The Baltavar *Hippotherium*: A mixed feeding Upper Miocene hipparion (Equidae, Perissodactyla) from Hungary (East-Central Europe)

by

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Abstract

The genus *Hippotherium* evolved in Central and Western Europe following the "Hipparion Datum" and is particularly remarkable for its complexly ornamented enamel plications on the maxillary and mandibular cheek teeth. The Baltavar hipparion assemblage is of importance because it represents one of the latest known populations of Central European *Hippotherium*. The Baltavar fauna accumulated during the regressive phase of the Late Miocene Pannonian Lake, and is most likely MN 12 correlative, circa 7.5-7 Ma. Baltavar represents the best assemblage of Central European Turolian mammals known. The paleoenvironments were likely much like Pikermi, being open country woodlands. The most abundant large mammal at Baltavar was the equid *Hippotherium* "*microdon*" We describe the morphology of a representative sample of maxillary and mandibular jaws and teeth from Baltavar. We also analyse metacarpal III's (MC III), metatarsal III's (MT III) and 1st phalanx III's. The MC III's are relatively elongate and moderately robust, while the MT III's are relatively elongate and slender. Dental and postcranial remains share a number of discrete and continuous characters with *Hippotherium*, invalidating the referral to *Hipparion* s.s. However, for the sake of taxonomic stability, we prefer to recognize the nomen *Hippotherium* „*microdon*" for the majority of the Baltavar specimens and *Hippotherium* cf. *intrans* for the two metapodials cited herein. The mesowear method is used to assess the dietary behavior of *Hippotherium* "*microdon*" at Baltavar. The dietary reference species for the Baltavar population is the modern impala (*Aepyceros melampus*), a balanced mixed feeder which has a grass / browse ratio of 50/50% in its diet. The impala lives in tropical east Africa in grass dominated open environments like bushland and *Acacia* savannahs but also in *Acacia* forests and other deciduous woodlands. It further has one of the most abrasive diets among extant mixed feeders and is consistently classified next to the grazers in mesowear evaluation. The comparatively abrasive diet of *H.* "*microdon*" suggests the presence of grass or other abrasive vegetation in the Baltavar paleohabitat. Compared to *Hippotherium* cf. *intrans*, the larger bodied equid species at Baltavar, we suggest that *Hippotherium* "*microdon*" probably favored more open conditions and was likely a more efficient cursorial form. We suspect that *Hippotherium* "*microdon*" favored open, deltaic habitats where fresh grass was abundant and carnivores prevalent.

Keywords: *Hippotherium*, Equidae, Miocene, Hungary

Kurzfassung

Die Gattung *Hippotherium* entwickelte sich nach dem "Hipparion Datum" in Mittel- und Westeuropa. Kennzeichnend sind die komplex ornamentierten Schmelzplikationen der oberen und unteren Backenzähne. Die Hipparionen von Baltavar sind vor allem deshalb so bedeutsam, weil es sich bei ihnen um die jüngste bekannte mitteleuropäische Population von *Hippotherium* handelt. Die Fauna von Baltavar repräsentiert die regressive Phase des obermiozänen pannonischen Sees, und ist mit großer Wahrscheinlichkeit mit MN 12 (7,5-7 Ma) zu korrelieren. Baltavar repräsentiert die umfangreichste bekannte Ansammlung turolischer Säugetiere in Mitteleuropa. Als offene Waldlandschaften waren die Paläo-Lebensräume wahrscheinlich denen von Pikermi sehr ähnlich. Das häufigste überlieferte große Säugetier in Baltavar war der Equide *Hippotherium* "*microdon*". Es wird die Morphologie einer repräsentativen Stichprobe maxillärer und mandibulärer Kiefer und Zähne von Baltavar beschrieben. Ferner werden Metacarpalia III (MC III), Metatarsalia III (MT III) und erste Phalangen III analysiert. Die MC III sind relativ lang gestreckt und mäßig robust, während die MT III relativ lang gestreckt und schlank sind. Dentale

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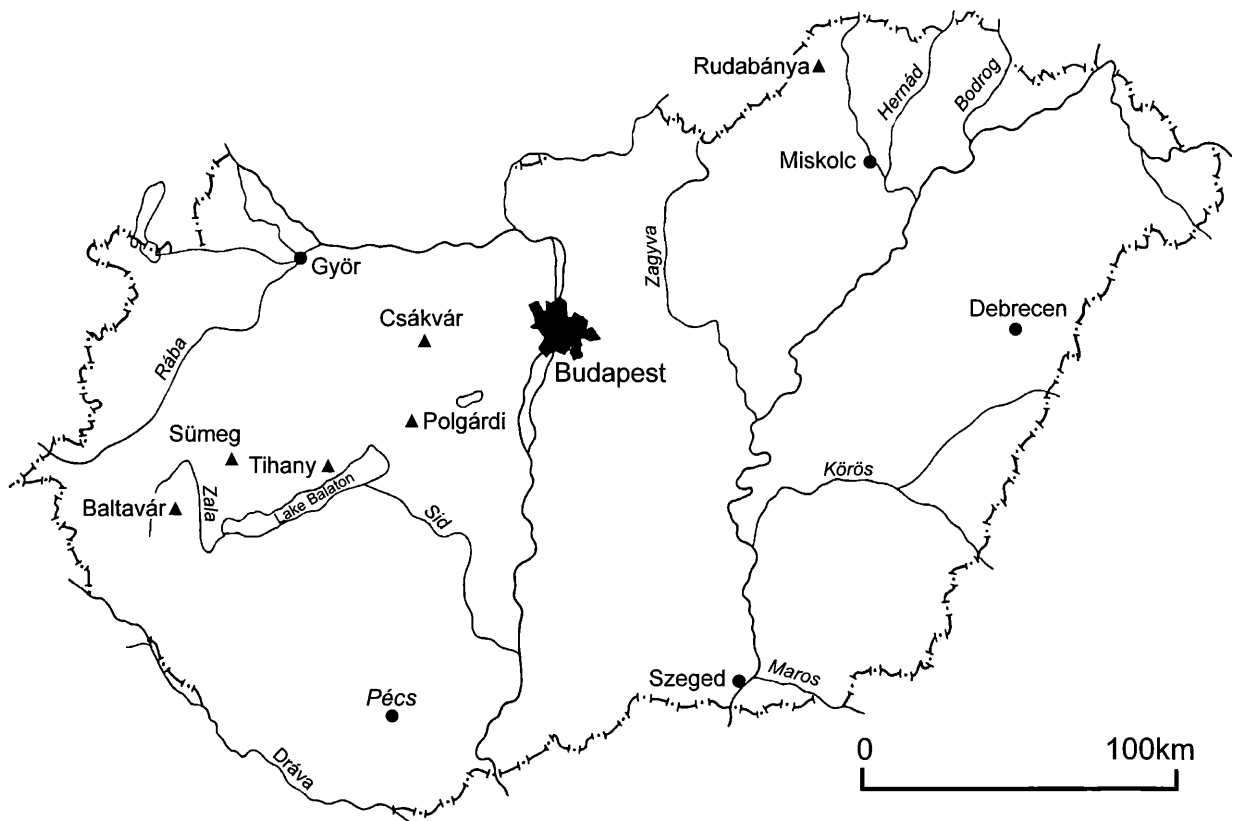
Figure 1: Locator map of Baltavar and other Hungarian Neogene stratotype localities (after Bernor et al., 1999).

und postkraniale Überreste teilen eine Reihe von Gemeinsamkeiten in diskreten und metrischen Merkmalen mit *Hippotherium*, die eine Zuweisung zu *Hipparion* s.s. ausschließen. Aus Gründen der taxonomischen Stabilität wird das Nomen *Hippotherium „microdon"* der Mehrzahl der Stücke von Baltavar zugewiesen, sowie *Hippotherium* cf. *intrans* für zwei hier vorgestellte Metapodien. Die Mesowearmethode wird eingesetzt, um das Ernährungsverhalten von *Hippotherium "microdon"* von Baltavar abzuschätzen. Die auf die Diät bezogene rezente Referenzart für die Population von Baltavar ist die Impalaantilope (*Aepyceros melampus*), ein ausgewogener Mischkostfresser mit einem Gras / Konzentrat-Verhältnis von 50/50 %. Impalas leben im tropischen Ostafrika und bevorzugen dort grasdominierte offene Lebensräume wie Buschland und akaziendominierte Baumsavannen. Sie sind jedoch auch in Akazienwäldern und anderen laubwerfenden Waldhabitaten anzutreffen. Die Impalaantilope hat ferner unter den rezenten Mischkostfressern eine der abrasivsten Diäten und wird in Mesowearanalysen stets in der Nachbarschaft der Grasfresser klassifiziert. Die vergleichsweise abrasive Diät von *H. "microdon"* verweist auf die Gegenwart von Gräsern oder anderen abrasiven Vegetationskomponenten im Paläo-Lebensraum von Baltavar. Verglichen mit *Hippotherium* cf. *intrans*, der großwüchsigsten Equidenart von Baltavar ist es nahe liegend, dass *Hippotherium "microdon"* wahrscheinlich eher offene Bedingungen bevorzugte und eine eher cursoriale Form war. Es ist zu vermuten, dass *Hippotherium "microdon"* offene Deltahabitate mit reichlich frischem

Gras, aber auch einer großen Carnivorendichte als Lebensraum bevorzugte.

1. Introduction

Hipparionine horses originated in North America circa 16 Ma and underwent an extensive evolutionary radiation there (Woodburne, in press) prior to their entry into the Old World between 11.2 and 10.8 Ma. The first occurring Old World hipparion belonged to the genus *Cormohipparion*, known to occur in Turkey and Ethiopia shortly following the so-called "Hipparion Datum" (Bernor et al., 1996b; Woodburne et al., 1996; Bernor et al., 2003a, b; 2004). The genus *Hippotherium* evolved in Central and Western Europe following the "Hipparion Datum" and is particularly remarkable for its complexly ornamented enamel plications on the maxillary and mandibular cheek teeth. Recent research on Central European *Hippotherium* (Bernor & Franzen, 1997; Bernor et al., 1993a, b, 1997, 1999, 2003a, b; Kaiser et al., 2000, 2003; Scott et al., 2005a, b) has established that the earliest locally occurring members of this clade had highly complex enamel plications, but had a body size and metapodial proportions not dissimilar to first occurring Turkish *Cormohipparion, C. sinapensis* (Bernor et al., 2003c). An extensive analysis of the postcranial skeleton (Bernor et al., 1997, 1999; Scott et al., 2005b) suggests that German, Austrian, Hungarian and Italian members of the *Hippotherium* clade underwent a modest evolutionary radiation that included character

displacement in size and postcranial proportions. The Baltavar hipparion assemblage is of importance because it is substantial in its number of identifiable elements, and represents one of the latest known populations of Central European *Hippotherium*. The assemblage's referral to *Hippotherium "microdon"* is discussed further, below.

Baltavar is a vertebrate locality situated in western Hungary, west-northwest of Lake Balaton. The locality was discovered in 1850 during the construction of a postal road between Budapest and Graz. An unnamed Austrian engineer working on the edge of the small Hungarian town of Berbaltavar was undertaking a cut in the hill known to local people as "Kancsal" when his team of excavators uncovered abundant bones and teeth of fossil mammals. He contacted the Court Museum at Vienna (now the Naturhistorisches Museum, Wien) about their discovery and the museum, in turn, sent Mr. Eduard Suess, a renowned stratigrapher to the site to retrieve the bones. While not publishing a report on the Baltavar bones per se, SUESS (1861) stated that the species occurring at Baltavar were most like those of Pikermi, Greece (BENDA, 1927). Excavations occurred sporadically between 1850 and 1926, the most notable by PETHÖ (1883) and later KORMOS (1914) who amassed a large fauna that is mostly housed in the Museum of the Hungarian Geological Institute (MAFI, Budapest), the Naturhistorisches Museum, Wien, the Natural History Museum, London, and the Natural History Museum of Szombathely, Hungary.

Bernor and Kordos organized excavations at Baltavar and associated museum studies in the summers of 2000 and 2001 in an attempt to better understand the fauna, its age, sedimentary environments and paleoenvironmental context. This work is ongoing in collaboration with a number of European and American colleagues and will be published in the near future. Our preliminary results have established some very fundamental facts about the fauna and its context. First, the Baltavar fauna accumulated in a fluviatile channel. Second, the fauna is indeed similar to Pikermi (Greece), but, besides having mammalian taxa common to Pikermi, there are also large mammal species that are endemic to Central Europe. The Baltavar fauna accumulated substantially later than the famous Rudabánya fauna (BERNOR et al., 2003b, 2005), during the regressive phase of the Late Miocene Pannonian Lake, and is most likely MN 12 correlative, circa 7.5-7 Ma. As such, Baltavar represents the best assemblage of Central European medial Turolian age mammals known. The paleoenvironments were likely much like Pikermi, having recently been reported to be open country woodlands (BERNOR et al., 1996c; SOLOUNIAS et al., 1999). The most abundant large mammal at Baltavar was the equid, *Hippotherium "microdon"*

2. Materials and Methods

Table 1 provides a list of the localities used in this study, and their correlation following SCOTT et al. (2005b). Table 2 here lists the complete Baltavar hipparion assemblage

Symbol	Name	Pannonian Zone	MN unit
M	Maragheh, NW Iran		11 to 12
	Austria (all Locality 6 entries)	unknown	
b	Inzersdorf	E	9
	Gols	H?	11?
d	Schwechat	unknown	
	Rendezvousberg	unknown	
f	Prottes	H?	11 or 12
g	Wieden am See	unknown	
h	Atzelsdorf	C	9
	Mariental	C	9
j	Laaerberg	E	9
k	Stratzing	unknown	9?
l	Vösendorf	E	9
m	Belvedere	unknown	9
	Oswaldgasse	D?	9
	Siebenhirten	E	9
p	Grusse-Meiseldorf-Ziersdorf	unknown	
q	Mannersdorf B. Algern	H	11?
H	**Höwenegg**		**9**
D	**Dorn Dürkheim**		**11**
E	**Eppelsheim**		**9**
L	Mt. Luberon (= Cucuron)		12
S	Samos		12
R	**Rudabánya**		**9**
U	**Sümeg**		**10 to 11**
C	Csakvar		11
B	**Baltavar**		**12**
G	Polgardi		12 to 13
N	Baccinello		12 to 13

Table 1: List of localities used in this study. Age is based on MN correlations. Localities employed in dietary analysis are set bold.

measured by Bernor. For the purposes of our systematic work herein, we describe the morphology of a representative sample of maxillary and mandibular jaws and teeth from Baltavar. We follow BERNOR et al.'s (1997) measurement protocols, and here M = measurements as defined therein. M in each case refers to measurement, so for a given bone M1 equals the measurement as defined by BERNOR et al. (1997). To show metric ranges of variablility for the teeth we use maxillary P2 and calculate plots of occlusal length (M1) versus width (M3) (Fig. 2A, B) as well as protocone width (M11) versus length (M10) (Fig. 2C). We plot these dimensions against 95% confidence ellipses using the Eppelsheim (West Germany, Dinotheriensande, MN 9) sample. This sample is superior because it belongs to a single species of *Hippotherium*, it is the type locality of *Hippotherium primigenium*, a primitive Old World hip-

parion, and it is a robust statistical sample. We also analyse metacarpal III's (MC III), metatarsal III's (MT III) and 1st phalanx III's. For analysis of MC III's and MT III's we first use a series of bivariate plot comparisons (Figs. 3A-C) to several other late Miocene Central European localities from Germany Austria and Hungary, as well as the Greek locality of Samos, Iranian locality of Maragheh and the Italian localities of Baccinello (Table 1). For these bivariate plots we follow BERNOR et al. (1997 and elsewhere) in using the Höwenegg sample as our statistical standard for calculating 95% confidence ellipses. This population is "biologically uniform", including several complete, articulated skeletons belonging to a single primitive species, *Hippotherium primigenium* MEYER, 1833 (BERNOR et al., 1997), and is particularly useful for postcranial comparisons. We will initially plot our entire analytical sample (Table 2), then the Austrian sample and finally the Hungarian sample to gain insight into the Baltavar hipparion's systematic position. We further use the Höwenegg sample as a standard for calculating a log10 mean for all Baltavar MC III's (Fig. 3D), MT III's (Fig. 4D) and 1PH III's (Fig. 5). We will compare these log10 ratio plots against the mean Höwenegg sample to gain insight on how the Baltavar hipparion vary compared to the Höwenegg population. Our measurements follow EISENMANN et al. (1988), and BERNOR et al. (1997). Our analytical procedures have been most recently reviewed by SCOTT et al. (2005b). The rationale for these bivariate comparisons is to compare relative morphological, and inevitiably species diversity between these different geographic areas following SCOTT et al. (2005b). For the taxonomy of Western Eurasian hipparions we follow BERNOR et al. (1996) and highlight the strong provincial differences between Central European and Southeast European-Soutwest Asian localities.

Paleodietary analysis so far has focused on several upper and lower tooth positions. Upper M2 were originally employed by FORTELIUS & SOLOUNIAS (2000), KAISER et al. (2000), and SOLOUNIAS & SEMPREBON (2002). The tooth model has further been extended to upper and lower molars and fourth premolars in equids (KAISER & SOLOUNIAS, 2003; KAISER & FORTELIUS, 2003) and to both M2 and M3 in ruminants (FRANZ-ODENDAAL & KAISER, 2003).

The mesowear method of FORTELIUS & SOLOUNIAS (2000) has proven to be a powerful tool for reconstructing dietary traits of herbivorous ungulates (KAISER et al., 2000). It is based on facet development of cheek tooth occlusal surfaces. The degree of facet development reflects the relative proportions of tooth-to-tooth contact (attrition) and food-to-tooth contact (abrasion). Attrition creates facets while abrasion obliterates them. The entire surface of the teeth is affected by tooth wear but mesowear analysis has focused on the buccal cutting edges of the enamel surfaces where the buccal wall (ectoloph) meets the occlusal surface. The mesowear method treats ungulate tooth mesowear as two variables: occlusal relief and cusp shape. The sharper buccal cusp of a cheek tooth (either the paracone or the metacone) is scored. Occlusal relief (OR) is classified as high (h) or low (l), depending on how high the cusps rise above the valley between them. The second mesowear

variable, cusp shape, includes three scored attributes: sharp (s), round (r) and blunt (b) according to the degree of facet development. The mesowear method after FORTELIUS & SOLOUNIAS (2000) investigates mesowear using the upper second molar (M2) as a model. KAISER & SOLOUNIAS (2003) extended the method to four tooth positions (P4-M3) in order to make the method available for fossil equid assemblages, which mostly consist of small numbers of tooth individuals assignable to a certain tooth position. This extension allows to reconstruct and compare the dietary regime of different populations of closely related species from different paleohabitats. The "extended" mesowear method as introduced by KAISER & SOLOUNIAS (2003) is applied to reconstruct the dietary regimes of *Hippotherium primigenium* and six Upper Miocene (Vallesian to Turolian) *Hippotherium* populations from Central and Eastern Europe (BERNOR et al., 1999; KAISER et al., 2003; KAISER, 2003; BERNOR et al., 2003a, b).

2.1. Statistics

For dietary analysis, chi-square tests were performed to test for significance in differences observed in the distribution patterns of mesowear variables of different Central and Eastern European *Hippotherium* assemblages. Axum6 software (licenced to TMK) was used to compute Chi-square corresponding probabilities for each combination of datasets giving the probability that the null hypotheses of independence should be rejected (at an error probability of 0.05). The absolute frequencies of mesowear variables (high, sharp, and round) were tested for significance. Cluster statistics was performed for four groups of datasets using Systat 11.0 (SYSTAT Software Inc., Richmond, CA) software (licenced to TMK) and using default settings. Hierarchical cluster analysis with complete linkage (furthest neighbours) was applied following the standard hierarchical amalgamation method of HARTIGAN (1975). The algorithm of GRUVAEUS & WEINER (1972) was then used to order the cluster tree using the three mesowear variables (% high, % sharp and % blunt).

As a comparative dataset for dietary classification, we use 27 extant mammalian ungulate species reported as "typical" dietary categories by FORTELIUS & SOLOUNIAS (2000). For the fossil comparison species presented in this study we employ data published by: BERNOR et al. (1999; 2003a, b) for *Hippotherium intrans* from Rudabánya (DS6); KAISER et al. (2003) for *Hippotherium* aff. *primigenium* (DS3) and *Hippotherium kammerschmittae* (DS2) from Dorn-Dürkheim; KAISER (2003) for *Hippotherium primigenium* from Höwenegg (DS4) and Eppelsheim (DS5) and BERNOR et al. (1999) for *Hippotherium sumegense* from Sümeg (DS7).

We further apply Principal Components Analysis (PCA) on mesowear parameters % (% high, % sharp and % blunt) of each of the above mentioned datasets (DS). As in Cluster analysis, we include 27 "typical" extant ungulate species after FORTELIUS & SOLOUNIAS (2000) as comparative species with known diets.

3. Systematic Paleontology

Taxonomy:
Ordo Perissodactyla OWEN 1848
Subordo Hippomorpha WOOD 1937
Superfamilia Equoidea GRAY 1821
   Familia Equidae GRAY 1821
     Subfamilia Equinae GRAY 1821

Hippotherium „microdon" KORMOS, 1914

Holoype: MAFIVOB3193 (Vt. 109), a left mandible with very worn p3-m3 (Plate 1, G-H [photograph of cast]).
Type locality: Baltavar, Western Hungary
Referred specimens: listed in Table 2
Age: Late Miocene, medial Turolian age (MN 12), ca. 7.5-7.0 Ma.
Geographic range: Western Hungary.
Emended diagnosis (with derived characters compared to *Hippotherium primigenium* in bold):
A smaller member of the Central European *Hippotherium* lineage with complex plications of the maxillary and mandibular cheek teeth; **cheek tooth crowns, as demonstrated in P2's, becoming modestly more hypsodont with unworn P4-M1 likely being substantially more than 50 mm; protocones with flattened-to concave lingual borders; pli caballins reduced often being single;** hypoglyphs deeply incised in middle wear; metaconids mostly rounded; metastylids showing some squaring; protoconid enamel band always rounded; linguaflexids shallow V-shape in premolars, broader and somewhat deeper in molars; ectostylids absent in adult cheek teeth; **MC III's and MT III's somewhat smaller and more slender than in *M. primigenium*.**
Description of the material: Table 2 lists 508 specimens of hipparionine equids from Baltavar. This is acknowledged as being a partial, perhaps majority sample of the hipparions known from Baltavar. As cited earlier, the Baltavar assemblage is principally housed in London, Vienna, Budapest and Szombathely, but many specimens were likely sold and traded to natural history museums around the world. The majority of specimens are believed to belong to *Hippotherium "microdon"*, there being a rarer form present at Baltavar (SCOTT et al., 2005b). We describe a representative sample of these elements below.
Skulls and dentitions: There are no complete skulls of the Baltavar hipparions to describe. There are premaxillary and maxillary fragments and individual cheek teeth.
Plate 1A, B is an edentulous premaxilla, MAFIV13180A, A being a dorsal view and B being an occlusal view. This specimen has a large canine alveolus revealing that this was a male individual (Plate 1B). The most significant aspect of this specimen is the shape of incisor arcade which is arcuate and as such suggestive of a selective feeding adaptation, not dedicated grazing (BERNOR & ARMOUR-CHELU, 1999).
One of the most complete and best represented cranial fragments is a right maxilla with P2-M2, MAFOB13195 (Plate 1C). In this specimen all cheek teeth are character-

ized as having: complex plications of the pre- and postfossettes, hypoglyphs that are deep to very deep; protocones that have flattened-to-lingually concave surfaces and are moderately elongate; mesostyles that are a slender U-shape; P2 has an elongate anterostyle; pli caballin varying from being highly reduced on P2, P4 and M2, double on P3 and single on M2. Of these features, the protocone and pli caballin morphologies are derived for the *Hippotherium* clade.
Plate 1E, F is a P2, MAFIV13169 in a moderate stage-of-wear, less worn than the P2 of MAFI3195. Plate 1F shows that the crown is high for *Hippotherium* (43.2 mm), and Plate 1E shows that enamel plication morphology is complex on all fossette borders, a hallmark for this genus. Likewise, the pli caballins are clearly double, hypoglyph is moderately deeply incised and protocone is oval-shaped. The crown height in this specimen is greater than any measured for the Höwenegg hipparion, whose maximum measured crown height is 37 mm (BERNOR et al., 1997), and is an advanced feature for this species of *Hippotherium*.
Mandibles and dentitions: MAFIOB338 (Plate 1D) is a nearly adult mandibular symphysis with right and left i1-c, and with i3 not yet in complete occlusion. The canines are very large with a broad lingual pillar indicating that this was a male individual. The most significant feature of this specimen is the rounded-arcuate incisor arcade which effectively mirrors the premaxillary fragment described above: this is the pattern of a selective feeder.
Plate 2A and B show a left mandible, MAFIVBalt1, with p3-m3. Plate 2A exhibits p3-m3 in a relatively moderate stage-of-wear, with the following salient features: metaconids are rounded; metastylids all exhibit some degree of distal squaring; linguaflexid is shallow on p3, shallow V-shape on p4, deeper V-shape on m1-m3; ectoflexid is shallow on p3, slightly deeper on p4 and deep, invading the metaconid-metastylid isthmus on m1-m3; preflexid enamel plications exhibit complexity of their mesial borders, while postflexids appear too worn to preserve enamel plications; all cheek teeth have rounded protoconid enamel bands; no cheek teeth preserve either protostylids or ectostylids.
In that we define two taxa of hipparions at Baltavar based on metapodial proportions (below), we have calculated a series of plots on maxillary P2. BERNOR et al. (1997, 2003c) have shown that P2 is always certainly identifiable and the most metrically stable cheek tooth through wear; other cheek teeth are not so useful. Figure 2A plots our complete analytical sample against the Eppelsheim 95% confidence ellipse for occlusal width (M3) versus occlusal length (M1). There are a number of points, and in particular Samos and Maragheh, that plot outside the ellipse. Figure 2B has a slightly changed X-axis scale to better render the distribution of the sizeable Baltavar P2 sample for M3 versus M1. The majority of points plot within the Eppelsheim ellipse, with some falling below, some to the right and some to the left of the ellipse. There is no clear indication of two or more size clusters in this plot. Figure 2C plots protocone width (M11) versus protocone length (M10) and exhibits all Baltavar points, except one, plotted within the Eppelsheim 95% confidence ellipse. Further-
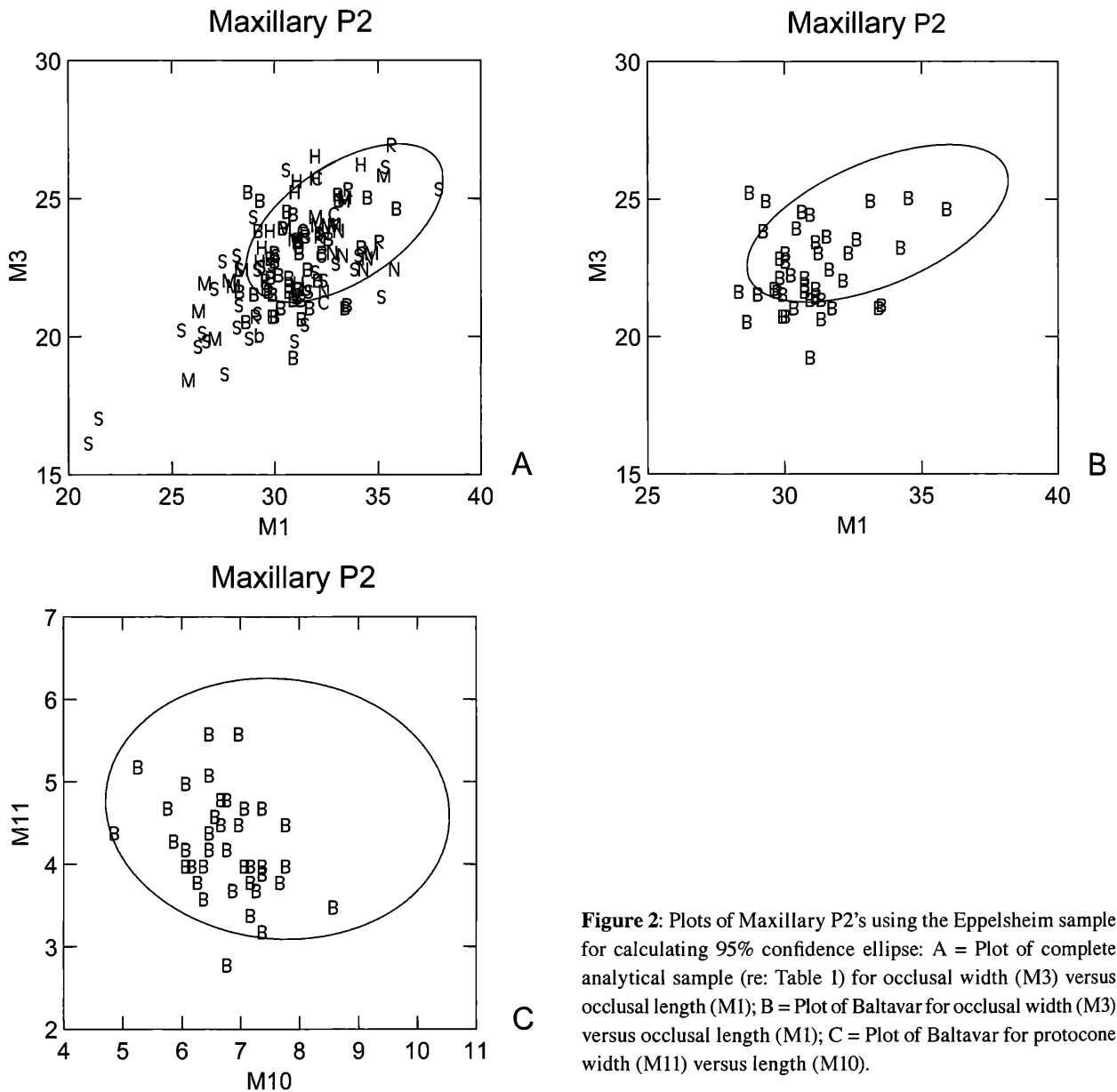
Maxillary P2

A

Maxillary P2

B

Maxillary P2

C

Figure 2: Plots of Maxillary P2's using the Eppelsheim sample for calculating 95% confidence ellipse: A = Plot of complete analytical sample (re: Table 1) for occlusal width (M3) versus occlusal length (M1); B = Plot of Baltavar for occlusal width (M3) versus occlusal length (M1); C = Plot of Baltavar for protocone width (M11) versus length (M10).

more, there are no discrete clusters within the Eppelsheim ellipse. We can only conclude from this analysis that two species of Baltavar hipparion cannot be discriminated by cheek tooth metrics.

Metacarpal III's: Plate 2C-E renders three complete Baltavar hipparion right MC III's: MAFIV417/2, MA-FIV417/3 and MAFI418/5 which are relatively elongate and moderately robust.

Figure 3 provides a series of plots made on MC III. Figure 3A includes all the localities listed in Table 1. The ellipse in the right center of the bivariate field represents the 95th percentile ellipse of the Höwenegg population. When considering all the localities in our analytical sample, one can see that there are many plotted points outside the Höwenegg ellipse, particularly to the right and above. As pointed out by SCOTT et al. (2005a, b) the Eastern Mediterranean – Southwest Asian localities of Samos (= S here; Greece) and Maragheh (= M here; Iran) are particularly remarkable for their elongate slender hipparion species that differ significantly from Central European *Hippotherium*. We plot here also the Mt. Luberon (= L; MN 12,

France) sample to show that these hipparions had more slender metapodial III proportions than the Höwenegg sample, overlapping considerably portions of the Samos and Maragheh sample.

Figure 3B plots only the Austrian Late Miocene hipparions. Nearly all the Austrian localities under consideration fall within the ellipse. The most remarkable exception to this is a single specimen from Prottes (f) which falls far to the left and slightly higher than the rest of the population. Gols (c) has one specimen outside the upper left portion of the ellipse, and one inside. Inzersdorf has one specimen outside the lower right of the ellipse, and three inside the ellipse. Of these, Prottes is likely the youngest of the sample and therefore likely the closest in age to Baltavar.

Figure 3C plots only the Hungarian hipparion MC III's. The Baltavar sample falls in the lower portion, and outside the lower portion of the Höwenegg ellipse. The only other individual that falls below the ellipse is represented by a U, and is the type specimen of *Hippotherium sumegense* (BERNOR et al., 1999). The Csakvar sample (C) is distributed into a population within the center of the ellipse
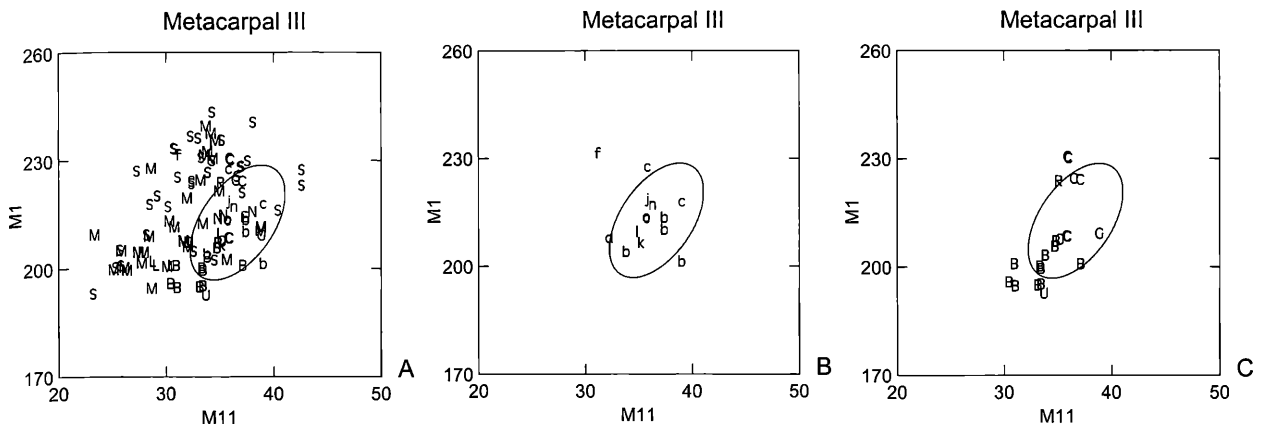
Figure 3: Metacarpal III statistical plots using the Höwenegg population standard: A = bivariate plot of maximum length (M1) versus distal articular width (M3) of entire analytical sample; B = bivariate plot of maximum length (M1) versus distal articular width (M3) of the Austrian late Miocene sample; C = bivariate plot of maximum length (M1) versus distal articular width (M3) of the Hungarian late Miocene sample; D = log10 ratio diagram of Baltavar MC III's.
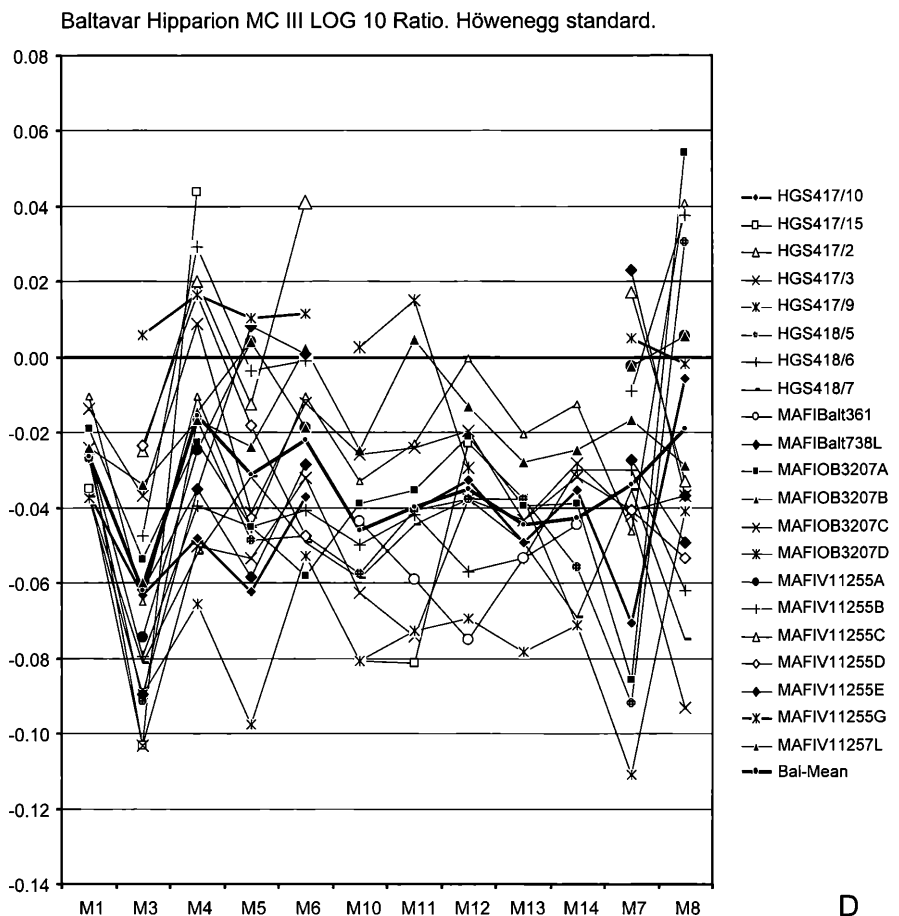
and another at the top of the ellipse. Associated with the uppermost distribution of Csakvar, is a single MC III of *Hippotherium intrans* from Rudabánya (R). Associated with the smaller sample of Csakvar are two specimens of Polgardi hipparion. In conclusion, the MC III bivariate plots for the Hungarian sample includes three morphological groupings:

1. a larger, elongate MC III sample from Rudabánya (*Hippotherium intrans*), apparently also represented at Csakvar; 2. a smaller morph from Baltavar, with length-width dimensions most similar to *Hippotherium sumegense*; 3. a Höwenegg sized form from Csakvar and Polgardi.

Figure 3D is a log10 ratio diagram of the Baltavar MC III's compared to the mean Höwenegg standard. The sample exhibits remarkable uniformity, except for one fragmentary

individual, MAFIV12555G (with star symbol). Compared to the Höwenegg log10 mean, the Baltavar MC III sample has: shorter maximum length (M1), more slender midshaft width (M3), somewhat shallower midshaft depth (M4); but note the slenderness of the mid-shaft); proximal articular width (M5) and depth (M6) and distal articular dimensions (M10-14) overlap or are smaller than the Höwenegg sample. This plot supports a species-level distinction from the Höwenegg *Hippotherium primigenium* sample.

Metatarsal III's: Plate 2F and G renders the cranial view of two Baltavar MT III's, on the left (F) MAFIOB420-4 and on the right (G) MAFIOB419-12. Both are relatively elongate and slender in their morphology.

Figure 4A provides a plot of our complete comparative sample, which again shows that Western Mediterranean
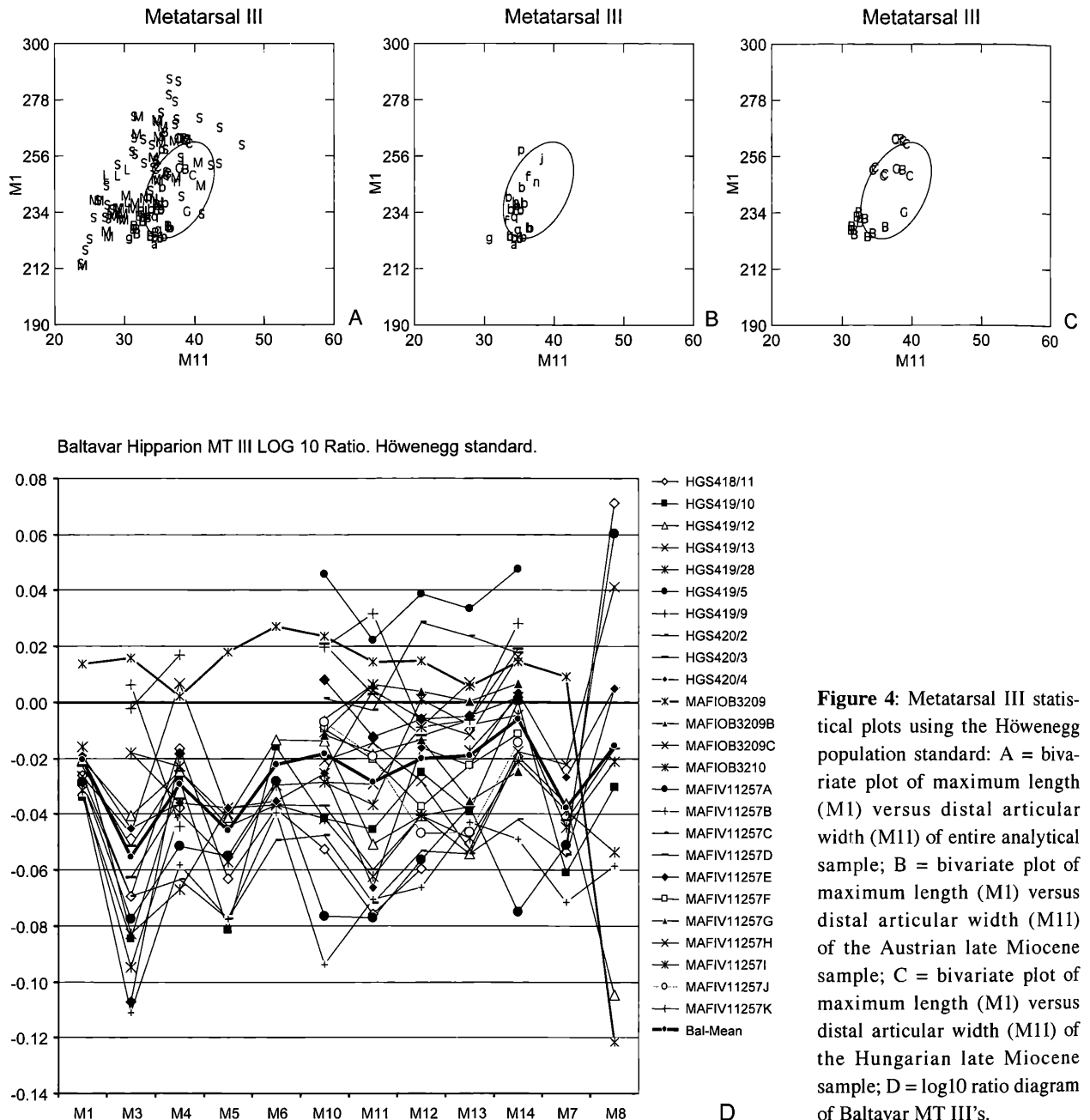
Figure 4: Metatarsal III statistical plots using the Höwenegg population standard: A = bivariate plot of maximum length (M1) versus distal articular width (M11) of entire analytical sample; B = bivariate plot of maximum length (M1) versus distal articular width (M11) of the Austrian late Miocene sample; C = bivariate plot of maximum length (M1) versus distal articular width (M11) of the Hungarian late Miocene sample; D = log10 ratio diagram of Baltavar MT III's.

(L = Mt. Luberon) and Eastern Mediterranean (Samos = S) and Southwest Asian (M = Maragheh) collectively have a large number of specimens plotting outside the Höwenegg ellipse. There are also individuals which are much more elongate than the Höwenegg sample, and a few more massive, revealing considerable species diversity.

Figure 4B plots the Austrian sample only. Nearly all of the sample is distributed within the ellipse. One specimen (p) from Grusse-Meiseldorf-Ziersdorf is found to the left of the upper portion of the ellipse. A specimen from Wieden am See (g) is smaller and found below and slightly to the left of the ellipse. The Inzersdorf sample (b) falls in the lower portion of the Höwenegg range, and in this regard resembles the Sinap early MN 9 sample of *Cormohipparion sinapensis*. Inzersdorf is likely a primitive member of the *Hippotherium* clade, because of its very complex enamel plications, that retained primitively small MT III's (Scott et al., 2005b).

Figure 4C plots the Hungarian sample. All Baltavar MT III's, except one, plot at the lower end of the Höwenegg ellipse. There is a single specimen from Polgardi that plots close to these Baltavar specimens. The Csakvar sample includes two clusters: one in the upper portion of the Höwenegg ellipse (with the single Baltavar specimen), and another cluster overlapping the upper border of the ellipse (with a single Rudabánya specimen of *Hippotherium intrans*). This plot suggests that there are as many as three populations represented in this cluster, and that the two extreme clusters are likely species of *Hippotherium* other than *H. primigenium*. The elongate Csakvar form is referable to *Hippotherium* cf. *intrans*, whose type is from Rudabánya (Bernor et al., 1993a, 1999, 2003a; Scott et al., 2005b).

Figure 4D is a log10 ratio diagram of Baltavar MT III's. The sample is mostly uniform in its dimensions, with one obvious exception: MAFIOB3209, which is larger and

**Figure 5**: Log10 ratio diagram of Baltavar 1PH III's, Höwenegg standard.

more elongate. The majority of the sample has log10 ratio proportions closely tracking the MC III sample in its comparison to the Höwenegg mean: maximum length (M1) is less; midshaft width (M3) is far narrower; midshaft depth (M4) is somewhat narrower (but note that the M3-M4 ratio reveals both absolute and relative narrowness); proximal and distal articular dimensions (M5-M6; M10-M14) overlap, but are mostly less than the Höwenegg sample. The larger MT III, MAFIOB3209, is remarkable for its great length, massive midshaft dimensions, and large proximal and distal articular dimensions. This analysis supports the existence of a rare large species of *Hippotherium* from Baltavar best referable to *Hippotherium* cf. *intrans*, also occurring at Rudabánya and Csakvar.

1PH III's are relatively rare at Baltavar, and elsewhere, so we have not calculated any bivariate plots. Figure 5 is a log10 ratio plot of four Baltavar 1PH III's. They all four closely covary except for the smaller midshaft depth dimension of MAFIBalt724L. The Baltavar 1PH III sample compares to the Höwenegg population as follows: length (M1 and M2) marginally less; midshaft width (M3) overlapping or somewhat less; proximal articular width (M4) overlapping or somewhat less; proximal articular depth (M5) mostly similar; distal width at tuberosities (M6) somwhat smaller; distal articular width (M7) somewhat greater; distal articular depth (M8) less; caudal trigonmum phalangis scar markedly variable (typical for hipparions). In effect, there is little morphometric difference between the Höwenegg and Baltavar hipparions.

Remarks: The Baltavar hipparions are evidently a late occurring assemblage of *Hippotherium* species. There is a predominant species clearly represented by a large homogeneous sample of MC III's and MT III's, and a rare species best represented by a single, complete MT III, MA-FIOB3209. A fragmentary MC III, MAFIV11255G may also represent this rare species. The rare species mostly closely compares morphometrically with the Rudabánya hipparion, *Hippotherium intrans*. This leaves us seeking a viable nomen for the dominant, smaller and more gracile form at Baltavar.

„*Hipparion microdon*" was erected by KORMOS (1914) based on a very worn mandibular dentition (MAFIVOB-3193 (VT-109); Plate 1, fig. G, H). KORMOS (1914) noted that the teeth were the size of the diminuitive hipparion, "*Hipparion*" *minus* from Samos. However, the very small size of the teeth of the type specimen of "*Hipparion microdon*" is due entirely to this individual's old age.
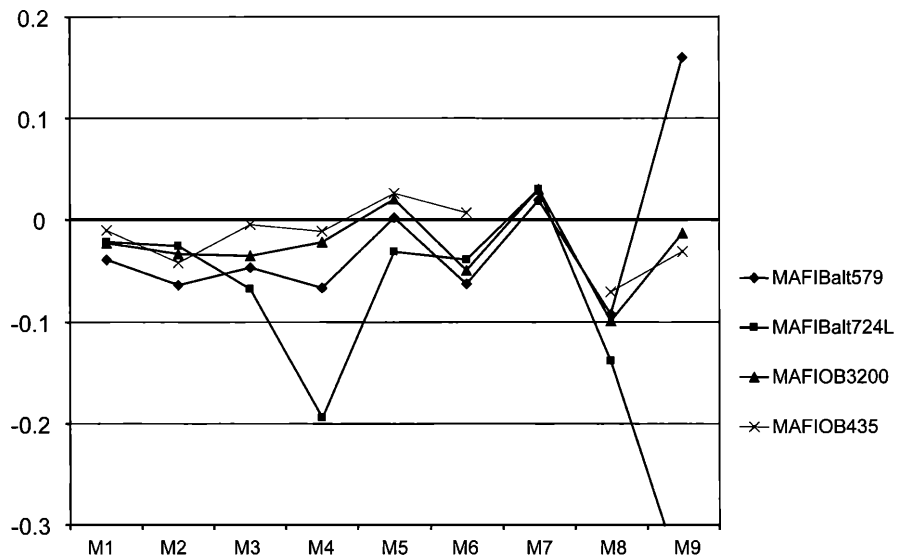
It is well known now that as hipparion teeth wear, they become smaller, particularly in their occlusal length measurement. Additionally, because the dentition is so worn, the occlusal surface details have become obliterated, and as such the type specimen is undiagnostic at the species level. As such, the Baltavar nominal taxon *Hipparion microdon* lacks efficacy. Moreover, both the dental and postcranial remains share a number of discrete and continuous characters with *Hippotherium*, invalidating the referral to *Hipparion* s.s. (WOODBURNE & BERNOR, 1980; BERNOR et al., 1996b). However, for the sake of taxonomic stability, we prefer to recognize the nomen *Hippotherium* „*microdon*" for the majority of the Baltavar specimens and *Hippotherium* cf. *intrans* for the two metapodials cited herein.

4. Paleodiet

4.1. Macroscopic Occlusal Wear Features

***Hippotherium* populations included**: We select six populations of *Hippotherium* from Vallesian and Turolian Central and Eastern European localities additionally to the Baltavar hipparion population in order to compare dietary signals and to test for the influence of climatic signals on the mesowear signature of these populations.

***Hippotherium* "*microdon*" from Baltavar (Hungary)**: After excluding specimens in very early wear, and specimens with less than 15 mm remaining crown height, 99 dental specimens of cheek tooth positions P4-M3 of *Hippotherium microdon* were available for this investigation.

***Hippotherium* aff. *primigenium* and *H. kammerschmittae* from Dorn-Dürkheim (Germany)**: The Dorn-Dürkheim hipparion fauna (MN 11) is intermediate in age compared to the Baltavar fauna and the Vallesian hipparion faunas of central Europe. As a whole, the fauna indicates a forested biotope with an abundantly watered
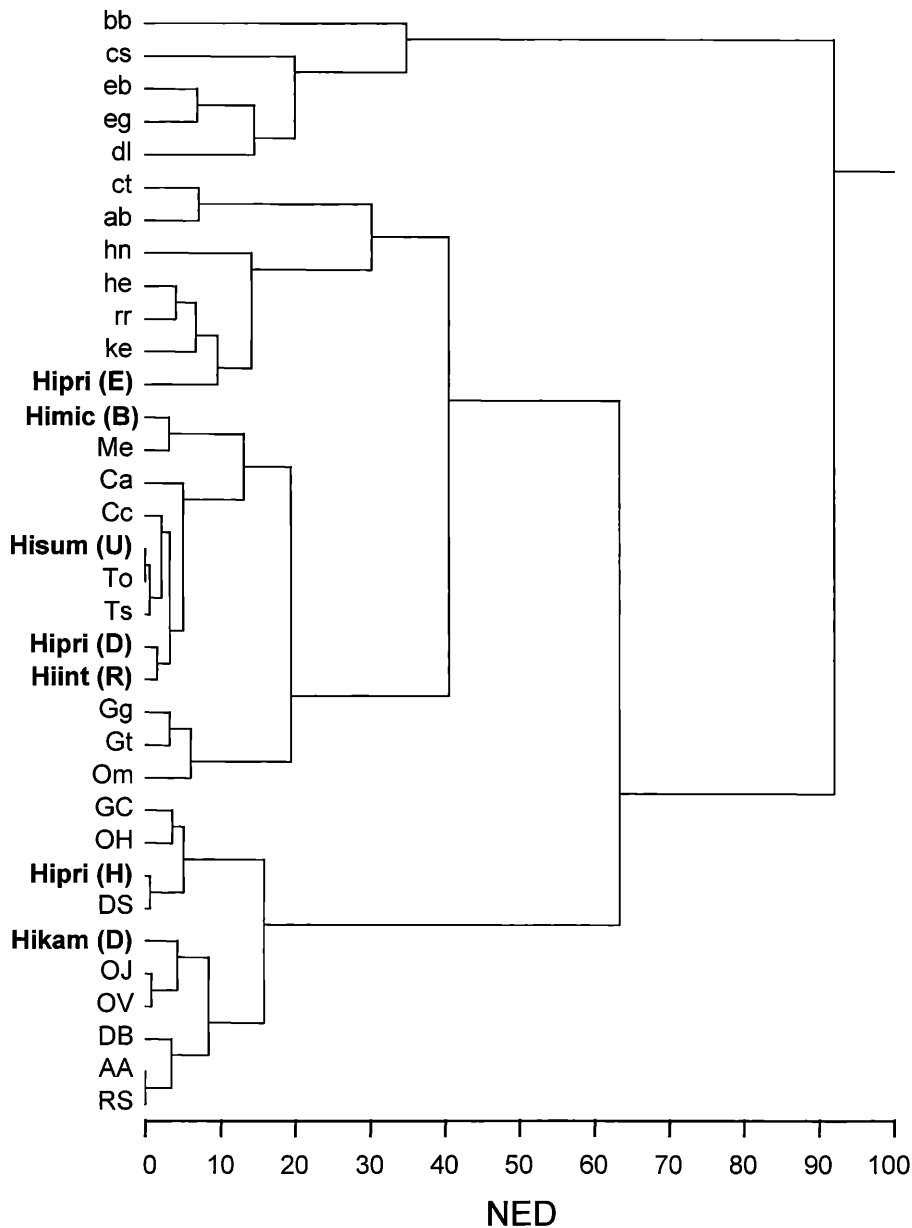
Dürkheim (MN 11), Hicam (D) = *Hippotherium kammerschmittae* from Dorn-Dürkheim, Himic (B) = *Hippotherium "microdon"* from Baltavar (MN 12).

Mesowear scorings for *Hippotherium* sp. base on the upper P4-M3 according to the "extended" mesowear method (KAISER & SOLOUNIAS, 2003). Distances are Euclidean distances.

Capital initials = browser, lower case initials = grazer, mixed capital and lower case initials = mixed-feeder.

Browsers: AA = *Alces alces*, DB = *Diceros bicornis*, DS = *Dicerorhinus sumatrensis*, GC = *Giraffa camelopardalis*, OH = *Odocoileus hemionus*, OJ = *Okapia johnstoni*, OV = *Odocoileus virginianus*, RS = *Rhinoceros sondaicus*. **Grazers**: ab = *Alcelaphus buselaphus*, bb = *Bison bison*, cs = *Ceratotherium simum*, ct = *Connochaetes taurinus*, dl = *Damaliscus lunatus*, eb = *Equus burchellii*, eg = *Equus grevyi*, he = *Hippotragus equinus*, hn = *Hippotragus niger*, ke = *Kobus ellipsiprymnus*, rr = *Redunca redunca*. **Mixed feeders**: Ca = *Capricornis sumatraensis*, Cc = *Cervus canadensis*, Gg = *Gazella granti*, Gt = *Gazella thomsoni*, Me = *Aepyceros melampus*, Om = *Ovibos moschatus*, To = *Taurotragus oryx*, Ts = *Tragelaphus scriptus*.

Figure 6: Hierarchical cluster diagrams based on a set of 27 "typical" species from FORTELIUS & SOLOUNIAS (2000). *Hippotherium* datasets are in bolt. Hipri (E) = *Hippotherium primigenium* from Eppelsheim (MN 9), Hipri (H) = *Hippotherium primigenium* from Höwenegg (MN 9), Hiint (R) = *Hippotherium intrans* from Rudabánya (MN 9), Hisum (U) = *Hippotherium sumegense* from Sümeg (MN 10), Hipri (D) = *Hippotherium* aff. *primigenium* from Dorn-

landscape. Dorn-Dürkheim 1 is the only German locality securely correlated with MN 11, and as such it occupies a critical paleogeographic tie-point between comparably aged localities of Spain, France, Austria, Hungary and the Czech Republic (FRANZEN & STORCH, 1999). The Dorn-Dürkheim hipparion sample includes teeth and isolated postcranial elements (BERNOR & FRANZEN, 1997). Besides *Hippotherium* aff. *primigenium* (BERNOR & FRANZEN, 1997), KAISER et al. (2003) and KAISER et al. (2005) identify a second hipparion species at Dorn-Dürkheim, *Hippotherium kammerschmittae*. *Hippotherium kammerschmittae* is slightly smaller than *H. primigenium* (body mass near 190 kg), MC III are moderately long, displaying

a craniocaudally expanded crista sagittalis and a reduced minimal lateral condyle depth. Cheek tooth morphology is essentially the same as in *H. primigenium* (as defined by BERNOR et al., 1997 and BERNOR & FRANZEN, 1997), but cheek teeth are slightly narrower and shorter than in *Hippotherium primigenium*. Dietary analysis of the two Dorn-Dürkheim hipparions undertaken by KAISER et al. (2003) indicates that the large bodied species [Hipri (D)] had a mixed diet at Dorn-Dürkheim which was very similar to that of *Hippotherium intrans* in the MN 9 at Rudabánya. The small bodied species (*H. kammerschmittae*) [Hikam (D)] differs from *H.* aff. *primigenium* in having been a more dedicated browser at Dorn-Dürkheim.

Figure 7: Principal components factor plot based on a set of 27 "typical" species from FORTELIUS & SOLOUNIAS (2000). *Hippotherium* datasets are in bold. Mesowear scorings for *Hippotherium* sp. base on the upper P4-M3 according to the "extended" mesowear method (KAISER & SOLOUNIAS, 2003). Capital initials = browser, lower case initials = grazer, mixed capital and lower case initials = mixed-feeder (species legends as in Figure. 6).
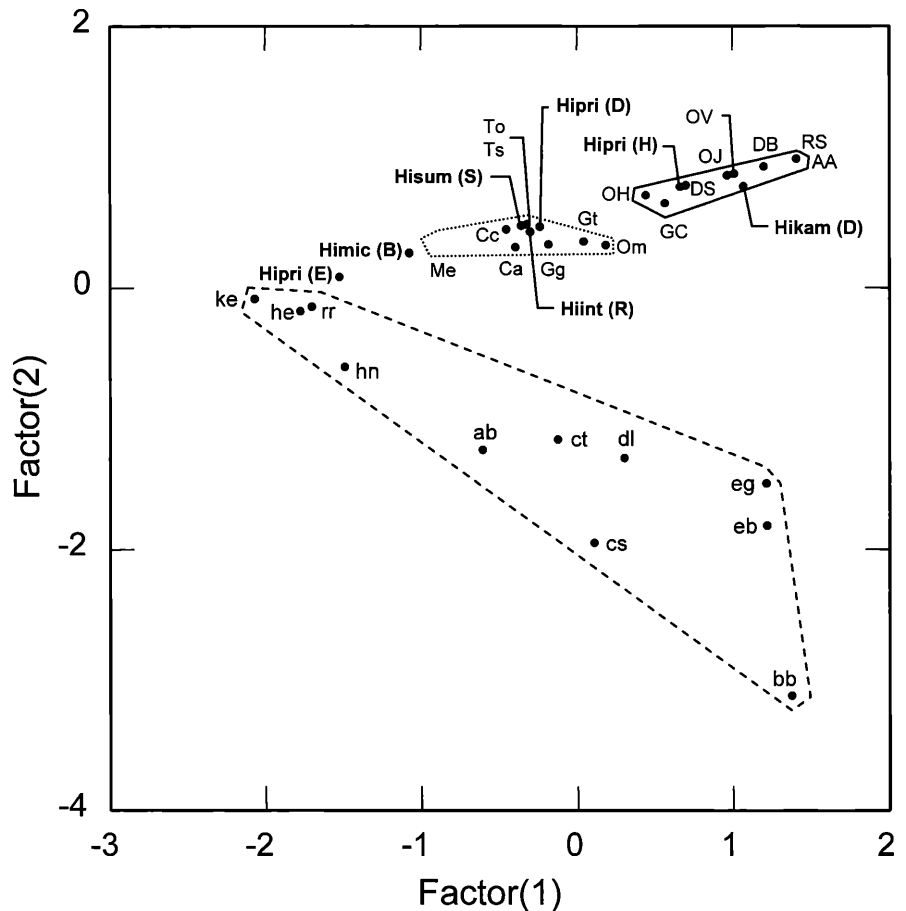
Hippotherium primigenium from Höwenegg (Germany): The Upper Miocene fossil locality of Höwenegg (Hegau, Southern Germany) has yielded articulated mammal skeletons as well as isolated skeletal elements from various species of the Perissodactyla and Artiodactyla among which the hipparionine equid *Hippotherium primigenium* [Hipri (H)] makes up the most frequently preserved. Recent chronostratigraphic work suggests a MN correlation which places the „Höwenegg - Schichten" in the early Vallesian = MN 9 (BERGGREN & VAN COUVERING, 1974; BERNOR et al., 1988; BERNOR et al., 1980, 1989; MEIN, 1989; STEININGER et al., 1989; TOBIEN, 1986). The Höwenegg population of *H. primigenium* is particularly well suited as a reference population for the Central European biogeographic region in the upper Miocene, because the mesophytic forest habitat reconstructed for this population is considered typical for large parts of Central Europe in the Vallesian period. This reconstruction is as well supported by the mammalian fauna (TOBIEN, 1986) as also by the trophic signal of the hipparions, which are shown to have incorporated a large proportion of browse in their diet (KAISER, 2003: fig. 1).

Hippotherium primigenium from Eppelsheim (Germany): The Upper Miocene sequence of sands, silts, gravels and conglomerates exposed at Eppelsheim (Germany) has yielded a rich mammalian fauna, which is estimated at about 10.5 Ma (STEININGER et al., 1996a, ANDREWS & BERNOR, 1999). This assemblage comprises the genotypic sample of *Hippotherium primigenium* (MEYER, 1829)

(FRANZEN, 2000; KAISER et al., 2000). The chronological homogeneity of the Dinotheriensande sample is uncertain, but there is no reason to believe at present that more than one species of hipparion is present in this sample. Besides being the largest sample of teeth known of *Hippotherium primigenium* [Hipri (E)], the Dinotheriensande sample is almost known entirely from isolated teeth allowing crown height measurements to be taken, which is important for ultimately knowing the wear stage and age of the individual at death. The latter facts make Eppelsheim the most favourable reference sample for the Dinotheriensande complex. KAISER (2003) has reconstructed the dietary regime of the Eppelsheim population of *H. primigenium* as that of a grazer. The African extant common waterbuck (*Kobus ellipsiprymnus*), a grazer inhabiting reedbeds and also foraging into woodlands is identified as the dietary analogue for the Eppelsheim population. KAISER (2003) concludes that the paleohabitat of Eppelsheim would be recognised as representing at least seasonally extended grassy areas as reed flats in the proximity of the Miocene Rhine River that served as meadows for *H. primigenium*.

Hippotherium intrans from Rudabánya (Hungary): KRETZOI (1983) named a new species of *"Hipparion"* from Rudabánya based on a complete metatarsal III, *Hipparion intrans* [Hiint (R)]. In a preliminary description of the Rudabánya hipparion (BERNOR et al., 1993a) and a subsequent comparison with the Götzendorf (MN 9/10, Vienna Basin, Austria) hipparion assemblage, BERNOR et al. (1993b) later agreed that the Rudabánya hipparion

represented an advanced population of *Hippotherium primigenium* lineage and suggested a late MN 9 correlation for Rudabánya. Ecomorphological evaluation of *H. intrans* by BERNOR et al. (2003a, b) identified the species as a mixed feeder at Rudabánya based on mesowear analysis in their study. The entire upper cheek tooth material of *H. intrans* from Rudabánya (BERNOR et al., 1993a) collected between 1977 and 1994 was included, which made 25 teeth available to this investigation.

***Hippotherium sumegense* from Sümeg (Hungary)**: The late Vallesian vertebrate locality of Sümeg is a fissure fill formed in the late Cretaceous limestone Gerinc Quarry (Ugod Limestone Formation) and is situated in the Central Transdanubian Mountains, Hungary. BERNOR et al. (1999) indicate Sümeg to have a minimum age of not less than 9.0 Ma giving a congruent result with previous correlations of MN 10 being between 9.5 and 9.0 Ma (STEININGER et al., 1996a; RÖGL & DAXNER-HÖCK, 1996). BERNOR et al. (1999) describe a smaller member of the Central European *Hippotherium primigenium* - lineage from Sümeg, *Hippotherium sumegense* [Hisum (U)] which is characterized by a short MC III that has a relatively broad and flat midshaft dimension. BERNOR et al. (1999) suggest that *Hippotherium sumegense* was a non-cursorial forest denizen with a significant browse component in its diet.

4.2. Frequency of mesowear variables

The frequency of mesowear variables scored is shown in Table 3. High occlusal reliefs make up 100% in the Baltavar upper cheek tooth sample. Round cusps predominate (59%) and sharp cusps make up 25%. There are no blunt cusps in this population. If proportions of mesowear variables high, sharp and round are tested for significance of differences observed in the distribution pattern, p-values ranging between <0.0001 and 0.72 indicate that *H. "microdon"* is likely to be different in its mesowear signature from the following Central European Upper Miocene hipparion populations: 1. The Dorn-Dürkheim population of *Hippotherium kammerschmittae* ($p = 0.0079$), the Dorn-Dürkheim population of *Hippotherium* aff. *primigenium* ($p = 0.0037$) and the Höwenegg *H. primigenium* ($p < 0.0001$). P values > 0.05 indicate, that at the given error probability of 0.05 *H. microdon* is not different from *H. primigenium* from Eppelsheim ($p < 0.172$), *Hippotherium intrans* from Rudabánya ($p = 0.148$), and *H. sumegense* from Sümeg ($p = 0.72$).

Linkage patterns in cluster (CA) and PCA plots: The cluster diagram computed shows relations of datasets by joining them in the same clusters. The closer the data are, the smaller is the normalized Euclidean distance (NED) at the branching point. However, the exact sequence and direction of species arrangement in the diagram may not be interpreted as an expression of sequential differences, because clusters in the diagram may flip. Cluster analysis using the mesowear variables %high, %sharp and %blunt polarise the set of 27 extant ruminant and rhinocerotid

species and the seven fossil hipparion populations under study into a pattern with grazers and browsers at the extremes and with mixed feeders in between (Fig. 6). There are four main clusters, one containing those grazers with the most abrasion dominated diet, one containing the grazers with less abrasive diet, one containing all mixed feeders from the comparative sample, and one containing all the browsers.

Cluster analysis using all mesowear variables polarize the entire set of 27 'typical' extant species by FORTELIUS & SOLOUNIAS (2000: fig. 6). The Baltavar hipparion is joined in a cluster of NED = 13.1 which besides the Rudabánya, Sümeg and the Dorn-Dürkheim sample of *Hippotherium* aff. *primigenium* (KAISER et al., 2003), comprises five mixed feeders. Amongst those, the Baltavar sample is closely linked with *Aepyceros melampus* (Me), the impala antelope. The Höwenegg sample of *H. primigenium* (KAISER, 2003) and the Dorn-Dürkheim population of *Hippotherium kammerschmittae* (KAISER et al., 2003), however, are joined in a cluster of NED = 15.8 which comprises exclusively browsers. Here the Sumatran rhinoceros (*Dicerorhinus sumatrensis*; DS) is the closest linked extant species (Fig. 6). The only *Hippotherium* population linked in the grazer spectrum is *Hippotherium primigenium* from Eppelsheim (KAISER, 2003).

Principal components analysis (PCA) plots the Baltavar population of *H. "microdon"* in the transitional space between the mixed feeders and the grazers (Fig. 7). We realize that within the factor space this species is much closer to the mixed-feeder kernel, while the Eppelsheim population of *H. primigenium* [Hipri (E)] is much closer to the grazer kernel. From the PCA it becomes obvious, that the hipparions from Sümeg [Hisum (S)], Dorn-Dürkheim [Hiprim (D)] and Rudabánya [Hiint (R)] are very close in their mesowear signatures, as indicated by their crowded classification in the center of the mixed-feeder factor kernel. As in the CA, the Höwenegg hipparion [Hipri (H)] and *H. kammerschmittae* from Dorn Dürkheim [Hikam (D)] are the only populations classified in the browser kernel.

5. Discussion

The dietary signal for the Baltavar population of *Hippotherium "microdon"* is in the mixed feeder range close to the transition to the grazers. In this regard, it is significantly different from most other Central European Vallesian and Turolian populations of *H. primigenium*, *H. sumegense*, *H. intrans* and *H. kammerschmittae*. The dietary reference species of the Baltavar population, the impala (*Aepyceros melampus*) is an inhabitant of mainly open country. It is water dependent but can go without water for considerable time. The impala is found frequently in grass dominated open environments like bushland and Acacia savannahs but also in *Acacia* forests and other deciduous woodlands.

The impala has a diet that may be considered to be a perfectly balanced mixed diet. The status of the impala as a mixed (intermediate) feeder is uniformly acknowledged

DS	Taxon	Sample	sym	n	l	h	s	r	b	%l	%h	%s	%r	%b
1	*Hippotherium microdon*	Baltavar (Hungary)	Himic (B)	99	0	99	25	59	0	0.0	100.0	29.8	70.2	0.0
2	*Hippotherium kammerschmittae*	Dorn-Dürkheim (Germany)	Hikam (D)	14	1	13	7	1	0	7.0	93.0	88.0	13.0	0.0
3	*Hippotherium* aff. *primigenium*	Dorn-Dürkheim (Germany)	Hipri (D)	91	3	88	41	32	0	3.3	96.7	56.2	43.8	0.0
4	*Hippotherium primigenium*	Höwenegg (Germany)	Hipri (H)	43	0	43	30	8	0	0.0	100.0	78.9	21.1	0.0
5	*Hippotherium primigenium*	Eppelsheim (Germany)	Hipri (E)	58	2	56	8	43	0	3.4	96.6	15.7	84.3	0.0
6	*Hippotherium intrans*	Rudabánya (Hungary)	Hiint (R)	25	1	24	12	12	0	4.0	96.0	50.0	50.0	0.0
7	*Hippotherium sumegense*	Sümeg (Hungary)	Hisum (S)	4	0	4	1	1	0	0.0	100.0	50.0	50.0	0.0

DS1/2	X-square = 9.6929, df = 2, *p*-value = 0.0079
DS1/3	X-square = 11.1756, df = 2, *p*-value = 0.0037
DS1/4	X-square = 25.8026, df = 2, *p*-value = <0.0001
DS1/5	X-square = 3.521, df = 2, *p*-value = 0.172
DS1/6	X-square = 3.8208, df = 2, *p*-value = 0.148
DS1/7	X-square = 0.6504, df = 2, *p*-value = 0.7224

Table 3: Mesowear variable distribution in the populations investigated. Himic (B) = *Hippotherium "microdon"* from Baltavar (Hungary); Hicam (D) = *Hippotherium kammerschmittae* from Dorn-Dürkheim (Germany); Hipri (D) = *Hippotherium* aff. *primigenium* from Dorn-Dürkheim (Germany); Hipri (H) = *Hippotherium primigenium* from Höwenegg (Germany); Hipri (E) = *Hippotherium primigenium* from Eppelsheim (Germany); Hiint (R) = *Hippotherium intrans* from Rudabánya (Hungary); Hisum (S) = *Hippotherium sumegense* from Sümeg (Hungary); n = number of specimens available; Mesowear variables: l = absolute scorings low, h = absolute scorings high, s = absolute scorings sharp, r = absolute scorings round, b = absolute scorings blunt; % l = percent low occlusal relief, % h = percent high occlusal relief, % s = percent sharp cusps, % r = percent rounded cusps, % b = percent blunt cusps.

by all workers who have evalutated ungulate dietary classification (JANIS, 1988; JANIS & ERHADT, 1988; GRZIMEK, 1988; HOFMANN, 1989; VAN WIEREN, 1996; FORTELIUS & SOLOUNIAS, 2000; GAGNON & CHEW, 2000; SPONHEIMER et al., 2003). VAN WIEREN (1996) gives a grass/browse ratio of 60/40 % based on BREYMEYER & VAN DYNE (1980) and SKINNER & SMITHERS (1990). Based on stable isotopes SPONHEIMER et al. (2003) found a C4 grass ration of 51% in the Southern African population of *A. melampus* and 54% in the East African population of the species. Based on faeces, CODRON et al. (2005) suggest a grass / browse ratio of 50/50 % for *A. melampus*. Among the extant comparison species the impala is the only species that consistently eats substantial amounts of grass. The remaining mixed feeders in this comparison have far less extensive grass components in their diet. The impala has therefore the most abrasive diet among all known mixed feeders and is consistently classified next to the grazers in all mesowear evaluations.

Among the Central European *Hippotherium* populations so far investigated, only the Eppelsheim (MN 9) population of *H. primigemium* appears to have a more abrasive diet than *H. "microdon"* (KAISER, 2003). The Eppelsheim signature, however, cannot be regarded as being representative for MN 9 Central European *H. primigenium*, because the spatially and temporally closely related Höwenegg population of the same species has a clear browsing signal. KAISER (2003) interprets this as to represent the local habitat and foraging conditions at the two contemporaneous localities and thus to indicate a high degree of dietary flexibility of *Hippotherium* rather then reflecting a specific dietary adaptation. We do not yet know of a second European occurrence of *H. "microdon"*, and hence are not able to assess the degree of dietary flexibility for this species.

The Baltavar hipparion paleodietary signal represents strong evidence for the presence of grass or other abrasive vegetation in the Baltavar paleohabitat.

The Baltavar fauna exhibits a shift from subtropical forest conditions resident at Rudabánya at 10 Ma (BERNOR et al., 2003b) to more open country conditions best approximated by the Pikermi (Greece) fauna (BERNOR et al., 1996c; SOLOUNIAS et al., 1999). While declining earth temperature was an attribute of this change, the regional regression of the Central Paratethys, and in particular the Pannonian Lake was a dominant feature of paleoenvironmental change in the Hungarian Late Miocene. Whereas the Pannonian lake occupied nearly all of Hungary in Rudabánya times, by the middle Turolian it had regressed substantially southward to such an extent that Baltavar supported fluviatile environments rather than lacustrine ones. We do not know how far the Pannonian Lake was from Baltavar, but we do know that it was a much smaller lake at this time, perhaps less than half its maximum size. Having less than half the lake's size compared to Rudabánya times means that there were likely more seasonal climates with more intensive seasonality. This increased seasonality caused a shift from subtropical forests to warm temperate open woodlands of the Pikermian type.

That there were two species of *Hippotherium* at Baltavar seems certain. The larger species, most similar to Rudabánya *Hippotherium intrans* was rare, and likely restricted to more wooded habitats. The smaller and more gracile species *Hippotherium "microdon"* apparently favored more open conditions, was likely a more effective running form, and included a mixed diet of graze and browse, or, the perfect mixed diet. We suspect that *Hippotherium "microdon"* favored open, deltaic habitats where fresh grass was abundant and carnivores prevalent.

6. Conclusions

The systematics and evolution of European hipparion has been undertaken for over hundred years, with concerted regional reconstruction undertaken for nearly forty years. Attempts to understand its paleodietary evolution is far more recent. We continue our work here on Central European hipparions to expand our base of empirical comparisons between fossil equids and extant ungulate species. Central European hipparions have consistently been shown to have relatively low morphologic and species diversity compared to Eastern Mediterranean-SW Asian hipparion taxa (re: BERNOR et al., 1996; SCOTT et al., 2005). For each of our statistical plots in this contribution, we render the diversity comparisons to highlight that during the late Miocene, 11.2-5.3 Ma, the known morphologic diversity was lower in Central Europe than Greece and Iran. It will be interesting in future studies to gain a closer understanding of paleodietary niche separation of the more diverse hipparion assemblages in Greece and Iran. We hope that the current study, as well as our recent published work on Central European hipparions serves as a basis for better understanding the paleodietary adaptation of diverse hipparion lineages, and its contribution to the evolution of the group.

7. Acknowledgements

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Table 2: List of Baltavar Hipparion specimens used for morphometric and mesowear analysis. SPEC_ID – Specimen number (MAFI – Hungarian Geological Institute (Budapest, Hungary); BONE = skeletal element (tx = tooth maxillary, tm = tooth mandibular); SIDE = side (r = right, l = left). OR = occlusal relief mesowear variables scoring (h = high, l = low); CS = cusp shape mesowear variables scoring (s = sharp, r = round, b = blunt); WEAR = wear stage (0 = unerupted, unworn; 1 = just erupted with early wear, but occlusal surface not yet entirely in wear; 2 = tooth with entire occlusal face in wear but pre- and postflexid still fused with anterior or posterior enamel band, respectively; 3 = pre-postflexid isolated from anterior or posterior enamel band, but tooth not yet worn to less than 30 % of maximum crown height).

SPEC_ID	BONE	SIDE	OR	CS	WEAR	SPEC_ID	BONE	SIDE	OR	CS	WEAR
MAFIBalt579	1stPhIII	l				HGS418/6	Metacarpal III	l			
MAFIBalt724L	1stPhIII	r				HGS418/7	Metacarpal III	l			
MAFIOB3200	1stPhIII	l				MAFIBalt361	Metacarpal III	r			
MAFIOB435	1stPhIII					MAFIBalt476L	Metacarpal III	l			
MAFIBalt580L	1stPhIV	r				MAFIBalt738L	Metacarpal III	l			
MAFIOB3199A	1stPhIV	l				MAFIOB3207A	Metacarpal III				
MAFIOB3199B	1stPhIV	l				MAFIOB3207B	Metacarpal III	r			
MAFIOB13189	2ndPhIII	l				MAFIOB3207C	Metacarpal III	l			
MAFIOB3198	2ndPhIII	l				MAFIOB3207D	Metacarpal III	3			
MAFIOB430	2ndPhIII	l				MAFIV11255A	Metacarpal III	l			
MAFIBalt621	3rdPhIII	l				MAFIV11255B	Metacarpal III	l			
MAFIBalt120	astragalus					MAFIV11255C	Metacarpal III	l			
MAFIBalt165	astragalus	r				MAFIV11255D	Metacarpal III	r			
MAFIBalt609	astragalus	l				MAFIV11255E	Metacarpal III	l			
MAFIOB3201	astragalus					MAFIV11255F	Metacarpal III	l			
MAFIOB432A	astragalus	r				MAFIV11255G	Metacarpal III	l			
MAFIOB432B	astragalus	l				MAFIV11257L	Metacarpal III	l			
MAFIOB432C	astragalus					HGS418/11	Metatarsal III	r			
MAFIOB433	astragalus	r				HGS419/10	Metatarsal III	l			
MAFIV13188A	astragalus	l				HGS419/12	Metatarsal III				
MAFIV13188B	astragalus					HGS419/13	Metatarsal III	r			
MAFIV13188C	astragalus					HGS419/28	Metatarsal III	l			
MAFIV13188D	astragalus					HGS419/5	Metatarsal III	l			
MAFIV13188E	astragalus					HGS419/9	Metatarsal III	l			
MAFIV13188F	astragalus					HGS420/2	Metatarsal III				
MAFIV13205	astragalus	r				HGS420/3	Metatarsal III				
MAFIBalt608	Calcaneum	l				HGS420/4	Metatarsal III	r			
MAFIBalt078	Cuneiform3					MAFIBalt313	Metatarsal III	l			
MAFIBalt153	Femur	r				MAFIOB3209	Metatarsal III	r			
MAFIBalt219	Femur	l				MAFIOB3209B	Metatarsal III	l			
MAFIBalt396	Femur	r				MAFIOB3209C	Metatarsal III	r			
MAFIOB3211	Femur	l				MAFIOB3210	Metatarsal III	l			
MAFIBalt742L	Humerus	l				MAFIV11257A	Metatarsal III	l			
MAFIBalt069	Mandible					MAFIV11257B	Metatarsal III				
MAFIBalt079	Mandible					MAFIV11257C	Metatarsal III	r			
MAFIBalt466L	Mandible					MAFIV11257D	Metatarsal III	l			
MAFIOB3196	Mandible	r				MAFIV11257E	Metatarsal III	l			
MAFIOB338	Mandible	l				MAFIV11257F	Metatarsal III	l			
MAFIOB390A	Mandible	l				MAFIV11257G	Metatarsal III	l			
MAFIOB390B	Mandible	r				MAFIV11257H	Metatarsal III	r			
MAFIOB391	Mandible	l				MAFIV11257I	Metatarsal III	l			
MAFIOB3196	Mandibular Canine	r				MAFIV11257J	Metatarsal III	l			
MAFIOB391	Mandibular Canine	l				MAFIV11257K	Metatarsal III	3			
MAFIOB338	Maxillary Canine	l				MAFIBalt136	Metatarsal IV	l			
MAFIBalt622	Mc/Mt2	3				MAFIBalt529L	Metatarsal IV				
MAFIBalt509L	Metacarpal II	l				MAFIBalt532L	Metatarsal IV				
MAFIBalt659	Metacarpal II	r				MAFIBalt633	Metatarsal IV				
MAFIBalt750L	Metacarpal II	l				MAFIOB3204B	Radius				
HGS417/10	Metacarpal III					MAFIOB378	Radius				
HGS417/15	Metacarpal III					MAFIOB425	Radius				
HGS417/2	Metacarpal III					MAFIVOB3204A	Radius				
HGS417/3	Metacarpal III					MAFIBalt623	Ulna	r			
HGS417/9	Metacarpal III					MAFIOB416A	Scaphoid	l			
HGS418/5	Metacarpal III					MAFIOB416B	Scaphoid				

SPEC_ID	BONE	SIDE	OR	CS	WEAR
MAFIOB416C	Scaphoid	l			
MAFIOB416D	Scaphoid	l			
MAFIOB431	Scaphoid				
MAFIV13180A	Skull				
MAFIBalt061	Tibia				
MAFIBalt260	Tibia				
MAFIBalt713L	Tibia	r			
MAFIOB3205	Tibia	l			
MAFIOB344A	Tibia	l			
MAFIOB344B	Tibia				
MAFIOB344C	Tibia				
MAFIOB344D	Tibia	r			
MAFIOB344E	Tibia	l			
MAFIOB377	Tibia	l			
MAFIOB421A	Tibia	l			
MAFIOB421B	Tibia	l			
MAFIOB421C	Tibia	l			
MAFIOB421D	Tibia				
MAFIBalt069	tmdP2				
MAFIBalt079	tmdP2				
MAFIBalt175	tmdP2				
MAFIBalt213	tmdP2				
MAFIBalt466L	tmdP2				
MAFIOB3194	tmdP2				
MAFIOB422	tmdP2	r			
MAFIV13170E	tmdP2	l			
MAFIV13171G	tmdP2				
MAFIV13171H	tmdP2				
MAFIV13171I	tmdP2	r			
MAFIV13184	tmdP2	l			
MAFIV13200A	tmdP2				
MAFIBalt069	tmdP3				
MAFIBalt079	tmdP3				
MAFIBalt213	tmdP3				
MAFIBalt466L	tmdP3	r			
MAFIBalt756L	tmdP3	l			
MAFIBalt8	tmdP3				
MAFIOB3194	tmdP3				
MAFIOB422	tmdP3	r			
MAFIOB427	tmdP3	l			
MAFIV13170E	tmdP3	l			
MAFIV13171I	tmdP3				
MAFI149	tmdP34				
MAFIV13174	tmdP34	r			
MAFIV13200B	tmdP34	l			
MAFIV13200C	tmdP34	l			
MAFIV13200D	tmdP34	r			
MAFI13184	tmdP4	l			
MAFIBalt001	tmdP4	l			
MAFIBalt069	tmdP4				
MAFIBalt079	tmdP4	r			
MAFIBalt107	tmdP4	l			
MAFIBalt419L	tmdP4				
MAFIBalt466L	tmdP4	r			
MAFIBalt560	tmdP4	l			
MAFIBalt756L	tmdP4	l			
MAFIBalt8	tmdP4				
MAFIOB422	tmdP4	r			
MAFIOB427	tmdP4	l			
MAFIV13170D	tmdP4	l			
MAFIOB3196	tmI1	r			
MAFIOB338	tmI1	l			
MAFIOB390A	tmI1	l			
MAFIOB390B	tmI1				

SPEC_ID	BONE	SIDE	OR	CS	WEAR
MAFIOB391	tmI1	l			
MAFIOB3196	tmI2	r			
MAFIOB338	tmI2	l			
MAFIOB390A	tmI2	l			
MAFIOB390B	tmI2	r			
MAFIOB391	tmI2	l			
MAFIOB3196	tmI3	r			
MAFIOB338	tmI3	l			
MAFIOB390A	tmI3	l			
MAFIOB390B	tmI3	r			
MAFIOB391	tmI3	l			
MAFI13169	tmM1				
MAFI13171A	tmM1				
MAFI13171C	tmM1	r			
MAFI13171D	tmM1	l			
MAFI13184	tmM1	l			
MAFIBalt1	tmM1	l			
MAFIBalt107	tmM1	l			
MAFIBalt2	tmM1	r			
MAFIBalt4	tmM1	l			
MAFIBalt5	tmM1	r			
MAFIBalt560	tmM1	l			
MAFIBalt7	tmM1				
MAFIBalt737L	tmM1	r			
MAFIBalt756L	tmM1	l			
MAFIBalt8	tmM1	r			
MAFIOB312	tmM1	l			
MAFIOB313	tmM1				
MAFIOB313	tmM1				
MAFIOB3194	tmM1				
MAFIOB400	tmM1				
MAFIOB401A	tmM1	r			
MAFIOB401C	tmM1	l			
MAFIOB401D	tmM1				
MAFIOB402	tmM1				
MAFIOB422	tmM1				
MAFIOB422	tmM1	r			
MAFIV13170B	tmM1	l			
MAFIV13170D	tmM1	l			
MAFIV13171J	tmM1				
MAFIV13171K	tmM1				
MAFIV13175	tmM1				
MAFIV13181	tmM1				
MAFIV13201	tmM1				
MAFIV13997	tmM1				
MAFIV3196B	tmM1				
MAFI13169	tmM2				
MAFI13171A	tmM2				
MAFI13171B	tmM2				
MAFI13171C	tmM2	r			
MAFI13171D	tmM2	l			
MAFI13184	tmM2	l			
MAFIBalt1	tmM2	l			
MAFIBalt107	tmM2	l			
MAFIBalt129	tmM2	r			
MAFIBalt4	tmM2	l			
MAFIBalt5	tmM2	r			
MAFIOB312	tmM2	l			
MAFIOB313	tmM2				
MAFIOB313	tmM2				
MAFIOB3194	tmM2				
MAFIOB401A	tmM2				
MAFIOB401D	tmM2				
MAFIOB402	tmM2				

SPEC_ID	BONE	SIDE	OR	CS	WEAR
MAFIOB422	tmM2	r			
MAFIV13170B	tmM2	l			
MAFIV13170C	tmM2	l			
MAFIV13170D	tmM2	l			
MAFIV13171J	tmM2				
MAFIV13171K	tmM2				
MAFIV13175	tmM2				
MAFIV13181	tmM2				
MAFIV13201	tmM2				
MAFIV13997	tmM2				
MAFIV3196B	tmM2				
MAFI13171B	tmM3				
MAFI13171C	tmM3	r			
MAFI13171D	tmM3	l			
MAFI13171F	tmM3	l			
MAFIBalt1	tmM3	l			
MAFIBalt4	tmM3	l			
MAFIBalt5	tmM3				
MAFIBalt6	tmM3				
MAFIOB3194	tmM3	r			
MAFIV13170C	tmM3	l			
MAFIV13170D	tmM3	l			
MAFIV13181	tmM3				
MAFIV13997	tmM3				
MAFIV3196B	tmM3				
MAFI13171A	tmP2				
MAFI13171E	tmP2				
MAFIBalt097	tmP2				
MAFIBalt2	tmP2				
MAFIBalt3	tmP2				
MAFIBalt7	tmP2	r			
MAFIOB13170A	tmP2	l			
MAFIOB312	tmP2	l			
MAFIOB313	tmP2				
MAFIOB313	tmP2				
MAFIOB3194	tmP2				
MAFIOB400	tmP2				
MAFIOB401B	tmP2				
MAFI13169	tmP3				
MAFI13171A	tmP3				
MAFI13171E	tmP3	r			
MAFIBalt1	tmP3	l			
MAFIBalt2	tmP3				
MAFIBalt3	tmP3				
MAFIBalt7	tmP3	r			
MAFIOB13170A	tmP3	l			
MAFIOB312	tmP3	l			
MAFIOB313	tmP3				
MAFIOB313	tmP3				
MAFIOB3194	tmP3				
MAFIOB400	tmP3				
MAFIOB401A	tmP3				
MAFIOB402	tmP3				
MAFIV13175	tmP3				
MAFIV13181	tmP3				
MAFI13169	tmP4				
MAFI13171A	tmP4				
MAFI13171E	tmP4	r			
MAFIBalt1	tmP4	l			
MAFIBalt2	tmP4	r			
MAFIBalt278	tmP4	l			
MAFIBalt3	tmP4	r			
MAFIBalt4	tmP4	l			
MAFIBalt459L	tmP4				

SPEC_ID	BONE	SIDE	OR	CS	WEAR
MAFIBalt5	tmP4	r			
MAFIBalt7	tmP4	r			
MAFIOB13170A	tmP4	l			
MAFIOB312	tmP4	l			
MAFIOB313	tmP4				
MAFIOB313	tmP4				
MAFIOB3194	tmP4				
MAFIOB400	tmP4				
MAFIOB401A	tmP4	r			
MAFIOB401C	tmP4	l			
MAFIOB402	tmP4				
MAFIOB422	tmP4	r			
MAFIV13173A	tmP4	l			
MAFIV13173B	tmP4	l			
MAFIV13173C	tmP4	l			
MAFIV13173C	tmP4	l			
MAFIV13173F	tmP4	l			
MAFIV13174	tmP4				
MAFIV13175	tmP4				
MAFIV13181	tmP4	r			
MAFIV13193D	tmP4	l			
MAFIV13195A	tmP4				
MAFIV13195B	tmP4				
MAFIV13195D	tmP4				
MAFIV13195E	tmP4				
MAFIV13196A	tmP4				
MAFIBalt704	txdP2				
MAFIV13152	txdP2	r			
MAFIBalt096	txdP34	l			
MAFIBalt168	txdP34	l			
MAFIBalt537L	txdP34	l			
MAFIV13172A	txdP34	l			
MAFIV13172B	txdP34	l			
MAFIV13172C	txdP34	l			
MAFIV13172D	txdP34	l			
MAFIV13172E	txdP34	l			
MAFIV13184	txdP34				
MAFIV13187A	txdP34				
MAFIV13187B	txdP34	r			
MAFIV13200E	txdP34	l			
MAFIBalt574L	txdP4	r			
MAFIV13180B	txI1	l			
MAFIV13180B	txI2	l			
MAFIV13180C	txI2	l			
MAFIV13180B	txI3	l			
MAFIV13180C	txI3	l			
MAFI-13169-157	txM1	l	h		3
MAFI-13169-216	txM1	l	h		3
MAFI-13172-14	txM1	l	h		3
MAFI-13172-152	txM1	l	h		3
MAFI-13172-155	txM1	l	h		3
MAFI-13172-5	txM1	l	h		3
MAFI-13172-72	txM1	l	h		3
MAFI-13187-106	txM1		h		3
MAFI-13194-37	txM1		h		3
MAFI-13194-80	txM1		h		2
MAFI-3195-271	txM1		h		3
MAFI-BAL-2000-31	txM1	r	h		3
MAFI-BAL-2000-6	txM1	l	h		2
MAFIBalt031	txM1	r			
MAFI-Ob-409-146	txM1	l	h		3
MAFI-Ob-409-149	txM1	l	h		3
MAFI-Ob-410-172	txM1	l	h		3
MAFI-Ob-414-165	txM1	l	h		3

SPEC_ID	BONE	SIDE	OR	CS	WEAR
MAFI-Ob-415-209	txM1	l	h	r	3
MAFIV13182	txM1	l			
MAFI-V-13197-163	txM1	l	h		3
MAFI-13169-215	txM12	l	h		3
MAFI-O-415-262	txM12		h		3
MAFI-V-13190-265	txM12	r	h		3
MAFI-13172-13	txM2	l	h		3
MAFI-13172-25	txM2	l	h		3
MAFI-13187-48	txM2		h		3
MAFI-13194-34	txM2		h		3
MAFI-13194-84	txM2		h		3
MAFI-13195-36	txM2		h		3
MAFI-3195-270	txM2	r	h		3
MAFI-BAL-2000-150	txM2	l	h		2
MAFI-BAL-2000-190	txM2	l	h		2
MAFI-BAL-2000-31	txM2	r	h		3
MAFI-BAL-2000-36	txM2	l	h		3
MAFIBalt006	txM2	l			
MAFIBalt027	txM2	l			
MAFIBalt031	txM2	r			
MAFIBalt150	txM2	l			
MAFIBalt530L	txM2	l			
MAFIOB3195	txM2	r			
MAFI-Ob-409-145	txM2	l	h		3
MAFI-Ob-409-148	txM2	l	h		3
MAFI-Ob-410-173	txM2	l	h		3
MAFI-Ob-415-208	txM2	l	h		3
MAFI-V-13169-268	txM2		h		2
MAFI-V-13190-264	txM2	r	h		3
MAFI-13172-15	txM3	l	h		3
MAFI-13172-18	txM3	l	h		3
MAFI-13187-43	txM3		h		3
MAFI-13187-50	txM3		h		3
MAFI-13187-55	txM3		h		3
MAFI-13194-33	txM3		h		3
MAFI-13194-38	txM3		h		3
MAFI-13194-6	txM3		h		2
MAFI-13194-7	txM3		h		3
MAFI-13194-8	txM3	r	h		3
MAFI-BAL-2000-167	txM3	l	h		3
MAFI-BAL-2000-48	txM3		h		3
MAFIBalt031	txM3	r			
MAFI-O-415-211	txM3	l	h		2
MAFI-O-415-261	txM3	r	h		3
MAFI-Ob-409-144	txM3	l	h		3
MAFI-Ob-409-148a	txM3	l	h		3
MAFI-Ob-410-169	txM3	l	h		3
MAFI-Ob-415-207	txM3	l	h		3
MAFIBalt028	txP2				
MAFIBalt220	txP2				
MAFIBalt583	txP2				
MAFIBalt689	txP2	r			
MAFINONUMB1	txP2	l			
MAFIOB13169AA	txP2	l			
MAFIOB13192	txP2				
MAFIOB2808	txP2				
MAFIOB2817	txP2				
MAFIOB3195	txP2	r			
MAFIV13169A	txP2	l			
MAFIV13169AAA	txP2	l			
MAFIV13169C	txP2	l			
MAFIV13169D	txP2	l			
MAFIV13169F	txP2	l			
MAFIV13169G	txP2	l			
MAFIV13169H	txP2	l			
MAFIV13169I	txP2	l			
MAFIV13169J	txP2	l			
MAFIV13169K	txP2	l			
MAFIV13169L	txP2	l			
MAFIV13169M	txP2	l			
MAFIV13169N	txP2	l			
MAFIV131690	txP2	l			
MAFIV13169P	txP2	l			
MAFIV13169Q	txP2	l			
MAFIV13172	txP2	l			
MAFIV13192B	txP2				
MAFIV13192C	txP2				
MAFIV13192D	txP2				
MAFIV13192E	txP2	r			
MAFIV13192E	txP2	l			
MAFIV13192F	txP2				
MAFIV13192G	txP2				
MAFIV13192H	txP2	r			
MAFIV13192I	txP2	l			
MAFIV13192J	txP2	r			
MAFIV13192K	txP2	l			
MAFIV13192L	txP2				
MAFIV13192M	txP2				
MAFIV13192N	txP2				
MAFIV13192N	txP2				
MAFIV13192P	txP2				
MAFIV13192Q	txP2				
MAFIV13192R	txP2				
MAFIV13192S	txP2	r			
MAFIV13192T	txP2	l			
MAFIOB3195	txP3	r			
MAFIV13172	txP3	l			
MAFI-13169-158	txP4	l	h		3
MAFI-13169-218	txP4	l	h		3
MAFI-13172-153	txP4	l	h		3
MAFI-13172-156	txP4	l	h		3
MAFI-13172-16	txP4	l	h		3
MAFI-13172-161	txP4	l	h		3
MAFI-13172-28	txP4	l	h		3
MAFI-13172-70	txP4	l	h		3
MAFI-13172-77	txP4	l	h		3
MAFI-13187-47	txP4		h		3
MAFI-13187-56	txP4	r	h		3
MAFI-13187-64	txP4	l	h		3
MAFI-13194-102	txP4		h		3
MAFI-13194-86	txP4		h		2
MAFI-13194-96	txP4		h		3
MAFI-13195-39	txP4		h		3
MAFI-3195-272	txP4		h		3
MAFI-BAL-2000-183	txP4		h		3
MAFI-BAL-2000-37	txP4	r	h		3
MAFI-BAL-2000-53a	txP4	l	h		3
MAFIBalt517L	txP4	l			
MAFI-Ob-409-147	txP4	l	h		3
MAFI-Ob-409-150	txP4	l	h		3
MAFI-Ob-410-171	txP4	l	h		3
MAFI-Ob-412-226	txP4	l	h		2
MAFI-Ob-414-166	txP4	l	h		3
MAFI-Ob-414-234	txP4		h		3
MAFI-Ob-414-235	txP4	r	h		3
MAFI-Ob-415-210	txP4	l	h		3
MAFIV13169	txP4	l			
MAFIV13172A	txP4	l			

SPEC_ID	BONE	SIDE	OR	CS	WEAR
MAFIV13172C	txP4	l			
MAFIV13182	txP4	l			
MAFI-V-13197-164	txP4	l	h		2
MAFI-13187-228	txP4M1		h		3
MAFI-13187-229	txP4M1		h		3
MAFI-13187-230	txP4M1	r	h		3
MAFI-O-415-212	txP4M1	l	h		3
MAFI-O-415-213	txP4M1	l	h		3

SPEC_ID	BONE	SIDE	OR	CS	WEAR
MAFI-O-415-258*	txP4M1	r	h	r	3
MAFI-O-415-263	txP4M1	r	h		3
MAFI-Ob-410-170	txP4M1	l	h		3
MAFI-Ob-415-185	txP4M1	l	h		3
MAFI-Ob-415-186	txP4M1	l	h		3
MAFI-Ob-415-187	txP4M1	l	h		3
MAFI-V-13169-269	txP4M1		h		3
MAFI-V-13190-266	txP4M1		h		2

PLATE 1

Fig. A   MAFIV13180A, premaxilla dorsal view

Fig. B   MAFIV13180A, premaxilla occlusal view

Fig. C   MAFIOB13195, right maxilla with P2-M2, occlusal view

Fig. D   MAFIVOB338, mandibular symphysis with right and left i1-c, occlusal view

Fig. E   MAFIV13169, lt. P2, occlusal view

Fig. F   MAFIV13169, lt. P2, labial view

Fig. G   MAFIVOB3193 (Vt. 109), a left mandible with very worn p3-m3 (type specimen of *Hippotherium „microdon"* Kᴏʀᴍᴏs 1914) occlusal view

Fig. H   MAFIVOB3193 (Vt. 109), labial view of dental row.

PLATE 1

20mm

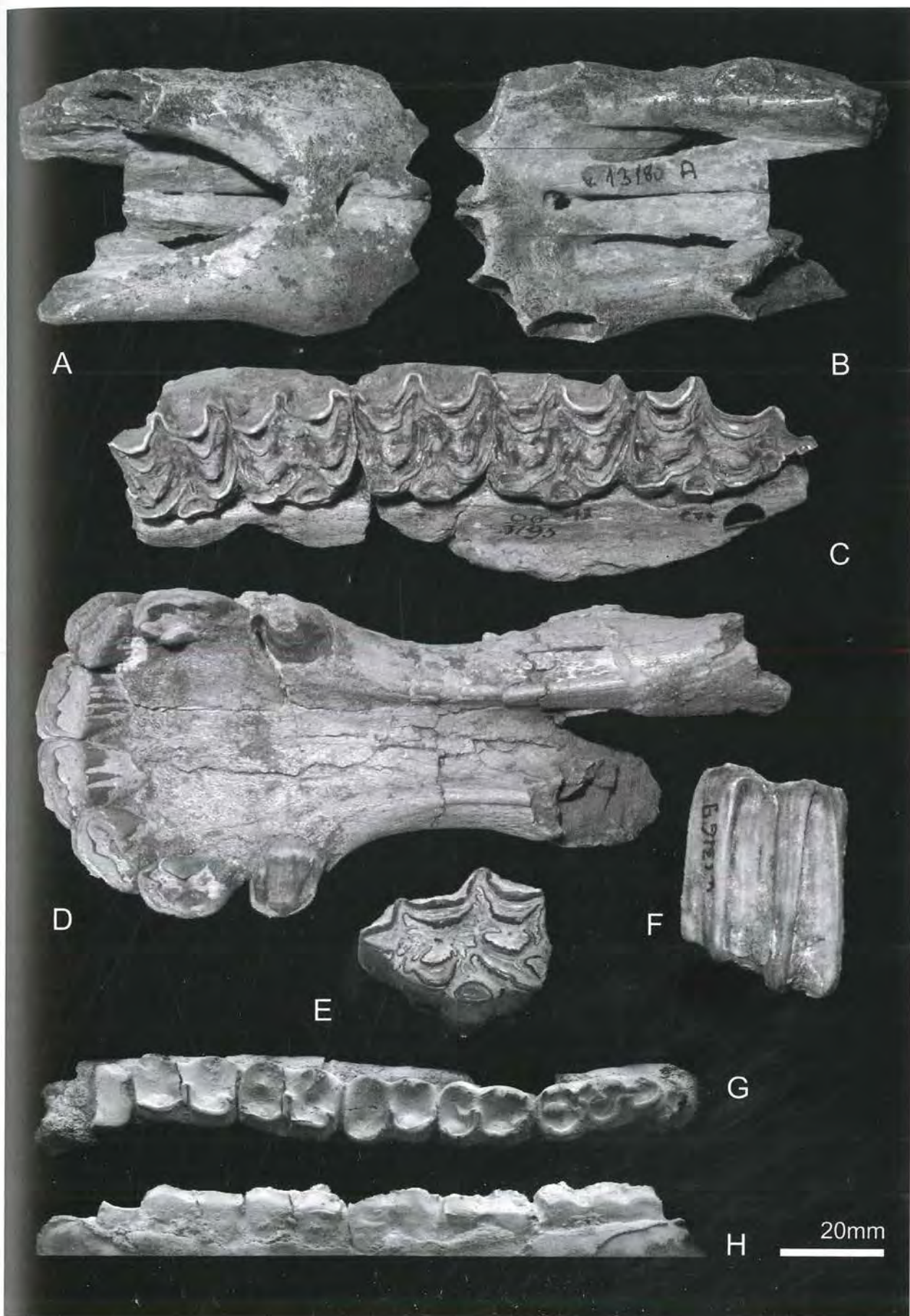# PLATE 2

Fig. A   MAFIVBalt1, left mandible with p3-m3, occlusal view.

Fig. B   MAFIVBalt1, labial view.

Fig. C   MAFIV417/2, Mc III, cranial view.

Fig. D   MAFIV417/3, Mc III, cranial view.

Fig. E   MAFI418/5, Mc III, cranial view, referable to *Hippotherium* "*microdon*"

Fig. F   MAFIOB420-4, Mt III, cranial view.

Fig. G   MAFIOB419-12, Mt III, cranial view.

PLATE 2