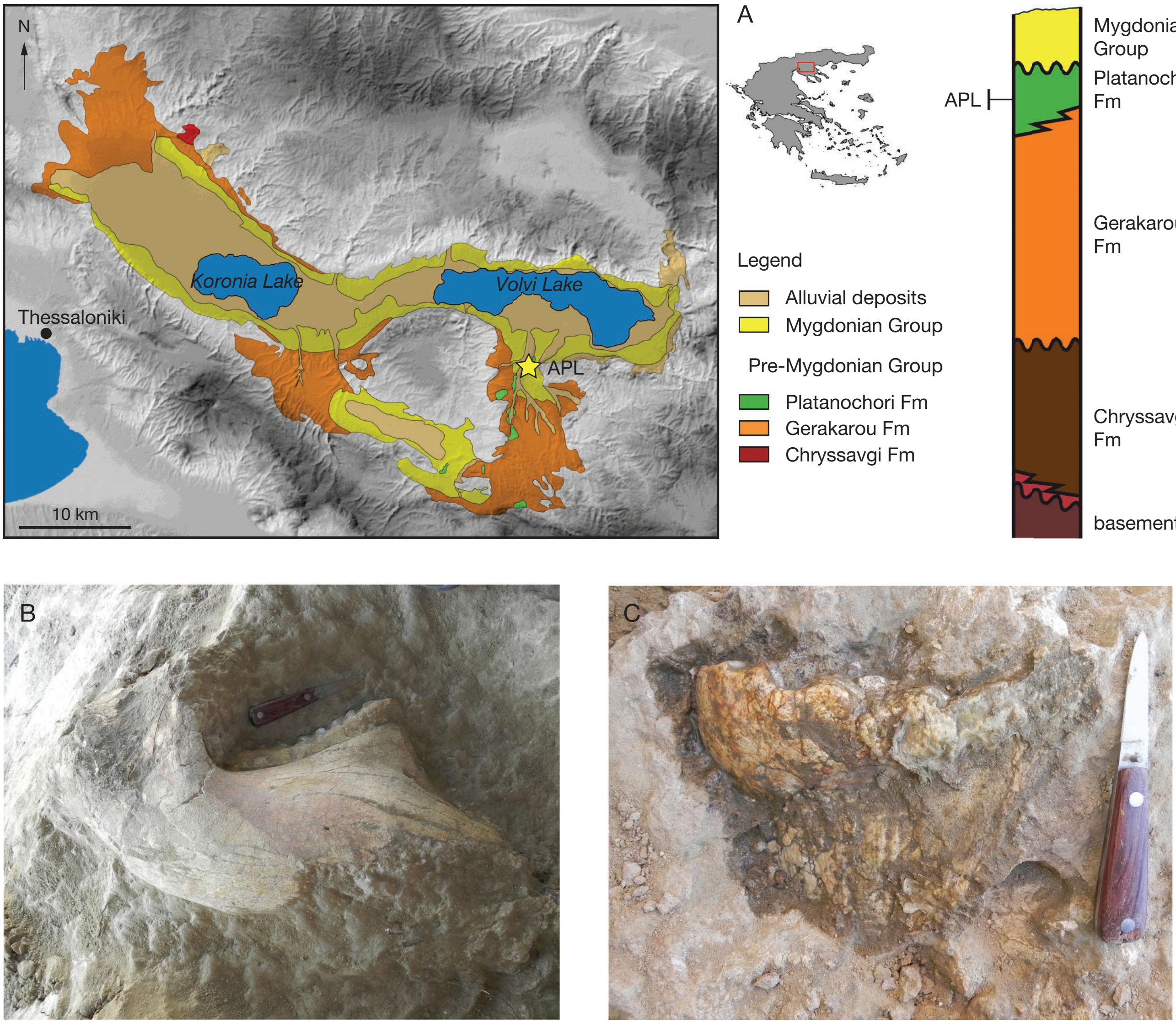

Fig. 1. — **A**, Geological map and simplified composite stratigraphic column of the Neogene and Quaternary lithostratigraphic units of Mygdonia Basin, showing the location of Apollonia-1 (map and column modified from Koufos *et al.* [1995] and Konidaris *et al.* [2015]); **B**, hemi-mandible APL-716 *in situ*; **C**, m3 APL-687 *in situ*.

enriched the APL collection (Kostopoulos *et al.* 2018; Koufos 2018; this study). The APL fossils are situated within the Platanochori Formation (Pre-Mygdonian Group; Fig. 1A), which consists of sands, sandstones, conglomerates, silty sands, silts, clays, marls and marly limestones, indicating the local development of small lakes and swamps (Koufos *et al.* 1995). The APL fauna is younger than Dmanisi (*c.* 1.8 Ma, Georgia; Lordkipanidze *et al.* 2007) and older than Untermaßfeld (*c.* 1.0 Ma, Epivillafranchian, Germany; Kahlke *et al.* 2011), showing faunal similarities with the Orce sites of Venta Micena, Fuente Nueva-3 and Barranco León (collectively *c.* 1.6-1.2 Ma, Spain; Martínez-Navarro *et al.* 2015) and Pirro Nord *c.* 1.6-1.3 Ma, Italy (Pavia *et al.* 2012; López-García *et al.* 2015); therefore, a correlation to the second half of the late Villafranchian is possible for APL. Further information on the geology, stratigraphy and fossiliferous localities of the Mygdonia Basin can be found in Koufos *et al.* (1995) and Konidaris *et al.* (2015).

Concerning the mammoth material, the maxilla fragment with deciduous dentition was discovered during the 1990s excavation campaigns and was briefly described by Athanassiou & Kostopoulos (2001). The rest of the specimens were discovered in 2012 (Fig. 1B, C). All the material is stored at the Museum of Geology-Paleontology-Paleoanthropology of the Laboratory of Geology and Palaeontology, University of Thessaloniki, Greece (LGPUT). Mandibular and dental terminology used for the description of the specimens follows Todd (2010). Mandibular measurements were taken after Beden (1983) and dental measurements after Lister & Sher (2015). The latter are given in Table 1.

For the comparison of the dental parameters, specimens from the following localities and publications were considered (including the measurements for Figs 5-8): Tulucești, Orodelu (Romania; Obadă 2010); Cernătești (Romania; Markov 2012); Red Crag (England; Lister & Van Essen 2003); Bossilkovtsi

Table 1. — Dental measurements of *Mammuthus meridionalis vestinus* (Azzaroli *in* Ambrosetti, Azzaroli, Bonadonna & Follieri, 1972) from Apollonia-1. Superscript numbers indicate the plate, where the parameter was measured. Abbreviations: **LF**, **ET**, average values; **p**, platelet.

Inventory number	Tooth	L (mm)	W (mm; including cement)	H (mm)	PN	LF	ET (mm)	HI	Plates in wear
APL-686B	left M3	(230.8)	$(87.0)^1$	128.8^6	+13 (?14)	5.5	2.80	1.48	6
APL-686A	right M3	(77.3)	$(84.8)^1$	118.2^4	+4	–	–	1.39	
APL-716	right m3	275.2	102.0^6	–	?12p	4.6	3.1	–	all
APL-687	left m3	217.4	88.8	–	+8	3.76 (basal)	3.24	–	all
APL-225	right DP2	21.9	16.8^2	–	4	20.3 (occlusal)	1.4	–	all
APL-225	right DP3	80.6	+34	34.5	8	10.4	–	–	2

(Bulgaria; Markov & Spassov 2003); Tsotylio (Greece; Kostopoulos & Koulidou 2015); Novotroitsk (Russia; Baygusheva *et al.* 2011); Taribana (Georgia; Gabunia & Vekua 1963); Liventsovka, Sinyaya Balka (Russia; Baygusheva & Titov 2012; HI values for Sinyaya Balka were kindly provided by V. Titov); Senèze (France; Maglio 1973); Upper Valdarno (Italy; Maglio 1973; Van Essen 2003; Lister & Stuart 2010; Lister *et al.* 2012; Ros-Montoya *et al.* 2012); Montopoli, Laiatico, Monte Tenda-Soave, Torrente Crostolo, Mugello, Farneta, Pietrafitta, Rio Pradella-Imola (Italy; Palombo & Ferretti 2005); Dmanisi (Georgia; Ros-Montoya *et al.* 2012); Ubeidiya (Israel; Beden 1986); Kapetanios (Greece; Steensma 1988); Venta Micena, Fuente Nueva-3, Incarcal-I (Spain; Ros-Montoya *et al.* 2012); Saint-Prest (France; Van Essen 2011); Dorst (the Netherlands; Van Essen 2003); Voigtstedt (Germany; Dietrich 1965); Edersleben (Germany; Van Essen 2003); Goldshäfe Sands, Stuttgart-Rosenstein (Germany; Van Essen 2011); Süßenborn (Germany; Lister & Stuart 2010; Lister *et al.* 2012); Loussika (Greece; Athanassiou 2012); West Runton (England; Lister & Stuart 2010).

Scatter plots and Principal Component Analysis (PCA) were acquired using PAST free software, version 3.15 (Hammer *et al.* 2001; https://folk.uio.no/ohammer/past/). In order to eliminate the size effect, dental measurements used in the PCA were prior transformed by the Mosimann's Log-shape ratio by dividing each value by the geometric mean of all the variables for each observation and logarithmizing the results. Missing values in PCA were treated by applying Iterative Imputation. Age at death was estimated using the dental-wear-based age criteria for the extant African savannah elephant *Loxodonta africana* provided by Laws (1966), and revised by Stansfield (2015) and Haynes (2017).

Dental abbreviations

DP	upper deciduous premolar;
ET	enamel thickness;
H	height;
HI	hypsodonty index (H × 100/W);
L	length;
LF	lamellar frequency;
m/M	lower/upper molar;
n	number of observations;
OA	angle between the tangent lines on the worn and unworn occlusal surfaces of the molar in lateral view (occlusal angle);
PN	plate number;
W	width.

SYSTEMATIC PALAEONTOLOGY

Order PROBOSCIDEA Illiger, 1811
Family Elephantidae Gray, 1821
Subfamily Elephantinae Gray, 1821

Genus *Mammuthus* Brookes, 1828

Type species. — *Mammuthus primigenius* (Blumenbach, 1799), fixed as type species by Garutt *et al.* 1990 (see also Reich *et al.* 2007 and Lister 2017).

Mammuthus meridionalis (Nesti, 1825)

Lectotype. — Cranium with M3, IGF-1054 (Natural History Museum, Geology and Paleontology Section, University of Florence, Italy), designated by Depéret & Mayet (1923: 126).

Type locality. — Upper Valdarno (Italy).

Mammuthus meridionalis vestinus (Azzaroli *in* Ambrosetti, Azzaroli, Bonadonna & Follieri, 1972) (Figs 2-4)

Holotype. — Skeleton including the skull with the m3/M3 (Spanish Fortress, L'Aquila, Italy).

Type locality. — Madonna della Strada (Scoppito, L'Aquila, Italy).

Locality. — Apollonia-1 (Mygdonia Basin, Macedonia, Greece).

Age. — Late Villafranchian (Early Pleistocene).

Material examined. — Right maxilla fragment with DP2-DP3, APL-225; right M3 fragment, APL-686A; left M3 fragment, APL-686B; right hemi-mandible with m3, APL-716; left m3, APL-687.

Description

The right maxilla fragment APL-225 preserves the DP2 and DP3 (Fig. 2). The DP2 has rectangular shape and is formed of four, only slightly worn plates, with the posterior one attached to the third one. Cementodonty is present, but weak. The still not completely erupted DP3 consists of eight mostly unworn plates, which are parallel-sided and separated. The tooth presents a weak lingual curvature. In lingual view, the first two plates are slightly

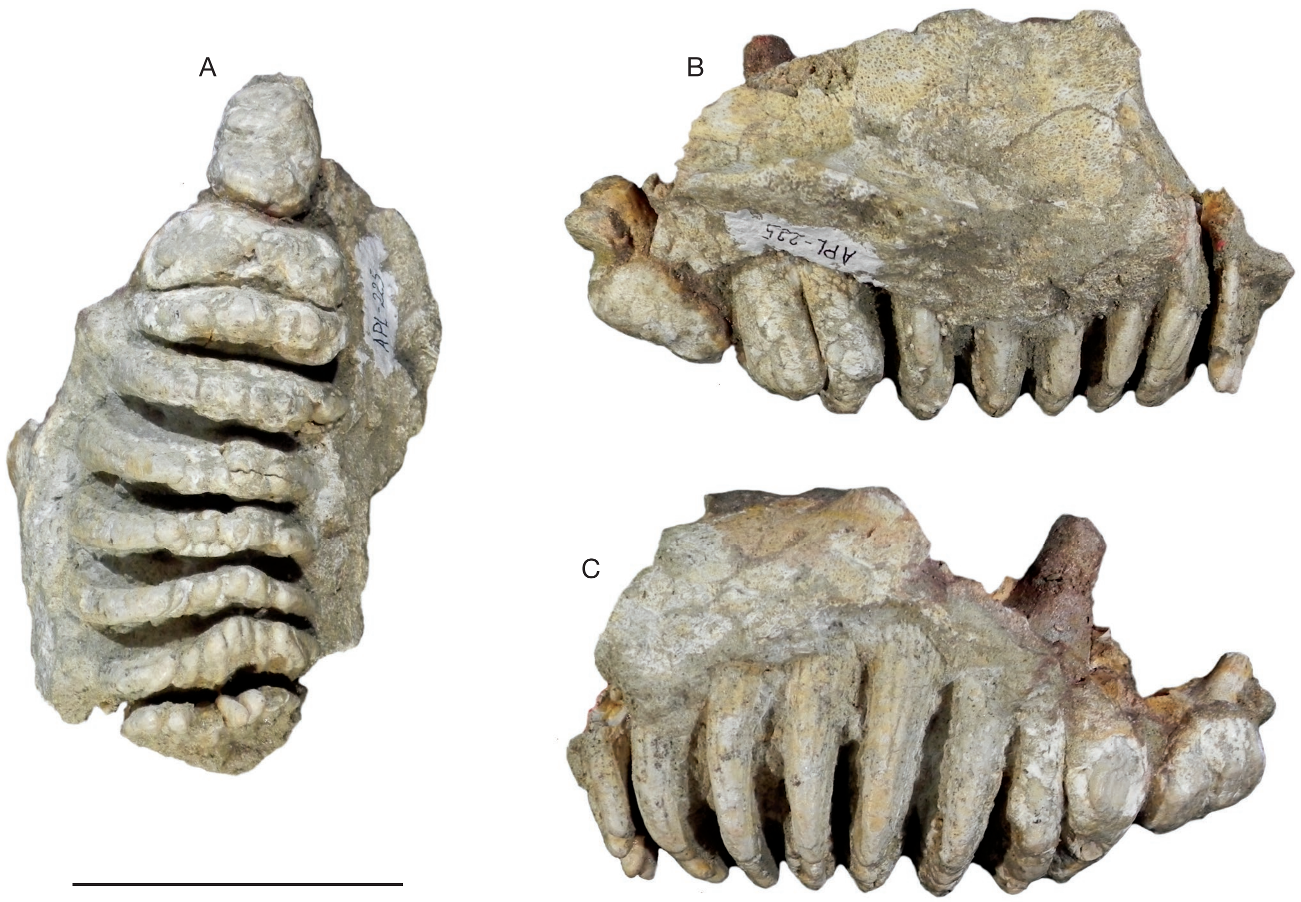

Fig. 2. — Right maxilla fragment with DP2-DP3 (APL-225) of *Mammuthus meridionalis vestinus* (Azzaroli *in* Ambrosetti, Azzaroli, Bonadonna & Follieri, 1972) from Apollonia-1: ventral (**A**), medial (**B**), and lateral (**C**) views. Scale bar: 5 cm.

inclined relative to the occlusal surface, whereas the rest are almost vertical.

APL-686B (Fig. 3A-C) is identified as upper molar based on the obtuse angle that is formed between the occlusal surface to the vertical plane of the lamellae, and on the rootward tilt for the last 6-7 lamellae (Lister *et al.* 2013). It represents the third (last) molar due to the tapering form at the posterior end of the crown (Lister *et al.* 2012). The plates were found loose and isolated in the sediment, and they were subsequently glued together. Preserved are thirteen plates, although at least one more should have been anteriorly, increasing thus the PN to possibly 14. The tooth is curved at the lingual side. In labial and lingual views, the plates are slightly inclined relative to the horizontal occlusal surface, and they are rather straight. The only complete enamel loop is the anterior-most preserved one. The enamel loops at the anterior part of the tooth are parallel-sided, separated, perpendicular to the long axis of the tooth, and their lateral sides are rounded and evenly directed (not curving anteriorly or posteriorly). Apical digitations (appearing on the occlusal surface as rounded loops) are present at the third and fourth preserved lamellae. The fourth lamella, which is at an early wear stage, shows four subequal rings. The enamel folding is weak. The last eight plates are ovoid of wear. APL-686A corresponds to a fragmented upper molar and preserves only four plates. It was found close to APL-686B and represents possibly its right counterpart.

The hemi-mandible APL-716 preserving the m3 (see below) lacks the anterior part of the ventral border of the corpus, the condyle and the coronoid process (Fig. 4). The mandibular symphysis is not well-preserved, but its preserved dorsal surface is straight and steeply directed downwards. In lateral and medial views, the hemi-mandible is relatively short and deep. The corpus is moderately swollen and more evident in the medial side. In lateral view, the depth of the corpus is higher at the level of the anterior part of the m3. The lateral side of the ramus is flat. Corpus and ramus form obtuse angle due to the posterior inclination of the ramus. The rostral margin of the ramus is positioned at a minor obtuse angle, but almost vertical, to the alveolar planum. Two anterior mental foramina (AMF) are located at the posterior border of the symphysis, at the level of the anterior end of the m3, and a large medial mental foramen (MMF) is present approximately at the same level as the AMF. Measurements [in mm; according to Beden (1983)], are A = (220); B = (120); C = 260; F = 150 and J = (225).

The molar on the hemi-mandible APL-716 (Fig. 4) is considered as the third one due the long antero-posterior dimension (length) and the narrowing of the crown towards the posterior end. The anterior part is worn down to a dentine platform and the original plate number can only be estimated, due to the wear of the enamel loops. However, the rostral part of the anterior root is visible, indicating that no substantial loss should had happened due to wear, which resulted possibly in the loss of only the anterior talon (Lister & Sher 2015). Therefore, the number of plates is estimated as 12, plus a platelet/talonid at the posterior end. The shape of the molar is elliptic, being wider in the middle, and with a minor curvature at the labial side. In lingual view, the plates are slightly inclined relative to the occlusal surface. In labial view, the tooth shows a slight depression at the middle. Cement deposition is strong on the occlusal surface, as well as on the labial, lingual and posterior sides; however, the enamel is high above the cement. The enamel loops (five complete at the anterior part) are parallel-sided and separated. Anteriorly, the loops are oblique relative to the long axis of the tooth and become perpendicular to that at the posterior end. Apical digitations are few and present posteriorly. The enamel folding is undulating and present at the entire length of the enamel figure. The lateral sides of the enamel figures are rounded and directed anteriorly, stronger on the lingual side.

The identification of the APL-687 (Fig. 3D-F) as a third lower molar is based on the significant preserved length despite the advanced dental wear (a condition possible only in the last molars when the forward progression of them has been terminated), and on the presence of a single root; the anterior first and second roots had been lost, and therefore a substantial part of the original anterior end of the tooth is missing (Lister *et al.* 2012; Lister & Sher 2015). The tooth preserves seven visible plates, whereas at least one more should be added in the anterior part, where the dentine is confluent. Due to its strong wear, the original plate number, as well as the crown height, cannot be estimated. The lamellar frequency, measured at the base of the crown, results in a low value (Table 1), because of the divergence of the plates towards the base in elephantids (Lister & Sher 2015). The shape of the molar is almost parallel-sided. In labial and lingual views, the tooth shows a slight depression at the middle. Cement covers the regions between the enamel loops as well as the labial, lingual and posterior sides. At the anterior-medial part of the tooth, complete enamel loops are present, which are parallel-sided with anterior and posterior median swellings that are slightly offset from the long axis of the molar (asymmetry). The enamel loops are separated, albeit in some lamellae they are almost in contact, and are oblique relative to the long axis of the tooth. The lateral sides of the enamel figures are rounded. Apical digitations are present on the two distal plates; the last plate, which is at an early wear stage shows four subequal rings. The enamel folding is regular, more intense than APL-716, due to the advanced stage of wear (Van Essen 2011); it is present at the entire length of the enamel figure.

Age at death

The ontogenetic age is estimated using the dental-wear-based age criteria for the extant African savannah elephant *Loxodonta africana* provided by Laws (1966). The m3 APL-716 (Fig. 4) falls within Laws' group XXV, which corresponds to the average age of 49 in African Equivalent Years (AEY). Recent revisions on Laws' age assignments propose that this age group corresponds to an upper limit of 50 AEY with 70+ longevity for the African elephant (Stansfield 2015; Haynes 2017). *Mammuthus meridionalis* had a significantly larger body size than extant African elephants, and due to the general positive scaling of longevity to body size across mammals, also probably had a longer total lifespan (Eisenberg 1990; Maiorana 1990); therefore, a slightly older true age is expected for APL-716. When the formula of Blueweiss *et al.* (1978) (longevity in days proportional to body mass in grams$^{0.17}$) is applied, assuming a longevity of 70 years and a body mass of 6.0 tonnes for males of *L. africana*, and an average body mass of 11.0 tons for *M. meridionalis* (Larramendi 2016), a longevity of approximately 77.5 years can be hypothesized for the latter. Consequently, the estimated upper limit of the ontogenetic age for APL-716 is 47 × 77.5/70 = 52 years. Accordingly, the estimated upper limit of the ontogenetic age for the m3 APL-687 (Laws' group XXVII; Fig. 3D-F) is 66-73 years, for the M3 APL-686B (Laws' group XX; Fig. 3A-C) is 37 years and for the maxilla APL-225 (Laws' group II; Fig. 2) is *c.* 1 year.

DISCUSSION-COMPARISON

COMPARISON WITH OTHER PLEISTOCENE ELEPHANTIDS

Apart from *Mammuthus*, two more elephantids were present during the Pleistocene in Eurasia, *Palaeoloxodon* and *Elephas* (the lineage leading to the Asian elephant *E. maximus*); a fourth genus, *Loxodonta*, is also included in the comparison, albeit not found so far outside of Africa. The straight-tusked elephant *Palaeoloxodon* is represented in Europe from the Middle to the Late Pleistocene by the single species *P. antiquus* (Falconer & Cautley, 1847). The taxonomically important cranium and tusks for the distinction between the two genera are missing from the APL collection; however, several lines of evidence exclude an assignment to *Palaeoloxodon*: a) *Palaeoloxodon* is characterized by tight enamel folding and presence of midline sinuses; in the APL molars, the moderate enamel folding (APL-687, 716) and midline swellings (APL-687) are traits seen generally in much worn elephantid molars, and are without taxonomic significance; b) in early wear, the plates of *Palaeoloxodon* are typically subdivided into two short lingual and labial rings, and with a long central ring; in contrast, in all APL molars, their plates in early wear consist of sub-equal rings; c) the M3 of *P. antiquus* are more hypsodont (mean value HI > 1.9) than the APL one; d) the lamellae of *Palaeoloxodon* commonly have "cigar-shape" and blunt lingual and labial ends; in the APL molars the enamel bands run almost parallel to each other; and e) a medial mental foramen is absent in *P. antiquus*, whereas it is present in the APL mandible (Palombo & Ferretti 2005; Ferretti & Debruyne 2011; Lister *et al.* 2012; Stimpson *et al.* 2016). The APL molars are further differentiated from *Elephas*, which is characterized by: a) dental wear, which progresses from a row of small rings at the apex, to three subequal rings that finally fuse to form

FIG. 3. — Dental remains of *Mammuthus meridionalis vestinus* (Azzaroli *in* Ambrosetti, Azzaroli, Bonadonna & Follieri, 1972) from Apollonia-1: **A-C**, left M3 fragment (APL-686B) in occlusal (**A**), buccal (**B**), and lingual (**C**) views; **D-F**, left m3 (APL-687) in occlusal (**D**), lingual (**E**), and buccal (**F**) views. Scale bar: 5 cm.

the lamella; b) tightly folded enamel; and c) lack of a medial mental foramen in its Plio-Pleistocene Asian representatives *E. planifrons* Falconer & Cautley, 1845 and *E. hysudricus* Falconer & Cautley, 1845 (Ferretti & Debruyne 2011; Lister *et al.* 2013). Finally, the lozenge-shaped dental wear figure in contact in the successive lamellae in the midline, typical for *Loxodonta* (Maglio 1973), is not present in the APL molars. Therefore, the following comparison will focus on the *Mammuthus* representatives.

Comparison within European *Mammuthus*

Morphological features of the molars, and particularly of the last molars, are primarily used for the identification of mammoth species. This is not only because molars are more frequently preserved in the fossil assemblages, but also because the morphology of the mammoth molars has adaptive and evolutionary significance. Features of important taxonomic value include the relative crown height (expressed with the HI), the occlusal angle (OA); the plate number (PN), the enamel thickness (ET) and the lamellar frequency (LF). The evolution of these attributes in the mammoth lineage is related to the greater emphasis on shearing mastication and the enhancement of its effectiveness, as well as in the verticalization of the skull architecture. In particular: 1) increased hypsodonty provided greater tooth life, and resulted in the deepening of the maxillary region of the cranium and the corpus of the mandible; 2) in the more primitive mammoths the molars were in a more horizontal position (higher OA) relative to the occlusal plane, whereas in the more advanced ones they were more verticalized (lower OA), associated with the more vertical architecture of the skull; 3) the increased number of plates provided greater shearing power and tooth life; and 4) the density of the plates increased and was accompanied by a reduction in the thickness of the enamel, enhancing the shearing action (Lister 1996; Van Essen 2011).

The earliest and most primitive mammoths of Eurasia are commonly attributed to *M. rumanus*. Due to the limited, sometimes incomplete and not securely dated material, our knowledge about this species remains vague. The European sample includes specimens from Tuluceşti, Cernăteşti, Orodelu (all Romania), Tsotylio (Greece), Bossilkovtsi (Bulgaria), Red Crag (England), Montopoli, Laiatico (both Lower Valdarno, Italy) and Novotroitsk (Russia), and indicates its existence broadly during 3.5-2.5 Ma (Lister & Van Essen 2003; Markov & Spassov 2003; Lister *et al.* 2005; Palombo & Ferretti 2005; Maschenko 2010; Baygusheva *et al.* 2011; Markov 2012; Kostopoulos & Koulidou 2015). *Mammuthus rumanus* is distinctly more primitive than later mammoths and collectively is characterized in its m3/M3 by low crown height (HI: 1.09-1.35), low number of plates (PN: 8-10), low lamellar frequency (LF: 3.0-4.93) and thick enamel (ET: 3.0-5.0) (see above references). In these parameters, the sample of *M. meridionalis* from its type locality Upper Valdarno (Italy; Nesti 1825; Weithofer 1890; Azzaroli 1966, 1977) is more derived in having slightly higher m3/M3 (HI: 1.13-1.47), more plates (PN: 12-15), higher lamellar frequency (LF: 3.8-6.6) and thinner enamel (ET: 2.2-4.2) (Van Essen 2003). The typical material from Upper Valdarno, attributed to *M. m. meridionalis*, lacks precise stratigraphic information, but it is collectively correlated to the Olivola and Tasso Faunal Units (FU), and therefore to the beginning of the late Villafranchian (Azzaroli 1977); the Olivola/Tasso FU boundary is magnetostratigraphically calibrated close to the top of the Olduvai subchron, at 1.78 Ma (Napoleone *et al.* 2003; Rook & Martínez-Navarro 2010; Rook *et al.* 2013). As a more primitive morphotype than the typical *M. meridionalis* (*M. m. meridionalis*) two subspecies have been proposed:

– *M. m. gromovi* (Garutt & Alexeeva, 1964); type locality: Liventsovka (Sea of Azov, Russia). Originally erected as "*Archidiskodon gromovi*" (Alexeeva & Garutt 1965), this subspecies is recorded from several Khapry fauna localities in the Northeast Sea of Azov (Russia), correlated to the middle Villafranchian (MNQ 17) (Garutt & Baygusheva 1981; Baygusheva & Titov 2012, 2018; Baygusheva *et al.* 2016).

– *M. m. taribanensis* (Gabunia & Vekua, 1963); type locality: Taribana (Georgia). A skeleton of this subspecies was found within normally magnetized strata (no other accompanying fauna), interpreted as the Olduwai subchron (1.95-1.78 Ma), and therefore corresponding to the first part of the late Villafranchian (Gabunia & Vekua 1963; Vekua *et al.* 2010; Bukhsianidze & Koiava 2018). Obadă (2014) suggested that the Taribana mammoth is more primitive than the holotype of *M. m. gromovi* and that it has nomenclatural priority.

Mammuthus meridionalis is further differentiated from the more derived *M. trogontherii* from Süßenborn (type locality, Germany; within the early Brunhes magnetochron, 0.7-0.6 Ma; Kahlke *et al.* 2011), the latter having significantly higher m3/M3 (HI: 1.41-2.06), more plates (PN: 17-22), higher lamellar frequency (LF: 4.45-8.94), thinner enamel (ET: 1.7-3.0) and lower OA (Van Essen 2011; Lister & Stuart 2010; Lister *et al.* 2012). Again, several morphotypes/evolutionary stages of more derived *M. meridionalis* have been proposed:

– *M. m. vestinus* (Azzaroli *in* Ambrosetti, Azzaroli, Bonadonna & Follieri, 1972); type locality: Madonna della Strada, near Scoppito (L'Aquila, Italy). Azzaroli (1977) included into this subspecies an almost complete skeleton from Madonna della Strada, described by Maccagno (1962) (see also Rossi *et al.* [2017]), as well as material from Farneta and Mugello (Italy; Azzaroli 1977: pl. 1, fig. 2, pl. 2, fig. 2; fig. Palombo & Ferretti 2005: fig. 4a, b; Cioppi & Mazza 2010: fig. 18.15), considering more derived cranial features and larger body size than the Upper Valdarno typical *M. meridionalis* (see below). The deposits bearing the Madonna della Strada skeleton are possibly slightly older than *c.* 1.3 Ma (Magri *et al.* 2010) and the Farneta Faunal Unit (FU) of the Italian biostratigraphy is dated at *c.* 1.7-1.5 Ma (Masini & Sala 2011). Therefore, a post-Upper Valdarno and pre-Epivillafranchian correlation can be assumed for the above occurrences. Stratigraphical information for the L'Aquila Basin can be found in Mancini *et al.* (2012).

– *M. m. depereti* Coppens & Beden, 1982; type locality: Saint-Prest (France). This locality has yielded abundant remains of the southern mammoth, which show more derived dental features than the Upper Valdarno ones, and

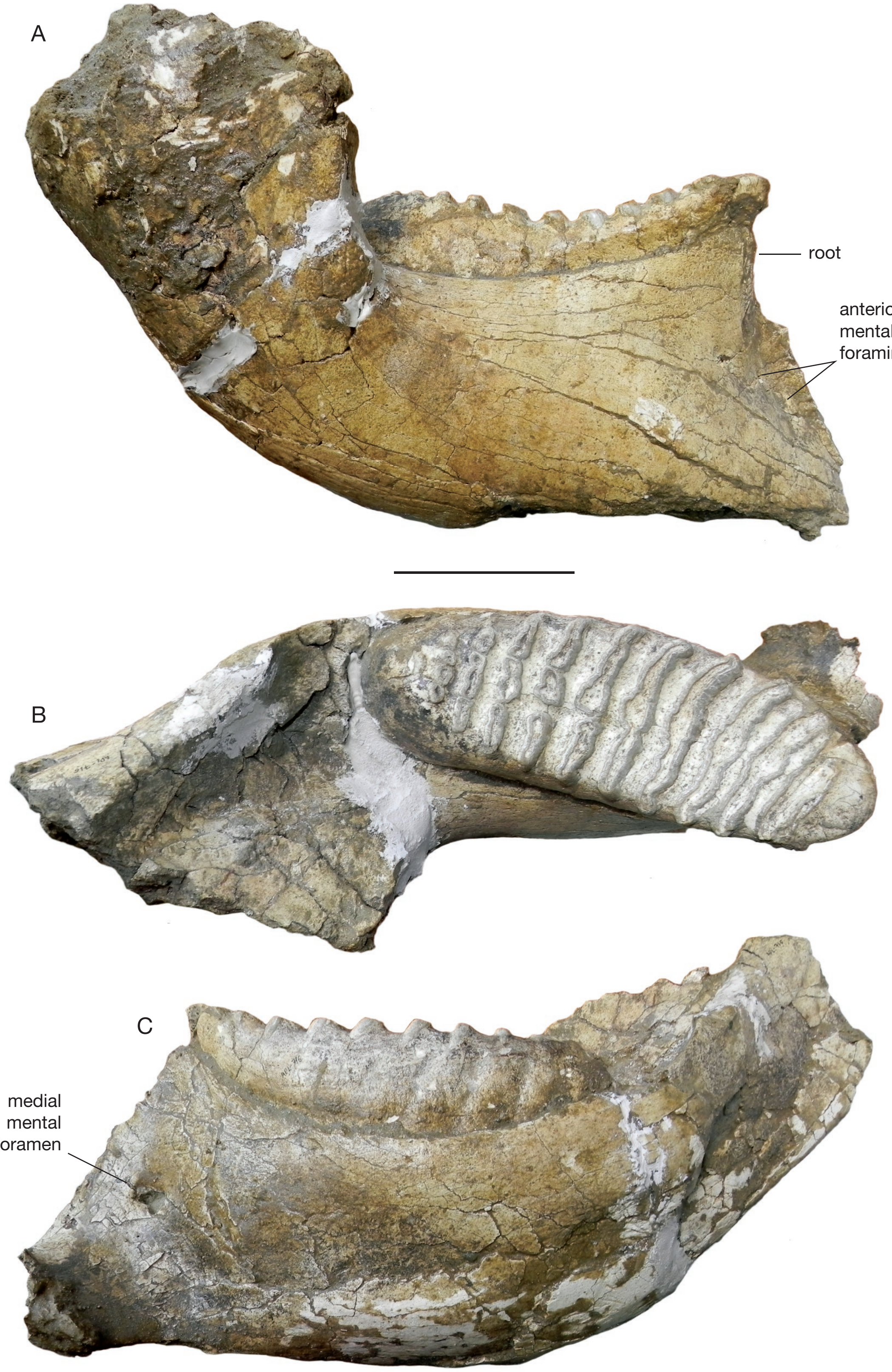

Fig. 4. — Right hemi-mandible with m3 (APL-716) of *Mammuthus meridionalis vestinus* (Azzaroli *in* Ambrosetti, Azzaroli, Bonadonna & Follieri, 1972) from Apollonia-1 in lateral (**A**), dorsal (**B**), and medial (**C**) views. Scale bar: 10 cm.

therefore a new subspecies was erected; the locality is correlated to the Epivillafranchian, at *c.* 1.0-0.9 Ma (Coppens & Beden 1982; Guérin *et al.* 2003; Kahlke *et al.* 2011; Bellucci *et al.* 2015). According to Coppens & Beden (1982) the large skeleton (shoulder height: 3.83 m; Lister & Stuart 2010) from Durfort in France, exhibited in the Muséum

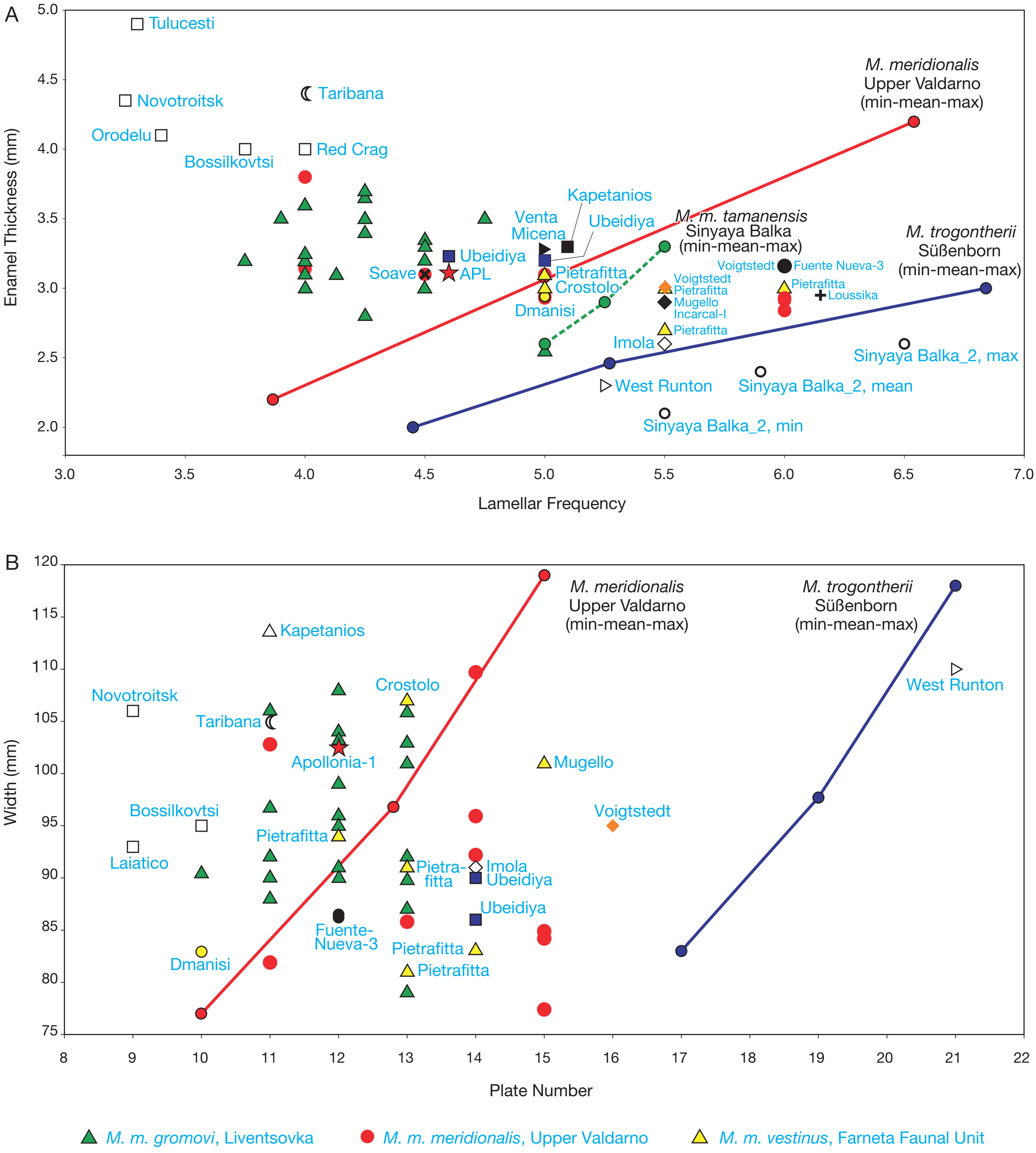

Fig. 5. — Scatter plots comparing LF-ET (**A**) and PN-W (**B**) of the m3 of various mammoth taxa from various localities in Europe. Sinyaya Balka_2 (in **A**) corresponds to the second mammoth taxon with affinities to *M. trogontherii*. Data from references cited in Material and methods.

national d'Histoire naturelle in Paris and described by Gaudry (1893), belongs probably also to this subspecies. The more advanced stage of its molars had been already marked by Gaudry (1893), Depéret & Mayet (1923) and Azzaroli (1977) (note that the skull is mostly reconstructed, and only the tusks and the molars are original [*fide* Osborn 1942; Azzaroli 1977]). Durfort is correlated to the Epivillafranchian, with an age close to that of Saint-Prest (Kahlke *et al.* 2011; Bellucci *et al.* 2015).

– *M. m. tamanensis* (Dubrovo, 1964); type locality: Sinyaya Balka (Taman Peninsula, southern Sea of Azov Region, Russia). This subspecies is best known from its type locality, but material from several other localities is also included (Baygusheva & Titov 2012; Baygusheva *et al.* 2016). Several

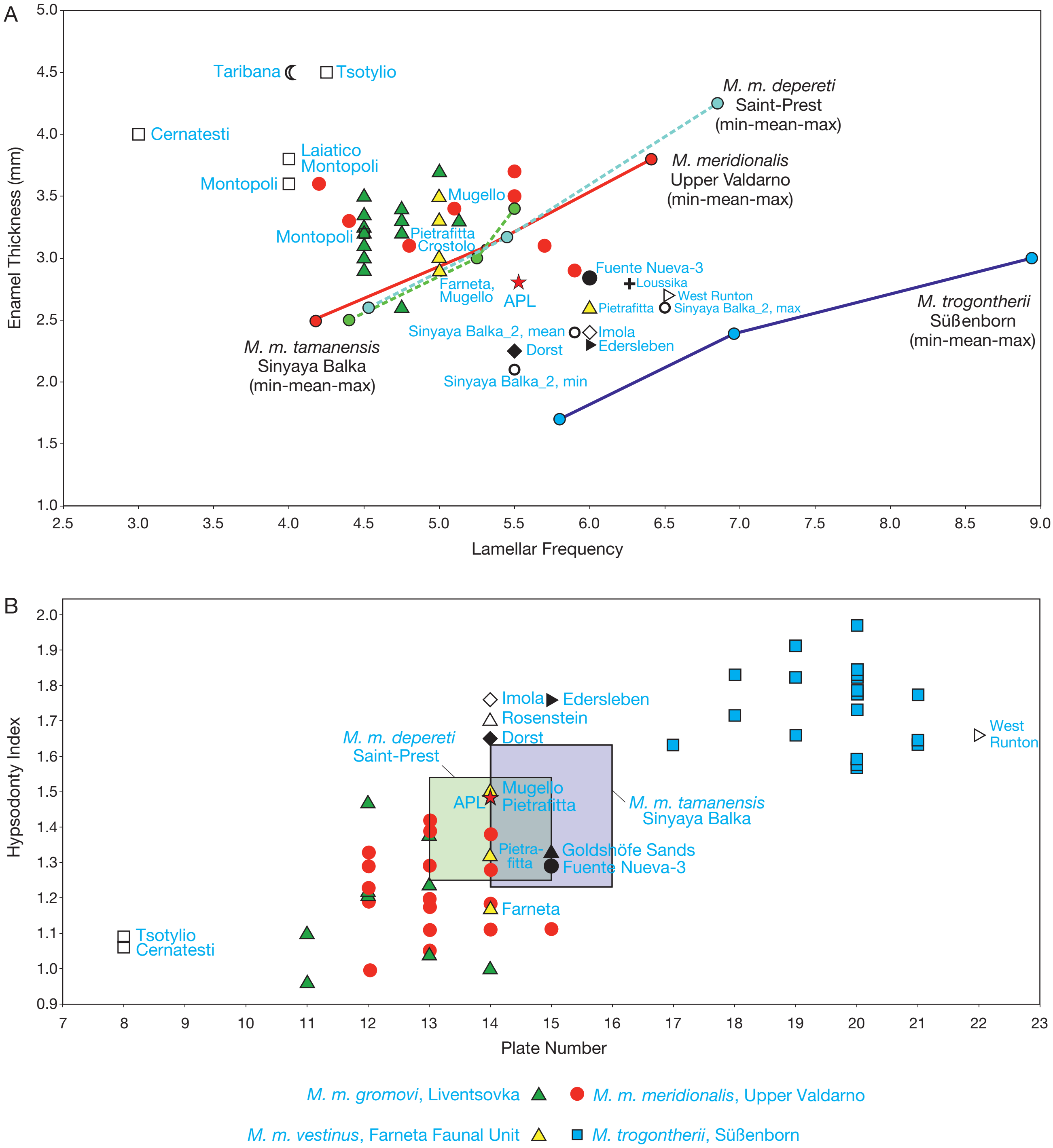

FIG. 6. — Scatter plots comparing LF-ET (**A**) and PN-HI (**B**) of the M3 of various mammoth taxa from various localities in Europe. Data from references cited in Material and Methods; B modified from Lister & Stuart (2010: fig. 19).

researchers have pointed the bimodal distribution of dental features, indicative of the presence of two mammoth taxa, the one attributed to an advanced morph of *M. meridionalis* (*M. m. tamanensis*), the second to a morph with affinities to *M. trogontherii* (Sher 1999; Lister *et al.* 2005; Baygusheva & Titov 2012). Previously regarded as an Epivillafranchian locality, recent research suggests an age not younger than 1.2-1.1 Ma, which in combination with other faunal elements favors a late Villafranchian age, between 1.5-1.2 Ma (Shchelinsky *et al.* 2010, 2016). Mixing of material belonging to different depositional phases, reworking or addition of surface findings should be considered for Sinyaya Balka, and could perhaps explain the presence of mammoths of two different evolutionary stages (Baygusheva & Titov 2012), especially in light of the early age of the locality. The description of new material from the locality will possibly shed light on this issue.

Table 2. — Comparison of the DP2 and DP3 of various Eurasian mammoths. [1], Baygusheva *et al.* (2016); [2], Ros-Montoya (2010); [3], Tong & Chen (2016); [4], Mashenko *et al.* (2006); [5], Maschenko (2002).

	Species	Locality	Age	n	L	W	PN	LF	ET
DP2	*M. meridionalis*	Apollonia-1	late Villafranchian	–	21.9	16.8	4	20.3	1.4
	(Nesti, 1825)	Maglio (1973)	–	2	21.2-22.2	17.9-19.9	3-4	–	–
		Liventsovka (Russia)[1]	middle Villafranchian	–	25.8	20.4	4	–	–
		Liventsovka[1]	middle Villafranchian	–	31.0	29.2	3	12.0	1.0
		Liventsovka[1]	middle Villafranchian	–	32.0	22	4	–	–
		Venta Micena (Spain)[2]	late Villafranchian	–	27.3	22.7	4	–	1.6
		Venta Micena[2]	late Villafranchian	–	24.3	21.1	4	–	1.4
		Venta Micena[2]	late Villafranchian	–	23.4	21.5	4	–	1.4
	M. trogontherii	Shanshenmiaozui (China)[3]	late Early Pleistocene	–	22.7	17.3	4	18.3	–
	(Pohlig, 1885)	Shanshenmiaozui[3]	late Early Pleistocene	–	21.8	16.9	4	18.6	–
		Shanshenmiaozui[3]	late Early Pleistocene	–	26.9	20.9	5	18.9	–
		Shanshenmiaozui[3]	late Early Pleistocene	–	26.5	20.4	5	–	–
	M. primigenius (Blumenbach,	Berelekh, Eliseevichi, Sevsk (Russia)[4]	Late Pleistocene	–	12.6-18.0	11.5-17.8	3-5	–	0.4-0.8
	1799)	several localities in Russia[5]	Late Pleistocene	9-13	15.0-20.5	11.5-17.0	3-6	–	0.5-0.8
DP3	*M. meridionalis*	Apollonia-1	late Villafranchian	–	80.6	> 34	8	10.4	–
		Maglio (1973)	–	2	52.4-63.0	32.2-38.1	5-6	9.7-10.0	1.3-1.4
		Kobiakova Balka (Russia)[1]	middle Villafranchian	–	> 59.5	34.8	6	10.0	0.8
		Kuruksay (Tadzhikistan)[1]	middle Villafranchian	–	> 52	34.8	5	9.0	–
		Georgievsk (Russia)[1]	late Villafranchian	–	> 65	35	6	10.0	1.0
		Venta Micena[2]	late Villafranchian	–	69.6	42.6	6	–	–
		Venta Micena[2]	late Villafranchian	–	65.2	39.9	6	–	–
		Venta Micena[2]	late Villafranchian	–	72.5	36.0	7	–	–
		Venta Micena[2]	late Villafranchian	–	51.9	35.1	7	–	–
		Venta Micena[2]	late Villafranchian	–	59.6	37.3	7	–	–
		Akhalkalaki (Georgia)[1]	Epivillafranchian	–	72.0	42.0	7-8	9.0	0.9
	M. trogontherii	Shanshenmiaozui[3]	late Early Pleistocene	–	62.9	34.2	7	11.1	–
		Shanshenmiaozui[3]	late Early Pleistocene	–	65.7	34.2	7	10.7	–
		Shanshenmiaozui[3]	late Early Pleistocene	–	65.5	37.2	7	10.7	–
		Shanshenmiaozui[3]	late Early Pleistocene	–	–	35.9	6	–	–
	M. primigenius	Berelekh, Eliseevichi, Kostenki XI, Sevsk (Russia)[4]	Late Pleistocene	–	64.7-140.0	48.0-68.0	7-10	–	0.7-1.3
		several localities in Russia[5]	Late Pleistocene	14-15	54.0-67.0	32.0-43.0	7-8	–	0.5-1.0

Several other subspecies, such as *Mammuthus m. voigtstedtensis* (Dietrich, 1965), *M. m. cromerensis* (Depéret and Mayet, 1923), *M. m. jockgrimensis* (Dietrich, 1958), *M. m. uromensis* (Vörös, 1979) and *M. m. nesti* (Pohlig), are considered either that fall within *M. trogontherii* or invalid (Lister *et al.* 2005; Virág 2009; Van Essen 2011).

Comparison of the teeth

In all the scatter plots comparing PN, LF, HI, ET and OA, the APL specimens are clearly outside the range of the *M. trogontherii* sample from its type locality Süßenborn having lower PN, LF and HI values, thicker enamel and more obtuse OA (Figs 5-7). On the other side, the APL molar sample is also different from *M. rumanus*, the latter having lower PN, LF and HI, and higher ET values. The values of all these parameters of the APL molars are plotted comfortably within the range of *M. meridionalis*, showing the diagnostic features of this species (Maglio, 1973; Lister, 1996), and unambiguously indicate an attribution to the southern mammoth, in accordance with the morphology of the APL mandible (see below).

Within *M. meridionalis*, the m3 APL-716 is plotted at the upper LF and lower ET values of *M. m. gromovi* from Liventsovka and within *M. m. meridionalis* from Upper Valdarno, having similar values with Monte Tenda-Soave (Italy) and a molar from Ubeidiya (Israel) (Fig. 5A). Molars from Kapetanios (Greece), Torrente Crostolo, Mugello, Pietrafitta (all Italy and all Farneta FU), Venta Micena and Fuente Nueva-3 (both Spain) and another molar from Ubeidiya have similar ET, but slightly higher LF (5.0-6.0). Compared with the molars from Fuente Nueva-3 and Pietrafitta (PN: 12-13), the APL m3 is longer (albeit the original tooth would have been slightly even longer) and wider (Fig. 5B), but it shows a lower LF.

The M3 APL-686B is plotted at the upper LF and lower ET values of Upper Valdarno, and together with the molars from Farneta, Torrente Crostolo, Mugello, Fuente Nueva-3 and partially Pietrafitta in the region of LF: 5.0-6.0, ET: 2.5-3.5 and PN: 14-15 (Fig. 6A). The Saint-Prest sample shows a wide range in both LF and ET, reaching the mean LF value of *M. trogontherii*, but also the thick enamel of the primitive mammoths. The specimen from Rio Pradella-Imola (Italy), although similar in PN with the APL one, is distinguished both in the higher LF and the lower ET, whereas the Dorst (the Netherlands) mammoth has similar LF, but thinner enamel.

One of the most crucial parameter that has to be examined is the HI, because it can distinguish between relatively primitive (low-crowned) and relatively advanced (high-crowned) molars, and is related with the deepening of the palatine and maxillary region of the cranium (Lister 1996; Van Essen 2011). APL-686B presents slightly higher HI than the sample of *M. m. meridionalis* from Upper Valdarno (Fig. 6B; Van Essen 2003; Lister & Stuart 2010) and from Northern Caucasus (Baygusheva & Titov 2012: table 4), and together with an M3 from Mugello, it falls within the upper range of *M. m. depereti* from Saint-Prest, which has also similar PN. The APL M3 exceeds also the HI of Farneta, Pietrafitta and Fuente Nueva-3. Although its HI is within that of *M. m. tamanensis*, the latter has on average higher PN surpassing also *M. m. depereti*. The similar with the APL in PN M3 from Rio Pradella-Imola and Dorst have clearly higher HI, within the range of *M. trogontherii* (yet the latter has increased PN).

In order to acquire more comprehensive results, we applied a PCA, combining L, W, PN, LF, ET and HI (Fig. 8). PC1 axis, which accounts for the 63.46% of the total variance, separates rather well the species/subspecies and reveals additionally a remarkable chronological distinction. At the negative extreme are located the primitive early Villafranchian mammoths from Cernătești, Tsotylio, Montopoli and Laiatico characterized by high ET values and low PN, LF and HI, whereas at the positive extreme stand the Middle Pleistocene *M. trogontherii* from Süßenborn and West Runton (England), showing high PN, LF and HI, but low ET (Fig. 8). In intermediate position and partially overlapping, are the samples of the middle Villafranchian *M. m. gromovi* from Liventsovka and the late Villafranchian *M. m. meridionalis* from Upper Valdarno, with the former extending towards the negative values and being thus closer to the primitive European mammoths. The post-Upper Valdarno late Villafranchian sample from Farneta FU (*M. m. vestinus*, including Farneta, Pietrafitta, Mugello, Torrente Crostolo) and Fuente Nueva-3, is plotted outside the Upper Valdarno convex hull, as does also the APL one. In this region of the graph is located also the sample from Saint-Prest, which shows great range mostly along PC2 axis, as well as the M3 from Goldshäfe Sands (Germany) and the sample of *M. m. tamanensis*. The M3s from Rio Pradella-Imola, Dorst, Stuttgart-Rosenstein and Edersleben (both latter in Germany) are plotted further to the positive values of PC1 and closer to *M. trogontherii*.

Concerning the deciduous dentition, the eight plates in the DP3 from APL are above the range of 5-6 of *M. meridionalis* provided by Maglio (1973) (Table 2; see also Weithofer [1890: pl. 13, fig. 2, 2a] and Garutt & Baygusheva [1981]). DP3s with high PN are known in *M. primigenius*. Within *M. meridionalis* and *M. trogontherii* (China), the APL specimen is the only so far with this high PN, yet it is also the longest one. However, some DP3s from Venta Micena and Akhalkalaki (Georgia) show also an increase to 7-8 plates (Vekua 1986; Ros-Montoya 2010; Baygusheva *et al.* 2016). The LF is placed between the *M. meridionalis* and *M. trogontherii* samples. Regarding the DP2, the PN and length are within the range provided by Maglio (1973) for *M. meridionalis*, whereas the width is slightly smaller; however, only two specimens were available to Maglio. These values are also close to the DP2 with four plates of *M. trogontherii* from China, although longer DP2 with five plates are also present (Tong & Chen 2016). The DP2 of *M. m. gromovi* are more robust than the APL one (Baygusheva *et al.* 2016), whereas those of *M. primigenius* are smaller and have thinner enamel (Table 2).

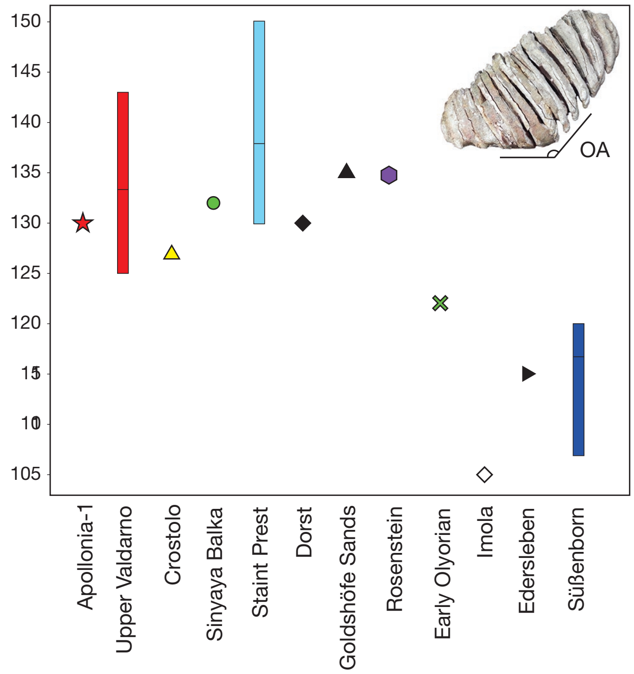

Fig. 7. — Comparison of the occlusal angle (**OA**) of various mammoth taxa from various localities in Europe. Data from Van Essen (2011) and obtained from illustrations from Palombo & Ferretti (2005) and Lister *et al.* (2005).

Comparison of the mandible

Mammoth mandibles (as well as of other recent and extinct elephantids) are characterized by evident intraspecific variability in morphology and dimensions affected mainly by the ontogenetic age and to a lesser degree by sex (e.g., Maschenko 2002; Álvarez-Lao & Méndez 2011; Paunović *et al.* 2017). In particular, studies on woolly mammoth mandibles showed that ontogenetic changes continue during the adult stages, and involve among others, increase in height and width of the corpus, whereas the relation of the greatest length of the mandible with age is statistically insignificant (Álvarez-Lao & Méndez 2011). Therefore, for any taxonomic conclusion, it is of primary importance to compare only mandibles of similar or at least approximate ontogenetic age [e.g., a comparison between the La Salita di Oriolo (Italy; Ferretti 1999) mandible with the m2 moderately worn and the Madonna della Strada with much worn m3 would not provide accurate conclusions]. Moreover, it should be noted that some mandibular features (e.g., outline of the rostral border of the ramus below the coronoid process) are subject to intraspecific variation even in individuals of similar ontogenetic age and sex (Van Essen 2011; Ros-Montoya *et al.* 2018).

There are several anatomical differences among the European mammoth species indicating evolutionary trends within the lineage, the most important of which are related to the

Table 3. — Comparison of the M3 (range and mean values) of various European mammoths: *M. rumanus* (Stefanescu, 1924), *M. meridionalis* (Nesti, 1825) and *M. trogontherii* (Pohlig, 1885). Numbers in parentheses indicate the sample size. [1], Lister & Van Essen (2003), Palombo & Ferretti (2005), Markov (2012), Kostopoulos & Koulidou (2015); [2], Baygusheva & Titov (2012); [3], Van Essen (2011); [4], Palombo & Ferretti (2005); [5], Ros-Montoya (2010); [6], Agostini *et al.* (2012); [7], Lister & Stuart (2010), Lister *et al.* (2012).

		M. rumanus	***M. meridionalis***								***M. trogontherii***
M3		several localities[1]	Liventsovka[2]	Upper Valdarno[3]	APL	Farneta FU[4]	Funte Nueva-3[5]	Madonna della Strada[6]	Saint-Prest[3]	APL, Farneta FU, Fuente Nueva-3 Madonna della Strada	Süßenborn[7]
	min	8	10	12	–	13	–	–	13	13	17
PN	mean	8.7 (6)	11.9 (16)	12.8 (20)	?14	13.8 (5)	15	–	13.8 (5)	14 (7)	19.7 (35)
	max	10	14	14 -?15	–	14	–	–	15	15	22
	min	3	4.5	4.2	–	5.0	–	–	4.53	5.0	5.8
LF	mean	4.1 (7)	4.6 (16)	5.3 (29)	5.5	5.2 (6)	6.0	5.0	5.5 (16)	5.3 (9)	7.0 (54)
	max	4.72	5.1	6.4	–	6.0	–	–	6.36	6.0	8.9
	min	3.0	2.6	2.5	–	2.6	–	–	2.6	2.6	1.7
ET	mean	3.7 (7)	3.2 (16)	3.1 (24)	2.8	3.0 (6)	2.8	3.5	3.2 (10)	3.0 (9)	2.4 (48)
	max	4.5	3.7	3.8	–	3.5	–	–	4.2	3.5	3.0
	min	1.06	0.96	1.13	–	1.17	–	–	1.25	1.17	1.53
HI	mean	1.15 (3)	1.18 (9)	1.28 (15)	1.48	1.4 (5)	1.29	–	1.37 (8)	1.39 (7)	1.77 (29)
	max	1.3	1.47	1.47	–	1.50	–	–	1.54	1.5	2.06

shortening of the skull and the increase in the hypsodonty of the molars (Lister 1996; Ferretti 1999; Lister & Stuart 2010). For the mandible in particular, progressively the corpus became shorter (decrease of the symphysis and rostrum, more upright ramus) and higher (increase in the HI of the molars), the coronoid process lengthened and the condyle was shifted higher (Lister 1996: figs 19.6, 19.9). Therefore, mandibles bearing the m3 in function, such as those from Chagny-Bellecroix and Senèze (both France; both attributed to *Elephas planifrons* by Mayet & Roman 1923: fig. 13: 2, 3), Liventsovka (Garutt & Baygusheva 1981), Chilhac (France; Boeuf 1983, 1990), Upper Valdarno (Azzaroli 1966: fig. 7; 1977: pl. 1, fig. 1) and Georgievsk (Russia; Garutt & Safronov 1965; Garutt 1998) are characterized by the primitive condition having relatively long (with prominent rostrum) and shallow corpora, and sufficiently caudally inclined rami (Fig. 9A-D; see also Lister 1996: fig. 19.6). On the other side, the more derived morphology, that is short (with reduced rostrum) and deep corpora with more upright rami, is present in mandibles of *M. trogontherii*, e.g., from West Runton (Lister & Stuart 2010) and Loussika (Greece; Athanassiou 2012). The degree of the elongation of the symphysis/rostrum, the length of the coronoid process and the position of the condyle cannot be evaluated in the APL mandible. However, the caudal inclination of the ramus of the APL mandible permits its attribution to *M. meridionalis* (Fig. 4). Yet, the mandibular corpus is relatively deep, a more derived trait associated with greater hypsodonty on the molars (Lister 1996). In this trait, it is similar to the mandibles of *M. m. vestinus* from Madonna della Strada (Azzaroli 1966: fig. 5b; Azzaroli 1977; Lister & Stuart 2010; Rossi *et al.* 2017: fig. 1; the rostral part of the symphysis is reconstructed), which belongs to an older individual (with much worn m3) and of *M. m. depereti* from Saint-Prest of approximately similar ontogenetic age (Coppens & Beden 1982) (Fig. 9E-G).

TAXONOMIC AND BIOSTRATIGRAPHIC CONCLUSIONS

The dentognathic remains of the APL mammoth permit its attribution to *M. meridionalis*. The relatively deep mandibular corpus is a derived condition, indicating possibly a rather high HI value. The dental features also indicate an evolutionary stage somewhat more derived than the Upper Valdarno mammoth (beginning of late Villafranchian) in terms of the higher PN in the DP3 (as has been already noted by Athanassiou & Kostopoulos [2001]) and the marginally higher HI in the M3. This is also revealed by the PCA, where several dental parameters are combined, and plot the APL M3 outside the range of Upper Valdarno and towards the more derived specimens (Fig. 8). In these aspects, the APL mammoth fits better with corresponding specimens from localities correlated to the second part of the late Villafranchian and the Epivillafranchian. These results are in agreement with the existing biochronological correlation of the APL fauna and further support the potential biostratigraphic significance of *M. meridionalis* within the Early Pleistocene. Whether this sample should be distinguished at subspecific level and, if so, which would be the proper name is open to discussion. However, the current data, including the APL specimens, show that some morphological/metrical features and especially those of the M3, could allow for a subspecific distinction and may have biostratigraphic importance.

Remarks on *Mammuthus meridionalis vestinus*

The holotype of *M. m. vestinus* is an almost complete skeleton from Madonna della Strada (see also above), described by Maccagno (1962). The skeleton belonged to a male individual with an ontogenetic age 50-55 AEY and shoulder height 3.65 m (Lister & Stuart 2010). According to Maccagno (1962, *fide* Azzaroli [1966]) the skull is different from those of Upper Valdarno: the cranium is very shortened anteroposteriorly and strongly

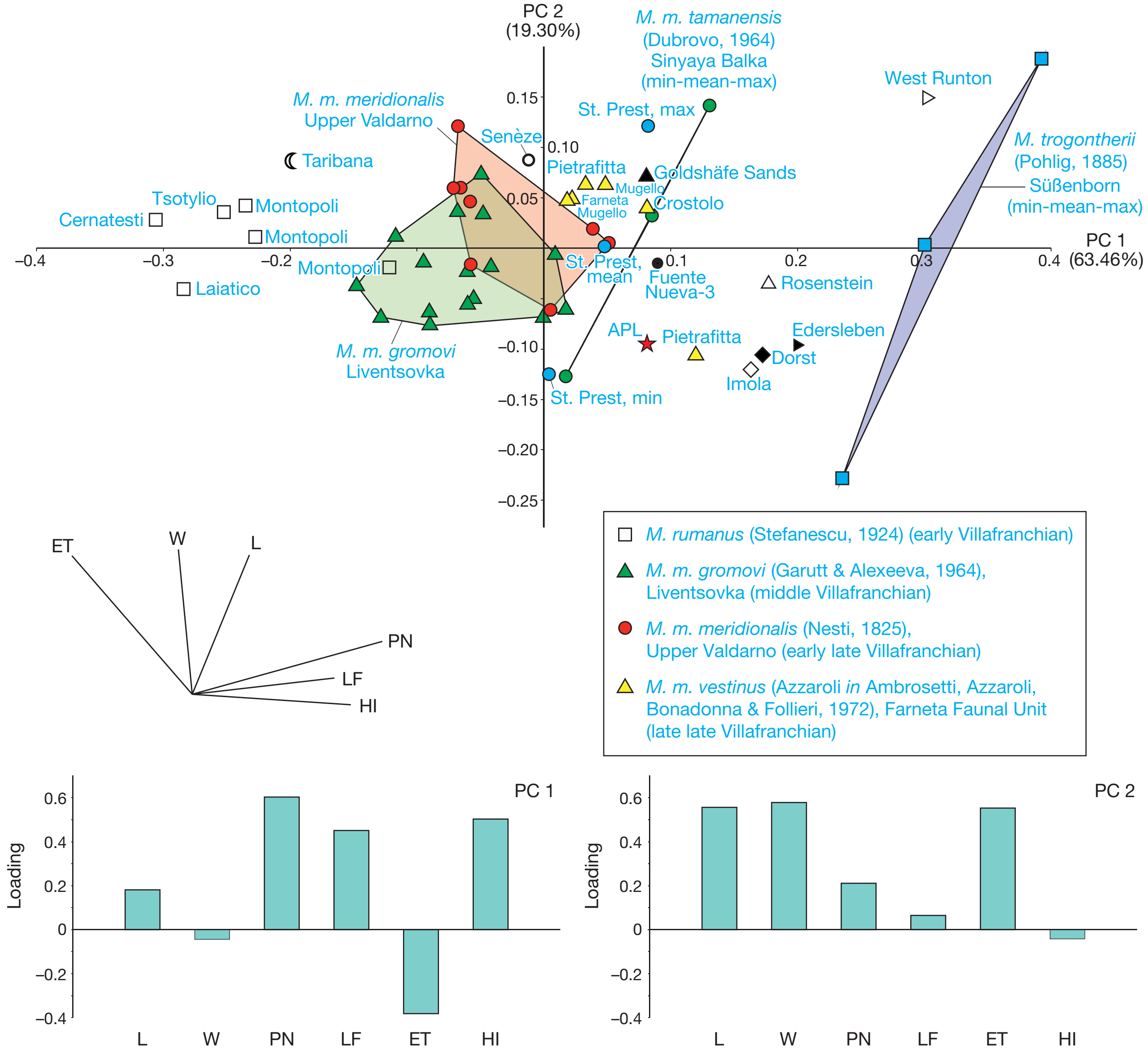

Fig. 8. — Principal Component Analysis (PCA) and loadings of six basic dental features (length, width, number of plates, hypsodonty index, lamellar frequency and enamel thickness) among M3 of various mammoth taxa from various localities in Europe using Mosimann's Log-shape ratio transformation (see "Fossiliferous locality, material and methods" for details). Principal component loadings for the PC1 and PC2 axes are also shown. Data from Maglio (1973; Senèze, Upper Valdarno), Gabunia & Vekua (1963; Taribana), Baygusheva & Titov (2012; Liventsovka and Sinyaya Balka), Van Essen (2003, 2011; Saint-Prest, Goldshäfe Sands, Dorst, Rosenstein), Palombo & Ferretti (2005; Montopoli, Laiatico, Farneta FU localities, Rio Pradella-Imola), Lister & Stuart 2010; Süßenborn), Markov (2012; Cernăteşti), Ros-Montoya (2010; Fuente-Nueva-3), Lister *et al.* (2012; Süßenborn), Kostopoulos & Koulidou (2015; Tsotylio) and V. Titov (pers. com. 2019 for HI of the Sinyaya Balka M3).

developed in height; the temporal fossa has different shape; the occipital condyles are in a more elevated position; the orbit has a different position in regard to the premaxillae and the nasal fossa; the tusk alveoli are close together and parallel; and, the mandible is very short and high. Azzaroli (1977) considering the above features, as well as the long premaxillae and the larger overall size than the Upper Valdarno typical *M. meridionalis*, erected for the Madonna della Strada skeleton the subspecies *M. m. vestinus*. Azzaroli attributed also into this subspecies, material from Mugello and Farneta, including a partial skeleton (age: 40+ AEY, shoulder height: 3.70 m; Lister & Stuart 2010) and two cranial fragments (Azzaroli 1977: pl. 1, fig. 2, pl. 2, fig. 2; Palombo & Ferretti 2005: fig. 4a, b; Cioppi & Mazza 2010: fig. 18.15). According to Ferretti (1999) the latter specimens are concordant with the diagnosis of *M. m. vestinus* in the large size, the strong vertical development, the very concave frontals and the laterally bulging parietals. All the *M. m. vestinus* material of Azzaroli was included by Maglio (1973) to his "*M. meridionalis* Bacton Stage", to distinguish it from the typical "*M. meridionalis* Montevarchi Stage". Later on, Ferretti (1999) assigned to *M. m.* cf. *vestinus* specimens from Pietrafitta, and proposed the affinities of the Monte Tenda-

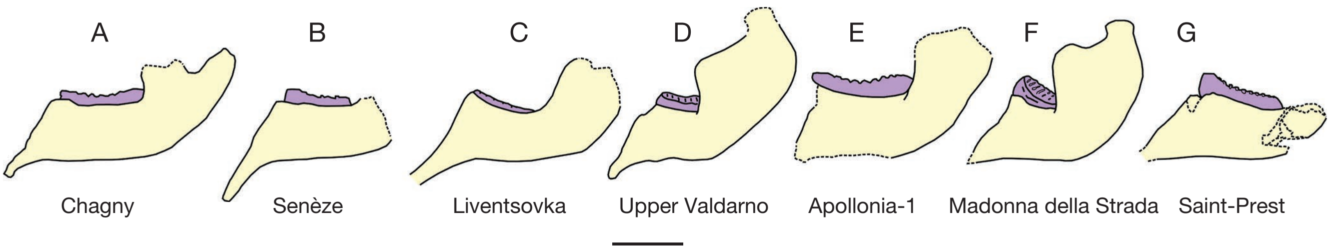

Fig. 9. — Comparison of mammoth mandibles from various localities in Europe in left lateral view: **A**, Chagny-Bellecroix (from Mayet & Roman 1923); **B**, Senèze (from Mayet & Roman 1923); **C**, Liventsovka (reversed, from Garutt & Baygusheva 1981); **D**, Upper Valdarno-Borro al Quercio (from Azzaroli 1966); **E**, Apollonia-1; **F**, Madonna de la Strada (from Azzaroli 1966); **G**, Saint-Prest (from Coppens & Beden 1982). Scale bar: 25 cm.

Soave and La Salita di Oriolo specimens with this subspecies. Ferretti & Croitor (2001) studied the functional anatomy of *M. m. meridionalis* and *M. m. vestinus*, and concluded on the different posture and mobility of the head, which could be related to different feeding habits, with *M. m. vestinus* being possibly a parkland-savanna inhabitant and a high-level feeder. Subsequently, Palombo & Ferretti (2005) questioned the validity of the subspecies, because it does not differ from *M. m. meridionalis* from Upper Valdarno in its dental features and the discrimination between the two subspecies becomes very difficult, if skulls are not available, considering also the certain degree of variability and the limited specimens. Lister & Stuart (2010) marked the more derived morphology of the Madonna della Strada mandible, while Van Essen (2011) considered *M. m. vestinus* a *nomen dubium*, although he acknowledged the marginally more derived dental traits and the more advanced mandibular morphology. A recent restoration of the skeleton led Rossi *et al.* (2017) to conclude that the only differences from the Upper Valdarno crania are the more concave forehead and the very long premaxillae with a deep furrow.

The M3s of the Madonna della Strada skeleton are very much worn, so that the taxonomically important PN and HI cannot be evaluated (their LF and ET are within the Early Pleistocene range). However, the sample from the Farneta FU localities attributed also *M. m. vestinus* (Azzaroli 1977; or to *M. m.* cf. *vestinus* by Ferretti 1999) and that from Saint-Prest of *M. m. depereti* (Coppens & Beden 1982) are very similar in their PN, LF, ET and HI values (Table 3). In these samples fit very well also the specimens from APL and Fuente Nueva-3. On average, all the above specimens show higher values in PN and HI. The similarities are also evident in the PCA, where all specimens from these localities fall outside the convex hull of *M. m. meridionalis* from Upper Valdarno, and towards the positive (more derived) values of the PC1 axis (Fig. 8). Known mandibular specimens from these localities share also the relatively deep corpus (Fig. 9). All the above suggest that they may belong to the same taxon, and that *M. m. vestinus* is valid and likely synonymous with *M. m. depereti*, a possibility that was already hinted by Van Essen (2011). If this is the case, the former has nomenclatural priority, with the latter being a junior synonym. *Mammuthus m. vestinus* (including *M. m. depereti*) is then characterized by the shift towards deepening and shortening of the cranium and the mandible, the very long premaxillae with a deep furrow and the strongly concave forehead of the cranium, the increase in the plates in the DP3, and the increase in its PN and HI values [the most important parameters for distinction according to Van Essen (2011)] in the M3 (Table 3; Fig. 10). This general shift in the M3 is well documented within *M. meridionalis*, from the average PN of 11.9 in *M. m. gromovi* (Liventsovka), to 12.8 in *M. m. meridionalis* (Upper Valdarno) and to 14 in *M. m. vestinus*. Likewise, from the average HI of 1.18 in *M. m. gromovi*, to 1.28 in *M. m. meridionalis* and to *c.* 1.4 in *M. m. vestinus* (Table 3; Fig. 10). We agree with Palombo & Ferretti (2005) that *M. meridionalis* crania are rare in the fossil record and indeed some features of the cheek teeth due to partial overlap are indistinguishable between the subspecies (see e.g., Figs 5, 6), making taxonomic conclusions at the subspecific level difficult or uncertain. However, we believe that it is the combination of the dental features that is proved to be diagnostic, rather than each trait or variable on their own. Indeed, the parameters of the M3 may permit the separation among the mammoth species/subspecies and the evolutionary trend within *M. meridionalis* has biostratigraphic significance (Table 3; Figs 6B, 8, 10). Moreover, isolated M3s (in order to obtain the HI) are relatively frequent in the fossil assemblages. Perhaps also the morphology of the mandible, in particular the heightening and shortening of the corpus, may contribute to this distinction, albeit the intraspecific and ontogenetic variability (Fig. 9). Therefore, in addition to Azzaroli's (Azzaroli *in* Ambrosetti *et al.* 1972; Azzaroli 1977) original diagnosis of the subspecies, based on the cranium and mandible morphology, and the larger overall size, we add here also the combination of dental parameters of the M3 (particularly with increase in the PN and HI values), and possibly also the increase in the PN of the DP3. In conclusion, we believe that *M. m. vestinus* can be recognized as a distinct subspecies in its own right, possibly encompassing *M. m. depereti*, and constitute a useful tool for the Early Pleistocene biostratigraphy (Fig. 11). Nonetheless, due to the partial overlap in the M3 values among the various mammoth taxa, any taxonomic/biochronologic conclusions based on a small sample should be always drawn with caution. Further specimens from this period, ideally cranial material correlated to the Epivillafranchian, but also more dental material that will increase the still relatively limited sample and improve the statistical analysis, are necessary to provide additional information.

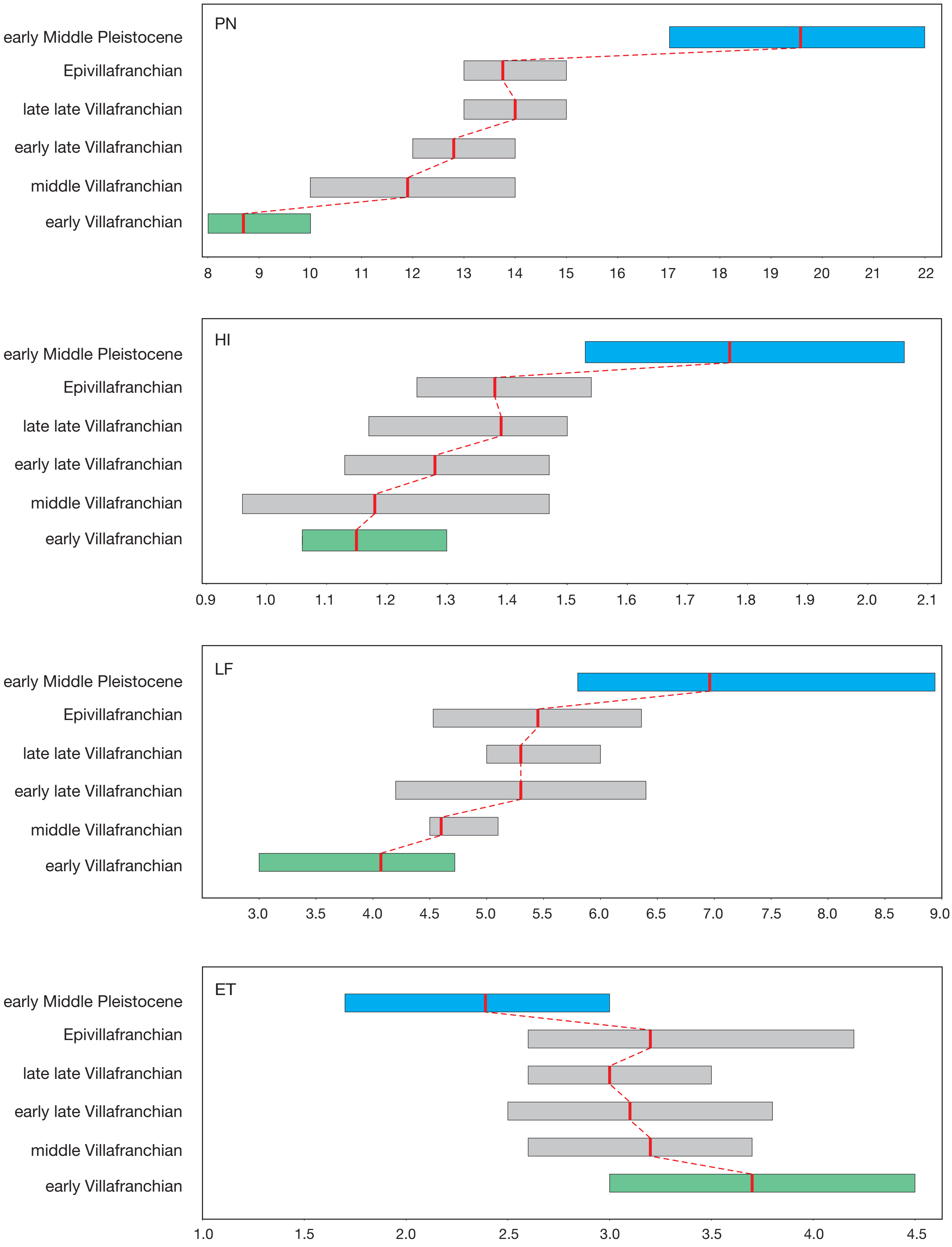

Fig. 10. — Evolutionary changes of the number of plates, hypsodonty index, lamellar frequency and enamel thickness in the M3 from selected *Mammuthus*-bearing localities of Europe. Early Villafranchian (n = 3-7): Tsotylio, Cernăteşti, Montopoli, Red Grag; middle Villafranchian (n = 9-16): Liventsovka; early late Villafranchian: Upper Valdarno (15-29); late late Villafranchian (n = 7-9): Farneta FU, Madonna della Strada, Fuente-Nueva-3, Apollonia-1; Epivillafranchian (n = 5-16): Saint-Prest; early Middle Pleistocene (n = 29-54): Süßenborn. Data from references cited in Table 3.

Mammuthus m. tamanensis from Sinyaya Balka is close to *M. m. vestinus*, as has been already noted by Baygusheva & Titov (2012). As similar conclusion was also drawn by Van Essen (2011) for the case of *M. m. depereti* and *M. m. tamenensis*. The current data indicate that the latter subspecies has added on average one additional plate from *M. m. vestinus* (including *M. m. depereti*) and two from the Upper Valdarno *M. m. meridionalis* (*c.* 15 in m3/M3, reaching 16 plates in M3 and 17 in m3) and achieved higher HI upper values (> 1.6 in m3/M3) (Sher 1999; Baygusheva & Titov 2012). Nonetheless, the mammoth sample from Sinyaya Balka belongs to old collections, including also a second (more derived) mammoth (see above). Therefore, the discovery and study of new, stratigraphically controlled material from the locality will help to define the exact range of the subspecies' values, and clarify the relationships and the degree of differences (if any) between *M. m. vestinus* and *M. m. tamanensis*. Pending new data, it is better for the moment to retain them as distinct taxa.

BIOCHRONOLOGICAL AND BIOSTRATIGRAPHICAL REMARKS

The *M. m. meridionalis* sample from Upper Valdarno lacks precise stratigraphic information, but is collectively correlated to the beginning of the late Villafranchian (Olivola and Tasso FU) with an estimated age between *c.* 2.0 and *c.* 1.7 Ma (Napoleone *et al.* 2003; Palombo & Ferretti 2005; Rook & Martínez-Navarro 2010). The occurrences of *M. m. vestinus* in the Farneta FU localities (*c.* 1.7-1.5 Ma; Napoleone *et al.* 2003; Rook & Martínez-Navarro 2010) and in Saint-Prest (*c.* 1.0 Ma; Guérin *et al.* 2003) indicate that the biostratigraphic range of the subspecies covers the second part of the late Villafranchian and the Epivillafranchian (see below; Fig. 11).

The replacement of *M. meridionalis* by *M. trogontherii* in Europe took place during post-Jaramillo–pre-Brunhes times (Lister *et al.* 2005; Van Essen 2011; Ros-Montoya *et al.* 2018). However, the mode and the exact time of this replacement are not totally clear, both due to the possible complex pattern of replacement, but also due to the unsecure dating of several pivotal localities. Crucial into this discussion of the last appearances of *M. meridionalis* are the samples from La Salita di Oriolo and Goldshöfe Sands, which both show clear "meridionaloid" features in their cranial, mandibular and dental morphology. Specimens from the former locality include a partial cranium with the tusks and the associated mandible with the m2s (Ferretti 1999). According to Muttoni *et al.* (2011) the locality correlates to post-Jaramillo–pre-Brunhes, whereas Toniato *et al.* (2017) suggest an early Brunhes correlation, an age when *M. trogontherii* was already present in Europe, as the data from Kostolac, Voigtstedt and West Runton indicate [but see Lister & Stuart (2010) for teeth from old West Runton collections]. Specimens from Goldshöfe Sands include a mandible with the m3 and upper M3 (Adam 1953; Van Essen 2011). The correlation of the locality is not secure, but possibly dates close to the Matuyama/Brunhes boundary (Van Essen 2011).

Apart from the aforementioned *M. meridionalis* occurrences, there are mammoth specimens from several localities of the post-Jaramillo–pre-Brunhes times, that appear to be intermediate/mosaic. Examples of these are the specimens from Rio Pradella-Imola and Dorst, dated close to the Early/Middle Pleistocene boundary (Kahlke *et al.* 2011; Ros-Montoya *et al.* 2018), and Stuttgart-Rosenstein, whose correlation is not secure, but possibly as in the case of Goldshöfe Sands, close to the Matuyama/Brunhes boundary, although age differences between the latter two localities are possible. The OA is "meridionaloid" for Dorst and Rosenstein, whereas "trogontherioid" for Rio Pradella-Imola (Fig. 7). However, all of them are characterized by low (primitive) PN, but high (derived) HI within the range of *M. trogontherii* from Süßenborn, implying a more "trogontherioid" cranium (Fig. 6B; Van Essen 2011). The combination of low PN with high HI (associated also with a low OA) is present in the M3 of the possible *M. trogontherii* from Edersleben, suggesting that the samples from Rio Pradella-Imola, Dorst and Rosenstein [attributed to "*M. meridionalis* advanced" by Lister *et al.* (2005) and Palombo & Ferretti (2005), and to *Mammuthus* sp. in Ros-Montoya *et al.* (2018)] could alternatively belong to *M. trogontherii* [Van Essen (2011); note that Maglio's (1973) lower range of the M3 PN for *M. trogontherii* is 14, yet he did not mention the origin of the specimens].

The earliest *M. trogontherii* is documented in China during the Early Pleistocene, at *c.* 1.7-1.6 Ma (Wei *et al.* 2010). From there, the species dispersed to the East, where it is recorded in the early Olyorian of Siberia, at 1.2-0.8 Ma (Sher 1986; Lister *et al.* 2005). Both the Chinese and Siberian samples are characterized by high HI values and PN > 17, that is higher than the mosaic specimens from Rio Pradella-Imola, Dorst and Rosenstein. This could possibly provide support to the scenario of a migration of *M. trogontherii* into Europe during post-Jaramillo–pre-Brunhes times and perhaps interbreeding with the local populations of *M. meridionalis* (Lister *et al.* 2005; Van Essen 2011). The earliest secure occurrence of "true" *M. trogontherii* in Europe is pre-Brunhes and is traced at 0.8 Ma in Kostolac (Serbia) (Fig. 11; Lister *et al.* 2012; Muttoni *et al.* 2015). Of approximately similar age is also Dorn-Dürkheim 3 (Germany; Franzen *et al.* 2000), whose sample includes both *M. meridionalis* and *M. trogontherii* due to reworking (Van Essen 2011). *Mammuthus trogontherii* is afterwards well documented during the early Brunhes in West Runton, Voigtstedt and Süßenborn (Stuart & Lister 2010; Kahlke *et al.* 2011).

Overall, the current evidence indicates that *M. meridionalis* existed until the Epivillafranchian as the samples from Saint-Prest, Durfort and Huescar-1 (Spain; Ros-Montoya *et al.* 2018) indicate (Fig. 11), while a penetration into the early Middle Pleistocene and a (temporal/geographic) co-existence for a short period with *M. trogontherii* cannot be excluded (depending on the precise age of La Salita di Oriolo, Goldshäfe Sands and the origin/dating of the West Runton old collection sample); possible genetic mixing between the two mammoth species is also likely for some populations. *Mammuthus trogontherii*, of Asian origin, entered Europe close to the Early/Middle Pleistocene boundary, thus roughly at the same time as the arrival of palaeoloxodont elephants (*Palaeoloxodon*)

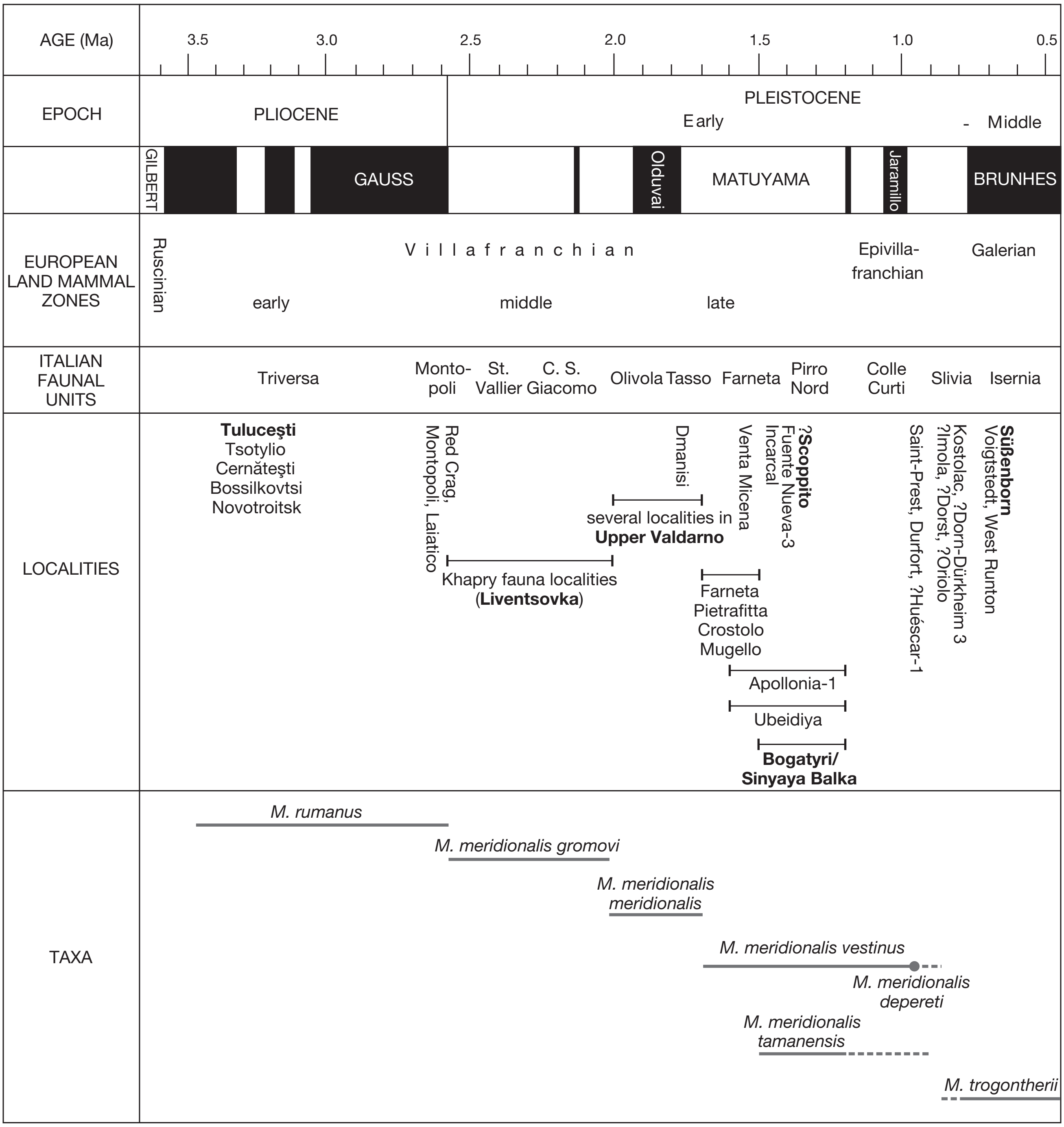

Fig. 11. — Biochronological and biostratigraphical distribution of Early-early Middle Pleistocene *Mammuthus* in Europe and chronology of selected localities mentioned in the text (in **bold** the type localities). Data from references cited in the text.

in Europe coming from Africa, representing thus both new Galerian megafauna immigrants (Palombo & Ferretti 2005; Saegusa & Gilbert 2008; Palombo 2014; Muttoni *et al.* 2018).

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