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An Evaluation of the Late MN 9 (Late Miocene, Vallesian Age), Hipparion Assemblage from Rudabánya (Hungary): Systematic Background, Functional Anatomy and Paleoecology

Evaluación de la asociación de Hipparion del Mioceno superior (Vallesiense, MN 9) de Rudabánya (Hungría): sistemática, anatomía funcional y paleoecología

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Abstract: KRETZOI 1983 recognized a new species of hipparion from Rudabánya, «*Hipparion» intrans*. Study of the entire Rudabánya II assemblage confirms that the predominante hipparion species at this locality is indeed the valid taxon *Hippotherium intrans*. A second, smaller and rarer species of hipparion, hitherto unnamed, is recognized only by cheek teeth originating from the overlying upper lignite levels. Our work on the postcranial anatomy of the *Hippotherium intrans* sample suggests that this species was an elongate-limbed advanced member of the *Hippotherium primigenium* VON MEYER 1829 lineage. Analysis of dental mesowear suggests that *Hippotherium intrans* was a mixed feeder: it ate both graze and browse. Based on evidence presented here, we believe that at Rudabánya *Hippotherium intrans* inhabited more open country environments than the swamp facies in which it was found: this primate-rich facies would appear to have been nothing other than a local hipparion watering-hole.

Key Words: Rudabánya, *Hippotherium*, postcrania, paleodiet

Resumen: KRETZOI 1983 reconoció una nueva especie de hipparion de Rudabánya, «*Hipparion» intrans*. El estudio de la asociación completa de Rudabánya II confirma que la especie de hipparion predominante en esta localidad es realmente el taxon válido *Hippotherium intrans*. Una segunda especie de hipparion menor y más rara aún sin nombre se reconoce por sólo sus dientes yugales procedentes de los niveles de lignito superiores. Nuestro trabajo sobre la anatomía postcraneal de la muestra de *Hippotherium intrans* sugiere que esta especie era un miembro avanzado con patas alargadas del linaje de *Hippotherium primigenium* VON MEYER 1829. El análisis del mesodesgaste dental sugiere que *Hippotherium intrans* era un herbívoro mixto: tanto ramoneador como pastador. Sobre la evidencia presentada, creemos que en Rudabánya *Hippotherium intrans* habitó ambientes más abiertos que los de las facies pantanosas en las que se encuentra: estas facies ricas en primates aparecen haber sido sólo un abrevadero local de hipparion.

Palabras clave: Rudabánya, *Hippotherium*, esqueleto postcraneal, paleodieta.

INTRODUCTION

KRETZOI 1983 named a new species of «Hipparion» from Rudabánya based on a complete metatarsal III, «*Hipparion» intrans*. In a more detailed description of the hipparion material collected solely under the direction of KRETZOI, BERNOR *et al.* (1993a) reported the occurrence of an advanced member of the *Hippotherium primigenium* lineage at Rudabánya. In a subsequent comparison with the

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Götzendorf (MN 9/10, Vienna Basin, Austria) hipparion assemblage, BERNOR *et al.* (1993b) later concurred that the Rudabánya hipparion represented an advanced population of the *Hippotherium primigenium* lineage and suggested a late MN 9 correlation for Rudabánya. A recent analysis of the Dorn Dürkheim (Germany, MN 11) hipparion assemblage by BERNOR & FRANZEN (1997), the Sümeg (Hungary, MN 10) assemblage by BERNOR *et al.* (1999), and a study of the entire Rudabánya hipparion assemblage collected between 1977 and 1994, suggests a potentially more complex interpretation of the systematics and biogeography of this assemblage.

SYSTEMATIC BACKGROUND

We leave the formal taxonomic allocation of Rudabánya hipparion specimens to the monographic treatment of the whole fauna. It is sufficient to say here that we recognize the nomen *Hippotherium intrans* as valid for a larger hipparion species at Rudabánya, and it is apparent that this species is the predominant one at all Rudabánya localities where hipparion is known. There is a rarer, smaller hipparion morph that has been found in the Upper Lignite levels of Rudabánya II, the youngest stratigraphic bed in this particular Rudabánya section. Because of the rarity of this smaller hipparion, we have chosen not to recognize a formal species name for it.

AGE CORRELATION AND BIOGEOGRAPHY

BERNOR *et al.* (1993 a and b) have suggested that Rudabánya II correlates with the latter part of MN 9. This is based on the observation that *Hippotherium intrans* is advanced over Vienna Basin Pannonian D-E populations of *Hippotherium primigenium*, while not being so advanced as the Götzendorf hipparion. RÖGL *et al.* (1993) argued for a latest MN 9 (= Pannonian Stage F) age for Götzendorf based on the absence of murids there. BERNOR *et al.* (1999) have recently studied the equids from Sümeg identifying two taxa in this fauna: a larger species, *Hippotherium sumegense* KRETZOI 1984, and a smaller species, «*Hipparion*» sp. small. Of these two, *Hippotherium sumegense* compares closely to the Götzendorf hipparion in its distinct mandibular premolar morphology. Biochronologic correlations based on Sümeg's small mammals strongly support the fauna's MN 10 age. Therefore, we can either accept the latest MN 9 attribution for Götzendorf based on the absence of murids, or accept the occurrence of *Eozapus* and *Hippotherium aff. H. sumegense* at Götzendorf as evidence of its MN 10 age. In either case, Rudabánya's hipparion is suggestive of a Pannonian F correlation and late MN 9 attribution, ca. 10.0 - 9.5 Ma (RÖGL & DAXNER-HÖCK, 1996; STEININGER *et al.*, 1996; BERNOR *et al.*, 1999). By the same argument, Götzendorf and Sümeg are most plausibly correlative with Pannonian G, circa 9.5 - 9.0 Ma (sensu RÖGL & DAXNER-HÖCK, 1996).

Rudabánya *Hippotherium intrans* is distinct from German and Austrian populations of *Hippotherium primigenium* in its longer metatarsal III. While there are few fossil hipparion from MN 10 localities in the Vienna Basin, material from Prottes would appear to be very similar in its molar occlusal morphology to the Götzendorf and Sümeg species. These observations suggest that by latest MN 9 time, or Pannonian F equivalent, the Pannonian Basin hipparions diverged from *Hippotherium primigenium*. BERNOR & FRANZEN's (1997) study of the early Turolian (MN 11) hipparion assemblage from Dorn Dürkheim (Germany) showed that this population retained conservative characters that ally it closely with older MN 9 hipparion from Eppelsheim and Höwenegg, Germany. Work in progress by KAISER *et al.* (in prep.) suggests that there are two closely related forms at Dorn Dürkheim, also related to the *Hippotherium primigenium* lineage. Given the current state of knowledge, the Pannonian late MN 9 (= Pannonian F) hipparion assemblages would appear to have become vicariantly separated from the German late MN 9 - MN 11 hipparions to the west. The small Sümeg hipparion appears to be most closely related to the small Greek MN 10 form *Cremohipparion macedonicus* KOUFOS, 1984, and would if that attribution were to prove to be true, be an indication of an opening biogeographic connection between the Central Paratethys and Macedonia.

FUNCTIONAL ANATOMY AND PALEOECOLOGY

Pilot studies have been made on *Hippotherium intrans* paleodietary and locomotor adaptations. Our preliminary results are reported below.

Tooth microwear comparison

We document tooth microwear patterns in the Rudabánya cheek tooth assemblage and compare them to specimens from the Dinotheriensande and from Sümeg. Rudabánya specimens available for this study included a maxillary P2-M3 (MAFIV12125) tooth row, a left and right mandibular p2-m3 (MAFIV15795) and a maxillary P3-M2 tooth row (MAFIV15749). We compared these with Sümeg specimens 1-7 (Bernor et. al, 1999) and 4 upper M2 specimens from the Dinotheriensande, the preservation of which proved to be good enough for microwear analysis. Figured specimens include (Figure 1): Rudabánya specimen MAFIV15749 (M1) and Dinotheriensande specimen HLMDDIN2716 (M2). While we would prefer having analysed the same tooth element for a large sample size of Rudabánya hipparions to standardize our analysis, the materials simply do not occur in sufficient abundance to do this. What we provide here is a preliminary assessment of Rudabánya *Hippotherium intrans* paleodiet based on microwear.

Microwear features predominating in all samples studied are scars dichotomised into pits and scratches (striations) by various workers (RENSBERGER, 1978; SOLOUNIAS *et al*., 1988; TEAFORD & WALKER, 1984; VAN VALKENBURG *et al*., 1990; Teaford, 1991; SOLOUNIAS & HAYEK, 1993). The Rudabánya sample of *Hippotherium intrans* has comparatively more scratches and less pits than either the Sümeg or Dinotheriensande samples considered; in the Sümeg sample both scratches and pits are equally present on the occlusal surface. The Rudabánya assemblage (Figure 1, A1) exhibits fewer similarities with specimens of *Hippotherium primigenium* from the Dinotheriensande (Figure 1, B1), which also show a pit dominated microwear pattern. Sümeg specimen #7 is the most similarities with the Rudabánya material studied (Bernor *et al*., 1999). In both the Rudabánya specimens and Sümeg specimen #7 there is only very little unscratched enamel surface exposed.

The frequency and morphology of enamel scars as pits and scratches are believed to be controlled by dietary regime and functional masticatory parameters (HAYEK *et al*., 1992; HUNTER & FORTELIUS, 1994). In herbivorous mammals, the proportion of pits to scratches is one of the microwear characters regarded important for species segregation by HAYEK *et al.* (1992), and is used for inferring dietary behavior (SOLOUNIAS & MOELLEKEN, 1992, 1993, 1994). SOLOUNIAS & HAYEK (1993) report that with some exceptions, recent browsers had fewer scratches and more pits than grazers; the converse is true in grazers. The predominance of scratches in the Rudabánya sample may thus suggest a relatively high proportion of grass in the last meal of these specimens. On the other hand, the more pitted overall appearance of the Dinotheriensande sample would indicate a relatively higher proportion of softer food matter. This is also suggested by the presence of extended polished areas. These polished and featureless areas are considered to be caused by occlusal enamel-enamel attrition, as demonstrated by TEAFORD & WALKER (1983). We thus expect considerable abrasion control in microwear features of the Rudabánya sample. We are aware of the fact that this qualitative comparison is provisional, however, it does point to differences in the microwear of Rudabánya *Hippotherium intrans*, Sümeg *Hippotherium sumegense*, and Dinotheriensande *Hippotherium primigenium*.

Mesowear analysis

The mesowear method was introduced by FORTELIUS & SOLOUNIAS (2000). KAISER *et al*. (2000) applied this methodology to a relatively large sample of Dinotheriensande (MN9, Germany) hipparion with substantial success and Kaiser & Solounias (in press) further extended the method. The mesowear methodology treats ungulate tooth wear as two variables: 1. occlusal relief and 2. cusp shape. 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 3 scored attributes: sharp (S), round (R), and blunt (B) according to the degree of facet development. A sharp cusp terminates to a point and has practically no rounded area between the mesial and distal phase I facets, a rounded cusp has a distinctly rounded tip (apex) with-out planar facet wear but retains facets on the lower slopes, while a blunt cusp lacks distinct facets altogether.

Occlusal relief and cusp shape are given in Table 1 as percentages of the five variables. We apply the mesowear method to the upper equid cheek teeth from Rudabánya and a comparative sample of *Hippotherium primigenium* from the Dinotheriensande. The tooth crowns of the Rudabánya specimens were moulded with BAYER Provil SOFT dental moulding putty. Epoxy resin casts were made using Reckli Injektionsharz EP epoxy resin. We collected data on teeth of medium wear stages; that is we excluded specimens

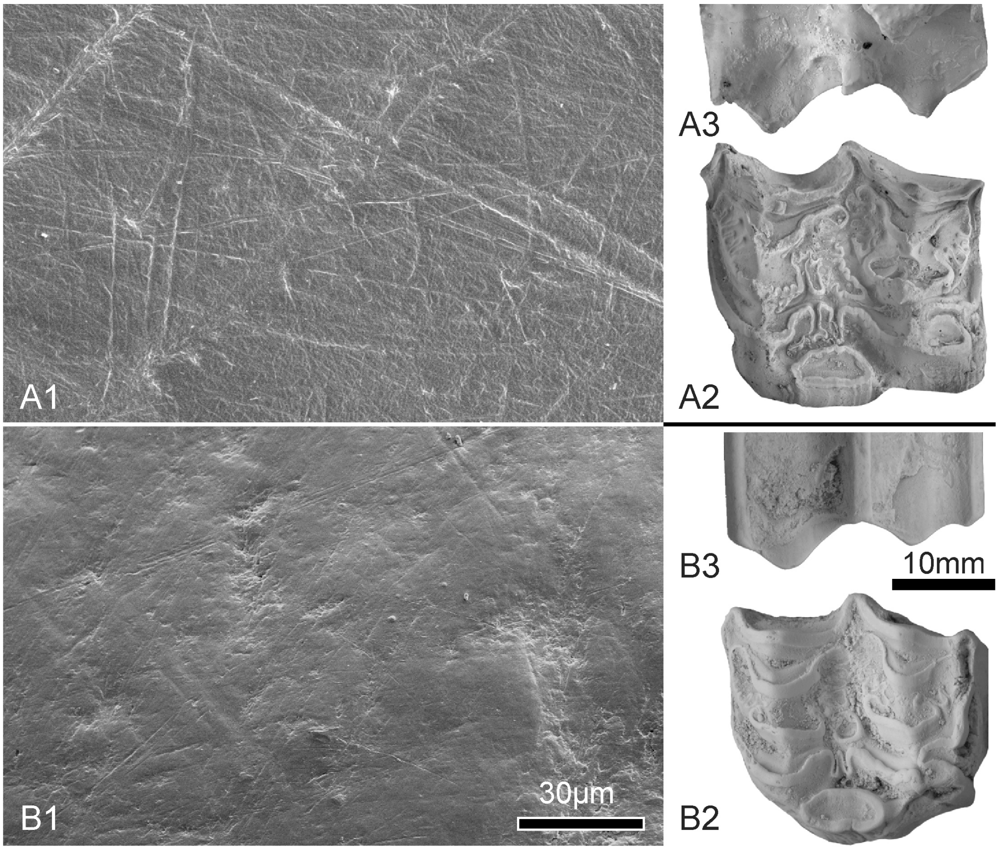

Figure 1A1, 1B1: SEM-micrographs of the occlusal surface of the ectoloph labial to the paracone (x500) showing representative microwear features. Buccal is towards the left. A1: Rudabánya MAFIV15749 (upper M1), B1: Eppelsheim HLMDDIN2716 (upper M2). A2,3, B2,3 Macroscopic occlusal features. A2, B2 occlusal aspect (left = mesial). A3, B3 ectoloph apical morphology. A2,3 Rudabánya MAFIV12125 (left upper M2); B2,3 Dinotheriensande specimen HLMDDIN 2716 (right upper M2, mirrored in figures).

Figure 1A1, 1B1: SEM-microfotos de la superficie oclusal del ectolofo labial del paracono (x500) con rasgos de microdesgaste representativos. Bucal a la izquierda. A1: Rudabánya MAFIV15749 (M1upper M1), B1: Eppelsheim HLMDDIN2716 (upper M2). A2,3, B2,3 Rasgos macroscópicos oclusales. A2, B2 aspecto oclusal (izquierda = mesial). A3, B3 morfologia apical ectolofo. A2,3 Rudabánya MAFIV12125 (M2 sup.sin.); B2,3 ejemplar de Dinotheriensande HLMDDIN 2716 (M2 sup. dex., imagen especular en las figuras).

that were either unworn or worn to less than 15 mm mesostyle height. A total of 14 upper P4 and M1-3 from Rudabánya and 164 upper P4 and M1-3 from the Dinotheriensande were used in this study for statistical analysis. Hierarchical cluster analysis was applied, with complete linkage (to enhance the distinctiveness of clusters), using four mesowear variables (%high, %sharp, %round and %blunt). For this analysis we use the original dataset of Fortelius & Solounias (2000) for the extant comparison species and the data presented in this study for *H. primigenium* and *H. intrans* (Table 1). All statistical tests were computed using Systat 9.0 (licensed to Kaiser). Photographed specimens were coated with ammonium chloride to reduce color contrast. Photographs were taken with a Kontron ProgRes 3012 (Carl Zeiss Jena) digital camera.

Occlusal relief was scored high in 100% of the Rudabánya specimens and 98% of the Dinotheriensande sample. Cusp shape scorings are 54% sharp in the Rudabánya sample and 18% sharp in the Dinotheriensande sample. Forty-six percent of the Rudabánya specimens have rounded cusps while 82% of the Dinotheriensande sample have rounded cusps. No blunt cusps occur in either sample (Table 1, Figure 2a, b).

Figure 3 is a cluster diagram that ranks the Vallesian European Hipparions from Rudabánya and the Dinotheriensande (Germany) within the browsing, intermediate and grazing hierarchy of extant ungulates reported by FORTELIUS AND & SOLOUNIAS (2000). The mesowear patterns of *Hippotherium intrans* from Rudabánya are closest to those of *Tragelaphus scriptus* (bushbuck), *Taurotragus oryx* (eland), *Cervus canadensis* (wapiti) and *Capricornis sumatraensis* (serow). The Dinotheriensande sample of *Hippotherium primigenium* shares most similarities in the mesowear signature with *Aepyceros melampus* (impala), *Kobus ellipsiprymnus* (common waterbuck), *Hippotragus equinus* (roan antelope), *Redunca redunca* (reedbuck), and *Hippotragus niger* (sable antelope). With the exception of the impala, all these species are grazers.

Our mesowear analysis suggests that *Hippotherium intrans* from Rudabánya had a mixed diet including grass and less abrasive browse components. Likewise, based on this methodology, the Dinotheriensande population of *Hippotherium primigenium* would appear to have been engaged in more grass eating. The microwear analysis provides a somewhat conflicting dietary signal, suggesting more abrasive food components in the diet of the Rudabánya sample than the Dinotheriensande population. Because of the sampling qualification we have given above, we do not wish to place much emphasis on the microwear evidence provided here, mainly because of the small number of specimens and the fact that sample sizes did not allow using the same facet on the same maxillary tooth across all the populations we sampled. We do believe however that the mesowear signal is more robust, and due to the extended method developed by KAISER & SOLOUNIAS (in press), we can now gain meaningful results from smaller samples than used originally on Dinotheriensande hipparions by KAISER *et al*. (2000). In the future we intend to utilize both the microwear and mesowear methods, but will rely much more on the mesowear method for our paleodietary interpretations.

Metapodial ecomorphology

In addition to the study of limb proportions using logarithmic ratio diagrams (BERNOR *et al*., in prep.), we have calculated principal components plots of the Rudabánya hipparionines compared to other Central European hipparion species. Principal components analysis (PCA) can be used to identify the major sources of variability in a sample and plots of principal components can be used to identify potential discrete subsets of a sample. We have elected to employ principal components analysis of continuous variables for evaluation of the third metacarpal III (MCIII) and the third metatarsal (MTIII). The continuous variables used follow Eisenmann *et al*. (1988) and Bernor *et al*. (1997). The six variables used in the MCIII analysis were M2, M3, M4, M5, M8, and M10. The nine variables used in the MTIII analysis were M2, M3, M4, M5, M10, M11, M12, M13 and M14. These measurements were selected to analyse the two complete metapodials from Rudabánya. The raw measurements for each element were all divided by the geometric mean of the measurements for that element (GEOMEAN), and these GEOMEAN corrected measurements were used in the principal components analysis (Jungers *et al*., 1995). Principal components analyses of the covariance matrix for complete MCIII's and MTIII's were computed using SAS. Principal components analysis included a total of 101 third metatarsals and 75 third metacarpals from Rudabánya, Csákvár, Sümeg, Sinap, Esme Akçakoy, Höwenegg, Inzersdorf, Eppelsheim, Dorn Dürkheim, Gols and Xmas Quarry (North America). The results cited below focus on the Rudabánya hipparion sample. A more extensive comparison with all the localities in question awaits our report on Central European hipparion postcranial evolution (SCOTT & BERNOR, in prep.).

The PCA of MCIII resulted in a first principal component that explained 97% of the total sample variance (Table 2a). Principal component one loaded heavily with the GEOMEAN corrected value of M2 and had a strongly positive eigenvector with M2. Thus, principal component one clearly expresses relative length. Principal component two may also be of interest because of its strongly positive eigenvector with GEOMEAN corrected M3 accompanied by a positive eigenvector for M10 and negative eigenvectors for M4, M5, and M8. Thus, positive scores on principal component two describe the morphologically interesting pattern of distal mediolateral expansion (Table 2b).

These morphological trends can be interpreted biomechanically and in turn be linked to locomotor adaptations and habitat preference (EISENMANN, 1995; BERNOR *et al*., 1999). A longstanding, implicit prediction is that hipparions adapted to open country

	Hippotherium primigenium (Dinotheriensande)					*Hippotherium intrans (Rudabánya)*				
	OR		CS			OR		CS		
Mesowear variable	L	H	S	R	B	L	H	S	R	B
Abs. counts	**3**	**164**	**25**	**117**	**0**	**0**	**14**	**7**	**6**	**0**
Percent	**2**	**98**	**18**	**82**	**0**	**0**	**100**	**54**	**46**	**0**

H, S, R: X-square = 9.8765, df = 2, p-value = 0.0072

Table 1. Mesowear variable distribution in upper P4, M1, M2 and M3 of *Hippotherium primigenium* from the Dinotheriensande and *Hippotherium intrans* from Rudabànya. OR = Occlusal Relief, L = low, H = high; CS = Cusp Shape, S = sharp, R = round, B = blunt.
Table 1. Distribución de variables de mesodesgaste en P4, M1, M2 and M3 sup. de Hippotherium primigenium *from the Dinotheriensande e* H. intrans *de Rudabànya. OR = Relieve oclusal, L = bajo, H = alto; CS = Forma de cúspide, S = afilada, R = redondeada, B = roma.*

running have craniocaudally deep metapodials (especially MTIII's), whereas forest dwelling species have craniocaudally shallow and mediolaterally wide metapodials (re: EISENMANN, 1995). Thus, we predict that more open country hipparionines are likely to have more negative values for principal component two while closed habitat dwellers are likely to have more positive values for principal component two. Similarly, the observation that cursorial forms generally have elongate limbs suggests that hipparionines with high scores for principal component one are likely to have low scores for principal component two. The MCIII's with positive scores for principal component one and negative scores for principal component two will be long and relatively slender suggesting adaptation for cursorial locomotion.

The Höwenegg hipparionine sample has previously been interpreted as belonging to a single forest dwelling species (BERNOR *et al.*, 1997). The Höwenegg MCIII sample forms a discrete cluster in the second quadrant of Figure 4a. Thus, the Höwenegg *Hippotherium primigenium* sample, is shown to have relatively short and broad (especially distally) MCIII's, the contrasting trend to that expected for cursorial species and confirming evidence of probable non-cursorial forest-dwelling adaptation (BERNOR *et al.*, 1997). This cluster of Höwenegg specimens is critical to our interpretation of all late Miocene hipparionine metapodial morphology from various sites including Rudabánya; it is used as a «key» population for assessing both population variability and functional adaptation of the distal limb. Hipparionine metapodials from a given locality that exhibit principal component scores similar to those from Höwenegg were possibly similarly forest-adapted while cursorial species would be predicted to plot opposite the Höwenegg sample in the fourth quadrant.

The single MCIII from Rudabánya complete enough for PCA analysis, MAFIV12039 is plotted here in Figure 4a as being well outside the range of the Höwenegg sample. It is distinguished by a high score for principal component one and can clearly be consi-

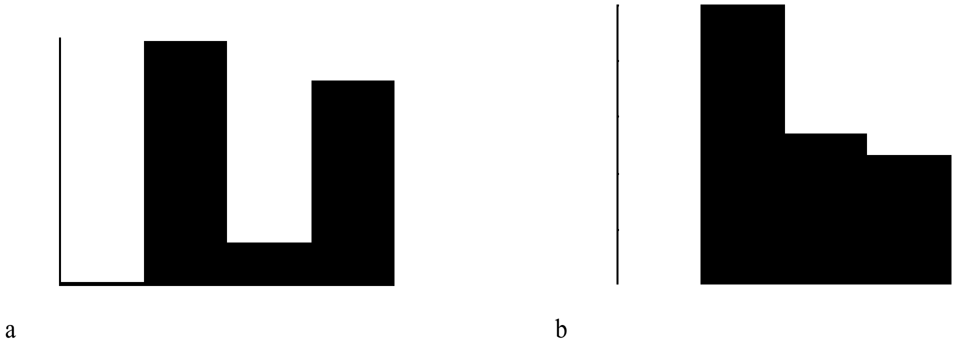

Figure 2a. Mesowear variable distribution in upper P4, M1, M2 and M3 of *H. primigenium* from the Dinotheriensande; 2b. Mesowear variable distribution in upper P4, M1, M2 and M3 of *H. intrans* from Rudabánya. L = low, H = high, S = sharp, R = round, B = blunt.
Figura 2a. Distribución de variables de mesodesgaste en P4, M1, M2 and M3 sup. de Hippotherium primigenium *from the Dinotheriensande; 2b. Idem. de* H. intrans *de Rudabànya. OR = Relieve oclusal, L = bajo, H = alto; CS = Forma de cúspide, S = afilada, R = redondeada, B = roma.*

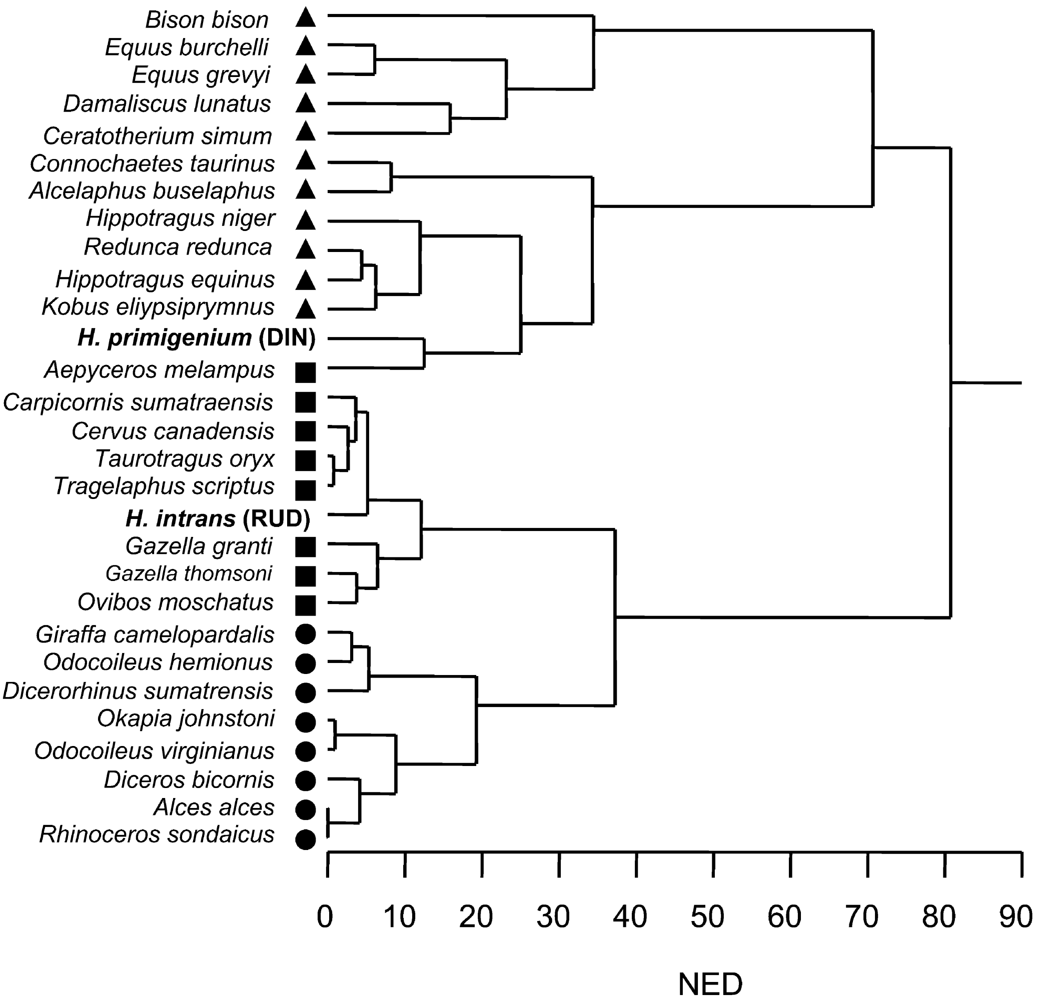

Figure 3. Hierarchical cluster diagram plotting the mesowear datasets of *H. intrans* from Rudabánya (RUD) and *H. primigenium* from the Dinotheriensande (DIN) together with 27 «typical» recent comparison taxa after Fortelius & Solounias (2000). Analyses based on the mesowear variables % high occlusal relief, % sharp cusps, % round cusps and % blunt cusps of the isolated upper cheek tooth positions P4, M1, M2 and M3, following the extended mesowear model of Kaiser & Solounias (in press). Symbols indicate dietary adaptations of recent reference species according to the consensus category of Fortelius & Solounias (2000): Circle = browser, rectangle = mixed-feeder, triangle = grazer. NED = normalised euclidean distance.

Figure 3. Dendrograma jerárquico agrupando los datos de mesodesgaste de H. intrans *de Rudabánya (RUD) y* H. primigenium *de Dinotheriensande (DIN) junto con 27 «típicos» taxa recientes de comparación según Fortelius & Solounias (2000). Análisis basad os en las variables de mesodesgaste % relieve occlusal alto, % cúspides afiladas, % cúspides redondeadas y % cúspides romas de los dientes yugales superiores aislados de las posiciones P4, M1, M2 and M3, según el modelo extendido de mesodesgaste de Kaiser & Solounias (en prensa). Símbolos de la dieta de especies recientes de referencia según las categorías consenso de Fortelius & Solounias (2000): Círculo = ramoneador, rectángulo = herbívoro mixto, triángulo = pastador. NED = distancia euclídea normalizada .*

dered elongate. Its nearest neighbor is one of the specimens from Gols (MN 10, Austria), but it also plots near a specimen from Csákvár (MN 11, Hungary). MAFIV12039 is similar to MNHNTRQ1126 from Sinap in its overall shape, which has been attributed to a small possibly cursorial species, in terms of principal component one but contrasts with MNHNTRQ1126 on principal component two. The estimated body mass for MAFIV12039 (= 194 kg) is less than the mean for the Höwenegg MCIII sample

Principal Component	Eigenvalue	% Variance Explained
One	0.2773	97.1%
Two	0.0035	1.2%
Three	0.0026	0.9%
Four	0.0014	0.5%
Five	0.0007	0.3%
Six	0	0.0%

Principal Component	Eigenvalue	% Variance Explained
One	0.2707	97.1%
Two	0.0025	0.9%
Three	0.0017	0.6%
Four	0.0014	0.5%
Five	0.0009	0.3%
Six	0.0007	0.2%
Seven	0.0004	0.2%
Eight	0.0004	0.1%
Nine	0	0.0%

Table 2b

Table 2a and 2b. Eigenvalues for Principal Components Analysis of MCIII.
Tabla 2.a y 2b. Eigenvectores del Analisis de Componentes Principales de MCIII.

		Eigenvector				
Variable	P.C.One	P.C.Two	P.C.Three	P.C.Four	P.C. Five	P.C.Six
M2/GEOMEAN	0.9979	0.0365	0.0081	0.0037	-0.0378	0.036
M3/GEOMEAN	-0.0409	0.8526	0.1448	-0.415	-0.0017	0.2799
M4/GEOMEAN	0.0219	-0.0631	-0.1026	0.1066	0.8966	0.412
M5/GEOMEAN	-0.0002	-0.3812	0.8287	-0.3327	-0.0023	0.2392
M8/GEOMEAN	-0.0323	-0.2378	-0.3707	-0.0784	-0.4132	0.7925
M10/GEOMEAN	-0.0306	0.2569	0.3797	0.8364	-0.1547	0.2556

Table 2c and 2d. Eigenvalues for Principal Components Analysis of MTIII.
Tabla 2c y 2d. Eigenvectores del Analisis de Componentes Principales de MTIII.

Variable	P.C.1	P.C.2	P.C.3	P.C.4	P.C. 5	P.C.6	P.C.7	P.C.8	P.C.9
M2/GEOMEAN	0.9969	0.0537	-0.0268	0.0092	0.0140	0.0012	0.0203	-0.0185	0.0401
M3/GEOMEAN	-0.0596	0.2685	-0.5335	-0.2743	0.0912	-0.1757	0.4662	-0.4066	0.3777
M4/GEOMEAN	0.0031	-0.0757	-0.3578	-0.4240	-0.3670	0.3138	-0.4185	0.3628	0.3827
M5/GEOMEAN	-0.0244	0.6384	0.6385	-0.3223	-0.0175	0.0339	-0.0124	0.0310	0.2788
M10/GEOMEAN	-0.0332	0.3296	-0.0953	0.7255	-0.4490	0.2047	-0.0866	-0.1858	0.2632
M11/GEOMEAN	-0.0296	0.2234	-0.1989	0.3115	0.6868	-0.0652	-0.1574	0.4759	0.2923
M12/GEOMEAN	0.0007	-0.3712	0.2357	0.0749	0.1035	0.5831	0.5620	0.1293	0.3431
M13/GEOMEAN	0.0026	-0.3641	0.2036	0.0073	0.2723	-0.0356	-0.4766	-0.5742	0.4400
M14/GEOMEAN	0.0103	-0.2878	0.1825	0.1092	-0.3136	-0.6943	0.1779	0.3070	0.4068

Table 2d

(=242 kg) (Bernor *et al.*, 1999). Thus, MAFIV12039 appears to represent a smaller species with elongate metapodials. It is possible that this species was somewhat cursorial but this issue remains uncertain. Comparison of MAFIV12039 with the type of *Hippotherium intrans* leaves the systematic attribution of this MCIII specimen somewhat equivocal.

The single MTIII specimen from Rudabánya analyzed here is the type specimen of *Hippotherium intrans*, MAFIV12038. The specimen was described originally as being very long (Kretzoi, 1983). Our analysis concurs with Bernor *et al.* (1999), placing MAFIV12038 just outside the range of relative length variation for Höwenegg (Figure 4b). Importantly, the contrast between MAFIV12038 and the Höwenegg sample of MTIII's is much smaller than the contrast noted between the MCIII MAFIV12039 and the Höwenegg MCIII sample.

This distinction in the degree of dissimilarity with the MTIII and MCIII from Rudabánya and the Höwenegg sample suggests three logical possibilities: 1) MAFIV12039, the MCIII, is referable to a species other than *Hippotherium intrans*, perhaps the smaller Rudabánya hipparion known by cheek teeth from the Upper Lignite bed at Rudabánya II; 2) the fore and hind limb proportions of *Hippotherium intrans* (as indicated by the MCIII and MTIII cited herein) may have been different than the Höwenegg hipparion in a very fundamental way not yet fully understood; 3) the two Rudabánya specimens represent extremes of intraspecies variation. This third possibility could be a case of sexual size dimorphism, but decidedly does not occur in the Höwenegg hipparion (Bernor *et al.*, 1997). The two Rudabánya specimens do appear to come from individuals of different size. The MTIII, MAFIV12038, yielded an estimated body mass of

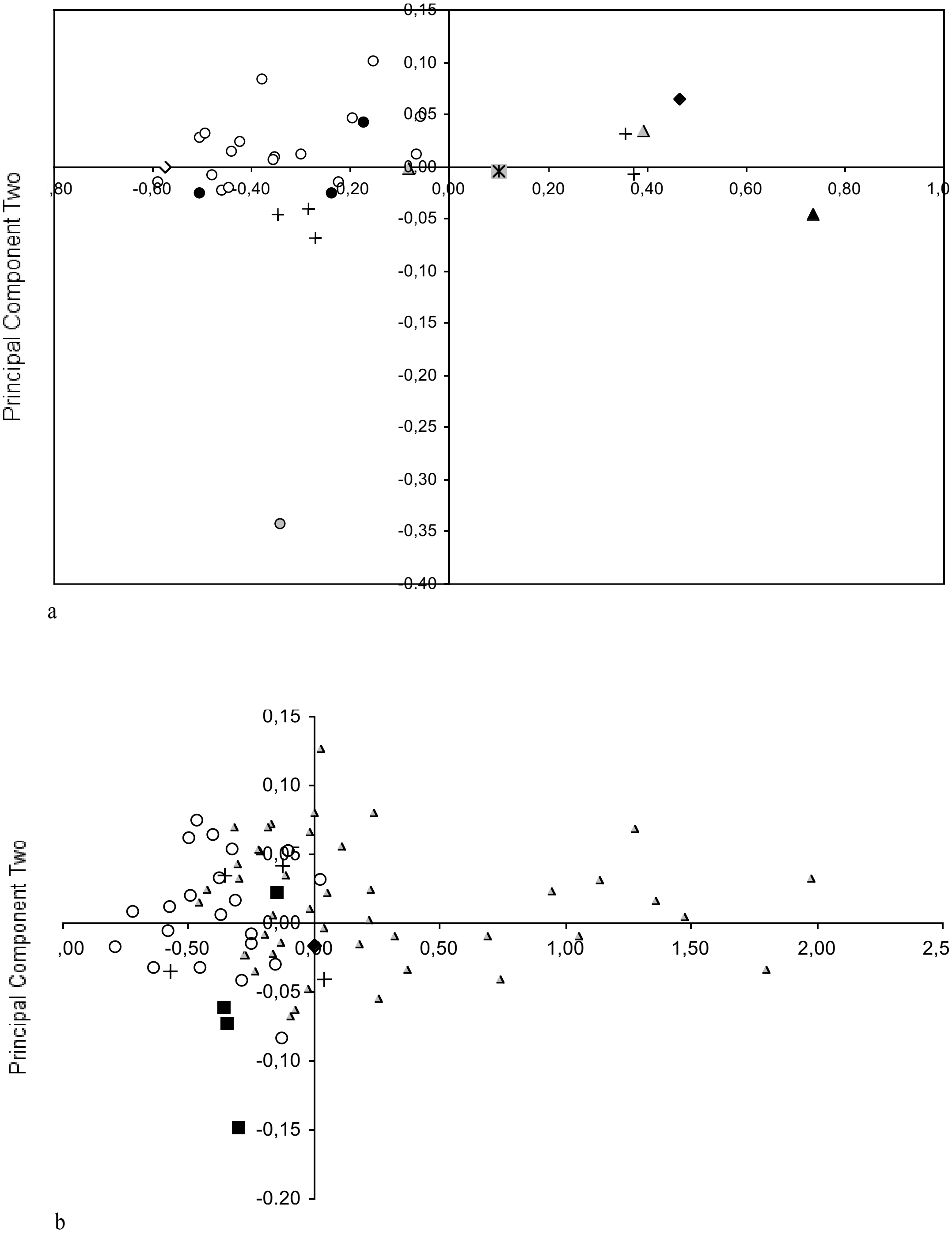

Figure 4 a. Principal Components Plot of Components 1 and 2 for MCIII; 4b. Principal Components Plot of Components 1 and 2 for MTIII.
Figura 4 a. Distribución de Componentes Principales para los components 1 y 2 del MCIII; 4b. Distribución de Componentes Principales para los components 1 y 2 del MTIII.

287 kg, the same as the mean estimated body mass for the Höwenegg MTIII sample (SCOTT & BERNOR, in prep.). However, as previously indicated, the MCIII MAFIV12039 was smaller than *Hippotherium primigenium* from Höwenegg (194 kg *versus* 242 kg as found in the Höwenegg hipparion; or 80% of the size). We cannot demonstrate decisively that any of the above possibilities is the best scientific interpretation, we can only suspect that we are either sampling the extremes of population variation, or that two species are represented by the complete metapodial material from Rudabánya II.

The small sample size of Rudabánya MPIII's (one MTIII and one MCIII) does not allow explicit statistical treatment of the species number question at Rudabánya. However, it is worth emphasizing that the range of variation for the two Rudabánya specimens is large compared to the Höwenegg sample and both Rudabánya specimens are outside the range of the Höwenegg sample (Fig. 4a and 4b). The Rudabánya MPIII specimens clearly suggest at least one species more cursorial than *Hippotherium primigenium* at Höwenegg and the possibility of two such species at Rudabánya.

The case of the two MCIII specimens from Gols parallels the situation at Rudabánya and again an inadequate sample size makes a definitive statement regarding species number of species at Gols impossible at this time. Csákvár (currently under study by Scott & Bernor) preserves five complete MCIII's and three complete MTIII's and two species appear likely at this site also. This is supported by a significant F-test ($p < .01$, d.f. = 4, 9) comparing the variation in Csákvár MCIII's (N=5 individuals) on principal component one to the variation in Höwenegg MCIII's (N=10 individuals, left side) on principal component one.

CONCLUSIONS

Rudabánya would appear to have harbored two hipparion species, the predominant large form *Hippotherium intrans* (KRETZOI, 1983), and a smaller rarer form known distinctly from the Upper Lignite levels of Rudabánya II. The predominant larger Rudabánya species, *Hippotherium intrans*, had an elongate MTIII which suggests a greater capability for sustained cursorial locomotion than exhibited for Central European *Hippotherium primigenium*. Analysis of microwear and mesowear patterns on Rudabánya *Hippotherium intrans* cheek teeth suggests a mixed grass-browse diet. While present in the local Pannonian lake-swamp facies, it is reasonable to deduce that Rudabánya's *H. intrans* inhabited more open country habitats distal to the lake water source. These lines of evidence suggest that the lake side equable subtropical forest environments with reeds were bounded distally by more open country mesophytic woodlands typical of the Central Paratethys during MN 9 (BERNOR *et al.*, 1988).

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