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Dental remains of *Elephas antiquus* FALCONER & CAUTLEY, 1847 (Mammalia, Proboscidea, Elephantidae) in Hungary

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(with 1 figure and 4 plates)

Despite the fact that hundreds of fossil proboscidean remains are known from Lower Miocene to Upper Pleistocene sediments in Hungary, only five specimens (four molars and a tusk fragment) from three different localities (Győrszabadhegy, Bükkábrány and the Castle Hill of Buda) can be referred securely as *Elephas antiquus*. The scant record and the lack of high-resolution stratigraphic information do not allow extensive conclusions. However it seems that forest elephants inhabited the territory in at least two periods (namely 800-700 ka and 500-400 ka).

Introduction

Fossil proboscideans are known from Lower Miocene to Upper Pleistocene sediments in Hungary. GASPARIK (1993, 2001, 2004, and 2007) made a comprehensive synthesis on the taxonomy, chronology and ecology of the deinotheres, gomphotheres and mastodons formerly inhabiting the region, whereas VÖRÖS (1979, 1981, 1983, 1985, and 2004) dealt with the elephantid remains. During the last few years several new finds came to light, and our knowledge on proboscideans greatly expanded, and so VIRÁG (2009) and VIRÁG & GASPARIK (2012) have begun the re-interpretation of some older material. As a continuation of this intention, this paper focuses on the revision of dental remains (molars and tusks) referable or previously referred as *Elephas antiquus* and some accompanying elephantid finds recovered from the territory of Hungary.

Elephas antiquus was a large sized proboscidean characterized by straight tusks and often associated with woody vegetation of warmer interglacial periods during the Middle and Late Pleistocene of Europe, hence its common name is forest or straight-tusked elephant. The taxon was introduced by FALCONER & CAUTLEY (1847) based on the description of an incomplete mandible (with a second left lower molar) from England. The exact locality of the type specimen is unknown, however, based on its preservation, it is likely retrieved from the Middle Pleistocene terrace deposits of the Thames River at Grays (see PALOMBO & FERRETTI 2005 for details). The skeletal and dental variability of this species is well-known, since abundant material was found from the continental Europe (especially from Germany and Italy) to date. Despite this fact, different opinions can still be found in the literature on the nomenclature and interpretation of this taxon. AGUIRRE (1968-1969) and ALBAYRAK & LISTER (2012) attributed the species to the genus *Palaeoloxodon* MATSUMOTO, 1924, whereas MAGLIO (1973), MOL et al. (2007), and TSOUKALA et al. (2011) placed it in the genus *Elephas* LINNAEUS, 1758. BEDEN (1983) and PALOMBO & FERRETTI (2005) considered *Palaeoloxodon* as a subgenus of *Elephas*. MAGLIO (1973) considered the Asiatic *Elephas namadicus* FALCONER & CAUTLEY, 1845 as a senior synonym of the European *E. antiquus*, whereas Adrian LISTER (see note E2 of appendix C1 in SHOSHANY & TASSY 1996) provisionally suggested a geographic separation for the two species until additional evidence becomes available. Since this problematic issue is beyond the scope of the present study, *E. antiquus* is used here for European material with only one exception.

Material and methods

The tusk and the molars (9) used in the present paper are stored in the Hungarian Natural History Museum (HNHM) and the Geological and Geophysical Institute of Hungary (GIH). An additional molar fragment from Bükkábrány (collected by Márton PALOTAI on October 24, 2007) was provided for analysis by the courtesy of Miklós KÁZMÉR. The examined specimens were recovered from 4 different Hungarian localities (Fig. 1). Standard morphometric parameters (such as the number of plates, the so called laminar frequency, the thickness of enamel, as well as the length, width, and height of teeth) were recorded following the methodology of VIRÁG (2009) and VIRÁG & GASPARIK (2012) with a digital caliper with a precision of 0.003 mm. 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.

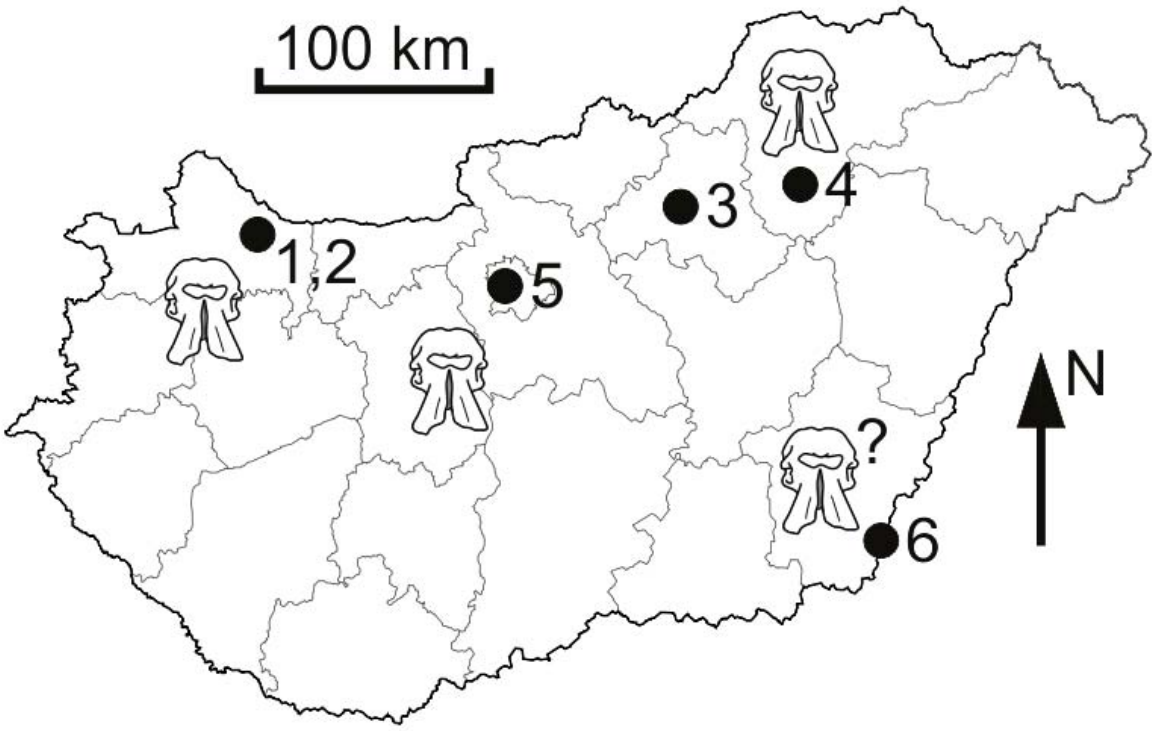

Fig. 1. Map of the Hungarian localities mentioned in the text. Skulls are indicating *E. antiquus* finds.
Legend: 1: Győrújfalu, 2: Győrszabadhegy, 3: Visonta, 4: Bükkábrány, 5: Castle Hill of Buda, 6: Lökösháza.

Localities

Győrújfalu and Győrszabadhegy

More than 35 m thick fluvial sediments were transected during the gravel mining activity near Győrújfalu, which is situated in Northwestern Hungary, 5 km northwest from the centre of Győr, south from the river Danube. Numerous plant, mollusc and vertebrate remains were found since 1983 from the sandy gravel layers located at a depth of 20-31 m from the surface (see the details in JÁNOSSY & KROLOPP 1994 and PONGRÁCZ 1993, 1996). The microvertebrate fauna, especially the co-occurrence of *Mimomys savini* and voles belonging to the *Microtus* (*Pitymys*) *hintoni-gregaloides* group suggests a late Early or an early Middle Pleistocene age (approximately 1.0-0.6 Ma) for the locality. The mammalian assemblage can be correlated with the *Mimomys savini* Rodent Zone and the Nagyharsányhegyian or Templomhegyian Substage of the local biochronological system (see in KRETZOI & PÉCSI 1979). Considering the aforementioned age estimation, the only incongruous faunal element is

Mimomys reidi, the last occurrence of which in the Central European region can be dated back to 1.8-1.7 Ma according to MAUL & MARKOVA (2007). The identification of the latter species is however most likely erroneous, since it is based on only one first lower molar, that is more hypsodont than the typical representatives of the taxon and shows no signs of cement in the re-entrant angles of the tooth.

Győrszabadhegy is located close to the above mentioned site, 3 km south from the centre of Győr. A few elephantid molars have been recovered from the gravels in the vicinity of this municipality, but unfortunately neither detailed stratigraphic information, nor the exact localities are available.

Bükkábrány and Visonta

A large open-cast lignite mine is situated on the southern foothills of the Bükk Mountains (Northeastern Hungary) in the vicinity of Bükkábrány. The Upper Miocene lignite is covered by Pliocene, fluvial, yellow or gray coloured clays and clayey or sometimes pebbly sands. The overlying sediments for the latter sequence are Pleistocene gravels. A few large mammal remains came to light from the gravels during the extensive mining activity, but unfortunately, detailed stratigraphic data are not available.

Another open-cast lignite mine with a similar section is located on the southern foothills of the Mátra Mountains near Visonta, 50 km west from Bükkábrány. Numerous vertebrate remains (including mammoths) were recovered so far from the Pleistocene gravels covering the rest of the sequence.

Castle Hill, Budapest

The top of the Castle Hill (or Várhegy) at the Buda side of Budapest is covered with a 7 to 10 m thick travertine layer. The underlying sediments are weakly cemented, calcareous, and clayey silts as well as fluvial, cross-bedded, sandy gravels, which provided numerous vertebrate remains (including proboscideans) since the middle of the 20th century. Several sections were opened or sealed behind masonry to date due to construction works in the cave and cellar system located under the Castle District. According to the faunal revision made by KORDOS (2004), the age of the fluvial gravels can be correlated with Marine Isotope Stage (MIS) 14 or 12, whereas the overlying calcareous, clayey silt deposited during MIS 11. The latter can be correlated with the *Lagurus transiens–Arvicola cantiana* Rodent Zone (see the details of the zonation in KORDOS 1994) which can be dated to 500-400 ka. According to the U/Th dating of KELE (2009) the age of the covering travertine is 400-350 ka. Microvertebrate remains were recovered from the reddish brown clay infilling of the karstic cavities in the freshwater limestone during the construction works of the Hilton Hotel. Based on the latter fauna, JÁNOSSY (1976) introduced the so called Castellum Phase to the local biochronological system. KORDOS (2004) correlated the age of the infilling sediments with MIS 7 or 6 (which means approximately 200 ka).

Characteristics of *E. antiquus*

The skull of *E. antiquus* has a flat dorsal profile and a characteristic double-domed vertex. The premaxillaries are fan shaped and extremely wide distally. The mandible is short with a weakly developed symphyseal rostrum. Tusks are large, and weakly curved. The molars are usually narrow and extremely high compared to a mammoth. The relative crown height or hypsodonty index (i.e. the ratio of the height and the width of the tooth) of the last molars varies from 1.8 to 2.0, or exceeds 2.0 in some cases. The number of plates (excluding talons and platelets) on the aforementioned teeth is usually 16 or 17 but can reach up to 20 according to PALOMBO & FERRETTI (2005) or varies between 15 and 21 according to ALBAYRAK & LISTER (2012). The plates have an S-shaped curvature from lateral view. Laminar frequency (which represents the number of plates that occur within 10 cm along the longitudinal plane of the molar) varies between 5 and 6. The enamel is 2.0-3.0 mm thick, usually heavily wrinkled and one to three acute folds (or sinuses) are frequently present on both the anterior and posterior sides of each loop. The incipient wear figures on the occlusal surface are often formed by a large oval central loop and two small circular lateral loops. This is the so called dot-dash-dot or ring-loop-ring pattern which usually appears on several consecutive plates in the case of *E. antiquus*, whereas not typical in the case of mammoths.

Reappraisal of dental remains

Győrújfalu

The HNHM V.84.105 specimen (Plate I/A-B), which is a right m_3, was referred by JÁNOSSY & KROLOPP (1994) to the "archaic form of *Palaeoloxodon antiquus*" based on the opinion of István VÖRÖS. The tooth is built up from 13 plates and a posterior platelet. The occlusal wear reached the base of the crown at the anterior part of the molar, however the base of the first root is still visible and its position suggests that only one anterior plate is missing. The plates are more or less straight in lateral view. The laminar frequency is approximately 4. The thickness of enamel varies between 2.9 and 3.6 with an average of 3.4 mm. The tooth crown is relatively wide (91 mm) and low (92 mm). The unworn height can be estimated up to maximum 130 mm, which results in a maximum 1.4 hypsodonty index. Based on the low plate count and laminar frequency, the thick enamel, and the relatively low tooth crown, the specimen most likely belongs to *Mammuthus meridionalis* (NESTI, 1825). The only characteristics that could support *E. antiquus* are the acute posterior enamel folds appearing on the medial part of the occlusal surface and the wear figures of the 5th an 6th plates (counted from posterior to anterior direction) which are broadly similar to the typical dot-dash-dot pattern but the lateral loops are more elongated.

The m_3 depicted Plate I/C-D shows remarkably similar, maybe a bit more advanced morphology compared to the HNHM V.84.105 specimen, but its measurements still remain in the range of *M. meridionalis* (the data and the photographs were made available for me by the courtesy of Hans van ESSEN in the case of this molar). The exact locality of the specimen is unknown, but it was recovered from sandy gravel in the vicinity of Győr. The tooth has 15 plates, an anterior talonid, and a posterior platelet. The first root is visible and the occlusal wear has never reached the base of the crown, although it is close to the latter in the most anterior part of the molar. The plates are more or less straight in lateral view in this case too. The laminar frequency is approximately 4.5, which is somewhat higher than in the case of the HNHM V.84.105 specimen. The enamel thickness ranges from 3.0 to 3.7 with an average of 3.1 mm. The tooth crown is wide (97 mm) and low (126 mm) compared to an advanced mammoth or a typical *E. antiquus*. The hypsodonty index is approximately 1.3. The incipient wear resulted in three equally wide loops (i.e. dash-dash-dash pattern) on the 3rd plate (counted from anterior to posterior direction) and the enamel is only moderately folded.

The other specimen from Győrújfalu stored in the paleontological collection of the HNHM is the V.84.106 molar fragment. It has now 7 plates and a posterior talon, but the anterior part is missing. The anterior sides of the enamel loops are convex, whereas the posterior sides are concave, which occurs more often in the case of the upper dentition. The tooth is tapering towards the posterior end, which suggests that it is a third molar. The maximal width of the specimen is now 80 mm, but the missing anterior plates may have been wider. The laminar frequency is 6.8. The enamel is 2.2-2.8 mm thick with an average of 2.5 mm and heavily wrinkled. The incipient occlusal wear resulted in dot-dash-dot pattern on the 1st and 2nd, dash-dash-dash pattern on the 3rd and 4th, and dash-dot-dash pattern on the 5th and 6th plates (counted from posterior to anterior direction). The latter two configurations rarely occur on *E. antiquus* molars. Despite the fragmentary preservation of the molar, based on the aforementioned data, it is most plausibly referable to *M. trogontherii* (POHLIG, 1885).

In addition to the above mentioned material, PONGRÁCZ (1996) depicted a molar fragment on his Fig. 5/B with 8 remaining plates under the name of "ancient form of forest elephant". The laminar frequency seems low and the enamel is remarkably thick. The tooth is heavily worn and fragmented even from the lateral sides. The apical region of an elephantid molar is usually subdivided into three so called pillars by two clefts (van ESSEN 2011). The widths of these pillars determine the characteristics of the incipient wear pattern. Since the occlusal wear proceeded beyond the lowest level of the clefts in this specimen, the loops are completely fused from side to side of the crown. However, two infolding of the loops are visible close to the medial part of the occlusal surface, and it could be a clue for a dash-dot-dash pattern, which makes the original determination unlikely. The specimen is most plausibly referable to *M. meridionalis.*

In summary, the presence of *E. antiquus* at Győrújfalu can not be verified based on the available data, although there are several other finds from the site in the private collection of László PONGRÁCZ, which have not been studied by the present author to date. It seems that specimens

formerly referred to this taxon from this locality are representatives of the genus *Mammuthus* BROOKES, 1828.

Győrszabadhegy

The most complete molar from this site is a left m_3 without inventory number (Plate II/A-B). It is built up from 17 plates, and a platelet is missing on the posterior end of the tooth based on the remaining cement interval. It is possible, that the original tooth had one more lamella on the anterior end as well, therefore the original number of plates was most plausibly 18. The plates have an S-shaped curvature from lateral view. The laminar frequency is 5.1. The enamel thickness varies between 1.9 and 2.6 with an average of 2.3 mm. Acute folds are visible on both the anterior and posterior sides of several loops. The incipient wear resulted in dot-dash-dot pattern on the 7th, 8th, 9th, and 10th plates (counting from posterior to anterior direction). The tooth crown is narrow (74 mm) and high (138 mm), resulting in a hypsodonty index around 1.85.

There is an other tooth from the locality without inventory number stored in the paleontological collection of the HNHM (Plate II/B-C). The molar has 11 plates and a posterior talonid. Two anterior plates are missing based on the position of the first root, therefore the original number of the plates can be estimated up to 14. The occlusal surface is slightly concave in lateral view and curved when viewed from the top, which occurs usually in lower dentition. The tooth is not tapering towards the posterior end and the posterior wall of the last plate is approximately perpendicular to the occlusal surface. In addition the posterior root is triangular and widens towards the end of the tooth. These features suggest that it is a second molar (a left one based on its curvature). The plates have an S-shaped curvature from lateral view. The laminar frequency is 5.6. The thickness of enamel ranges from 1.9 to 2.9 with an average of 2.4 mm. A well-developed median sinus and some additional acute folds are visible on the anterior and posterior sides of almost all loops. Dot-dash-dot pattern is visible in the case of the 2nd, 3rd, 4th, 5th, and 6th plates (counting from posterior to anterior direction). The crown of the tooth is narrow (62 mm) and high (138 mm but the unworn height can be estimated up to 140 mm), resulting in a hypsodonty index around 2.2. Greater estimates are also possible, since the bases of the so called cement islets are 40-45 mm lower at the medial part of the molar compared to the lateral basal enamel extremes which were the starting points for height measurements in the present study.

The HNHM V.79.32 specimen is a fragment built up from the remains of 6 plates, the anterior and posterior ends of the molar are both missing. The plates have an S-shaped curvature from lateral view, similarly to the above discussed teeth. A transversal fracture in the case of the most anterior lamella reveals 25-30 mm deep medial clefts which are dividing the apical region into three pillars. The lateral pillars are significantly narrower than the medial one, consequently, the incipient occlusal wear would have resulted in dot-dash-dot pattern on the plate. The laminar frequency is 5.6. The enamel is 2.8-2.9 mm thick. The tooth crown is narrow (65 mm) and high (155 mm), resulting in a hypsodonty index around 2.3.

Considering all evidence, the above discussed specimens can be referred as typical representatives of *E. antiquus*.

Castle Hill, Budapest

The GIH V.21665 specimen (Plate III/G-H) depicted by both JÁNOSSY (1986 on his Fig. 1 of Plate III) and VÖRÖS (2004 on his Fig. 4/3) was the first forest elephant find recognised in the Hungarian material. According to MOTTL (1943) the tooth was recovered from the weakly cemented, calcareous, and clayey silt layers sectioned by a cellar system lying under 14, Országház Street and 7, Szentháromság Street. The specimen is only a molar fragment which can be referred to *E. antiquus* based on the occlusal wear pattern, although it is important to note, that similar pattern can be seen in some cases on heavily worn teeth belonging to the genus *Mammuthus*. The enamel is heavily and regularly wrinkled and 2.5 mm thick in average. An acute fold is visible on both the anterior and posterior sides of the lozenge-shaped loops.

In addition, MOTTL (1942, 1943) described and depicted several mammoth teeth which were found in the fluvial gravels under 72, Úri Street. Some of these remains (GIH V.21619, GIH V.21620 and GIH V.21621, Plate III/A-F) were available for the present author as well. The teeth can be identified as second lower and upper molars with a reconstructed number of 11-13 plates, a laminar frequency between 5.5 and 6.5, and an enamel thickness between 2.0 and 3.0 mm. The width of the molars varied between 80 and 90 mm, whereas the unworn height most plausibly ranged from 140-150 mm. These estimates result in hypsodonty indices around 1.6-1.8. According to MAGLIO (1973), plate number on second molars of *M. meridionalis* hardly ever reached 11. Referring

these specimens to *M. trogontherii* is therefore more plausible. As MOTTL (1943) noticed, the remains are morphologically indeed very similar to the material recovered from Mosbach (Germany), a site which can be dated to approximately 500 ka (see e.g. LISTER et al. 2005). This observation, on the on hand, is in agreement with the stratigraphical interpretation of KORDOS (2004) and, on the other hand, gives a maximum age for the overlying calcareous and clayey silt layer from which the above mentioned *E. antiquus* molar was recovered.

Bükkábrány

VIRÁG (2012) reported a tusk fragment (HNHM PAL 2012.13.1) from Bükkábrány (Plate IV/A-B) which can be referred to *E. antiquus* based on the so called Schreger pattern visible on the cross section of a tusk. Angles, formed by the intersecting and curved Schreger lines, open towards the pulp cavity, and not farther than 10 mm from the cement dentine junction, varied between 96° and 136° with an average of 115°, which is much larger than the typical values for a mammoth according to the comparative data of PALOMBO & VILLA (2001).

In addition, a molar fragment with only the remains of 4 plates came to light from the locality on October 24, 2007. All of the plates are broken into half along the sagittal plane. The remaining loops (the medial and one of the laterals) are elongated and approximately equally wide which suggest a dash-dash-dash occlusal wear pattern. Based on this assumption, the original width of the tooth can be estimated up to 80-90 mm. The elevated laminar frequency (7-8) and the thin enamel (1.1-1.7) suggest a form more advanced than *M. meridionalis*, and so the molar is tentatively referred here as *M. trogontherii*.

Lökösháza

In addition to the above discussed material, VÖRÖS (2004 on his Fig. 4/2) depicted a narrow molar fragment with 9 remaining plates, relatively thin and more or less regularly wrinkled enamel. Based on the available data, it can not be ruled out that the molar belonged to an *E. antiquus* as he stated, however it should be noted that the incipient wear result in dash-dash-dash wear pattern which is more typical for mammoths in the case of two lamella and the remaining plates have a bipartite structure which is an anomalous and possibly atavistic condition in the case of elephantids. The molar was recovered from the gravel quarry at Lökösháza (Southeastern Hungary) and was unfortunately not available for the present author.

Discussion and conclusions

According to ALBAYRAK & LISTER (2012), representatives of the lineage that gave rise to *E. antiquus* migrated outside Africa through the Levant approximately 900 ka. One of the earliest records of the group in Eurasia could be Dursunlu in Turkey which is close to the presumed migration route. According to their opinion, forest elephants became widespread in the continent by the time *M. meridionalis* went extinct and more advanced *M. trogontherii* migrated into the region (at around 800-700 ka).

Due to the lack of high-resolution stratigraphic information, the exact date of the arrival of *E. antiquus* to Hungary is not clear at the present state of knowledge, however it is plausible that the specimens from Bükkábrány and Győrszabadhegy represent an early immigration of the taxon. At Győrszabadhegy, only the presence of *E. antiquus* was detected, but at Győrújfalu, a geographically close site with a similar gravel sequence, both *M. meridionalis* and *M. trogontherii* were recognized. The situation is somewhat similar in the case of Bükkábrány, from where *E. antiquus* and *M. trogontherii* were described in the present article. In a similar section at Visonta, *M. meridionalis* and *M. trogontherii* were recovered from stratigraphically close horizons (see FODOR & VÖRÖS, 1990 and VIRÁG 2009 for details). Unfortunately *E. antiquus* fossils have not been found at the locality to date. It is probable, that similarly to the Ponte Galeria Formation in Italy (see PALOMBO & FERRETTI 2005 for details), the aforementioned sections contain the period of the faunal turnover discussed above.

It was accepted for a long time that *E. antiquus* went extinct in Europe at the end of the Eemian interglacial (MIS 5e), approximately 115 ka, although STUART (2005) and MOL et al. (2007) presented some reasonable but not conclusive evidence for the survival of some isolated populations to approximately 50 ka or as late as 34-33 ka. Nevertheless, the last known occurrence of the species in Hungary at the Castle Hill of Buda can be dated between 500 and 400 ka which is significantly older compared to data from the rest of Europe. It seems that several gaps are exist

in the Hungarian forest elephant record, which suggests that *E. antiquus* was not a permanent element of the fauna but migrated into the region only for geologically short periods of time as stated by István VÖRÖS (see in JÁNOSSY & KROLOPP 1994).

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Plate I

M. meridionalis molars from Győr and Győrújfalu.

A. *M. meridionalis* right m_3 (HNHM V.84.105) in occlusal view from Győrújfalu.
B. *M. meridionalis* right m_3 (HNHM V.84.105) in lingual view from Győrújfalu.
C. *M. meridionalis* left m_3 in occlusal view from the vicinity of Győr (photo by courtesy of Hans van ESSEN).
D. *M. meridionalis* left m_3 in buccal view from the vicinity of Győr (photo by courtesy of Hans van ESSEN).

Plate 1

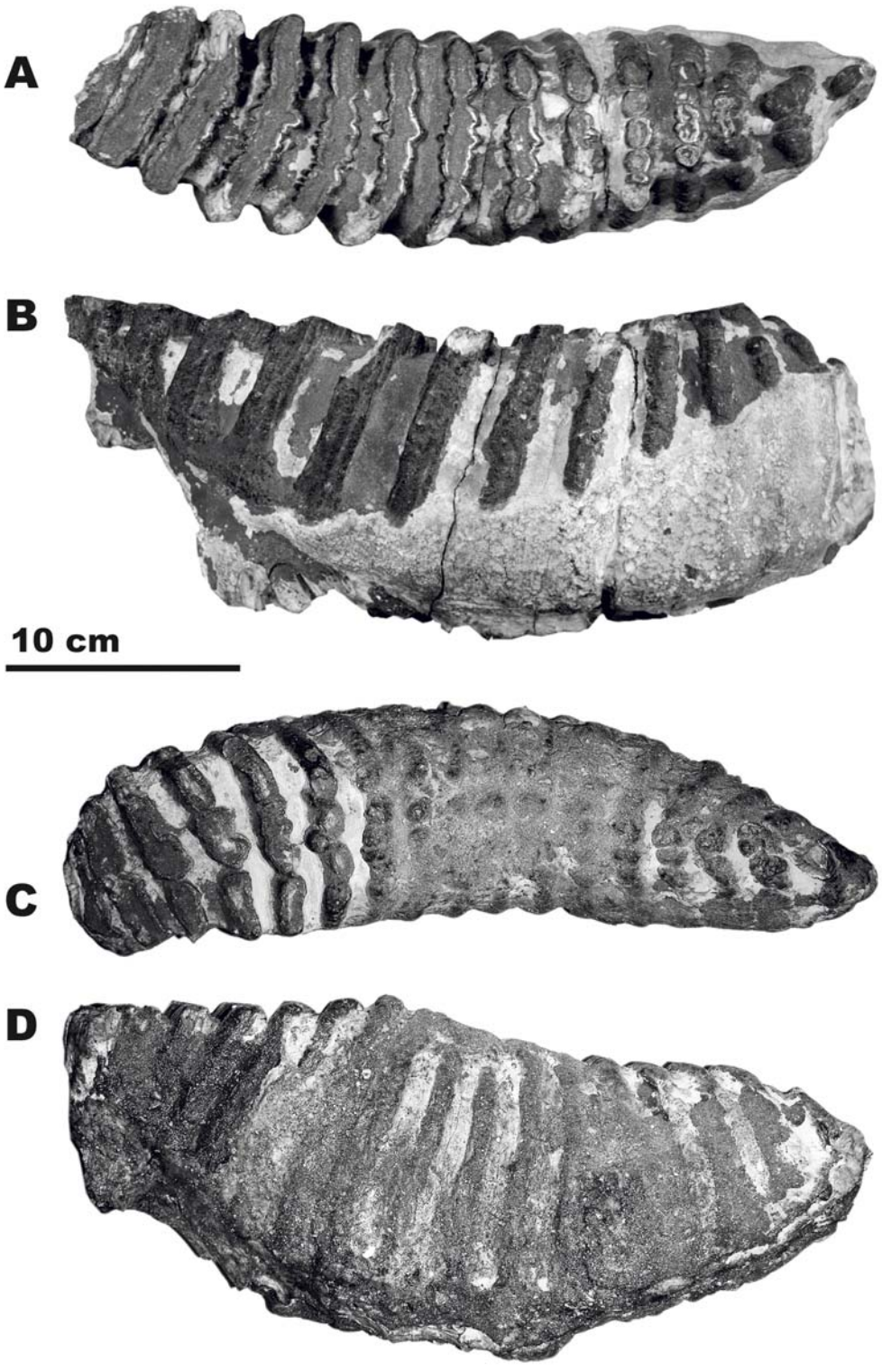


Plate II

E. antiquus molars from Győrszabadhegy

A. *E. antiquus* left m_3 in occlusal view from Győrszabadhegy.
B. *E. antiquus* left m_3 in buccal view from Győrszabadhegy.
C. *E. antiquus* left m_2 in occlusal view from Győrszabadhegy.
D. *E. antiquus* left m_2 in lingual view from Győrszabadhegy.

Arrows are indicating plates with dot-dash-dot wear pattern.

Plate II

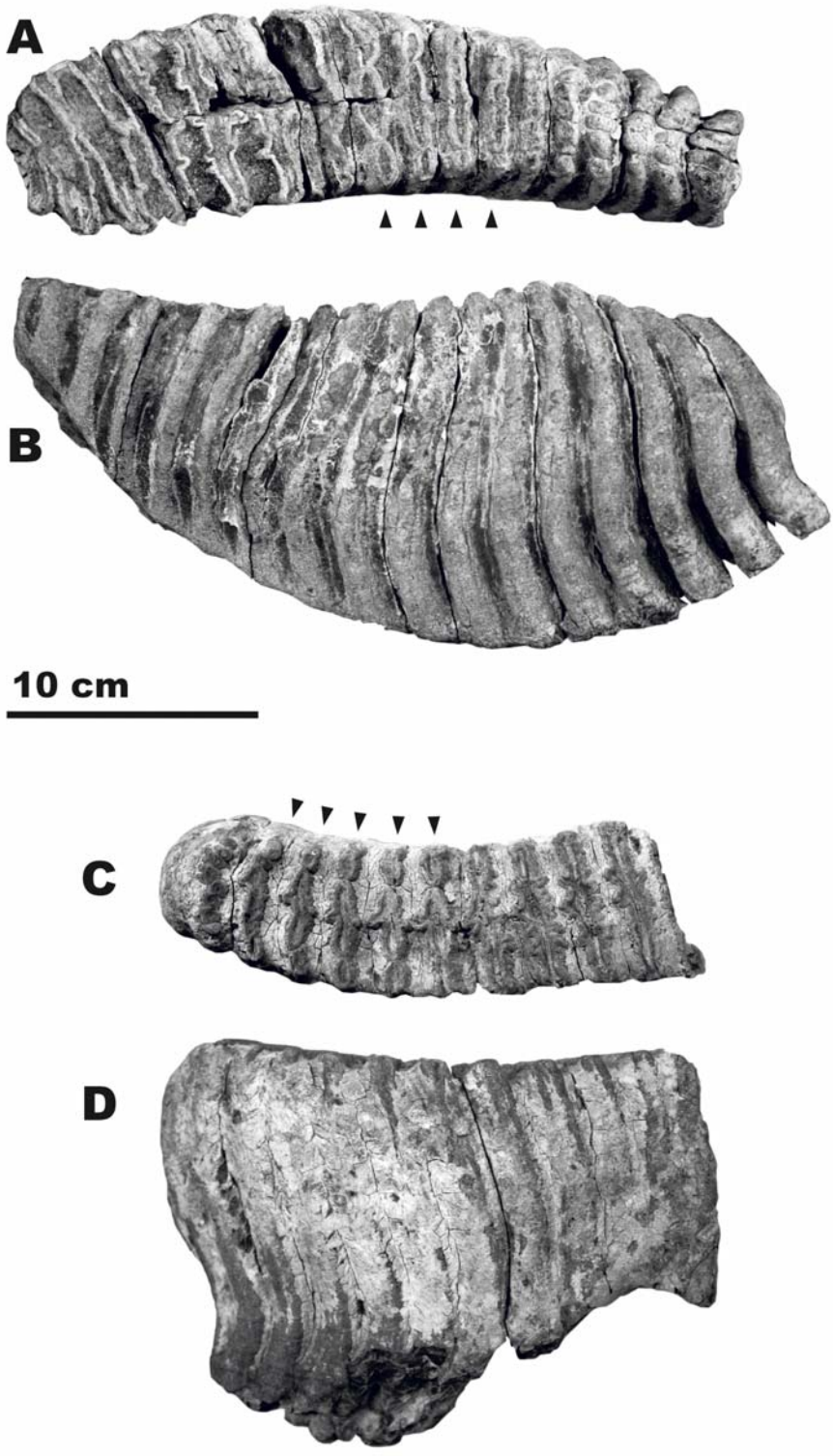


Plate III

M. trogontherii and *E. antiquus* molars from the Castle Hill of Buda.

A. *M. trogontherii* left M^2 (GIH V.21621) in lingual view from the Castle Hill of Buda.
B. *M. trogontherii* left M^2 (GIH V.21621) in occlusal view from Castle Hill of Buda.
C. *M. trogontherii* M^2 (GIH V.21620) in lateral view from Castle Hill of Buda.
D. *M. trogontherii* M^2 (GIH V.21620) in occlusal view from Castle Hill of Buda.
E. *M. trogontherii* left m_2 (GIH V.21619) in occlusal view from the Castle Hill of Buda.
F. *M. trogontherii* left m_2 (GIH V.21619) in lingual view from Castle Hill of Buda.
G. *E. antiquus* molar (m?) in occlusal view from Castle Hill of Buda.
H. *E. antiquus* molar (m?) in lateral view from Castle Hill of Buda.

Plate III

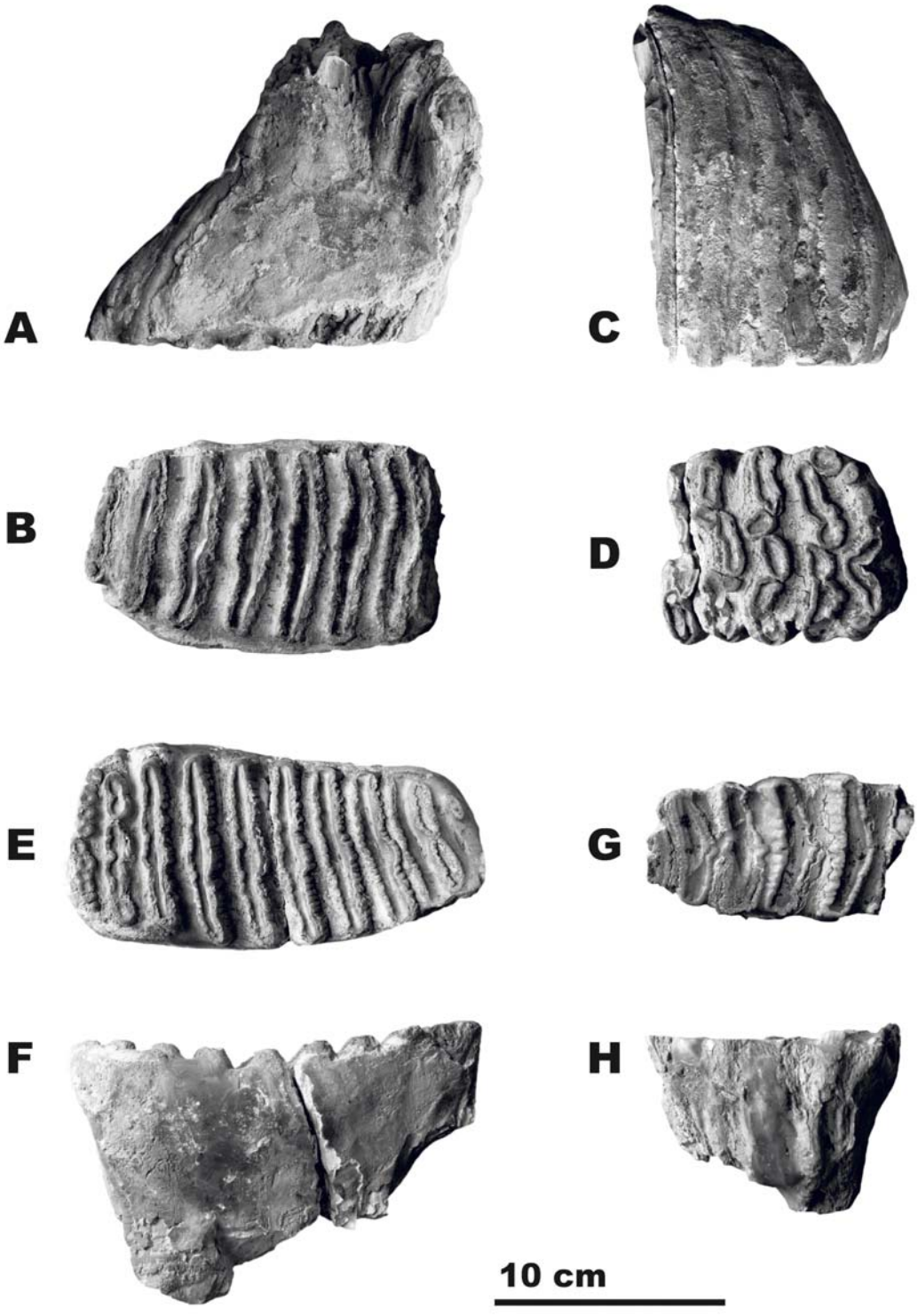


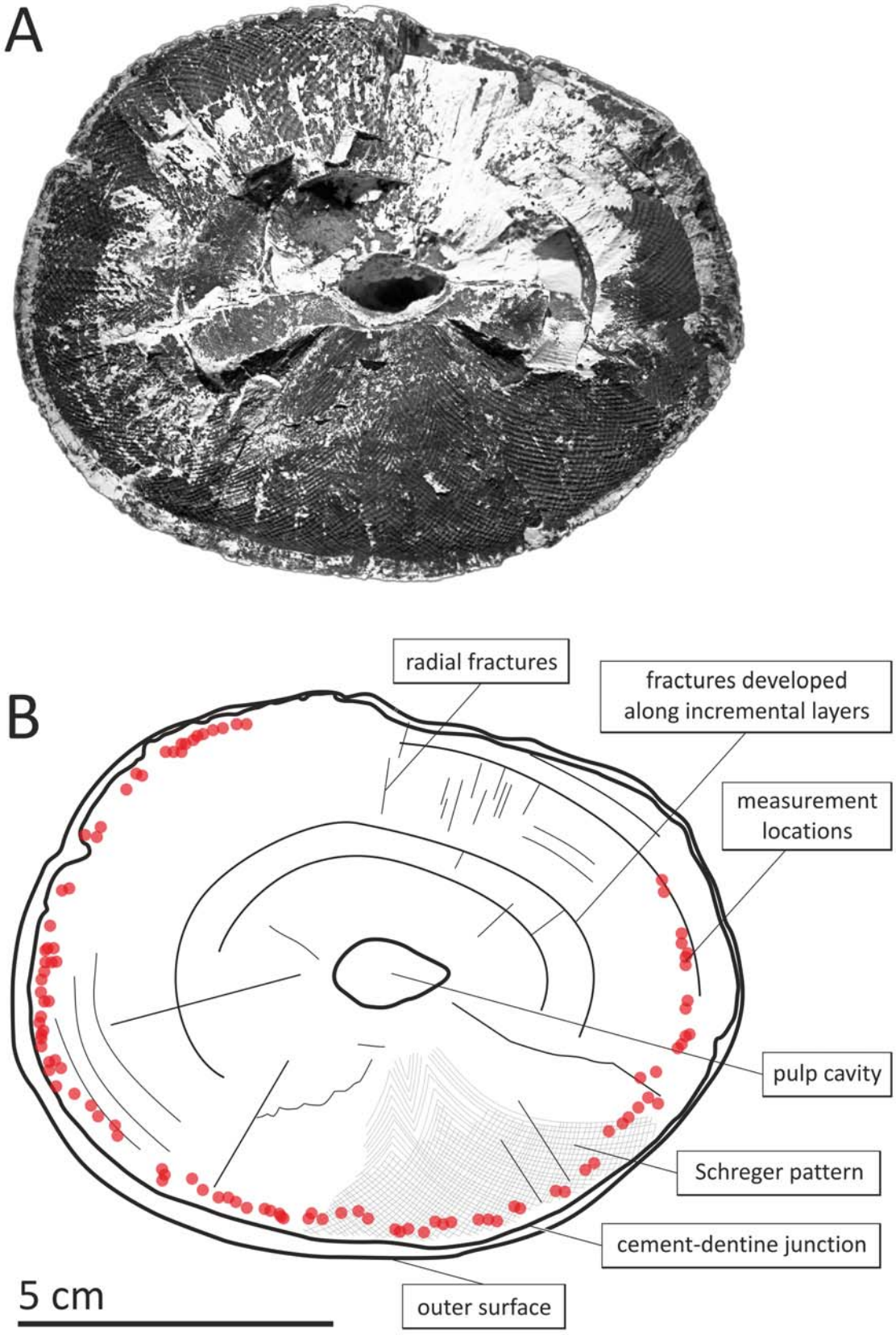
Plate IV

E. antiquus tusk from Bükkábrány

A. *E. antiquus* tusk fragment (HNHM PAL 2012.13.1) in transverse profile from Bükkábrány.

B. Schematic drawing of an *E. antiquus* tusk fragment (HNHM PAL 2012.13.1) in transverse profile from Bükkábrány.

Plate IV


A
B
radial fractures
fractures developed along incremental layers
measurement locations
pulp cavity
Schreger pattern
cement-dentine junction
outer surface
5 cm