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Relative chronology of Late Pliocene and Early Pleistocene mammoth-bearing localities in Hungary

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(with 3 figures, 1 table and 1 plate)

Present study provides a comprehensive picture of the major Late Pliocene and Early Pleistocene mammoth-bearing localities of Hungary and places them within the framework of the early evolution of *Mammuthus* lineage in Eurasia. The evolutionary scenery is discussed from the biozone MN16 with the earliest representatives of the lineage in Hungary (i.e. *M. rumanus* from Ócsa and "primitive" *M. meridionalis* from Aszód) to the *M. meridionalis*-*M. trogontherii* transition around the Early-Middle Pleistocene boundary (i.e. Üröm-hegy with a specimen, which shows mosaic tooth morphology). In addition, the relationship between the geological age and four standard morphometric characters measurable on the molars (i.e. plate number, hypsodonty index, lamellar frequency and enamel thickness) were analysed. Similarities of the local evolutionary changes with the European patterns were pointed out. Reliable age estimates can be made for mammoth-bearing localities on the basis of the morphometric data presented in the article.

Introduction

The emergence of the family Elephantidae from Miocene gomphotheres reflects a major adaptive shift in their method of chewing, probably as a response to shifts in habitat utilization during the Pliocene and the Pleistocene. The accelerating evolution of the shearing ability of the molars at the expense of the grinding capabilities triggered a series of morphological changes. The increasing plate number resulted in denser packing of the lamellas. To maintain the appropriate cement-enamel-dentine ratio of the occlusal surface, the enamel and the enclosed dentine became increasingly thinner. The more rapid abrasion of the thinner enamelled teeth of later elephants and mammoths was compensated by the increasing height of the molars (Fig 1.).

As a consequence of the aforementioned evolutionary trends the molar morphology of the consecutive *Mammuthus* chrono-species differs from each other. The differences on the one hand have taxonomic implications, on the other hand offer a basis of a stratigraphic scheme for the latest Pliocene and Pleistocene. In other words, fossil deposits can be dated – within limits – based on the evolutionary pattern of mammoth molars.

The present study aimed to collect tooth morphological and geochronological data from major Hungarian Late Pliocene and Early Pleistocene mammoth-bearing localities. With the placing of these data in the context of the evolution of Eurasian mammoths, similarities of the local patterns with the regional one can be tested.

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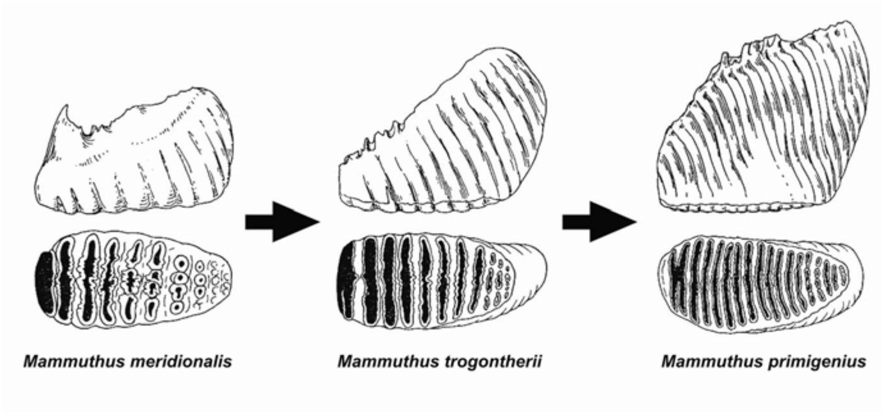

Fig. 1. The evolution of the upper third molar within the *Mammuthus* lineage (modified from THENIUS 1969).

Material and Methods

Standard morphometric measurements (see below) were taken on molars referable to the genus *Mammuthus* stored in two great collections in Budapest (GIH = Geological Institute of Hungary, HNHM = Hungarian Natural History Museum). The examined specimens are from nine Hungarian localities. In addition, three molars embedded in the freshwater travertine at Dunaalmás (more specifically at Leshegy) were studied in situ. Letter "m" followed by a number in subscript was used for indicating the exact positions of the lower molars. Letter "M" with a superscript number concerns to upper molars.

Aszód: M^3, HNHM V.59.1120; M^3, HNHM V.82.6. m_2 dext; HNHM V.64.903.

Ercsi: M^3 sin., GIH Ob-230; M^1 dext., GIH Ob-231; m_3 sin., GIH Ob-953A; m_3 sin., GIH Ob-953B.

Kisláng: m_3 dext., GIH 10306; m_3 sin., GIH 10307; m_3 sin., GIH 10309 and 10310; m, GIH 10311; M^3 sin., GIH 10313; m, GIH 10315; M2 dext., GIH 10316; m3 dext., GIH 10317; m3 dext., GIH 10318; m_3 sin., GIH 10319; M^3 dext., GIH 10320; M, GIH 10321A; m_3 sin., GIH 10321B; m_3 sin., GIH 10322; M^2 dext., GIH 10323; M, GIH 10325; M, GIH 10326; m, GIH 10328; ?, GIH 10329; M, GIH 10330; M^3 sin., GIH 10331; m, GIH 10332; ?, GIH 10333; m_3 dext., GIH 10334; M, GIH V.13343A; M, GIH V.13343B; m, GIH V.13343C; M, GIH 29/14; m, GIH V.13340B; m, GIH V.13343D; m, GIH V.13343E; m, GIH V.13346B; M, GIH V.13347A; M, GIH V.13347B; ?, GIH V.13336; ?, GIH V.13338; ?, GIH V.13340A; ?, GIH V.13341; ?, GIH V.13342; ?, GIH V.13344A; ?, GIH V.13344B; ?, GIH V.13344C; ?, GIH V.13344D; ?, GIH V.13344E; ?, GIH V.13345; ?, GIH V.13419; ?, GIH V.13434; ?, GIH V.13435; ?, GIH V.13436.

Mezőkomárom: M^3 sin., GIH Ob-2899; m_3 sin., GIH Ob-2900.

Ócsa: m_3, without inventory number, stored in the collection of the HNHM.

Süttő: m, HNHM V.72.113.

Szabadhídvég: M^3 sin., GIH Ob-1768; m_3 dext., GIH Ob-1769; m_3 dext., GIH Ob-1770; m_3 sin., GIH V. 11135.

Szomód, Csúcsoshegy: m3 sin., HNHM 75.35.1; m3 dext., HNHM V.82.49.; M, HNHM V.82.50; m, HNHM V.88.11.

Üröm-hegy: M^3 sin., HNHM V.72.116.

The method for measuring morphological parameters of elephantid molars is based on the methods of MAGLIO (1973) and BEDEN (1979). These methods were later adapted and modified by other authors (e.g. van den BERGH 1999; van ESSEN 2003). The measurements were performed with digital calipers with a precision of 0.3 millimeters. The biometrical parameters used in this paper (Fig. 2.) are the following:

P: Number of plates (or lamellae) present in one molar. A dash (–) in front or behind the plate number indicates the incompleteness of the molar. If a plate is incompletely preserved, $^1/_2$ or $^1/_4$ is put in front or behind the plate number. Posterior and anterior talons and platelets are not counted; they are indicated with "x". The estimated number of plates missing is given between brackets if possible. The estimation can be based on the alveolar outline or on the extent of loss of the first root. Thus

$(x?2)^{1}/_{2}7x$ means that, of a molar fragment with 8 plates (the first of which is broken) and a posterior talon or platelet remaining, two plates and possibly an anterior talon are lacking at the front.

L_m: Maximum length of the molar, measured along the longitudinal axis, perpendicular to the planes of the intermediate plates.

W_m: Maximum width of the molar, measured on the widest plate of the molar, parallel to the anterior and posterior surfaces of the plate. To avoid bias it is better to measure Wm without the cover cement.

H_m: Maximum height of the molar, measured vertically on the lateral side of the highest plate, between the crown base (the lateral-basal enamel extreme of the plate) and the apices of the digitations. Values taken on slightly worn plates are indicated with "+" behind the measured value.

H_m/W_m: Hypsodonty index (or relative crown height) represents the ratio of the maximal height and the maximal width.

LF: Laminar frequency represents the number of plates that occur within 10 cm along the longitudinal plane of the molar. The LF values were obtained by measuring the distances between at least two valley separating three or more plates, both on the lingual and buccal side of the molar. If these distances (expressed in millimeters) are indicated with d_l (lingually) and d_b (buccally), and the number of plates between the two measuring points with n, than the LF was calculated using the formula: $LF=(100n/d_l+100n/d_b)/2$.

ET: Enamel thickness is measured perpendicular to the anterior or posterior enamel surface of molar plates. Within one molar the enamel thickness is not constant and maximum and minimum value are given if possible. As the enamel usually decreases in thickness towards the base of the plates, only those measurements are included, which could be taken in plates that are worn less than two-thirds. In unworn but broken molar fragments the ET could be obtained on vertical broken enamel surfaces.

The P, H_m/W_m, LF and ET measurements are summarized in Table 1. Measurements on incomplete molars or bones are followed by "+", indicating that the value of the original element was larger than the recorded value. If a measurement represents an estimated value, that value is succeeded by "e".

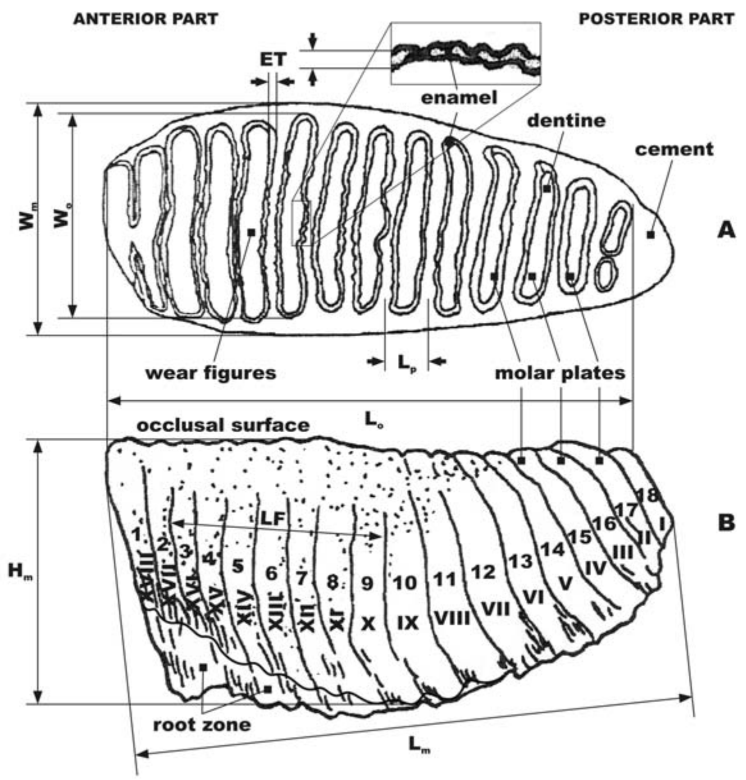

Fig. 2. Terminology and measurements of mammoth molars (further explanation in the text) (modified from FORONOVA 2007). Legend: A = m_3 in occlusal view, B = m_3 in buccal view, L_m = maximum length of the molar, L_o: maximum length of the occlusal surface, L_p: average length of a single plate, W_m: maximum width of the molar, W_o:

maximum width of the occlusal surface, H_m: maximum height of the molar, LF: lamellar frequency on 100 mm, ET: enamel thickness. Molar plates are marked with Arabic numerals when counting from anterior in posterior direction and with Roman numerals when counting from posterior in anterior direction, as indicated in fig. B.

Table 1. Summary statistics of P, H_m/W_m, LF and ET of mammoth molars from various Hungarian localities.

Site	**Age**	**P (for third molars)**			**H_m/W_m**			**LF**			**ET**		
		n	mean	range	n	mean	range	n	mean	range	n	mean	range
Ócsa	late MN16	1	7+ 9e		1	0.95+ 1.14e		1	3.5		1	2.45	2.03-2.66
Aszód	late MN16				3	1.1	1.0-1.3	3	4.2	4.0-4.4	3	3.95	3.8-4.0
Dunaalmás, Leshegy	early MN17							3	4.9	4.4-5.6	3	3.7	3.2-4.2
Szabadhídvég	early MN17	3	11	11-12	2	1.0	0.97-1.02	4	4.7	3.9-5.9	4	3.4	3.25-3.6
Szomód, Csúcsoshegy	early MN17	1	14		3	1.47	1.38-1.69	4	4.9	4.6-5.4	4	3.4	3.2-3.6
Süttő	late MN17				1	1.02		1	4.7		1	3.18	3.16-3.20
Kisláng	late MN17	3	13	12-13	13	1.2	1.07-1.38	34	5.3	4.3-7.2	49	3.0	2.6-3.2
Ercsi	late MN17				3	1.17	1.08-1.27	4	5.3	4.2-5.8	4	2.9	2.6-3.2
Mezőkomárom	Early Pleistocene	1	11+		2	1.13	1.09-1.16	2	5.8	5.6-6.0	2	2.7	2.6-2.8
Ürömhegy	0.8-0.7 Ma	1	15+ 17e		1	1.5+ 1.65e		1	6		1	3.2	3.1-3.4

The earliest mammoths in Eurasia and their representatives in Hungary

Elephantids referable to genus *Mammuthus* had entered Europe, apparently from Africa, not later than 3 Ma. Members of the earliest evolutionary stage (namely *M. rumanus*) spread across Europe and eastwards to China (LISTER et al. 2005).

The name "*rumanus*" was originally applied as "*Elephas antiquus rumanus*" to an incomplete upper third molar (M^3) from Tuluceşti (Romania) by ŞTEFĂNESCU (1924). OSBORN (1942) referred to the same specimen as "*Archidiskodon planifrons rumanus*". Following the trend for assimilating all early mammoths within the genus *Mammuthus*, RADULESCU & SAMSON (1995, 2001) referred to it as *Mammuthus rumanus* (see LISTER & van ESSEN 2003 as well as LISTER et al. 2005 for a detailed discussion).

The holotype specimen has a very primitive morphology when compared to later mammoth taxa. The plates are very widely spaced, the lamellar frequency (LF) is somewhere between 3 and 4 and the total plate count (P) cannot have been more than 9-11 according to ATHANASIOU (1915) or 9-10 according to LISTER & van ESSEN (2003). The maximum length of the molar (L_m) cannot have been more 300 mm considering the estimation of LISTER & van ESSEN (2003).

On the basis of the fragmentary nature of the holotype, LISTER & van ESSEN (2003) proposed a complete lower third molar (m_3) from Cernăteşti (Romania) as a neotype of the taxon. The maximum length of the neotype is 293 mm. The lamellar frequency is extremely low (3.07), the tooth probably had maximum 8 or 9 plates. The tooth crown is low; the hypsodonty index (H_m/W_m or HI) is 1.18. The average thickness of the enamel (ET) is 4.25 mm.

On the basis of the associated mammalian fauna (which includes e.g. *Mammut borsoni* and *Anancus arvernensis*) RADULESCU & SAMSON (1995, 2001) placed Tuluceşti and Cernăteşti in the mammalian biozone MN16a.

In addition to the aforementioned localities, LISTER & van ESSEN (2003) and LISTER et al. (2005) referred some material from the Red Crag Formation (Great-Britain), from Montopoli and Laiatico (Italy) to the above described taxon and reported some primitive molars from the sediments of the Mazegou and Youhe Formations in the Yushe Basin (China). PALOMBO & FERRETTI (2005) regarded the Montopoli material as an early form of *M. meridionalis*, although they noticed its more primitive morphology than the typical form. The age of these localities can be correlated with the biozone MN16.

MARKOV & SPASSOV described primitive mammoths referable to *M. rumanus* from Bossilkovtsi (Bulgaria). The latter MN16 locality provided a mandible with both m_3. The plate number of the molars (P) is 10, the lamellar frequency (LF) is approximately 3.75 and the enamel thickness (ET) is 4 mm. Both molars are 260 mm long (L_m), 95 mm wide (W_m).

A tooth similar to the above described specimens was reported by GASPARIK (2010) from the gravel-pit of Ócsa (Hungary). The specimen is a lower left m_3 (?) of a *Mammuthus rumanus* (Pl. 1/A-B). The lamellar frequency is remarkably low (LF = 3.5). The estimated length (L_m) of the teeth is 240 mm or less within which probably 8 or plausibly 9 full plates could have been accommodated. Any longer value would create an unnatural shape. The maximal width (W_m) of the molar is 101 mm and the worn height is 96 mm, therefore the hypsodonty index of the original tooth (W_m/H_m) must have been more than 0.95. Probably it was approximately 1.14 taking into account to the estimated 115 mm for the maximum height (H_m). Nevertheless despite the listed similarities, the average enamel thickness (ET = 2.45 mm, range = 2.03-2.66 mm) is unusually thin for a typical early representative of the mammoth lineage. In fact the measured value is thinner than that in the case of *M. meridionalis* and even some *M. trogontherii* teeth. The co-occurrence of the above aforementioned molar with *Mammuthus meridionalis*, *Mammut borsoni* and *Anancus arvernensis* remains suggests the late MN16 age of the Ócsa locality (GASPARIK 2010).

Early Pleistocene mammoth-bearing localities of Hungary in the light of the evolution of *Mammuthus meridionalis*

In the interval between 2.6 and 2.0 Ma, *M. rumanus* was replaced by mammoths which were dentally more advanced (*M. meridionalis* and its early representatives), but the details of this transition, including the question of where and how it occurred, are unknown (LISTER et al. 2005). The latter taxon was defined by NESTI (1825) on the basis of material from the 2.0-1.75 million years old fluvio-lacustrine deposits of Upper Valdarno (Italy).

ALEXEEVA & GARUTT (1965) created the species "*Archidiskodon gromovi*" for early mammoth material from the Khapry faunal complex, especially from Liventsovka (Russia). TITOV (2001) placed the latter locality in biozone MN17 (c. 2.6-2.2 Ma), which means that these remains are intermediate in age between *M. rumanus* and typical *M. meridionalis*. LISTER & van ESSEN (2003), LISTER et al. (2005) and PALOMBO & FERRETTI (2005) shared the opinion that the type material from Khapry (with even 12-14 full plates on third molars and with 1.2 as average relative crown height) actually does not differ in the key features significantly from *M. meridionalis*, and should be considered as a junior synonym of the latter. However in lamellar frequency and enamel thickness, the Khapry teeth are slightly more primitive than *M. meridionalis* from Upper Valdarno, but these features alone are insufficient for taxonomic separation. Nevertheless fossils from various other localities in Europe have been referred to this taxon. AZZAROLI (1977) for example interpreted the specimens from Laiatico and Montopoli as "*A. gromovi*". In contrast, MAGLIO (1973) included the remains from the latter two localities in his "Laiatico Stage" of *M. meridionalis*, the earliest of three stages into which he subdivided that species, while LISTER & van ESSEN (2003) and LISTER et al. (2005) referred some of these specimens as *M. rumanus* (see above).

According to GASPARIK (2010) there are four other localities (namely Aszód, Süttő, Kisláng and Ercsi) in Hungary besides Ócsa where the co-occurrence of *Mammut borsoni* or *Anancus arvernensis* or both with the early representatives of genus *Mammuthus* suggests similar age (late MN16 or MN17) as in the case of Khapry. VÖRÖS (1985, 2004) described "*A. gromovi*" specimens from Aszód and later in addition from Szomód and from the open-cast lignite mine at Visonta.

Two incomplete M^3 (Pl. 1/F-G) and a lower right m_2 (Pl. 1/D-E) from Aszód were available for the present study. The molars showed primitive *M. meridionalis* morphology with low crown (H_m/W_m = 1.0 for both M^3 and 1.3e for the m_2) moderately low lamellar frequency (LF = 4.0 and 4.2 for the two M^3, 4.4 for the m_2) and thick enamel (ET = 3.8-4.0 mm).

Two m_3 and two molar fragments from Szomód (more specifically from Csúcsos-hegy) showed slightly more derived morphology with greater LF (mean = 4.9, range = 4.6-5.4) and thinner enamel (mean = 3.4 mm, range = 3.2-3.6 mm). The relative crown height varied between 1.38-1.69 with 1.47 as an average. A complete third lower right molar had 14 plates.

In addition, from the gravels of Szabadhídvég (Hungary) three m_3 and one M^3 were examined. The observed plate number (11-12), the lamellar frequency (mean = 4.7, range = 3.9-5.9), the enamel thickness (mean = 3.4 mm, range = 3.25-3.6 mm) and the relative crown height (mean = 1.0, range = 0.97-1.02) was similar than the material from Szomód.

Three molars with similar morphology, embedded in the freshwater travertine at Dunaalmás, Leshegy (Hungary) were studied in situ. The ET varied between 3.2-4.2 mm with 3.7 mm as an average, and the LF ranged between 4.4-

5.6 with 4.9 as an average. The preliminary result of the cosmogenic nuclide (Be, Al) burial dating of the quartzite gravel of the same site is c. 2.9-2.4 Ma (Zsófia RUSZKICZAY-RÜDIGER, pers. comm., 2010), namely late MN16 or early MN17.

The material from Süttő (1 molar), Kisláng (49 molars) and Ercsi (4 molars) showed slightly more derived morphology than the latter localities and therefore did not differ significantly from typical *M. meridionalis*. According to GASPARIK (2010) late MN17 age is plausible for these localities.

The hypsodonty index of the Ercsi material varied between 1.08-1.27 (mean = 1.17), the LF ranged from 4.2 to 5.8 (mean = 5.3), and the ET varied between 2.6-3.2 mm with 2.9 mm as an average. The relative crown height of the Kisláng material ranged from 1.07-1.38 (mean = 1.2), the lamellar frequency varied between 4.3-7.2 with 5.3 as an average, while the average ET was 3.0 mm (range = 2.6-3.2 mm). Only one molar was studied from Süttő. The hypsodonty index of the molar was low (1.02), the plate frequency was 4.7 and the enamel was only moderately thick (ET = 3.18 mm).

Typical *M. meridionalis* morphology (in all respects) in Europe (with 11 to 14 full plates on last upper and lower molars and with 1.3 as a mean H_m/W_m and 3.2 mm as an average ET) is achieved by approximately 1.75 Ma. The taxon had already been widely dispersed in Eurasia by this time. Subsequently, the lamellar frequency and the enamel thickness underwent further evolution, but the plate number and the hypsodonty index remained in a stasis.

The material from Mezőkomárom (Hungary) represents the aforementioned slightly derived morphology with moderately higher LF (5.6 and 6.0) and noticeably narrower enamel (2.7 mm in average) but with a conservative relative crown height (1.09 and 1.16).

A Hungarian find related to the transition between *M. meridionalis* and *M. trogontherii* in Europe around the Early-Middle Pleistocene Boundary

By 0.6 Ma at Süssenborn (Germany) and elsewhere, *M. meridionalis* has been completely replaced by a new species, called *M. trogontherii* (with 19 plates in average and with 1.75 as a mean hypsodonty index). In the interval 1.0–0.7 Ma, a series of European samples illustrates a complex transitional period, which has been discussed in details by LISTER & SHER (2001) and LISTER et al. (2005).

The earliest detected *M. trogontherii* morphology in Europe is at the easternmost part of the continent (Taman Peninsula, Russia). The contemporaneous Western European samples (e.g. the material from Saint-Prest, France) shows slight advancement in P (range = 13-15) but altogether remains at *M. meridionalis* level. The material from the Taman Peninsula therefore has been posited as a key "intermediate" between the two species. Although this sample as a whole is intermediate in both P and H_m/W_m, it has rather broad morphological range (P = 14 to 19, H_m/W_m = 1.6 to 1.9), and the distributions of these characters are bimodal (LISTER & SHER 2001).

Two smaller and slightly younger samples from Voigtstedt (Germany) and West Runton (England) at around 0.8-0.7 Ma have not only *M. trogontherii* (with P = 19 to 22, and H_m/W_m = 1.6 to 1.9) and "advanced" *M. meridionalis* molars, but also specimens showing mosaic morphology (e.g. *trogontherii*-like hypsodonty index but *meridionalis*-like plate number, or vice versa).

WEI et al. (2003) described mammoth material including molars with 17 or even 18 plates from China. The locality was dated to 2.0–1.8 Ma on the basis of rodent biostratigraphy. LISTER & SHER (2001) presented specimens from the territory between the Lena and Kolyma River valleys (north-eastern Siberia), dated by paleomagnetism and microfauna to the interval 1.2–0.8 Ma, with similar tooth morphology to typical European *M. trogontherii* from Süssenborn.

The aforementioned earlier appearance of the derived morphology suggests that the *M. trogontherii* morphology had arisen allopatrically from an indigenous population of *M. meridionalis* in eastern Asia in the interval c. 2.0–1.5 Ma. The European *M. trogontherii* populations derived from immigrants either from Siberia or from China. However, as pointed out by LISTER & SHER (2001) and LISTER et al. (2005), the mosaic morphology of several European representatives in the transitional period (as discussed above) does not support a "clean" allopatric replacement whereby the European ancestor (typical *M. meridionalis*) was simply displaced by an incoming daughter species (typical *M. trogontherii*).

The above mentioned observations led to the conclusion, that the entire Eurasian *M. meridionalis*-*M. trogontherii* complex might had a "metapopulation" structure (a series of populations with greater or lesser degrees of connection between them), and that the transition between the two species in Europe was achieved by input from the East, either in the form of migrating herds, and/or by gene flow without the long distance movement of individual animals. As proposed by LISTER (1996) and van ESSEN (2003) populations of *M. meridionalis* and *M. trogontherii* morphology plausibly have occupied different areas of the European continent (*meridionalis* occurred in more temperate conditions, *trogontherii* in cooler), perhaps shifting their distributions seasonally or with short-term climatic cycles. The genetic mixing between the adjacent populations resulted in a hybrid zone, which was responsible for individuals with mosaic or intermediate characters (e.g. from Voigtstedt and from West Runton) as well as for those which correspond to the parent populations in all characters.

As VIRÁG (2009) pointed out, a single M^3 (Pl. 1/C) from the locality Üröm-hegy (Hungary) shows similar morphology as the material from Voigtstedt and West Runton. The most probable reconstruction of the plate number is x17x, which means that the specimen is most likely belongs to an *M. trogontherii*, since the late populations of the "true" *M. meridionalis* never reached the 17 lamellae. The enamel is *meridionalis*-like, somewhat thicker (mean= 3.2 mm, range = 3.1-3.4 mm) than in the case of the typical *M. trogontherii* morphology. The estimation of the relative crown height (1.65e) is intermediate or slightly advanced. The molar plates are thin and closely spaced (LF = 6). Most likely the above described hybridization could be the responsible for the observed mosaic morphology of the tooth. VIRÁG (2009) dated the Üröm-hegy locality to c. 0.8–0.7 Ma on the basis of rodent biostratigraphy, therefore the aforementioned tooth is not only similar but essentially time equivalent with the material from Voigtstedt and West Runton.

Application of mosaic evolution of the molar characters as a biostratigraphic tool

VANGENGEIM & PEVZNER (2000) as well as PEVZNER & VANGENGEIM (2001) fitted a mathematical curve in order to relating LF to the geological age on the basis of the data of three localities with idependent age determination. The ages of several other European samples were then calculated from their LF data using the equation of the resulting curve. As pointed out by LISTER (2001) this methodology produced some unexpected and false ages for well-known mammoth-bearing deposits. Nevertheless it is obvious from the above described complex evolutionary scenery that the evolution of the molar morphology of European mammoths cannot be approached by such an extremely gradualistic way. However, the observed mosaic nature of the transition of some characters could be a reliable base for a stratigraphic scheme used in coarse age determination of mammoth-bearing localities.

The evolutionary pattern of the P, H_m/W_m, LF and ET of mammoth molars in Europe are summarized on Fig. 3. The data was extracted from LISTER (1996), LISTER & SHER (2001) and FERRETTI (2003). Fig. 3. was supplemented by the data of the ten Hungarian mammoth-bearing sites discussed above. Since the local pattern seems consistent with the regional evolution, reliable age estimates can made for other mammoth-bearing localities on the basis of the measurable characters listed above, although the indications of possible reversals may complicate the situation.

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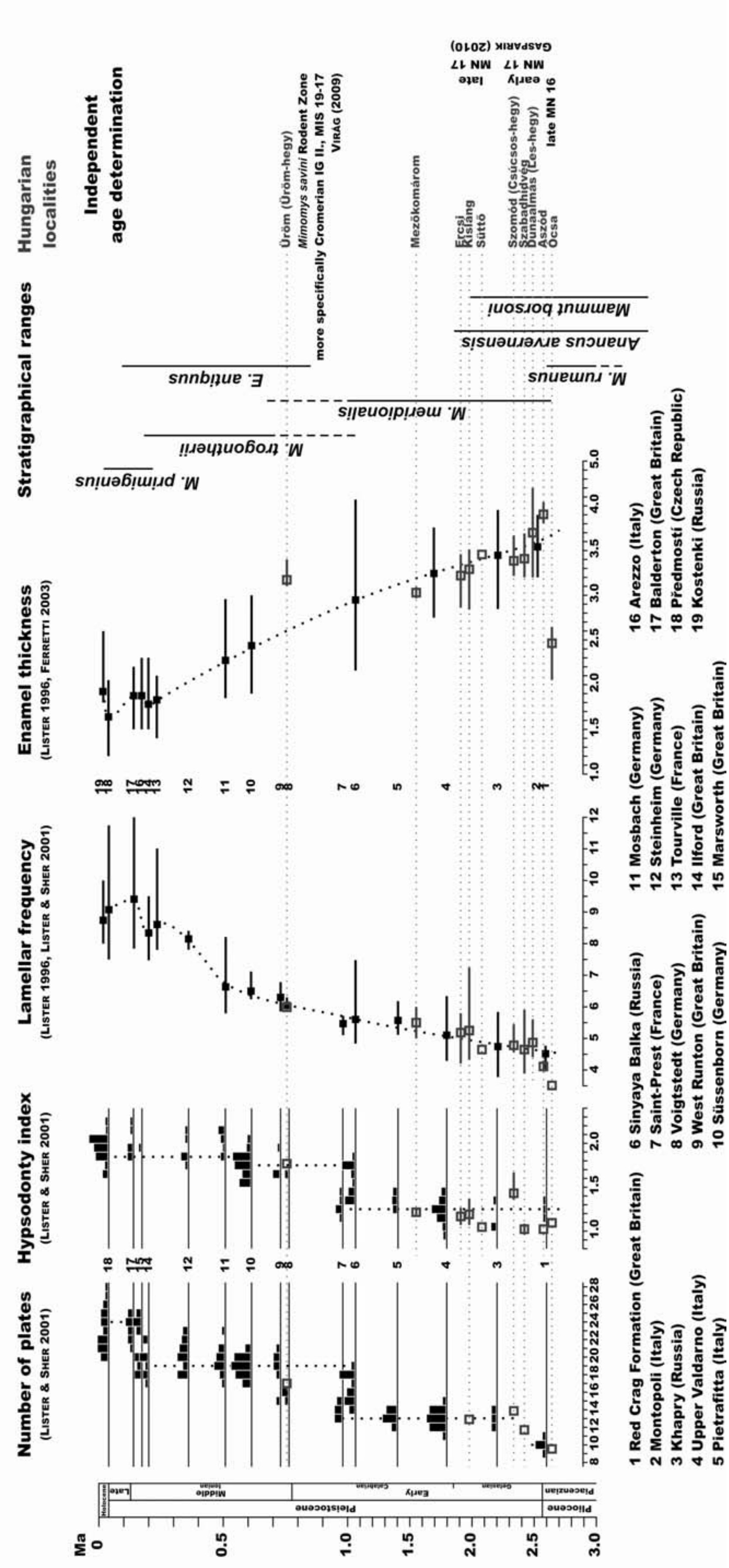
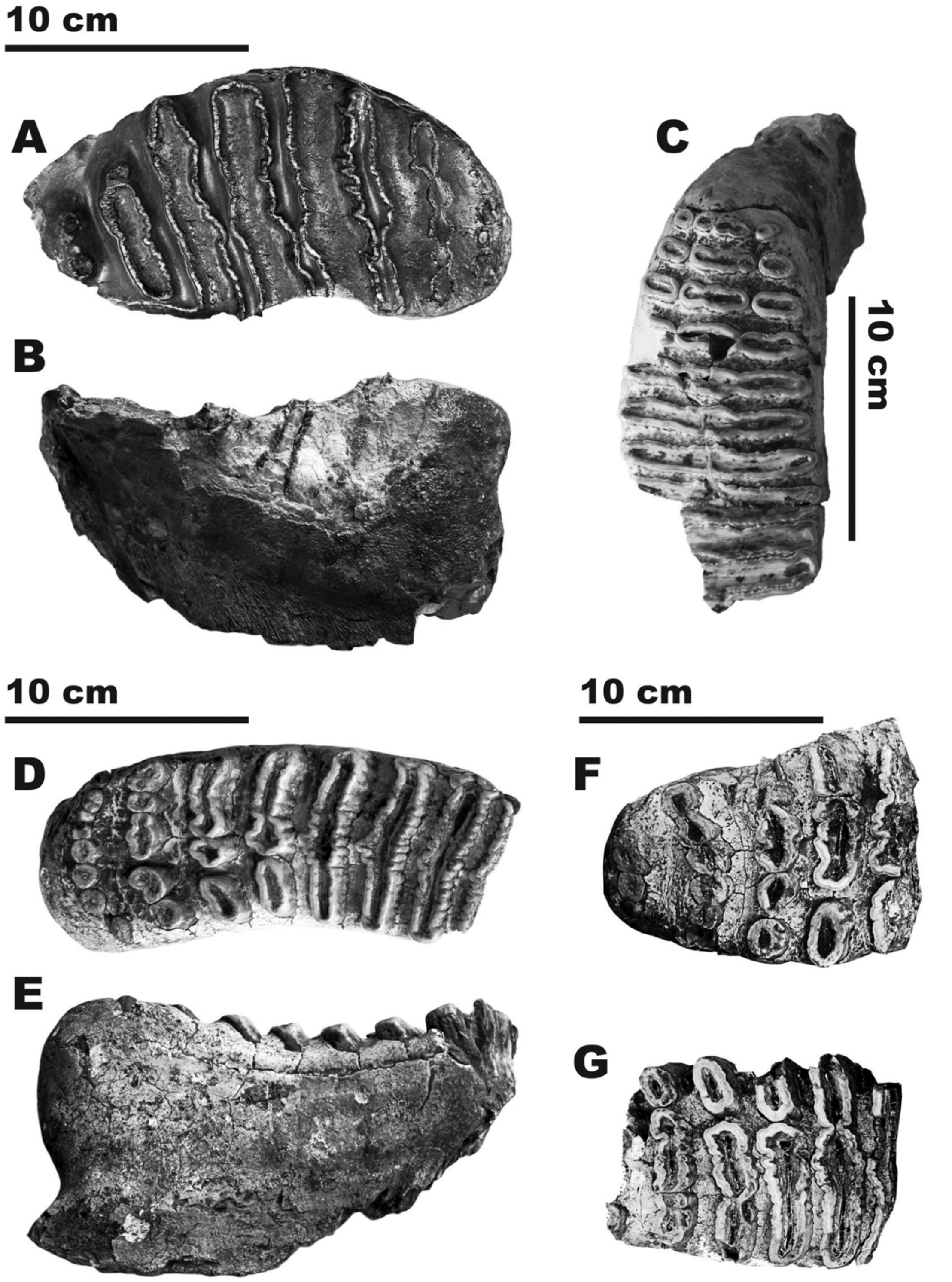


Fig. 3. The relation of P, H_m/W_m, LF and ET to the geological age (further explanation in the text).

Plate 1



A: *M. rumanus* lower left m_3 from Ócsa from occlusal view.
B: *M. rumanus* lower left m_3 from Ócsa from buccal view.
C: HNHM V.72.116. *M. trogontherii* left M^3 from Üröm-hegy from occlusal view.
D: HNHM V.64.903 Early *M. meridionalis* right m_2 from Aszód from occlusal view.
E: HNHM V.64.903 Early *M. meridionalis* right m_2 from Aszód from buccal view.
F: HNHM V.59.1120. Early *M. meridionalis* M^3 from Aszód from occlusal view.
G: HNHM V.82.6. Early *M. meridionalis* M^3 from Aszód from occlusal view.