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Systematics and Chronology of the Götzendorf “*Hipparion*” (Late Miocene, Pannonian F, Vienna Basin)

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(With 12 Figures)

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A b s t r a c t

We report here a small hipparion assemblage from Götzendorf, Austria. Recent study of the Götzendorf invertebrate and vertebrate faunas, and their comparison with the Central and Eastern Paratethys assemblages, correlate this locality with late Miocene Pannonian “zone” F. Mammalian correlations based upon recent analysis of micromammal faunas and the hipparions studied here give an MN 9/10 correlation, provisionally believed to be circa 9 Ma. The Götzendorf hipparion, *Hippotherium* aff. *primigenium*, is an advanced member of the lineage, being somewhat more primitive than the MN 10 and 11 hipparions from Sümeg and Csákvár, Hungary.

Z u s a m m e n f a s s u n g

Aus der jungmiozänen Wirbeltierfundstelle Götzendorf an der Leitha, NÖ., wird eine kleine Hipparionpopulation beschrieben. Es handelt sich um einen evoluierten Vertreter von *Hippotherium* aff. *primigenium* v. MEYER. Die vorliegende Art steht auf einer etwas niedrigeren Entwicklungsstufe als die Hipparionen der Säugetierzonen MN 10 und 11 von Sümeg und Csákvár in Ungarn, aber auf einem höheren Niveau als das *Hippotherium primigenium* s.str. aus den Fundstellen der “Zonen” D–E des Pannon (Säugetierzone MN 9). Nach den bisherigen Untersuchungen an Vertebraten- und Evertrebratenfaunen liegt die Fundstelle stratigraphisch im jüngeren Pannon (“Zone” F nach PAPP) und nach der Säugetierstratigraphie im Vallesien, an der Grenze der Zonen MN 9–10.

I n t r o d u c t i o n

The Austrian vertebrate locality of Götzendorf is late Miocene age and has yielded a diverse vertebrate fauna including the advanced hominoid primate, *Dryopithecus brancoi* (ZAPFE 1988, 1989, RÖGL & al. in press; ZAPFE in progress).

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Because of its faunal content and stratigraphic position, the Götzendorf locality has raised considerable controversy concerning its correlation to European MN zones (sensu MEIN 1989) and chronology (sensu STEININGER & al. 1989). Further resolution of these controversies will lead to significant refinements in Central European later Miocene correlations (BERNOR & al. in progress). The Götzendorf fauna currently appears to be closely correlative with the Central Paratethys Pannonian F "zone", and the European MN9/10 biochronologic unit (sensu FAHLBUSCH 1991) boundary.

An introduction to Götzendorf's history of investigations, regional geology and stratigraphic problems is given by RÖGL & al. (in press). Since RÖGL & al. (in press) is published in the German language, essential aspects of the history and geology will be distilled here.

Acknowledgements

The most informative large mammal specimens from Götzendorf have been found by a private collector, Mr. Hans SCHWENGERSBAUER (Mannersdorf am Leithagebirge). We are most grateful to him for lending us his collection for study and description, and for his help during the field campaigns which took place between 1988 and 1990. BERNOR wishes to acknowledge generous financial support from the Alexander Von Humboldt Stiftung for critical research leading to the interpretations published here. BERNOR also wishes to gratefully acknowledge the L.S.B. Leakey Foundation, National Geographic Society, the National Science Foundation and Professor Dr. Siegfried RIETSCHEL, Director of the Staatliches Museum für Naturkunde, Karlsruhe, for supporting field work and museum research related to the European Neogene Program. We thank Drs. Laszlo KORDOS and David BEGUN for reviewing this manuscript and offering many useful comments which improved it.

Abbreviations and Definitions

NHMW	Naturhistorisches Museum, Wien
RLB	preceding specimen numbers indicates private collection; RLB is BERNOR's initials, 91 in each assignment means observations made in year 1991.
M	indicates measurement number conforming to EISENMANN & al.'s (1988) standardized measurements (unless otherwise indicated)
Ma	Megannum, millions of years ago
mm	millimeters
tx	maxillary cheek tooth
tm	mandibular cheek tooth
a1ph2	anterior 1st phalanx II
a3ph3	anterior 3rd phalanx III
cal	calcaneum

hipparionine or hipparion – any horse with an isolated protocone of the maxillary premolar and molar teeth and, as far as known, tridactyl feet, including species of the following genera: *Hipparion*, *Neohipparion*, *Nannippus*, *Cormohipparion*, *Hippotherium*, *Proboscoidipparion*, "*Sivalhippus*", *Cremohipparion*, *Pseudhipparion* and "*Eurygnathohippus*" (= *Stylohipparion*). Characterizations of these taxa can be found in MACFADDEN (1984), BERNOR & HUSSAIN (1985), WEBB & HULBERT (1986), HULBERT (1987), and BERNOR & al. (1989).

"*Hipparion*" – hipparionine horses that belong to different lineages than those listed above, or which cannot be readily placed within a particular lineage.

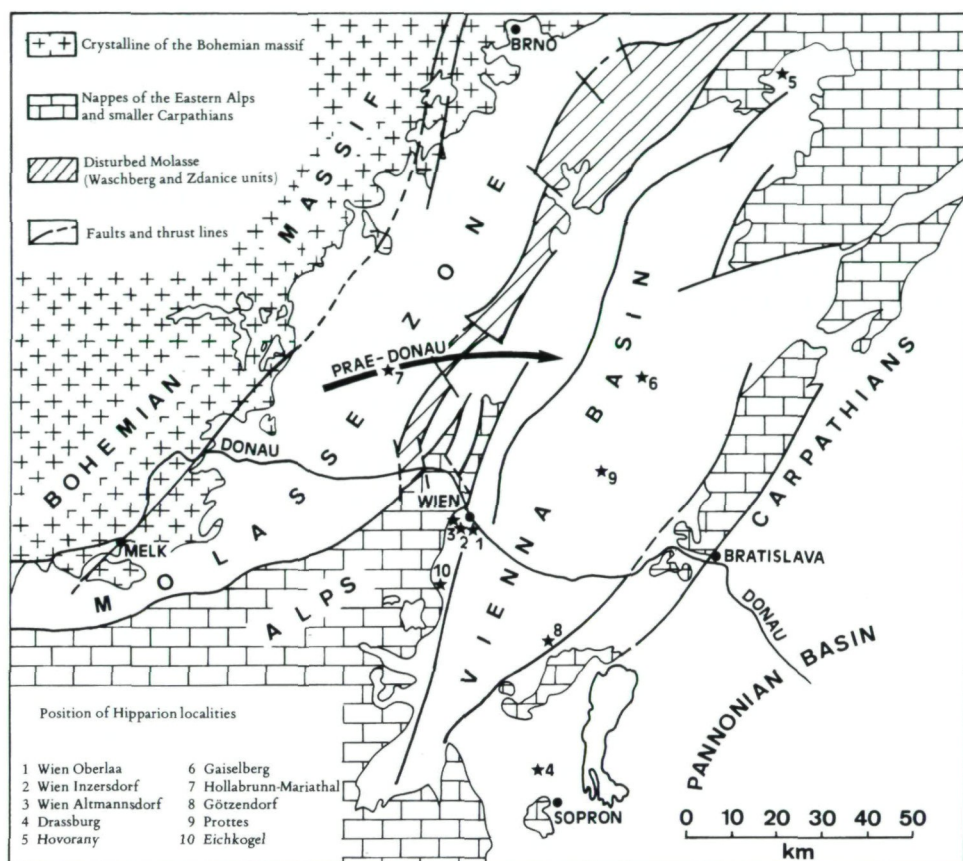


Fig. 1: Vienna Basin: Pannonian age mammal localities and structural geology (from BERNOR & al. 1988).

The Götzensdorf Locality, Geology and Stratigraphical Problems

The Götzensdorf locality has been misnamed since the earliest investigations on molluscs by PAPP (1951, 1953) and SAUERZOPF (1953), reptiles by BACHMAYER & MLYNARSKI (1977) and small mammals by BACHMAYER & WILSON (1984). The actual locality is a sand pit in the village of Sandberg, near the Leitha River and east of Götzensdorf. Sandberg belongs to the township of Mannersdorf am Leithagebirge, Lower Austria (Fig. 1). Although we correct this misnomer here, we retain the locality name Götzensdorf for historical continuity.

According to R. ROETZEL (Geological Survey, Vienna), the fossil-bearing unit represents a flood event. The sediment consists of a sand, silt and gravel mixture with interbedded clay clasts. Aquatic and terrestrial molluscs as well as vertebrate remains are found intermixed within this horizon. Vertebrate fossils are generally

worn and rolled, indicating their transport from a distal depositional community. The Götzendorf flood sediments are stratigraphically succeeded by fine-grained cross-bedded fluvial quartz sands.

Within the younger Miocene portion of the Vienna Basin sequence is a well recorded change of the aquatic environment (comp. STEININGER 1977). The marine middle Miocene Badenian deposits are directly succeeded by a Sarmatian reduced marine facies, with strongly developed molluscan and ostracod faunal endemism. Endemicity continued during the succeeding Pannonian stage, with progressive reduction of salinity (3–1 ‰). Paleogeographically, the Pannonian environment was restricted to the Pannonian Basin and its satellite basins located along the inner arc of the Alpine-Carpathian Mountain Range. In the adjacent peripheral Dacian Basin, and basins continuing to the east as far as the lake of the Aral area, the Sarmatian s.s. (as characterized and defined in the Vienna Basin) ecofacies continues into Pannonian time. The continuity of Eastern Paratethys Sarmatian facies into a Pannonian correlative time has caused confusion and controversy when attempting correlations between the Central and Eastern Paratethys sequences (Fig. 2).

The Central Paratethys Pannonian s.s. facies is characterized by the evolution of the endemic bivalves *Congeria* and *Lymnocardium*, and the gastropod *Melanopsis*. *Congeria*s finally become extinct in the Vienna Basin at the end of Pannonian “zone” F (PAPP 1948). In the succeeding stratigraphic units (“zones” G and H), sedimentation becomes limnofluvial and terrestrial. From this time onward, correlation to the Pannonian Basin, and even moreso to the Eastern Paratethys basins, becomes problematic in the succeeding Pontian stage.

The Vienna Basin’s late Miocene Pannonian and Pontian sediments have principally been subdivided by molluscan stage-of-evolution, which is partly comparable at the species level with the Hungarian Pannonian Basin (e.g. FUCHS 1875, FRIEDL 1937, STEVANOVIC 1985). A letter designation for stratigraphic subdivision was established by PAPP (1948, 1951) for the brackish-endemic Pannonian sedimentation and the succeeding fresh water beds. The stratigraphic position of the sediments younger than the *Congeria subglobosa* zone, or zone E of PAPP, has been alternatively included within either the Pannonian or Pontian stages (PAPP & al. 1974).

In terms of Vienna Basin stratigraphy, the Götzendorf locality is correlative with the *Congeria neumayri* / *Congeria zahalkai* zone, or “zone” F of PAPP. Since the latest compilation of the Pannonian stage (PAPP & al. 1985), “zone” F was referred to the Pontian. BACHMAYER & WILSON (1985) provisionally ranked Götzendorf as being MN10 based on small mammal stage-of-evolution. Current small mammal correlations under study by DAXNER-HÖCK, provide an MN9/10 correlation (RÖGL & al. in press). The hipparion stage-of-evolution we report here has proven to be congruent with RÖGL & al.’s determination.

STEVANOVIC & al. (1990) established a correlation between the Pannonian Basin and the Eastern Paratethys in the early Pontian stage based upon the immigration of molluscs and ostracods from the Pannonian Basin into the Dacian

ABSOLUTE AGES M. Y.	EPOCHS	STAGES		PANNONIAN - PONTIAN BIOZONATION		PAPP - "ZONES"	MAMMAL - AGES						
		MEDITERRANEAN	PARATETHYS		VIENNA BASIN			PANNONIAN BASIN					
			CENTRAL	EASTERN									
4	Pliocene	Zanclean	Dacian	Kimmerian	?		Ruscinian						
5													
5,3		Messinian	5,6	5,4				"Prosodacna" vutskitsi = Prosodacnomya - Zone					
6	Pontian		Pontian										
6,5							Turolian						
7	Late Miocene	Tortonian	Pannonian	Maeotian	Viviparus - Zone	Congeria balatonica / Lymnocardium decorum - Zone		H					
8													G
9										Congeria neumayri / C. zahalkai - Zone	Congeria unguilacprae / Melanopsis pygmaea - Zone	F	
10										Congeria subglobosa - Zone	Congeria subglobosa - Zone	D - E	
11										Congeria partschi - Zone	Congeria hoernesii / C. partschi - Zone	C	
11,0										Congeria hoernesii - Zone	Congeria ornithopsis / Melanopsis impressa - Zone	A/B	
12	Middle Miocene	Serravallian	Sarmatian	Sarmatian s.l.			Astaracian						
13													
14													

Fig. 2: Correlation Chart of the Late Miocene in the Vienna and Pannonian Basins (acc. RÖGL & al., in press).

and Euxinian basins. STEVANOVIC (1951, 1985) has correlated the *Congeria zahalkai* and *C. ungulacaprae* zone with the early Pontian in the Dacian Basin using the limnocyprids *Pseudoprosodacna* and *Pseudocatillus*. In contrast to this approach, MÜLLER & MAGYAR (1992 and in press) base their correlations on the bivalve evolutionary lineage *Lymnocardium* – *Prosodacnomya*. They argue that the first occurrence of *Prosodacnomya* is a distinct evolutionary step, and time equivalent in the Pannonian and Dacian basins, ca. 7 Ma. It is at this tie-point where we hope to solve a number of problems associated with Pannonian and Pontian correlation.

The MN 11 Hungarian locality of Tihany-Feherpart lies within Pannonian stratigraphic levels containing *Lymnocardium decorum* (ca. 8–7 Ma). The MN 13 Hungarian locality of Hatvan is positioned above the Pontian *Prosodacnomya vutskitsi* beds (6.4–6.0 Ma; MÜLLER & MAGYAR 1992), and is therefore younger than 6 Ma. If these correlations prove to be accurate, we estimate the Pannonian/Pontian boundary to be circa 7 Ma. This boundary is radioisotopically well developed in Crimea (CHUMAKOV & al. 1988).

With these correlations in mind, the Pannonian has a much longer chronological range than previously believed. The *Congeria zahalkai* and *C. ungulacaprae* zones are below the *Prosodacnomya* FAD, and therefore still Pannonian age. This also shows that all of the late Miocene Vienna Basin “zones” F to H are not correlative with the Pontian, but rather correlate to the late Pannonian stage in the Pannonian Basin. Therefore, the Austrian mammal localities of Götzendorf (MN 9/10), Kohfidisch (MN 10) and Eichkogel (MN 11) are all Pannonian age.

Methods

We use a combination of discrete character states and continuous metric measurements in identifying hipparionine species and assessing their phylogenetic relationships. Definition and use of discrete characters which we have adopted for the skull and mandible has developed, and been progressively refined, by WOODBURN & BERNOR (1980), BERNOR & HUSSAIN (1985), BERNOR (1985), BERNOR & al. (1988, 1989) and BERNOR & LIPSCOMB (1991 in review). Investigations of postcranial anatomy and functional morphology has been developed from TOBIEN (1959), SONDAAR (1968) and HUSSAIN (1971). Measurements follow those prescribed by the American Museum of Natural History International Hipparion Conference, 1981, are recorded in millimeters, and are amply illustrated and explained in EISENMANN & al. (1988). Data was entered into, and sorted, using dBase IV and statistically compared to other members of the “*Hippotherium*” *primigineum* evolutionary lineage (sensu BERNOR & LIPSCOMB in review) using Systat 5.03. Dbase IV and Systat 5.03 are licensed to BERNOR through the Smithsonian Institutions, Department of Paleobiology, Washington D.C. 20560.

Systematic Paleontology

Order Perissodactyla OWEN, 1848

Suborder Hippomorpha WOOD, 1937

Superfamily Equoidea HAY, 1902

Family Equidae GRAY, 1821

Subfamily Equinae STEINMANN & DÖDERLEIN, 1890

Hippotherium aff. *primigenium* VON MEYER, 1829

Referred Specimens: RLB9113, rt. txP3; RLB9114, rt. txP3; RLB9115, rt. txdP3; RLB9112, rt. txP4; RLB9111, lt. txM2; NHMW 1990/27/1, rt. txM2; RLB9116, lt. tmP4; RLB 9133, scapula articular surface fragment; RLB9131 distal tibia fragment; RLB9130, calcaneum fragment; NHMW 1990/27/3, 1st phalanx II or IV; RLB9132, distal 2nd Phalanx III fragment; RLB9117, 3rd phalanx III; NHMW 1990/27/2, 3rd phalanx III.

Geographic Range: Central Paratethys Bioprovince sensu RÖGL & STEININGER 1983 and BERNOR & al. 1988.

Diagnosis of *Hippotherium primigenium* s.s from Eppelsheim and the Pannonian D and E of the Vienna Basin (after BERNOR & al. 1988): A large hipparionine horse with moderate length snout; nasals retract maximally to just anterior to P2; preorbital bar long (46–57 mm), with anterior extent of lacrimal placed more than one-half the distance from the anterior orbital rim to the posterior rim of the fossa; preorbital fossa subtriangular shaped and anteroventrally oriented, deeply pocketed posteriorly, with great medial depth, medial wall lacking internal pits, peripheral border outline strong with a prominent anterior rim; nasal notch well anterior to txP2; cheek teeth relatively low crowned, in middle stage-of-wear adults, txP2–txM3 length dimension usually between 155 mm and 165 mm, fossette ornamentation complex, pli caballins bifid or complex, hypoglyphs deeply incised, protocones usually lingually flattened and labially rounded and txP2 anterostyle elongate; middle wear adult mandibular cheek teeth usually with well developed protostylids either present at occlusal level or on side of tooth, pre- and postflexids often with complexly plicated enamel margins, metaconids usually rounded, metastylids maybe rounded to somewhat square-shaped, metastylid spurs often occur on premolar teeth in earlier wear, linguaeflexids shallow to V-shape in premolars, may be deeper and more U-shaped in molars, ectostylids may be found not only in deciduous dentition, but primitive populations may only very rarely have ectostylids present on side of crown in latest stage-of-wear permanent dentition, protoconid enamel band usually well developed and a closed round structure; metapodials are generally short and rather robust, metacarpals have flattened distal sagittal keels, and the facet for the hamate/magnum articulation is rather low (120 to 130 degrees).

Description: The Götzendorf fauna includes a small sample of hipparion skeletal elements. Included are six maxillary cheek teeth, a mandibular

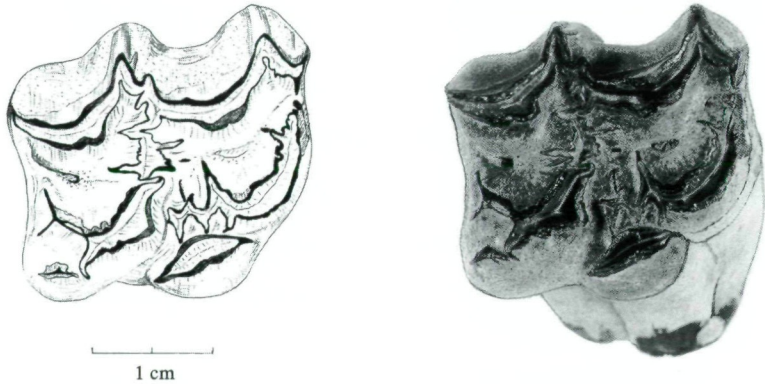


Fig. 3a: Line drawing of right upper premolar (txP3, RLB 9113), occlusal view.

Fig. 3b: Photograph of right upper premolar (txP3, RLB 9113), occlusal view.

cheek tooth, fragmentary scapula, distal tibia, calcaneum and four phalangeal fragments. Recent work on Central European later Neogene hipparionines provide us the data base to make detailed morphologic and morphometric comparisons.

There are two adult maxillary txP3's: RLB9113 (Fig. 3a, b) and RLB9114



Fig. 3c: Photograph of right upper premolar (txP3, RLB 9114), occlusal view.

(Fig. 3c). RLB9113 is in a very early stage-of-wear, and has the pre- and postfossette patterns poorly developed. The pli caballins (Fig. 3b) are beginning to show their complexity, and the protocone is very elongate and labiolingually compressed. RLB9114 lacks its labial wall, but preserves pertinent occlusal morphology. The protocone is small and lingually flattened, being much shorter than that of RLB9113, due to its more advanced wear. The occlusal enamel pattern has a bifid pli caballin and complex plications of the pre- and postfossettes and a very deeply incised hypoglyph.

There is also a fragmentary deciduous txdP3, RLB9115. This specimen is of a young foal, with only the anterior portion of the tooth showing any wear. The protocone is small, lingually flattened and labially rounded. The pli caballin is clearly bifid.

Fig. 4a compares Götzendorf RLB9113 occlusal crown length (M1) versus occlusal crown width (M3) to a 95% confidence ellipse for the Höwenegg hipparions (BERNOR, HAYEK & TOBIEN in preparation; note RLB9114 does not preserve the M3 dimension), and a broad sample of late Miocene Austrian and Hungarian hipparions. All txP3 shown here fall within the Höwenegg ellipse and reflect their overall close size similarity.

Fig. 4b compares the two adult txP3's (RLB9113, RLB9114) protocone length (M10) versus protocone width (M11). RLB9113, the young individual, has its

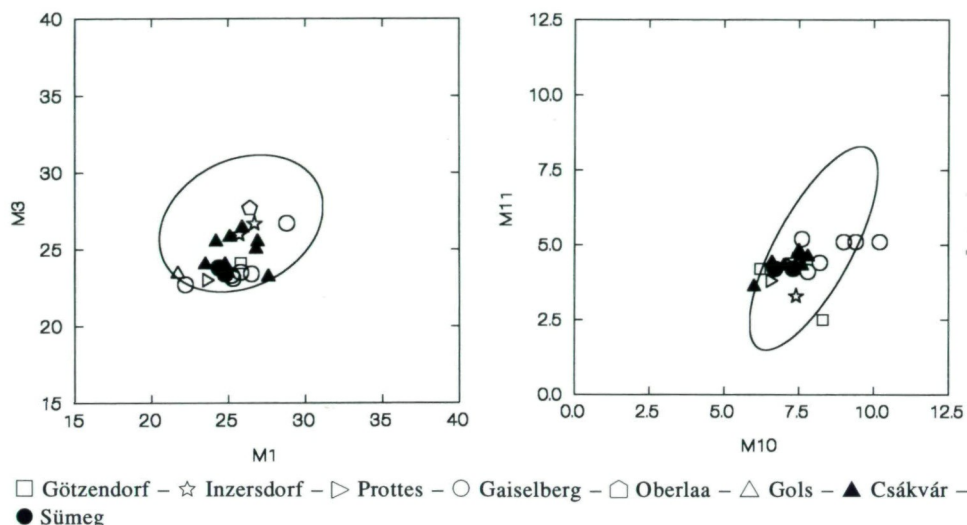


Fig. 4a: Bivariate plot of txP3: M1 (occlusal crown length) versus M3 (occlusal crown width). The encircled area here, and in ensuing figures below, represents the 95% confidence ellipse for *Hippotherium primigenium* based on the Höwenegg sample (BERNOR, HAYEK & TOBIEN in press). Götzensdorf (n = 1) is found within the ellipse, as is Gaiselberg (n = 6), Inzersdorf (n = 2), Oberlaa (n = 1), Gols (n = 1), Prottes (n = 1), Csákvár (n = 8) and Sümege (n = 2).

Fig. 4b: Bivariate plot of txP3: M10 (protocone length) versus M11 (protocone width). Götzensdorf (n = 2) with one specimen on the outer border of the Höwenegg ellipse (9114) and one specimen slightly outside of the ellipse with an elevated M10 dimension (9113). Gaiselberg (n = 6) 5 specimens within the ellipse and one outside the ellipse with an elevated M10 dimension; Inzersdorf (n = 2) two specimens within the ellipse; Prottes (n = 1) one specimen within the ellipse; Csákvár (n = 6) 5 specimens within the ellipse and 1 on the border of the ellipse; Sümege (n = 2) both within.

length dimension (M10) somewhat elevated compared to the width dimension (M11), giving a bivariate dimension just outside the ellipse. Quite to the contrary, RLB9114 has a relatively greater width (M11) and lesser length (M10), giving it a bivariate dimension which falls on the left border of the Höwenegg ellipse. All other hipparions considered in this sample fall within the Höwenegg 95% ellipse except for one specimen from Gaiselberg.

There is a single txP4, RLB9112 (Fig. 5), derived from a juvenile individual in early-middle wear. The protocone is elongate and subtriangular shaped with a flattened lingual border. The pre- and postfossettes have deeply incised plis, and the pli caballin has an asymmetrically bifid morphology. The hypoglyph is so deeply incised that it nearly encircles the hypocone. Fig. 6a shows that RLB9112 has a low occlusal width dimension (M3) compared to the Höwenegg

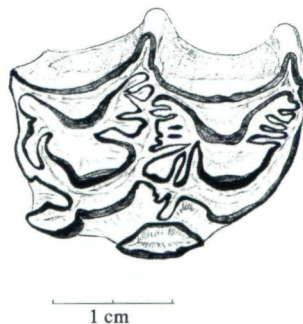
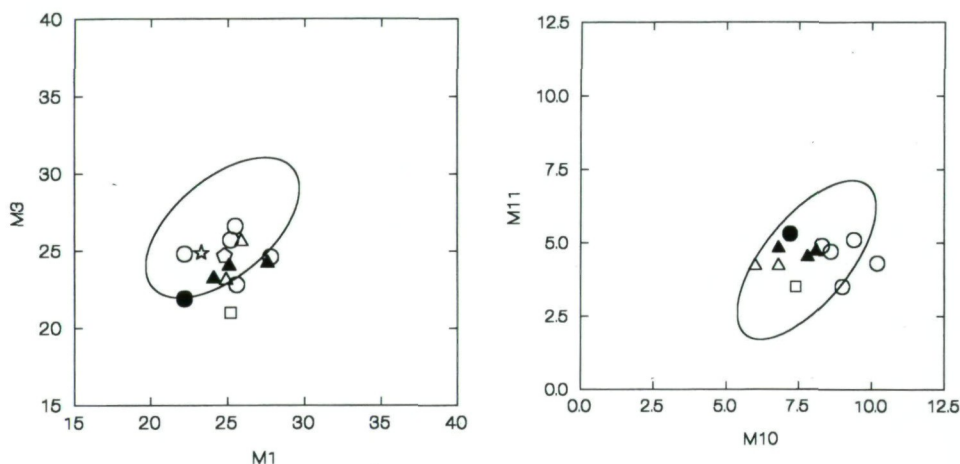


Fig. 5: Line drawing of right upper premolar (txP4, RLB 9112), occlusal view.



□ Götzendorf – ☆ Inzersdorf – ○ Gaiselberg – ◇ Oberlaa – △ Gols – ▲ Csákvár – ● Sümeg

Fig. 6a: Bivariate plot of txP4: M1 (occlusal crown length) versus M3 (occlusal crown width). Götzendorf's (n = 1) one known specimen has this bivariate dimension falling outside the Höwenegg 95% ellipse. Gaiselberg (n = 5) has 3 specimens within the ellipse and 2 specimens on the outside border of the ellipse; Inzersdorf (n = 1) has its one specimen occurring within the Höwenegg ellipse; Oberlaa (n = 1) has its one specimen occurring within the ellipse; Gols (n = 2) has its two specimens falling within the ellipse; Csákvár (n = 3) has two specimens falling within the ellipse and 1 specimen falling slightly outside the ellipse; Sümeg (n = 1) has one specimen on the edge of the ellipse with small values of M1 versus M3.

Fig. 6b: Bivariate plot of txP4: M10 (protocone length) versus M11 (protocone width). Götzendorf (n = 1) has one specimen found within the Höwenegg ellipse; Gaiselberg (n = 5) has 3 specimens found within the ellipse, one on the border of the ellipse (elevated protocone length = M10) and one outside the ellipse (elevated M10); Gols (n = 2) has both specimens within the ellipse; Csákvár (n = 3) has all specimens with the ellipse; Sümeg (n = 1) has its one specimen within the ellipse.

sample, giving it a bivariate dimension (M1 versus M3) well outside the Höwenegg ellipse, and indeed being the lowest of all other txP4's yet sampled. Fig. 6b reveals that RLB9112's protocone length (M10) versus width dimension (M11) falls well within the Höwenegg 95% ellipse. Of the sample considered, the Gaiselberg txP4's have one individual on the ellipse border, and another outside the Höwenegg 95% confidence ellipse. BERNOR & al. (1988, 1989) have noted that the somewhat elevated length and elongate oval shape of the Gaiselberg hipparions are characters that reflect a close phylogenetic relationship with North American *Cormohipparion occidentale*, the likely sister-taxon of all Old World hipparionine horses (BERNOR & LIPSCOMB in review).

There are two txM2's, RLB9111 (Figs. 7a,b) and NHMW 1990/27/1 (Figs. 7c, d). RLB9111 is in early wear and its occlusal pattern reveals a mediolingually compressed, triangular-shaped protocone with a flattened lingual wall. Pre- and postfossettes are beginning to show complexity, but the pli caballin is undeveloped. The hypoglyph is beginning to come into wear, and here can be seen to be a linear enamel feature on the posterolingual surface of the tooth. NHMW

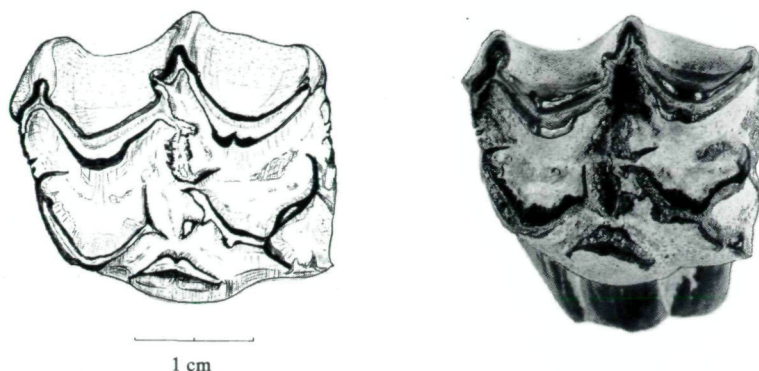


Fig. 7a: Line drawing of left upper molar (txM2, RLB 9111), occlusal view.

Fig. 7b: Photograph of left upper molar (txM2, RLB 9111), occlusal view.

1990/27/1 is in a slightly more advanced stage-of-wear. The protocone is still elongate, and the lingual border is nearly flattened. The pre- and postfossettes are clearly more developed in their complexity, and the pli caballin is bifid. The hypoglyph is clearly developed and so deeply incised that it surrounds the hypocone.

Fig. 8a is a bivariate plot comparing Götzendorf txM2 occlusal crown length (M1) versus width (M3) with the Höwenegg sample, and a number of other Austrian and Hungarian later Miocene hipparionines. Both Götzendorf specimens fall within the Höwenegg ellipse. Of the entire sample considered here, only the Austrian “Pontian” locality of Prottes falls outside the Höwenegg 95% confidence

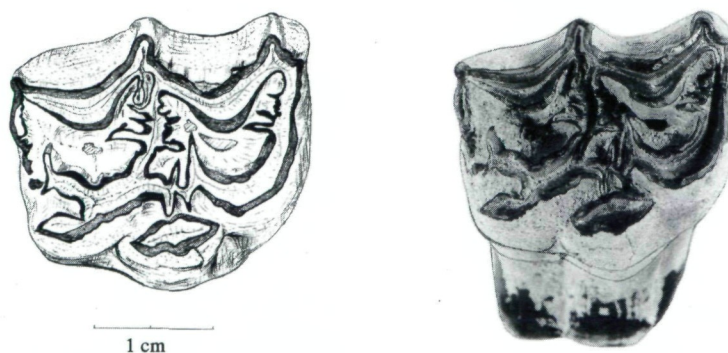


Fig. 7c: Line drawing of right upper molar (txM2, NHMW 1990/27/1), occlusal view.

Fig. 7d: Photograph of right upper molar (txM2, NHMW 1990/27/1), occlusal view.

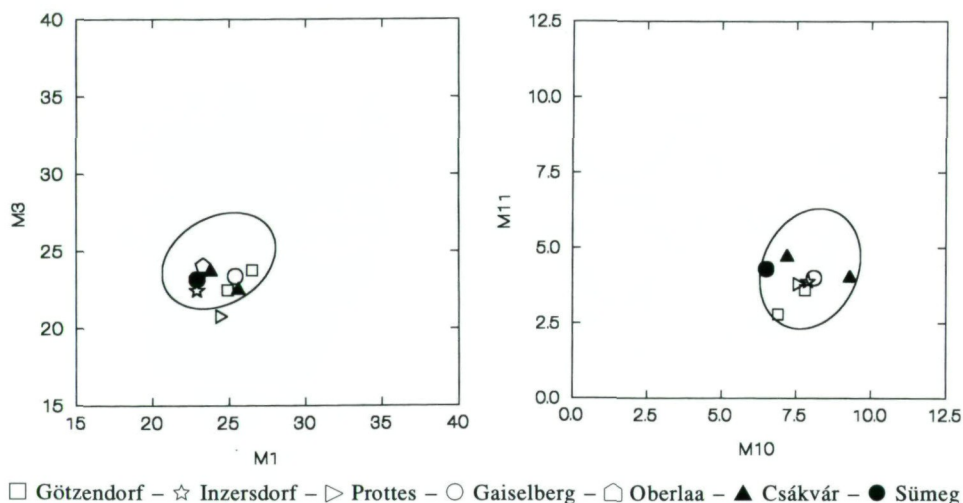


Fig. 8a: Bivariate plot of txM2: M1 (occlusal crown length) versus M3 (occlusal crown width). Götzendorf ($n = 2$) has both specimens within the ellipse; Gaiselberg ($n = 1$) has its one specimen within the ellipse; Inzersdorf ($n = 1$) has its one specimen within the ellipse; Oberlaa ($n = 1$) has its one specimen within the ellipse; Prottes ($n = 1$) has its one specimen just outside the ellipse with reduced $M1 \times M3$ measurements; Csákvár ($n = 2$) both specimens are found within the ellipse; Sümeg ($n = 1$) has its one specimen found within the ellipse.

Fig. 8b: Bivariate plot of txM2: M10 (protocone length) versus M11 (protocone width). Götzendorf ($n = 1$) both specimens are found within the ellipse. Also found within the Höwenegg 95% ellipse are: Gaiselberg ($n = 1$); Inzersdorf ($n = 1$); Prottes ($n = 1$), Csákvár ($n = 2$) and Sümeg ($n = 1$).

ellipse. Fig. 8b, protocone length versus protocone width, has both Götzendorf specimens, and indeed the entire sample under consideration, falling inside the Höwenegg 95% confidence ellipse.

The tmP4, RLB9116 (Figs. 9a, b), is an important specimen for determining the Götzendorf horse's stage-of-evolution. The occlusal pattern is distinguished by a metaconid and metastylid that are not rounded as in the most primitive members

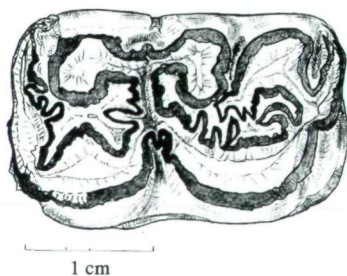
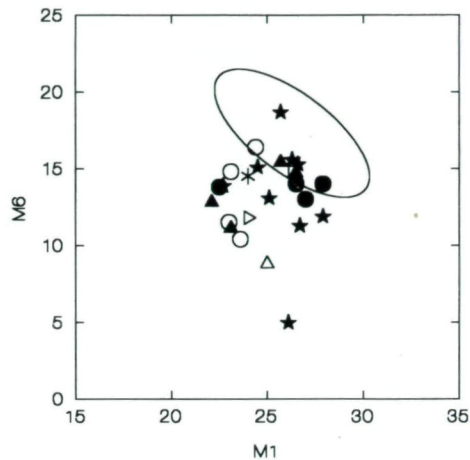
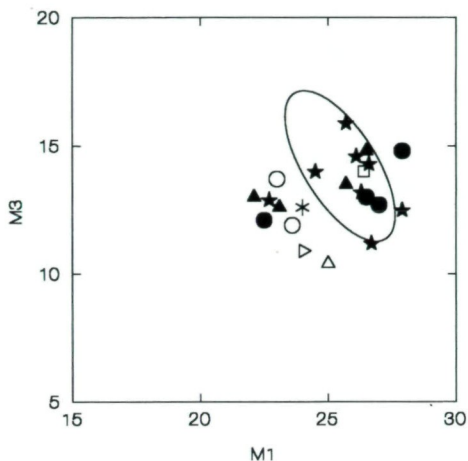
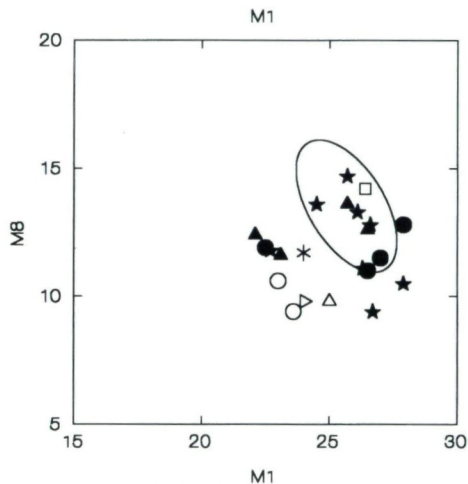


Fig. 9a: Line drawing of left lower premolar (tmP4, RLB 9116), occlusal view.

Fig. 9b: Photograph of left lower premolar (tmP4, RLB 9116), occlusal view.



□ Götzendorf – ▷ Prottes – ○ Gaiselberg –
△ Gols – * Meidling – ▲ Csákvár – ● Sümeg –
★ Rudabánya



sharply reduced M1 dimension; Csákvár (n = 4) has 2 specimens within the ellipse and 2 outside the ellipse with reduced values of M1; Sümeg (n = 4) has 2 specimens within the ellipse and 2 outside of the ellipse, one with elevated values of M1 and one with reduced values of M1.

Fig. 10b: Bivariate plot of tmP4: M1 (occlusal crown length) versus M6 (mid-crown width across the lingualflexid-ectoflexid). Götzendorf (n = 1) is found within the ellipse; Gaiselberg (n = 4) one specimen within the ellipse and 3 outside the ellipse with reduced values of M1 (2 also with reduced values of M6); Wien-Meidling (n = 1) one specimen with its M1 dimension reduced just outside the ellipse; Gols (n = 1) with its one specimen's M6 dimension well below the ellipse; Prottes (n = 1) specimen with reduced M6 outside ellipse; Rudabánya (n = 9) 3 specimens within the ellipse, 6 outside ellipse including one with sharply diminished M6 dimension; Csákvár (n = 4) two specimens within the ellipse and 2 specimens outside the ellipse having reduced M1 × M6 dimensions; Sümeg (n = 4) one specimen within the ellipse, one on lower border and two outside ellipse.

Fig. 10c: Bivariate plot of tmP4: M1 (occlusal crown length) versus M8 (occlusal crown width across metaconid/protoconid). Götzendorf (n = 1) is found within the ellipse; Gaiselberg (n = 2) has both individuals with sharply lower M1 versus M8 dimensions; Wien-Meidling (n = 1) has a lower M1 value than the Höwenegg horse; Gols (n = 1) has a lower M1 × M8 dimension; Prottes (n = 1) has a lower M1 × M8 dimension; Rudabánya (n = 8) has 4 individuals found within the ellipse, one on the lowermost border of the ellipse, one outside the ellipse with a sharply diminished M1 value and 2 other specimens outside the ellipse with diminished M8 values; Csákvár (n = 3) has 2 specimens within the ellipse and one specimen outside the ellipse with a reduced M1 value; Sümeg (n = 4) has one specimen within the ellipse, one on the lower border of the ellipse (reduced M8 value), one just outside the ellipse (increased M8 value) and one well outside the ellipse (reduced M1 value).

of *Hippotherium primigenium*, nor squared as is typical of more advanced forms. Rather, they have acquired an irregular, nearly kidney-shape morphology: the metaconid's distolabial border has been abbreviated by the expanded posterior surface of the preflexid, while the metastylid's proximolabial and distolabial borders have become restricted giving it a "waisted" morphology (see particularly the photo, Fig. 9b). Accompanying this derived metaconid-metastylid morphology is the unusually elongate isthmus connecting the metaconid/metastylid. The presence of a metastylid spur in this specimen is a character shared by members of the Central European *Hippotherium primigenium* evolutionary lineage (BERNOR & al. 1989; BERNOR & LIPSCOMB in review). The preflexid and postflexid borders are very complex, and again are indicative of an advanced stage-of-evolution of this taxon. Unlike primitive members of the *Hippotherium primigenium* evolutionary lineage, protostylid is very small and only faintly delimited, and restricted to the side of the crown; it would have never been presented on the occlusal surface. In its composite morphology, the tmP4 suggests that the Götzendorf hipparion was relatively advanced when compared to older Vallesian members of the *Hippotherium primigenium* evolutionary lineage.

A bivariate plot of tmP4 occlusal crown length (M1) versus metaconid/metastylid length (M3; Fig. 10a) places the Götzendorf specimen within the 95% confidence ellipse for the Höwenegg sample. Note that several Austrian and Hungarian specimens fall outside of this plot, and there does not appear to be a consistent, statigraphically based bias for bivariate distributions [localities include: Gaiselberg (lower MN9), Meidling (MN9), Gols (upper MN9), Prottes (MN11?), Rudabánya (upper MN9), Csákvár (MN10), Sümeg (MN11)]. A bivariate plot of occlusal crown length (M1) versus midcrown width (M6; Fig. 10b), again places the Götzendorf specimen inside the Höwenegg 95% ellipse,

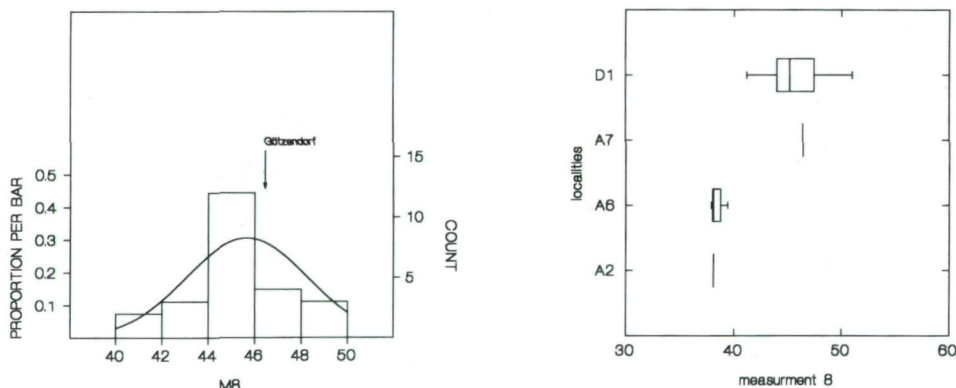


Fig. 11a: Univariate plot of Höwenegg tibia M8 (distal maximum depth) distribution indicating where the Götzendorf specimen falls.

Fig. 11b: Univariate "Box-and-Whisker's" plot of tibia M8 (distal maximum depth). Götzendorf (A7; $n = 1$) is found to fall within the center of the interquartile range of Höwenegg (D1; $n = 25$); Gaiselberg (A2; $n = 1$) and Prottes (A6; $n = 3$) fall below the range for Höwenegg (= within the inner fences, or $1.5 \times QI$ for Höwenegg here).

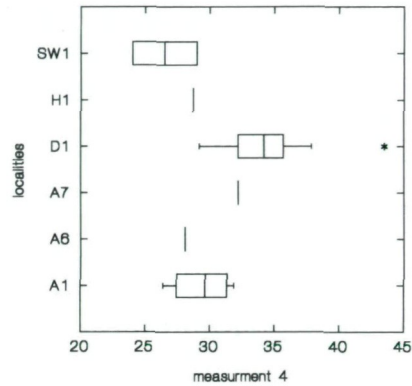
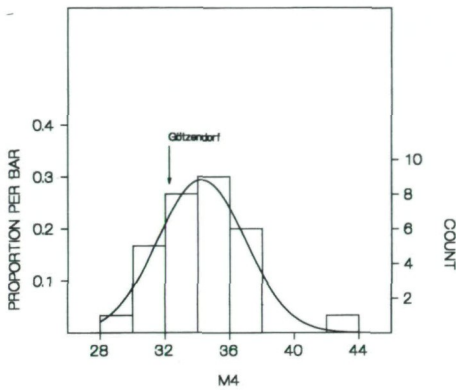


Fig. 12a: Univariate distribution of calcaneum M4 (mediolateral breadth of calcaneum tuber). Arrow indicates the point where the Götzendorf specimen falls.

Fig. 12b: Univariate "Box-and-Whisker's" plot of calcaneum M4 (mediolateral breadth of calcaneum tuber). Götzendorf (A7; $n = 1$) lies at the lower portion of the Höwenegg (D1; $n = 32$) interquartile range. Note that the Höwenegg sample has one value (indicated *) above the outer fence. SW1 (Charmoille; $n = 2$), H1 (Rudabánya; $n = 1$) and A6

(Prottes; $n = 1$) fall below the interquartile range and the values within the lower inner fence of Höwenegg). A1 (Inzersdorf; $n = 4$) and Götzendorf overlap the lower inner-fence range of the Höwenegg sample.

Fig. 12c: Bivariate plot of calcaneum M4 (mediolateral width of calcaneum tuber) versus M5 (anteroposterior depth of calcaneum tuber). Götzendorf ($n = 1$) is found within the ellipse; Inzersdorf ($n = 4$) 1 specimen is found within the ellipse and 3 specimens are found outside the ellipse with reduced values for M4 (2 individuals) and M5 (2 individuals; one of which has reduced both M4 and M5 dimensions); Prottes ($n = 1$) has reduced dimensions of $M4 \times M5$; Rudabánya ($n = 1$) has reduced dimensions of $M4 \times M5$; Csákvár ($n = 2$) has one specimen occurring within the ellipse and one just outside the lower border of the ellipse.

while several Vallesian and Turolian samples fall outside this range. Finally, a bivariate plot (Fig. 10c) of $tmP4$ occlusal crown length (M1) versus occlusal crown width (M8; taken across the metaconid/protoconid), again places the Götzendorf specimen within the Höwenegg ellipse, while several Austrian and Hungarian specimens fall outside the ellipse.

Of the postcranial elements that occur at Götzendorf, the tibia and calcaneum are the only elements which we believe to have morphometric significance. Fig. 11a presents a frequency distribution of Höwenegg tibia distal maximum depth (M8), indicating the place where the Götzendorf (NHMW9131) specimen's measurement for this variable ($= 46.4$ mm) falls; this is quite near the mean ($= 45.0$) and median ($= 44.9$) for Höwenegg. Fig. 11b gives a "Box-and-Whisker's" plot of the same (M8) tibia measurement. Again, the Götzendorf specimen (A7)

can be seen to fall almost in the middle of the interquartile range (25% of all measurements on either side of mean) of the Höwenegg sample, decidedly elevated above the Gaiselberg (A2) and Prottes (A6) samples. These statistics reveal a close similarity of this dimension to the Höwenegg hipparion.

Fig. 12a presents a frequency distribution of Höwenegg calcaneum tuber mediolateral breadth (M4), indicating the place where the Götzendorf specimen's (RLB9130) measurement for this variable (= 32.2 mm) falls. In this case, the Götzendorf specimen's measurement falls somewhat below the mean (= 34.3) and median (= 33.9) of the Höwenegg sample. Fig. 12b gives a "Box-and-Whisker's" plot of the same calcaneum dimension, again showing the close size identity of the Götzendorf and Höwenegg samples. Fig. 12c is a bivariate plot of calcaneum M4 versus M5 (anteroposterior depth). The Höwenegg ellipse calculated for these dimensions is so great as to discount the use of these variables for evaluation of calcaneum size.

Table 1: Measurements of Götzendorf and Gols *Hipparion* specimens.

Specimen No.	Element	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11
NHMW 1990/27/3	a1ph2											
RLB 9117	a3ph3	52.5	20.8	31.4								
NHMW 1990/27/2	a3ph3	52.3	56.6	35.9	21.0	30.0						
RLB 9130	calc	22.4	32.2	51.9	50.1							
RLB 9131	tibia	46.4										
RLB 9116	tmP4	26.4	23.4	14.0	8.4	12.8	14.8	16.0	14.2	14.8	42.7	
NHMW 1990/27/1	txM2	24.9	21.7	22.5	24.1	48.7	2.0	5.0	2.0	1.0	7.8	3.6
RLB 9111	txM2	26.5	22.4	23.8	24.3	47.6	6.9	2.8				
RLB 9113	txP3	25.8	22.5	24.1	22.6	45.6	8.3	2.5				
RLB 9114	txP3	26.6	23.9	35.3	3.0	4.0	2.0	1.0	6.2	4.2		
RLB 9118	txP3	25.9	21.5	24.5	23.5	45.3	0.0	0.0	0.0	0.0	8.5	3.0
RLB 9112	txP4	25.2	20.6	21.0	22.6	48.5	3.0	5.0	5.0	1.0	7.4	3.5
RLB 9115	txdP3	31.7	28.2	22.4	22.8	17.2	0.0	4.0	3.0	0.0	5.7	3.7
NHMW 1970/1376/1	txdP3	29.3	25.6	21.2	22.1	16.2	4.0	4.0	3.0	1.0	4.8	3.2

Discussion

BERNOR & LIPSCOMB (in review) have recently reported the phylogenetic relationships of the Central European *Hippotherium primigenium* evolutionary lineage. These steps are as follows, with the sister-taxon being North American *Cormohipparion occidentale*:

1) Pannonian C *Hippotherium primigenium* in comparison to its sister taxon *Cormohipparion occidentale* characterized by: increased plication frequency of pre- and postfossettes; pli caballins increase in number to become consistently double; pli caballinid has increased complexity; metapodials suggest some size increase (none are complete);

2) Pannonian D-E and Eppelsheim (Lectotype locality) populations of the *Hippotherium primigenium* s.s. evolutionary lineage, are characterized by: reduction or loss of lacrimal foramen; protocone becoming shortened so that it is

lingually flattened and labially rounded; metapodials reveal size increase over *Cormohipparion occidentale* condition;

3) Nombrevilla (Spain) *Hippotherium* “*koenigswaldi*” (perhaps already established as a separate lineage, vicariant from Central European populations) has protocone losing its lingual flattening and becoming somewhat compressed-ovate; autapomorphically, pli caballins become complex and metapodials become slightly lengthened;

4) the Höwenegg population of *Hippotherium primigenium* is characterized by lower cheek tooth metaconids and metastylids having evolved to being variably rounded or square morphology;

5) the Rudabánya population of *Hippotherium primigenium* is characterized by lower cheek tooth metaconids and metastylids being variably square to irregular-shaped, and metatarsal length (M1) \times distal articular width (M10) proportions are elevated outside the 95% and 99% confidence interval range of Pannonian C–E, Eppelsheim and Höwenegg populations (BERNOR & al. in press).

6) the last step is currently in need of future study and may include more than one evolutionary stage. We believe that the Götzendorf hipparion represents the most primitive population of a lineage recorded from the late Vallesian and early Turolian localities of Gols (also Pannonian F), Kohfidisch (MN10), Sümeg (MN10) and Csákvár (MN11) (comp. Fig. 2) and others in the Vienna Basin and Pannonian Basin districts (BERNOR & MITTMANN under study). This complex of hipparions is characterized by the presence of more complicated enamel plications of the maxillary and mandibular cheek teeth, irregular shaped metaconids and metastylids, elongate isthmuses separating metaconids and metastylids, and apparent reduction of protostylids. The Götzendorf assemblage, as well as the hipparions from other localities cited here, did not strikingly depart from earlier Vallesian Central European *Hippotherium primigenium* populations, except for lengthened metapodials in the Rudabánya sample and possible shift in Götzendorf protocone proportions (M10 \times M11; may be due to early ontogenetic stage of development however).

Currently, we believe that the various assemblages we refer to stages of *Hippotherium primigenium* are those of a single evolutionary lineage recognized especially in the later stages of evolution (Rudabánya and younger) solely from the Central Paratethys bioprovince.

DAXNER-HÖCK (in RÖGL & al. in press) correlates the Götzendorf rodent fauna to the MN9/10 boundary. She has noted that the absence of murids at Götzendorf, combined with the occurrence of “*Hipparion*”, and several species of middle Miocene small mammal holdovers, is indicative of an MN 9 age. However, the Götzendorf zapodid *Eozapus* first occurs elsewhere in Europe during MN10. If we accept DAXNER-HÖCK’s correlation, the occurrence of *Eozapus* would be taken to be its lowest stratigraphic occurrence, and within uppermost MN 9. Alternatively, *Eozapus* could be taken to be a marker for basal MN10, and the lack of murids would then have to be due to ecological barriers. Given these two equally plausible

hypotheses, we retain a correlation of the Götzendorf hipparion to be near the MN9/MN10 boundary.

Conclusions

The Götzendorf hipparion is an advanced member of the *Hippotherium primigenium* s.s. evolutionary lineage (sensu BERNOR & LIPSCOMB in review). This lineage is best characterized and defined within the Central Paratethys bioprovince (BERNOR & al. 1988), but may also be found in Greece (BERNOR & al. in review). The Götzendorf "*Hipparion*" is correlative with Pannonian F and near the MN 9/10 boundary (RÖGL & al. in press). The stage-of-evolution of the Götzendorf "*Hipparion*", suggests that it was near, but not at the terminus of the *Hippotherium primigenium* evolutionary lineage. The Hungarian "*Hipparion*" faunas from Sümeg and Csákvár are more derived than Götzendorf (ca. 9 Ma; BERNOR & al., in review), and would appear to be between Götzendorf and the basal Pontian (ca. 7 Ma) in their age.

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