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# Evolution of Late Miocene Hungarian Suinae (Artiodactyla, Suidae)

## Abstract

Neogene suids have been collected for over 100 years from Hungary, yet, until recently, there has been very little published about them. This contribution presents our current knowledge of Hungarian late Miocene Suinae and their evolutionary, chronologic and biogeographic relationships with other Eurasian suines. We analyse an evolutionary series of Miocene Suidae including *Hyotherium meissneri*, *Hyotherium soemmeringi*, *Propotamochoerus palaeochoerus*, *Propotamochoerus* sp. (Spain), *Microstonyx erymanthius/major* and *Hippopotamodon antiquus* in order to decipher evolutionary trends within the Suinae. Comparing bivariate plots and log-ratio plots for all cheek teeth of this series of suids we find that suines exhibit serially progressively longer M1/m1, M2/m2 and M3/m3 than hyotherines. Furthermore, *Hippopotamodon* would appear to be particularly distinct in its very large p4 length and width measurements. We find that *Propotamochoerus* and *Microstonyx* are distinct lineages that overlap in both time and space. *Propotamochoerus* would appear to be an index for warm equitable forests (typical for the late Astaracian/Vallesian of Middle Europe), while *Microstonyx* is an index for more seasonal open country woodlands typical of late Miocene "Pikermian" faunas.

## Kurzfassung

### Evolution ungarischer Suinae im späten Miozän (Artiodactyla, Suidae)

Seit über 100 Jahren wurden in Ungarn neogene Suiden gesammelt, doch gibt es darüber bis heute nur wenige Veröffentlichungen. Dieser Beitrag zeigt den derzeitigen Stand der Kenntnisse über die obermiozänen Suiden Ungarns und ihre evolutionären, chronologischen und biogeographischen Verhältnisse zu anderen eurasischen Suiden auf. Wir analysieren die evolutionäre Reihe von miozänen Suiden, einschließlich *Hyotherium meissneri*, *Hyotherium soemmeringi*, *Propotamochoerus palaeochoerus*, *Propotamochoerus* sp. (Spanien), *Microstonyx erymanthius/major* und *Hippopotamodon antiquus*, um die evolutionären Trends innerhalb der Suinae herauszuarbeiten. Durch Vergleiche von Bivarianz-Plots und Log-Ratio-Plots für alle Backenzähne dieser Suidenserie zeigen wir, daß die Suinae progressiv längere M1/m1, M2/m2 und M3/m3 aufweisen als die Hyotherinae. Darüberhinaus fällt *Hippopotamodon* durch einen sehr großen und breiten p4 auf. Wir zeigen außerdem, daß *Propotamochoerus* und *Microstonyx* zwei getrennte Linien sind, die einander in Raum und Zeit überlappen. *Propotamochoerus* scheint demnach ein Indikator für gemäßigt warme Wälder zu sein (typisch für das späte Astaracian/Vallesian Mitteleuropas), während *Microstonyx* als Indikator für eher durch Jahreszeiten beeinflusste offene Waldgebiete ist, typisch für die obermiozänen "Pikermian"-Faunen.

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## Introduction

Despite more than 100 years collection of fossil suines from late Miocene Hungarian strata, very little is known about the actual taxa represented or the material that it is based upon. A recent synthesis of Western Eurasian Suoidea by FORTELIUS et al. (1996) reported the following fossil suines from Hungary: *Propotamochoerus provincialis* GERVAIS, 1859 (possible occurrence at MN13? locality of Hatvan), *Microstonyx major* GERVAIS, 1848-52 (MN13 locality of Polgárdi) and *Microstonyx erymanthius* ROTH & WAGNER, 1854 (MN11 locality of Csákvár). A recent study of the Rudabánya suid fauna includes the MN8-9 suine *Propotamochoerus* (= *Korynochoerus* of SCHMIDT-KITTLER, 1971 and HELLMUND, 1995) *palaeochoerus* KAUP, 1833 (late MN9 locality of Rudabánya; FORTELIUS et al. 1999 and in press). These reported taxonomic records differ slightly from those listed in the curatorial records of the Hungarian Geological Survey (HGI or MAFI) which include: "*Hyotherium*" *palaeochoerus* from Rudabánya (KRETZOI et al. 1976); *Microstonyx* cf. *antiquus* from Csákvár (KRETZOI 1954); *Microstonyx erymanthius* from Polgardi (KRETZOI 1954) and another latest Miocene locality, Baltavar (KORMOS 1914). The aim of this paper is to conduct a quantitative comparison of the Hungarian material with other pertinent Miocene hyotherine and suine data to exact greater clarity in the evolution of Hungarian late Miocene suines. The Karlsruhe collections of late Miocene (medial Turolian) *Microstonyx erymanthius* from Mamutghazi, hitherto unpublished, serve as an important basis for our comparison and analysis.

## Materials and Methods

### Methods

We use both continuous and discrete variables here to analyse the Hungarian suine sample, which we compare to a series of hyotherine and suine pigs from Europe. The continuous variables used follow the conventions set forth in Table 1 (Legend). Our statistical analysis here includes calculation of bivariate plots of basal length versus maximum width for all available cheek teeth and the use of log-ratio plots of cheek tooth length between taxa. We use the extensive sample (over

400 specimens) of Rudabánya *Propotamochoerus palaeochoerus* as a standard for the log plots. We recognize maxillary teeth as upper case (i.e. P2, M3, etc.) and mandibular teeth as lower case (i.e. p2, m3, etc.).

### Materials

We compare the Hungarian suine species here (Table 1 here; excluding Rudabánya specimens reported in FORTELIUS et al., in press) to other populations of Central European hyotherine and suine taxa. These taxa are briefly characterized here.

*Hyotherium meissneri* – A well known, primitive hyotherine typical for the latest Oligocene - basal Miocene (MN1-2) of Europe, which we have sampled from Ulm-Westtangente, Germany (HELLMUND 1991). This species is characterized by small size, P1/p1 much smaller and lower crowned than P2/p2; P3 with tall pointed principal cusp and well defined posterolingual shelf; P4 with two distinct buccal cusps, a single lingual cusp and virtually continuous cingulum; M1-M3 with small, low bunodont cusps and cingulum on all but lingual margin; M3 with a short talon; p4 has a principal cusp that is moderately bifurcated lingually; mandibular molars with cingulum variably expressed on the buccal surface; m1-m2 rectangular shaped; m3 an elongate/triangular shape with decreased width from anterior to posterior aspects of the tooth.

*Hyotherium soemmeringi* – A well represented species of hyotherine pig which is larger than *H. meissneri*. Our comparative sample is derived from the late early Miocene (MN5) of Sandelzhausen, Germany (re: SCHMIDT-KITTLER 1971). This species is characterized by its relatively longer premolars than *H. meissneri*; P3 has a distinct posterolingual cusp; P4 cusps are essentially as in *H. meissneri*, but the crown outline is more quadrangular in shape and with the cingulum less continuous on the buccal and lingual surfaces; p4 with a more distinctly developed, lingually situated in-nenheugel; molars generally somewhat more elongate in their proportions than *H. meissneri*; m3 with a relatively more expanded trigonid bucco-lingual dimension.

*Propotamochoerus (= Korynochoerus) palaeochoerus* – A moderate sized stratigraphically early and primitive suine known from the late Astaracian and Vallesian of Western Europe, Vallesian of Central Europe (here, Germany [G], Hungary [H] and Spain [S]) and late Turolian of Greece; re: HELLMUND 1995). This species is larger than all hyotherines which we have studied, but smaller than *Microstonyx*. Our sample includes specimens from Spain (S), Germany (G) and Rudabánya (H).

*Propotamochoerus sp.* – A taxon known from the late Astaracian of Spain characterized by its longer anterior premolars.

*Microstonyx erymanthius/major* – An advanced late Miocene species of suine generally intermediate in size between *Propotamochoerus palaeochoerus* and *Microstonyx antiquus*. This species is characterized

by relatively short P2-3; P4 with similar length to *P. palaeochoerus*; molars exhibiting progressive serial increase in length compared with hyotheres and *P. palaeochoerus*.

*Hippopotamodon antiquus* – A very large suine with approximately twice the body mass of *Microstonyx erymanthius/major*, and apparently closely related to the *Microstonyx* clade; characterized by p1 being primitively long and p3 p4 longer larger and higher crowned than in *Microstonyx*.

### Statistical Analysis

Figures 1a-f present bivariate analyses of maximum width versus basal length of P2/p2 – P4/p4. P1/p1 are not plotted because of the scarcity of material, particularly in *Microstonyx* species which either lack or rarely preserve these teeth. P2 and p2 exhibit overlap of *H. soemmeringi* and *P. palaeochoerus*. The lower p2 exhibits overlap between these taxa and both the Dorn-Dürkheim and Turkish (Mamutghazi) *Microstonyx erymanthius*, and one specimen of *Hippopotamodon antiquus*. Clear outliers in the lower p2 cluster are the uncommon species of *P. n. sp.* from Spain and the Type material of *Hippopotamodon antiquus* from Eppelsheim.

Figures 1c and d again exhibit more extensive overlap in the p3's than the P3's. There is limited overlap between the Rudabánya sample of *P. palaeochoerus* and the *Microstonyx* sample of upper P3. Mandibular p3 plots *Hippopotamodon antiquus* and *P. n. sp.* well outside cluster of other plotted points. Figures 1e and 1f of upper P4 and lower p4 exhibit considerable overlap of plotted points with, once again, *H. antiquus* plotting as a separate cluster for lower p4.

Figure 2a-f presents bivariate analyses of width versus basal length of M1/m1 – M3/m3. Maxillary M1 exhibits overlap between the two hyotherine taxa and *P. palaeochoerus* taxa; the *Microstonyx* taxa cluster at the high end of the range demonstrating no overlap with *Propotamochoerus*. Mandibular m1 exhibits extensive width overlap between species of *Propotamochoerus* and *Microstonyx*, but also there is both width and length overlap between Spanish and Csákvár *Microstonyx*. *Hippopotamodon antiquus* is isolated at the top of the range.

The plot for M2 exhibits individual clusters for the hyotherines, *Propotamochoerus* and *Microstonyx* taxa; there is some limited overlap between *H. soemmeringi* and *Propalaeochoerus*, but the *Microstonyx* sample is well separated from the other taxa. The plots for m2 exhibit more overlap between *Hyotherium* and *Propotamochoerus* and there is a closer clustering, and even some overlap between *Microstonyx* and *Hippopotamodon*. Csákvár. *Microstonyx* again is at the lower end of the range but overlapping with the Dorn-

Dürkheim and Baltavar/Polgárdi samples in part. The greatest separation between taxa occurs with M3 and m3 (Fig. 2d, 2e). Here, *hyotheres*, *Propalaeochoerus* and *Microstonyx* are clearly separated from one another. Also, *Hippopotamodon* exhibits a near overlap with the Polgárdi/Baltavar sample of *Microstonyx*. Again, Csákvár's *Microstonyx* is the smallest member of this genus, but clusters most closely with a Baltavar specimen and 2 specimens from Dorn-Dürkheim.

Figure 3a, b presents a mean log-ratio plot of lengths of P2-M3 and p2-m3 of all taxa considered in the bivariate plots. The maxillary cheek tooth series reveals that the standard, *Propotamochoerus palaeochoerus* (Rudabánya), is intermediate in size between the hyotherine and suine taxa. It further shows that *Hyotherium soemmeringi* has elevated length values compared to *Hyotherium meissneri*; P2 and P3 are especially longer in their basal length dimension. The *Microstonyx* taxa have longer P2 and P3 length dimensions than both *Hyotherium soemmeringi* and *Propotamochoerus palaeochoerus*, and P4 is longer yet. The most substantial difference in upper cheek tooth basal length however is the progressive serial increase in M1, M2 and M3 basal length of all *Microstonyx* species. This is a fundamental and consistent difference between *Microstonyx major/erymanthus* and *Propotamochoerus palaeochoerus*.

The mandibular cheek teeth compare closely to the results seen in the maxillary cheek teeth (Fig. 3b). The significant difference here is that we have data on the Type material of *Hippopotamodon antiquus* from Epselsheim (MN9, ca. 10.5 Ma.). While larger than *Microstonyx* in molar length dimensions, the major difference between *M. major/erymanthus* and *H. antiquus* is in the proportionally longer p3, and to a lesser extent, longer p4-m3 measurements in the latter taxon. If this evidence is borne out in a larger sample of European and Asian *Hippopotamodon*, it could be indicative of a fundamentally different adaptation and evidence that *Hippopotamodon* and *Microstonyx* are truly distinct lineages.

The mean log width plots (Fig. 3c, d) are essentially similar to the mean log length plots in that the hyotheres track below the *Propotamochoerus* standard and the *Microstonyx* and *Hippopotamodon* taxa track above the standard. The mean log width plots are overall quite similar in their profile to the mean log length plots. The only difference we can detect here is that the separation between *Hippopotamodon* p3 and all *Microstonyx* p3 appears to be less in the mean log width dimension than the mean log length dimension. We finally note that the p3 and p4 of the Type series of *Hippopotamodon antiquus* would appear to be higher crowned and more stoutly built than the *Microstonyx* sample we present here.

Figures 4a-d are multivariate plots of p3 and p4. Figure 4a plots raw dimensions of basal length (M1), maxi-

mum width (M3) and height (M4) for wear stages 0, 1 and 2 (re: legend, Table 1). Figure 4b plots the same dimensions for p3 but using log dimensions. Figure 4a shows essentially the same dispersion and overlap shown in Figure 1d. Figure 4b however collapses taxa together for the length and width dimensions and commingles all taxa together for height except *Hippopotamodon antiquus* which maintains its separation from the rest of the sample. The p4 multivariate plots provide the same result (Fig. 4c, d), but with even further separation of *H. antiquus* height dimensions.

### Systematic Overview

We do not present a formal taxonomy section here because of the various unresolved controversies surrounding the suine taxa under consideration. Rather, we provide an abbreviated explanation as to the bases for these controversies and present here what we believe to be the "most prudent" taxonomic referral available to us with the material at hand. These referrals may well change with further research.

HÜNERMANN (1968) recognized *Hyotherium palaeochoerus* as being an advanced and large late member of the European "Hyotherium" clade. SCHMIDT-KITTLER (1971) nominated the new genus *Korynochoerus* for "*Hyotherium*" *palaeochoerus* arguing that characters of the skull and p4 united this taxon with the Suinae rather than Hyotheriinae. GINSBURG (1980) and VAN DER MADE & MOYÁ-SOLÁ (1989) further referred *Propotamochoerus provincialis* to *Korynochoerus provincialis*. HELLMUND (1995) followed SCHMIDT-KITTLER's (1971) taxonomy in recognizing a late occurring member of *Korynochoerus palaeochoerus* from the latest Miocene/earliest Pliocene locality of Maramena,

<i>Hy. meissneri</i>	⊗
<i>Hy. soemmeringi</i>	○
<i>P. paleochoerusG</i>	△
<i>P. paleochoerusH</i>	▽
<i>P. paleochoerusS</i>	◁
<i>P. spS</i>	▷
<i>H. antiquus</i>	□
<i>MicrostonyxCsk</i>	
<i>MicrostonyxB&amp;P</i>	⊙
<i>MicrostonyxDD</i>	
<i>MicrostonyxT</i>	☆

Legend for figures 1 & 2, see next pages

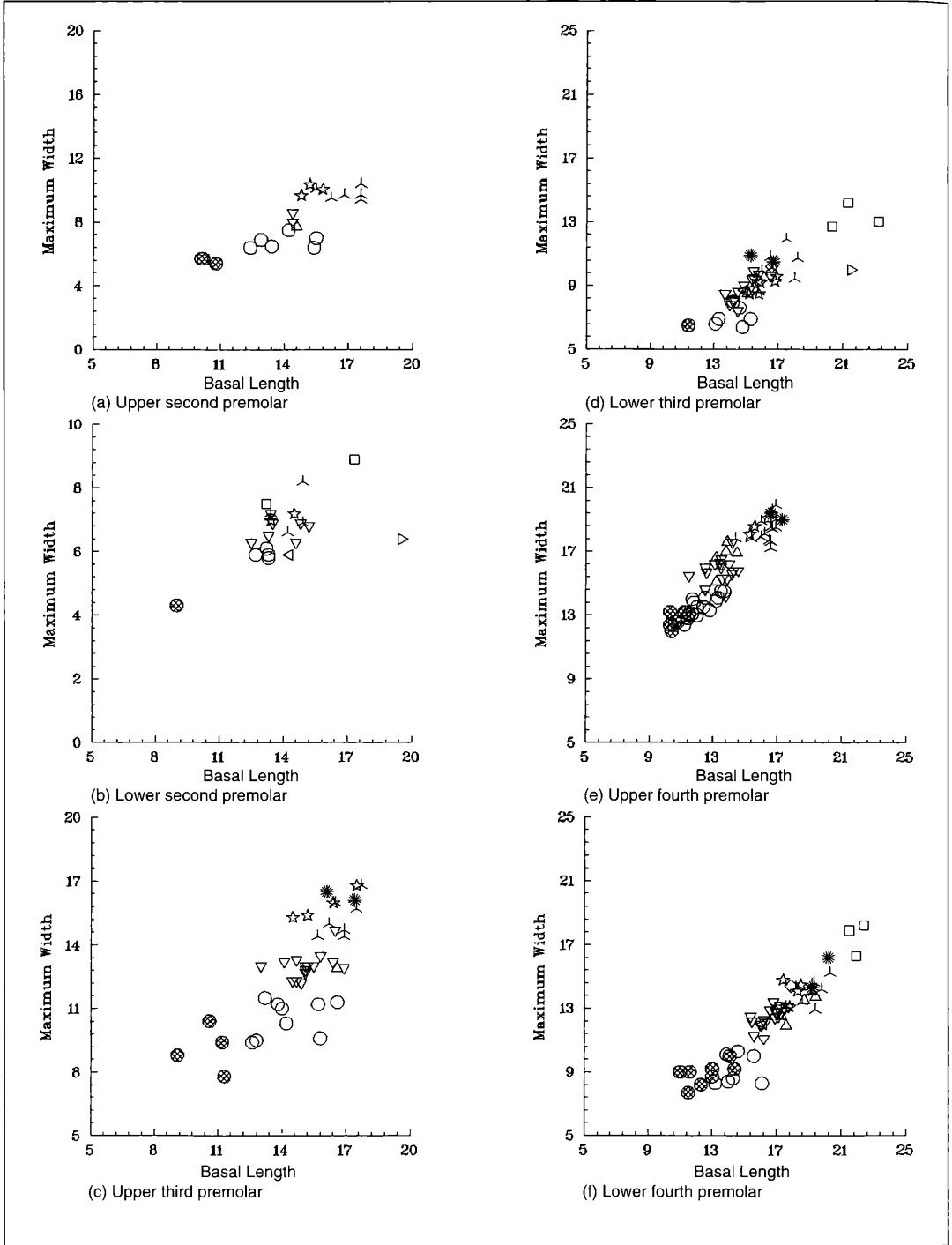


Figure 1. Bivariate plots of Basal Length versus Basal Width of Selected Hyotherine and Suine Premolars. a) P2, b) p2, c) P3, d) p3, e) P4, f) p4.

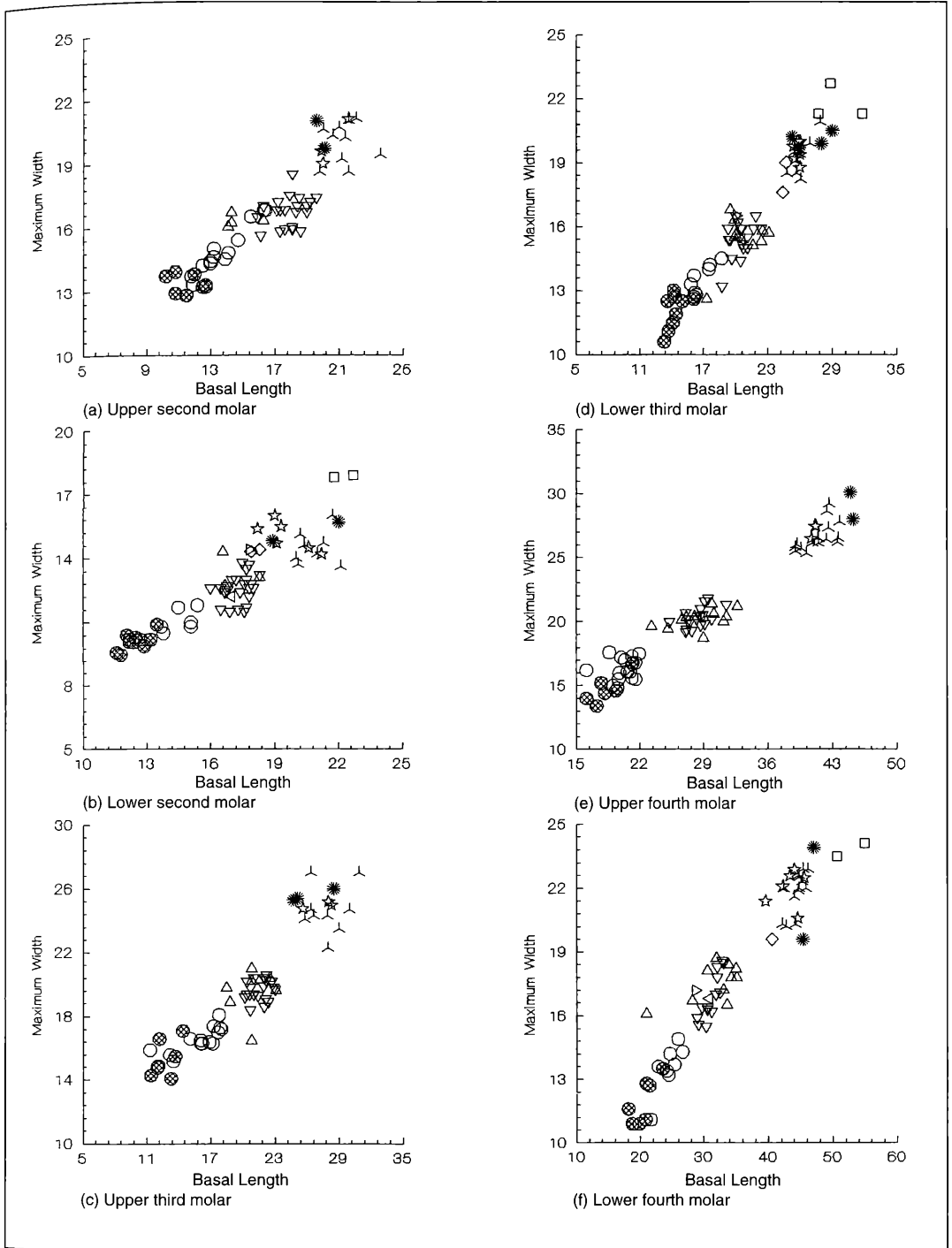


Figure 2. Bivariate plots of Basal Length versus Basal Width of Selected Hyotherine and Suine Molars, a) M1, b) m1, c) M2, d) m2, e) M3, f) m3.

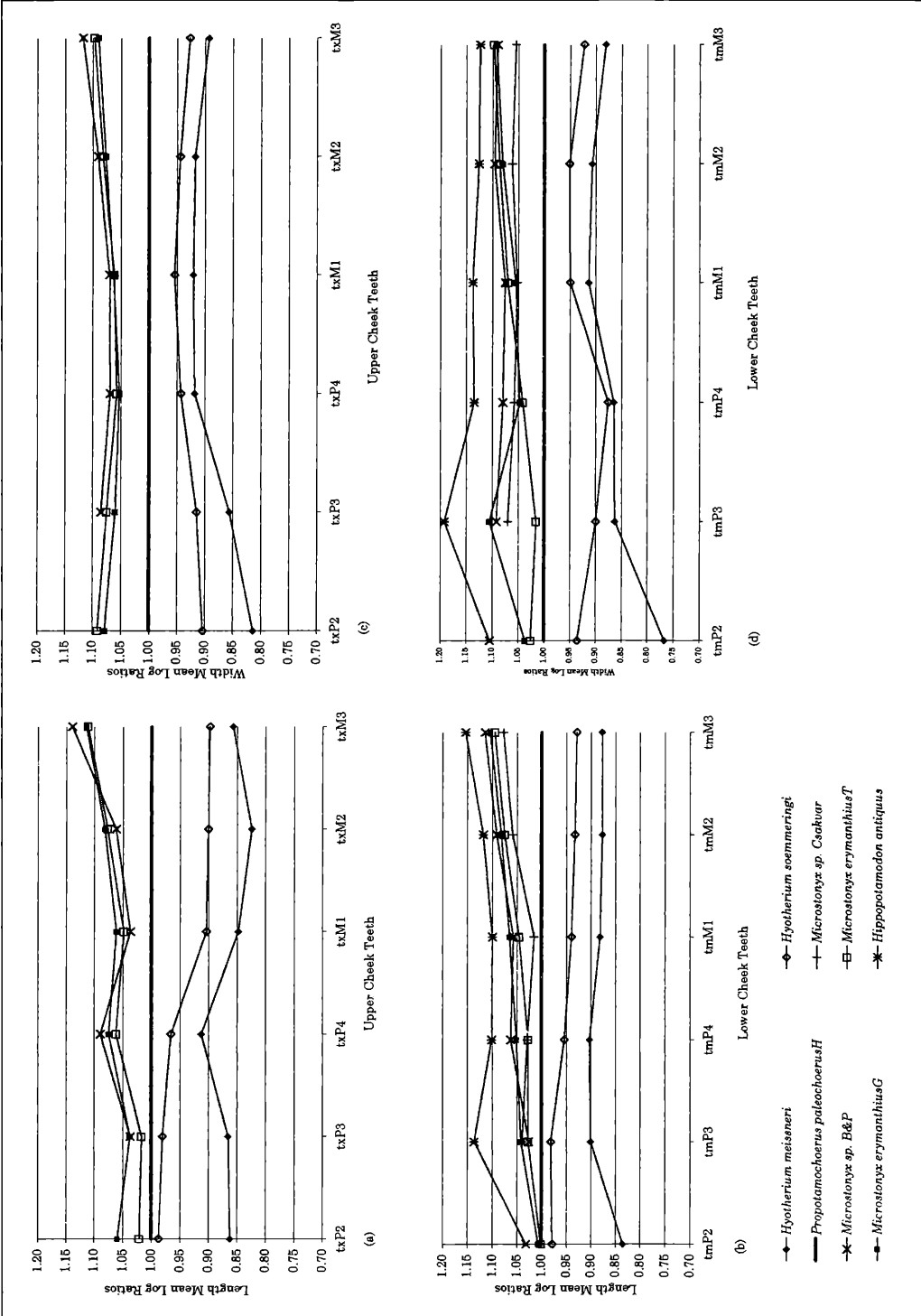


Figure 3. Length Mean Log-ratio Plots of Selected Hyotherine and Suine Species, Rudabánya *Propotamochoerus palaeochoerus* as a Standard. a) length maxillary cheek teeth, b) length mandibular cheek teeth, c) width maxillary cheek teeth, d) width mandibular cheek teeth.

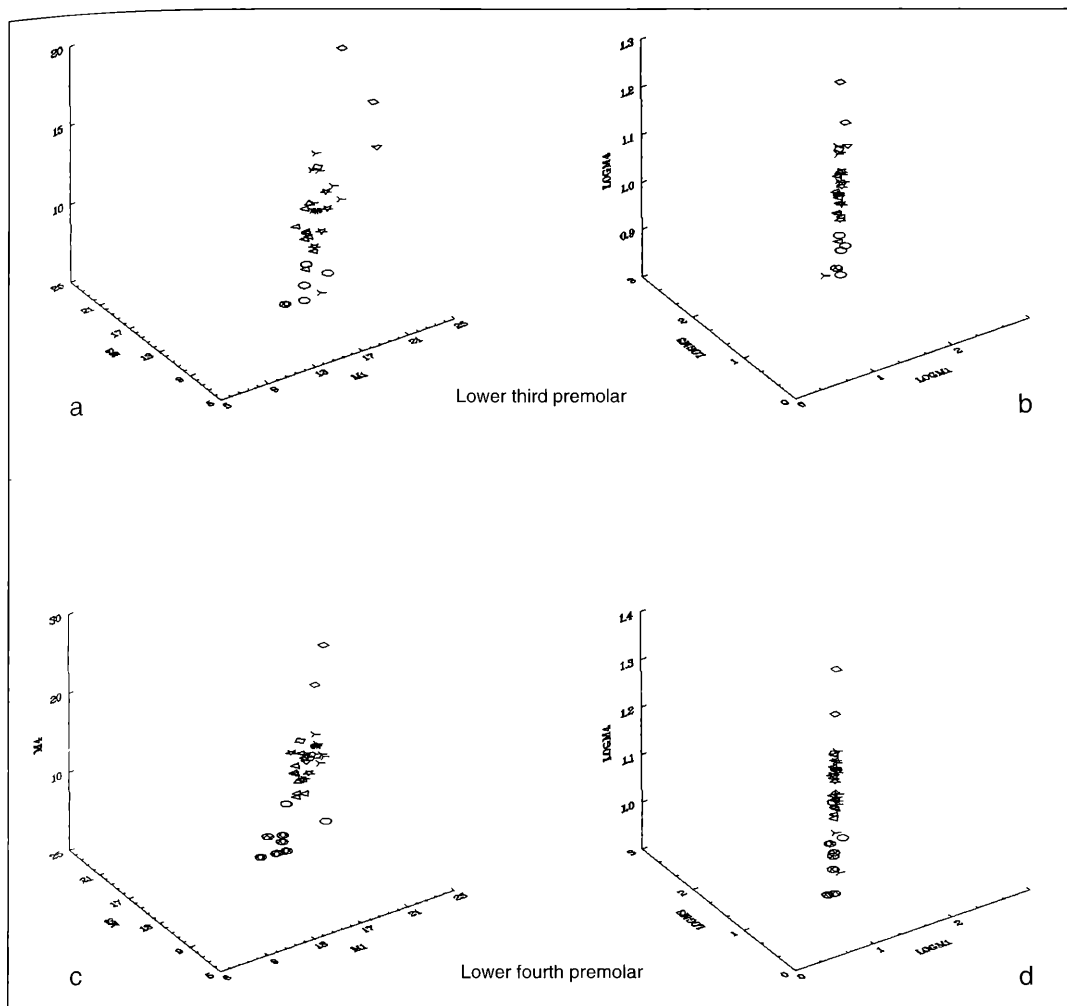


Figure 4. Multivariate Plots of p3 and p4 length, width and height measurements for wear stages 0-2, a) p3 raw measurement, b) p3 log measurements, c) p4 raw measurements, d) p4 log measurements.

Greece. FORTELIUS et al. (1996) argued that based upon the similarity of Central European *Korynochoerus palaeochoerus* to the Siwalik taxon *Propotamochoerus hysudricus*, that it should be referred to that genus. They acknowledged some problems with synonymising *Korynochoerus* with *Propotamochoerus* because of *Korynochoerus*' more conservative 11 morphology and morphology of its parietal crest and occiput stating that: "it [is] unlikely that *P. palaeochoerus* is the ancestor of any younger species of *Propotamochoerus* (FORTELIUS et al. 1996: 357)."

If we accept the synonymy of *Propotamochoerus* to include *P. provincialis*, *P. palaeochoerus* and *P. sp.* (Italy) from Europe, *P. salinus* and *P. hysudricus* from the Siwaliks, *P. hyotherioides* from south China (Lufeng,

latest Miocene) and *Propotamochoerus hysudricus* from Abu Dhabi (latest Miocene; BISHOP & HILL 1999), we would accept essentially a single clade, ranging from MN8 (circa 12 m.y.) to the latest Miocene/earliest Pliocene (circa 5 m.y.) of Eurasia and Arabia. The likelihood of a single suid lineage maintaining a continuous or semi-continuous geographic extension across the expanse of Eurasia for 7 million years seems unlikely. What would appear to be more likely is that a group of conservative small suinae united by plesiomorphic characters of the cheek tooth dentition maintained episodic biogeographic connections between Eurasia, Arabia and Africa during the late middle and late Miocene interval. These taxa would appear to all be adapted to closed woodland/forest conditions

Table 1 Measurements of the *Microstonyx* dental material from Csakvár, Baltavar, and Polgardi.

SPEC-ID	LOC	AGE	TOOTH	SEX	SIDE	M1	M2	M3	M4	M5	M6	M7	M8	M13
MAFIV18416	3	9,0	tmM1	3	1	17,9	16,8	14,3	6,3	15,0	5,0			5
MAFIV18403	3	9,0	tmM1	3	2	18,3	21,2	14,4	9,5	15,6	8,3			2
MAFIV18416	3	9,0	tmM2	3	1	24,4	26,3	17,6	10,1	18,6	8,7			4
MAFIV18403	3	9,0	tmM2	3	2	24,7	26,8	19,0	15,9	19,3	14,7			1
MAFIV18416	3	9,0	tmM3	3	1	40,5	39,1	19,6	12,8	18,8	12,9	15,7	10,1	2
MAFIV18403	3	9,0	tmP3	3	2	16,6	18,6	10,2	14,7					0
MAFIV18403	3	9,0	tmP4	3	2	17,9	19,9	14,4	15,4					1
MAFIVOB3157	4	7,0	tmM1	3	1	18,9	20,6	14,8	10,4	15,4	9,4			3
MAFIVOB325	4	7,0	tmM1	3	1	22,0	23,9	15,7	13,6	16,2	11,8			2
MAFIVOB3157	4	7,0	tmM2	3	1	25,9	26,1	19,7	13,8	19,6	13,0			2
MAFIVOB325	4	7,0	tmM2	3	1	29,0	29,1	20,5	18,9	20,3	16,3			1
MAFIVOB324a	4	7,0	tmM2	3	1	28,0	26,6	19,9	11,4	21,7	9,0			4
MAFIVOB3157	4	7,0	tmM3	3	1	45,3	39,9	19,6	18,3	20,5	17,6	17,4	15,0	1
MAFIVOB324a	4	7,0	tmM3	3	1	47,0	45,3	23,9	15,9	23,1	13,8	18,7	10,7	3
MAFIVOB324	4	7,0	tmP3	3	1	16,7	18,8	10,5	11,8					1
MAFIVOB3157	4	7,0	tmP4	3	1	19,2	20,1	14,3	14,2					1
MAFIVOB324	4	7,0	tmP4	3	1			15,2	14,3					0
MAFIVOB324a	4	7,0	tmP4	3	1	20,2	20,9	16,2	10,8					4
MAFIVOB309	4	7,0	txM1	3	1	20,1	19,8	19,7	7,9	19,8	8,4			5
MAFIVOB309	4	7,0	txM2	3	1	25,1	28,0	25,4	9,1	24,1	11,0			4
MAFIVOB309	4	7,0	txM3	3	1	45,2	36,9	28,0	14,2	25,7	14,0	16,4	12,1	2
MAFIOB2786	5	7,0	tmM2	3	1	25,3	27,3	20,2	13,5	20,8	12,4			3
MAFIOB2786	5	7,0	tmP3	3	1	15,3	14,0	10,9	7,0					4
MAFIVOB2784	5	7,0	txM1	3	2	19,6	21,1	21,0	5,2	19,9	6,0			5
MAFIVOB2784	5	7,0	txM2	3	2	24,7	28,4	25,3	15,0	24,9	11,6			3
MAFIVOB2707	5	7,0	txM2	3	2	28,5	29,9	26,0	6,8	25,2	9,2			2
MAFIVOB2784	5	7,0	txM3	3	2	44,9	41,1	30,1	12,8	28,3	13,6	19,6	10,6	2
MAFIVOB2707	5	7,0	txM3	3	2			28,6	12,5					1
MAFIVOB2784	5	7,0	txP3	3	2	16,1	16,6	16,5	10,7					3
MAFIOB2786	5	7,0	txP3	3	1	17,4	17,1	16,1	10,0					3
MAFIVOB2784	5	7,0	txP4	3	2	16,6	15,5	19,4	8,3					3
MAFIOB2786	5	7,0	txP4	3	1	17,3	15,1	19,0	11,2					2

M1: basal length, M2: occlusal length, M3: width (anterior), M4: height (anterior), M5: width (posterior), M6: height (posterior), M7: width (terminal talon/id), M8: height (terminal talon/id), M13: wear stage, LOC: locality

and likely were subject to episodic interprovincial migrations followed by protracted intervals of vicariant isolation.

A large suine, *Microstonyx antiquus* KAUP, 1833 is rarely found in MN9 of Central Europe (Type locality, Eppelsheim, Germany, ca. 10.5 Ma.). *Hippopotamodon sivalense* LYDEKKER, 1877 has been proposed as the senior generic taxon for "*Microstonyx*" *antiquus* and indicative of a biogeographic connection between the Siwaliks and Central Europe in the latest Astaracian/early Vallesian. THENIUS (1972), GINSBURG (1980) and VAN DER MADE & MOYÁ-SOLÁ (1989) have further proposed that *Microstonyx major* was derived from *Hippopotamodon antiquus*. FORTELIUS et al. (1996) accepted the referral of *Microstonyx antiquus* to *Hippopotamodon antiquus*, but FORTELIUS, BERNOR and

FESSAHA (pers. observ.) cast doubt on the efficacy of a *Microstonyx* – *Hippopotamodon* "transition" VAN DER MADE & FORTELIUS (in press) appear to be divided on this issue, but FORTELIUS has stated in this same manuscript that: "one of us (MF) finds it difficult to envision two closely related and highly similar species of generalist large mammal coexisting as distinct lineages on the same continent for over a million years. (The range of variation in the entire *Hippopotamodon-Microstonyx-Eumaiocoeris* Formenkreis is less than in the Recent genus *Sus*, with a similar geographic range)" We wish to add here that there are some differences which we believe are significant in the premolar dentition (cited above), particularly the stoutness and high-crowned profile of p3 and p4 of *Hippopotamodon antiquus* from the Dinotheriensande, and the



varying estimates of body mass for *Microstonyx erymanthius* (Pikermi; = 270 kg.), *Microstonyx major* (various localities; = 330 kg.) and *Hippopotamodon sivalense* (for *H. antiquus*; = 510 kg [nearly 2x that of the comparative *Microstonyx* species]). The fact is that these comparisons are made *almost entirely on cheek teeth*, and very little is known in time or space about the skull and postcranial morphology. We therefore prefer limiting our referral of *H. antiquus* and *H. sivalense* to the genus *Hippopotamodon* for now.

*Microstonyx erymanthius* ROTH & WAGNER, 1854 has been treated as the junior synonym of *Microstonyx major* GERVAIS, 1848-52 by several authors (TROFIMOV 1954, HÜNERMANN 1968: 60, 1969: 717, 718, THENIUS 1972, HÜRZELER 1982: 697, 700). VAN DER MADE & MOYÁ-SOLÁ (1989) treated these two "taxa" as subspecies, *M. major erymanthius* and *M. major major*, while VAN DER MADE & HUSSAIN (1989) recognized the species *Microstonyx major* from the type Nagri section, Pakistan. VAN DER MADE (1997) recognized yet a third subspecies, *M. erymanthius brevidens* for an early form from Dorn-Dürkheim (Rheinhesen) Germany which he believed was evolutionarily intermediate between the more conservative *M. major* and derived [Pikermi] *M. erymanthius*. VAN DER MADE (in FORTELIUS et al., 1996) added that a cast of a large M3 (in Naturhistorisches Museum Basel) from Polgárdi served as evidence that *Microstonyx major* was still present in MN13 of Hungary.

*Microstonyx* clearly had a broad Eurasian distribution for most of the late Miocene, MN10-13. There is little data supporting its transition in MN10 from *Hippopotamodon antiquus*. Rather, *Microstonyx* appears rather abruptly in middle Europe at the base of the Turolian (Dorn-Dürkheim, Germany and Csákvár, Hungary; both referred to MN11). It is interesting to note that these "early occurrences" of *Microstonyx*, and particularly the Csákvár form are amongst the smallest of our sample, disallowing the ready "transition" from the much larger *Hippopotamodon antiquus*.

We suspect that *Hippopotamodon* and *Microstonyx* are two different lineages. In Central Europe the former is associated with more closed woodland environment of Vallesian age while the latter is associated with more open country "Pikermian" faunas of latest Turolian age. JOHN BARRY (pers. commun.) reports that *Propotamochoerus hysudricus* and *Hippopotamodon* n. sp. first occur in the Potwar Plateau sequence at 10.2 Ma (equivalent to medial MN9 of Europe), however he recognized ?*Hippopotamodon* n.sp. in the Potwar Plateau at 11.3 Ma (inferred appearance at 11.4 Ma). FORTELIUS et al. (1996) report the first occurrence of *Propotamochoerus palaeochoerus* in MN8 of Western Europe while *Hippopotamodon antiquus* is earliest known from Yeni Eskihisar, Turkey (MN8) appearing first in Europe during MN9. So, our current understanding of the relevant West Asian record sug-

gests that *Propotamochoerus palaeochoerus* would appear to first occur in Europe while *Hippopotamodon* first appears in south and west Asia. It is clear that these two lineages (if indeed they are two separate lineages) are closely related and likely underwent biogeographic extensions between Europe and west and south Asia during the early Vallesian (MN9).

## Conclusions

The statistical analysis of Hungarian late Miocene suine assemblages coupled with this short overview of later Miocene suine taxonomy leads us to the following provisional conclusions about the Hungarian suine fauna:

*Propotamochoerus* (= *Korynochoerus*) *palaeochoerus* is well known from the subtropical environments of Rudabánya (MN9) and is most similar to other members of this clade in Germany. Spain may indeed have bonafide members of this species, but there also seems to be a new unrecognized species, *Propotamochoerus* (*Korynochoerus*) n. sp. with very elongate anterior premolars. There is good evidence of a pan Central European-Western European occurrence of this genus, and less evidence for the biogeographic continuity of Europe with other parts of Asia during the late middle Miocene-late Miocene interval.

*Microstonyx major* cannot be readily distinguished from *Microstonyx erymanthius* based on the Hungarian material. The MN11 locality of Csákvár has one of the smaller members of this clade, but the information at hand does not allow a species distinction. The latest Miocene localities of Polgárdi and Baltavar (MN12/13) have the same taxon which is referable to *Microstonyx major* s.l. (i.e. senior synonym of *Microstonyx erymanthius*). We suspect that *Microstonyx major/erymanthius* was a latest Vallesian immigrant from Asia or Asia Minor.

There is no record that we have uncovered of either *Hippopotamodon antiquus* or *Propotamochoerus provincialis* from Hungary. We find that *Propotamochoerus* and *Microstonyx* are distinct lineages that overlap in both time and space. *Propotamochoerus* is well represented in Central European warm temperate to subtropical forested regimes while *Microstonyx* is an index for more open country "Pikermian" woodland savanna mosaic habitats. The occurrence of *Propotamochoerus* in the latest Miocene/earliest Pliocene of Greece and the Siwaliks may serve as an environmental index at those localities: the existence of warm, equitable forest environments.

The Eurasian Miocene exhibits considerable provinciality in both time and space (BERNOR 1983, 1984, BERNOR et al. 1996, FORTELIUS et al. 1996b). This makes the possibility for a single lineage of either small or large mammal to maintain genetic continuity across

vast geographic distances for protracted periods of time unlikely. Large carnivores such as *Adcrocuta eximia* represent a notable exception to this generalization (WERDELIN & SOLOUNIAS 1996). The point to be made here is that suine cheek teeth tend to be rather conservative, while genus-level differences are more commonly recognized in skull and postcranial material when it is available (re: SCHMIDT-KITTLER 1971). The availability of this material is uncommon, and this makes synonymies of pan-Eurasian lineages, or even pan-European lineages of suine species problematical.

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