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The early Vallesian vertebrates of Atzelsdorf (Late Miocene, Austria)
9. *Hippotherium* (Mammalia, Equidae)

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(With 5 figures and 2 tables)

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Abstract

The *Hippotherium* sample from the Vienna Basin, Austria, represents one of the geologically oldest collections of this equid genus in the Old World. This report presents new information from the locality of Atzelsdorf, in conjunction with material previously known from Mariathal and Gaiselberg, also of Pannonian C (late Miocene) age. Whereas the number of specimens is small at some sites, collectively they show a dental morphology that is simpler and more plesiomorphic than that of *Hippotherium primigenium* from Eppelsheim or Höwenegg, Germany, and also resembles material assigned to *Cormohipparion* sp. from North America. The new Atzelsdorf specimens improve our understanding of the morphology of the taxon that represents the earliest entry of *Hippotherium* into the Old World, here allocated to *Hippotherium* sp.

Keywords: *Hippotherium primigenium*, Lake Pannon, Vienna Basin, Hollabrunn-Mistelbach Formation, *Hippotherium* Datum

Zusammenfassung

Die Hippotherium Fossilien aus dem Wiener Becken (Österreich) stellen das geologisch älteste Material dieser Pferdegattung in der Alten Welt dar. Diese Arbeit stellt die neuesten Ergebnisse basierend auf den Funden von Atzelsdorf, sowie auf weiteren Materialien aus Mariathal und Gaiselberg, vor, die allesamt ein Pannon C (Spätmiozänes) Alter aufweisen. Obwohl *Hippotherium* dort nur durch relativ wenige Stücke belegt ist, zeigen sie allesamt eine einfachere und plesiomorphere Zahnmorphologie als *Hippotherium primigenium* von Eppelsheim oder Höwenegg (beide Deutschland) und ähneln mehr *Cormohipparion* sp. aus Nord Amerika. Das neue Material aus Atzelsdorf erweitert unser Verständnis um die Morphologie dieses Taxons und wird hier als *Hippotherium* sp. beschrieben. Es repräsentiert das früheste Auftreten von *Hippotherium* in der Alten Welt.

Schlüsselwörter: *Hippotherium primigenium*, Pannon See, Wiener Becken, Hollabrunn-Mistelbach-Formation, *Hippotherium* Datum

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Introduction

BERNOR et al. (1988) reviewed the hipparions from the Vienna Basin (figs 1, 2) of early Pannonian (C-E) age, allocated it to *Hippotherium primigenium* MEYER, 1829, and suggested the presence of a lingually flattened protocone of the upper cheek teeth of these specimens signaled a phyletic relationship to *Cormohipparion occidentale* (LEIDY) 1856 of North America. WOODBURNE (2007) reviewed the *Cormohipparion occidentale* complex of hipparions, and segregated it into five species (fig. 5). WOODBURNE (2007) also reviewed hipparion specimens from the Vienna Basin as well as material from Höwenegg and Eppelsheim, Germany, classically identified as *Hippotherium primigenium* (SONDAAR 1961; BERNOR et al. 1997). WOODBURNE (2007) indicated that the *Hippotherium* material from Mariathal, Gaiselberg, Inzersdorf, and Atzelsdorf, of the Austrian Pannonian Basin, showed a morphology that apparently is more plesiomorphic than that exemplified by collections assigned to *Hippotherium primigenium*. WOODBURNE (2007) suggested that if the Austrian samples were united into a single species, that species would be separate from, and pre-date, *H. primigenium* from the German localities. The Austrian specimens are referred to here and in WOODBURNE (2007) as *Hippotheruim* sp.

As indicated by BERNOR et al. (1988) the Austrian specimens, rather than the German materials assigned to *H. primigenium*, reflect the oldest immigration of hipparionine equids to the Old World, an event commonly recognized as the *Hippotherium* Datum (e.g., WOODBURNE, 1996). It is therefore useful to provide a morphologic description of these Austrian samples and to assess the relationships of this potentially single species to the subsequent *H. primigenium* as well as to *Cormohipparion*, the likely North American progenitor of the Austrian taxon. The largest and best sample of the Austrian *Hippotherium* is recorded from Mariathal and its morphology, as well as material from Gaiselberg and Inzersdorf, is summarized here, after WOODBURNE (2007). The more plesiomorphic morphology of these samples is consistent with their older age, whereby the Vienna Basin material pre-dates *Hippotherium primigenium* from Höwenegg and Eppelsheim, as suggested in fig. 1. The sites discussed in the text are shown in fig. 2. The sample from Atzelsdorf is important because of its basal Pannonian C age, apparently similar to that of Mariathal and Gaiselberg. The Atzelsdorf material is morphologically plesiomorphic relative to some Mariathal and Gaiselberg specimens, and arguably could be somewhat older on that basis. The Atzelsdorf specimens were not available for detailed description in WOODBURNE (2007), but have since become so and are described and discussed below.

Methods

Length and width measurements on the isolated teeth are taken at the tooth occlusal surface rather than 1 cm above the base as recommended by EISENMANN et al. (1988). The tooth height is taken at the mesostyle (MSTHT; after MACFADDEN (1984)). The unworn MSTHT of the upper cheek teeth is estimated when not represented by actual specimens, so that the relative wear stage displayed by each tooth can be compared with that of other teeth. In tabs 1 and 2, the tooth ratio and protocone ratio comprise width/length. Plication counts of the upper cheek teeth follow EISENMANN et al. (1988), with a

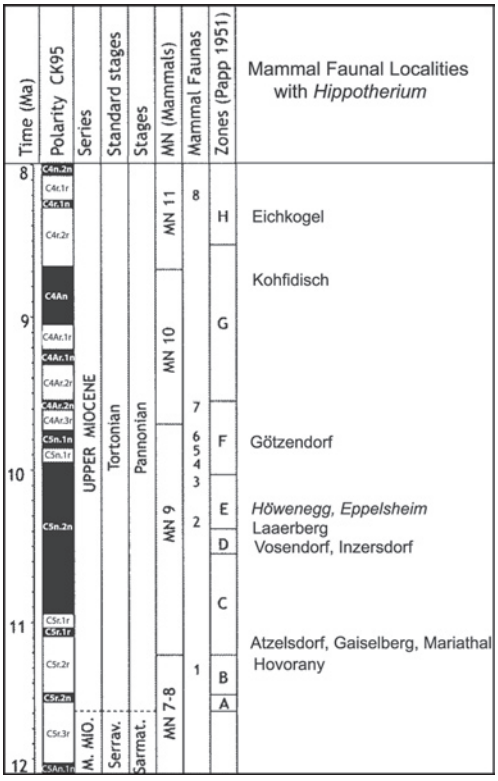

Fig. 1. Geochronology of selected *Hippotherium*-bearing sites in the Vienna Basin, modified from HARZHAUSER et al. (2004). The German sites of Höwenegg and Eppelsheim added, after SWISHER (1996).

notation such as 1;1;1;1 indicating that a single plication is present on the anterior border of the prefossette; the posterior border of the prefossette; the anterior border of the postfossette; the posterior border of the postfossette. See fig. 3L for examples of prefossette, postfossette, mesostyle, protocone, protoloph, plis caballin, hypocone, hypoconal groove; fig. 3B for pli protoconule. Fig. 4 shows that the protostylid, exemplified in p4 and m3, extends from the anterior base of the tooth toward its crown at the anterolabial corner of the tooth. The ectoflexid is shown in fig. 4A. Fig. 1 indicates that Atzelsdorf, Gaiselberg and Mariathal are essentially of the same age.

This study endeavors to make comparisons between adult wear stage specimens of the various samples. In general it appears from WOODBURNE (2007) that the interval of adult morphology ranges from about 20 % to 60 % wear. The beginning of the adult condition reflects the development of a fully expressed morphologic pattern, and appears to be associated with the presence of a bifurcate lingual-most pli on the anterior and posterior surfaces of the pre- and postfossettes (see P3 and P4 in fig. 3C and 3D for examples). These teeth have a MSTHT of about 32 mm, or about 40 % wear. For samples in which there is a relatively complete representation of this wear range, the advent of the bifurcate lingual-most pli on the anterior part of the prefossette corresponds closely with the development of a full plication count for all fossette borders, and the change from the condition of a bifurcate lingual-most pli of both anterior and posterior borders of the pre- and postfossettes to a condition in which the pattern is clearly simplified (only

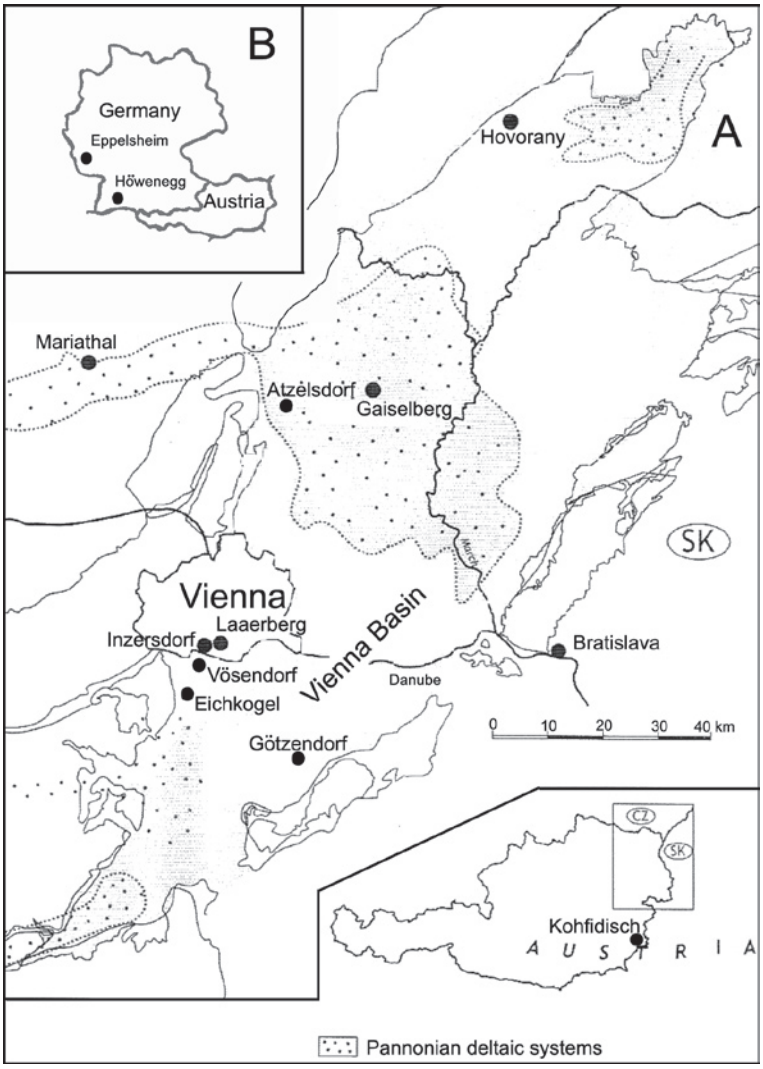

Fig. 2. Map of selected parts of the Vienna Basin and Germany, showing the location of *Hippotherium*-bearing sites discussed in the text. **A**. Main part of the Vienna Basin. **B**. Höwenegg and Eppelsheim,Germany. Based in part on fig. 2 in HARZHAUSER et al. (2004).

single plis at this position) heralds the transition to a senile wear condition. In samples that are well represented, such as P4 in the Mariathal collection for example, there are fourteen adult teeth, seven in a juvenile stage, and two that are senile. The adult interval embraces a range of 29 % to 55 % wear (WOODBURNE, 2007: tab. 22). In the following descriptions mean protocone ratios, mean plication counts, and mean pli caballin numbers are derived from the adult segment of the tooth population unless otherwise stated.

Abbreviations

HLMD	Hessisches Landesmuseum, Darmstadt, Germany
LACM	Natural History Museum, Los Angeles County, California
NHMW	Naturhistorisches Museum, Vienna, Austria
PIUW	Paläontologisches Institut, Universität Wien, Vienna, Austria
SMF	Senckenberg Museum, Frankfurt, Germany

Systematic Palaeontology

Family Equidae GRAY, 1821

Genus *Hippotherium* VON MEYER, 1829

Hippotherium sp.

M a t e r i a l : The *Hippotherium* material from Atzelsdorf described here belongs to the private collection of P. SCHEBECZEK (Pellendorf), but casts of all specimens are housed and inventoried at the Natural History Museum of Vienna. R: right, L: left, P/M: upper premolar/molar, p/m: lower premolar/molar.

The specimens are all isolated upper and lower cheek teeth, as follows: NHMW 2008z0062/0005, RP2; NHMW 2008z0062/0001, RP3; NHMW 2008z0062/0006, RP4; NHMW 2008z0062/0003, RM1; NHMW 2008z0062/0011, RM1; NHMW 2008z0062/0002, RM2; NHMW 2008z0062/004, Pp2; NHMW 2008z0062/0009, Lp4; NHMW 2008z0062/0012, Lp4; NHMW 2008z0062/0010, Rm2; NHMW 2008z0062/0007, Lm3; NHMW 2008z0062/0008, Rm3. During this study I was graciously supplied with casts and photographs of this material. Table 1 indicates that specimens allocated as p4 were documented by photographs only.

L o c a l i t y & a g e : The *Hippotherium* material is derived from the locality of Atzelsdorf, Lower Austria, located about 35 km NE of Vienna and geologically situated in the Vienna Basin (fig. 2). The deposits of the Atzeldorf site belong to the Hollabrunn-Mistelbach Formation – delta deposits, which have been discharged by the palaeo-Danube into Lake Pannon during the Late Miocene. According to HARZHAUSER et al. (2004) the Atzelsdorf section is correlated with the base of Pannonian Zone C (fig. 1), and is thus about 11.2-11.1 Ma old. See also the discussion by HARZHAUSER in this volume. Specimens from Gaiselberg and Mariathal (fig. 2) also are reviewed here. As indicated in fig. 1 these sites also correlate to Mammal Neogene (MN) zone 9, after DAXNER-HÖCK (1996) and HARZHAUSER et al. (2004).

D e s c r i p t i o n : Fig. 3 and table 1 indicate that the upper dentition of the Atzelsdorf samples is comprised of isolated teeth that pertain to P2 – M2, with un-illustrated specimens recognized as p2, m2 and m3. The nearly unworn Rm2, NHMW 2008z0062/0010, is about 50 mm tall at the metaconid (tab. 1) which suggests that p2 and m3 would have

Tab. 1. *Hippotherium* sp., Atzelsdorf, Austria; measurements (in mm).

	Specimen			Tooth			Protocone				Plication	Pli	Hypoconal	Remarks
Toot		S	Ht	Lth.	Wdth.	Rat	Lth	W	Rat.	Shape	index	caballin	groove	
P2	NHMW S106	R	21	-	23a	--	-	--	--	ovate	6;9;4;3	1	open,	Unworn MSTHT ca 45;
	0062/0005													ca 50% wear
P3	NHMW S22	R	6a	24,0	23.0	0.9	7.0	6.0	0.86	subcirc	1;10;5;2	3	narrow	Very late wear stage;
	0062/0001													ca 90% wear
P4	NHMW S107	R	32	23.6	22.0	0.9	8.3	4.0	0.48	ovate	5;11;8+;4	2	open,	Unworn MSTHT ca 55;
	0062/0006												narrow	ca 40% wear
M1	NHMW S103	R	18	23.7	23.2	0.9	8.7	5.2	0.60	ovate	4;9;8;2	1	open,	Unworn MSTHT ca 55;
	0062/0003												narrow	ca 65% wear
M1	NHMW S110	R	33	22.8	---	---	---	---	---	---	6;9;9;1	---	open	Unworn MSTHT ca 55;
	0062/0011													ca 40% wear
M2	NHMW S24	R	32.5	22.1	---	---	---	---	---	---	4;9;6;1	---	---	Unworn MSTHT ca 55;
	0062/0002													ca 40% wear
p2	NHMW S104	L	29.6	30	12.3									Strong ectoflexid; no pro-
	0062/0004													tostylid; ca 34% wear
m1	NHMW S23	L	15.2	20.4	13.2									Strong ectoflexid; proto-
	0062/0009													stylid present; ca 70% wr.
m1	NHMW S102	L	18.7	---	15.0									Strong ectoflexid; ca 63%
	0062/0012													wear; photo only.
m2	NHMW S25	R	50+*	27.0	11.2									Nearly unworn; protostyl-
	0062/0010													id ?present; occlusal
														pattern not developed
m3	NHMW S141	L	45*	27.0a	9.5									Nearly unworn; protostyl-
	0062/0007													id in lower 1/3 crown
m3	NHMW S142	R	39.5*	25.6	10.4									Protostylid in lower 1/3;
	0062/0008													not at occlusal surface; ca
														13% wear

Notes

S = side; Ht. = height; Lth. = length; Wdth. = width; Rat = ratio; W = width; subcirc = subcircular

For all specimens, complete notation is (for example) NHMW2008zS106 0062/0005. To save space, 2008z is not repeated here.

* = height at metaconid (paraconid unavailable)

Based on nearly unworn m2, upper molar unworn MSTHT likely 55 mm.

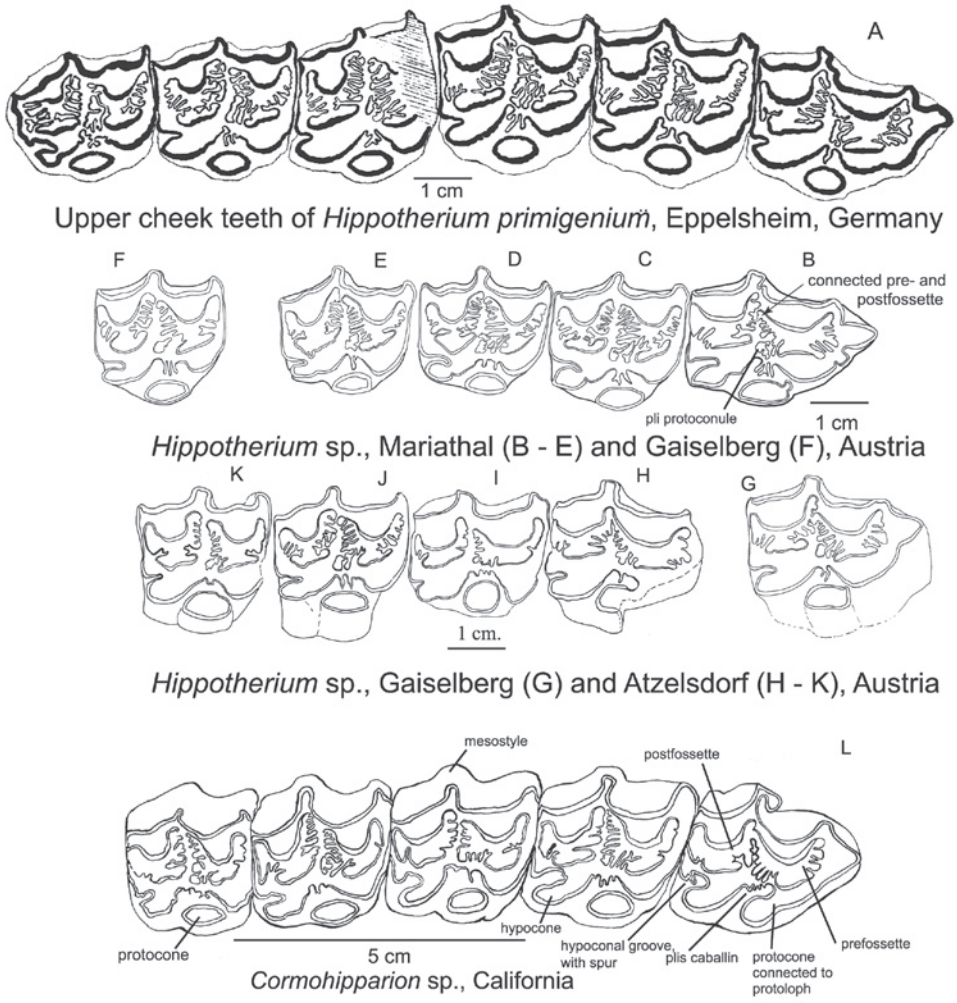

Fig. 3. Upper cheek tooth dentitions of *Hippotherium*. **A**. *Hippotherium primigenium*, Eppelsheim, Germany. HLMD Din. 1081, reversed. **B-E**. *Hippotherium* sp., Mariathal, Austria**. B**, PIUW 3540/3, LP2, reversed. **C**, PIUW 35403540/9, LP3, reversed. **D**, PIUW 3540/54, LP4, reversed. **E**, PIUW 3540/136, RM1 **F-G**. *Hippotherium* sp., Gaiselberg, Austria. **F**. NHMW 0024/26, RM2. **G**. NHMW 00224/19, RP2. **H-K**. *Hippotherium* sp., Atzelsdorf, Austria. **H**, NHMW 2008z0062/0005, RP2. **I**, NHMW 2008z0062/0001, RP3. **J**, NHMW 2008z0062/0006, RP4. **K**, NHMW 2008z0062/0003, RM1. **L**. *Cormohipparion* sp., California, RP to M2, LACM 150080. **A**. after SONDAAR (1961, fig. 12A)**. B-F** and **L** after WOODBURNE (2007, fig. 25). **G-K** original, based on photographs.

been about 45 mm tall (as in Lm3, NHMW 2008z0062/0007). In table 1, the unworn MSTHT for P2 is estimated at 45 mm, comparable with that of m3; the unworn MSTHTs for P3-M2 are estimated as 50 mm, comparable to the nearly unworn metaconid height of m2. The lower cheek teeth otherwise show no especial traits.

The dimensions of P2 are shown in table 1. In that the MSTHT of this specimen is only about 21 mm, it appears to be at about 50 % occlusal wear. The ovate shape of the protocone is clearly evident (fig. 3H), although its anterior edge is broken away. Even at about 50 % wear, the tooth displays a relatively complex fossette plication pattern (6;9;4;3) which could have been somewhat more complex in earlier (but still mature) wear stages. The fact that the protocone is connected to the protoloph at this wear stage likely is important, as is the fact that the pre- and postfossettes are confluent labially, rather than being isolated as in the other upper cheek teeth. The single pli caballin is unusual for this tooth, to judge from other samples of *Hippotherium* sp. from Austria (tab. 2).

As indicated in table 1, P3 is in very late (90 %) wear, so its simple plication count (1;10;5;2), at least as regards the anterior and posterior borders of the prefossette, and the posterior border of the postfossette, likely reflects that condition, as does the extremely ovate shape of the protocone and the shallow hypoconal groove. The fact that the protocone still is isolated at this extremely late stage of wear heightens the difference in protocone connection as shown in P2. The persistence of three plis caballin is common for P3 in these Vienna Basin teeth (tab. 2).

P4 (fig. 3J) displays a very complex enamel pattern, compatible with its approximately 40 % (adult) stage of wear. The plication count of 5;11;8+; 4 appears comparable to samples of the early Pannonian C interval of the Vienna Basin (tab. 2), and the presence of two plis caballin and a simple hypoconal groove is compatible with other material.

Remarks ►
*** = ages in Ma
H. koenigswaldi. P2 pre- and postfossettes ?rarely confluent ** = personal observation
Hippotherium primigenium
Höwenegg. P2 pre- and postfossettes rarely confluent
Eppelsheim; HLMD. P2 pre- and postfossettes rarely confluent
Eppelsheim; SMF. P2 pre-and postfossettes rarely confluent
Hippotherium sp.
Inzersdorf. * = single specimen
Mariathal. P2 pre- and postfossettes confluent; M2 juvenile
Gaiselberg. P2 pre- and postfossettes confluent
Atzelsdorf. P2 pre- and postfossettes confluent

Cormohipparion
Punchbowl Formation. * = single specimen. P2 pre- and postfossettes confluent

Notes
MSTHT refers to unworn mesostyle height of upper cheek teeth, P2-M2
Prot. ratio is protocone width/length ratio
Plication index is number of plications for the anterior border of the prefossette; posterior border of prefossette; anterior border of postfossette; posterior border of postfossette
Pli cab. is pli caballin
HLMD is Hessisches Landesmuseum, Darmstadt
SENK is Senckenberg Museum, Frankfurt
C, D, and E are Pannonian Zones, Vienna Basin, Austria
C. skinneri is a single specimen
XMas is Xmas Quarry, Nebraska. Ma ages for *Cormohipparion* are derived from WOODBURNE (2007)

Tab. 2. *Hippotherium* and *Cormohipparion*; summary dental statistics.

Species/Site/Age***	MSTHT	P2				P3				P4				M1				M2			
		Prot. ratio	plication index	pli cab.	N	Prot. ratio	plication index	pli cab.	N	Prot. ratio	plication index	pli cab.	N	Prot. ratio	plication index	pli cab.	N	Prot ratio	plication index	pli cab.	N
H. koenigswaldi																					
10.7	65-62**	0.67	9;6;5;4			0.60	10;12;9;3		35**	0.55	6;10;8;3		24**	0.54	4;10;9;4		26**	0.50	5;10;9.3		18**
Hippotherium primigenium																					
Höwenegg 10.3	45-52	0.56	9;12;12;4	5	3	0.44	8;12;9;3	4	3	0.50	9;12;11;3	5	3	0.51	8;12;10;5	4	3	0.41	6;10;7;4	4	3
Eppelsheim HLMD	49-58	0.67	7;10;11;2	2	2	0.57	6;10;9;3	3	10	0.58	7;12;9;4	3	14	0.60	7;12;9;3	3	7	0.51	6;14;10;3	4	2
Eppelsheim SENK	45-58	0.67	7;10;10;3	2	6	0.65	8;14;11;5	4	4	0.87	5;13;10;4	3	4	0.72	8;15;8;5	4	4	0.60	5;11;8;5	3	2
Hippotherium sp.																					
Pannonian																					
Inzersdorf* D/E	40-50	0.76	5;8;7;3	3	1	0.45	6;7;7;2	3	1	0.49	6;8;5;4	2	1	0.57	8;12;9;3	3	1	0.48	6;7;7;6	2	1
Mariathal C	44-56	0.56	8;9;6;3	3	7	0.60	8;9;6;3	3	5	0.51	6;13;9;3	2	14	0.50	6;11;9;3	3	9	0.47	4;10;6;6?	2	1
Gaiselberg C	50-55	0.56	4;10;6;3	2	3	0.68	6;9;8;3	3	2	0.41	6;12;6;?1	3	1	0.57	4;8;6;2	2	2	0.55	5;11;8;2	3	3
Atzelsdorf 11.2 C	?50		6;9;4;3	1	1	0.86	1;10;5;2	3	1	0.48	5;11;8+;4	2	1	0.60	5;9;9;1	1	2		4;9;6;1		1
Cormohipparion																					
Punchbowl Fm.,																					
Calif; * ca 11.5	?45-50	0.79	4;6;4;2	4	1	0.65	3;15;4;2	4	1	0.65	3;9;5;1	2+	1	0.59	1?;13;8;3	2	1	0.58	3?;8.6?;2	3	1
C. johnsoni 12-12.4	36-45	0.76		1	2	0.53	1;4;4;1	2	2	0.57	1;6;5;1	3	2	0.50	1;6;6;1	1	2	0.50	0;6;8;1	1	2
C. merriami 12-12.4	45-55	0.67	4;5;4;1	1	3	0.50	1;7;4;1	3	3	0.47	3;8;5;1	3	3	0.51	1;6;6;1	1	3	0.53	2;8;5;1	1	3
C. fricki 11.9-11.3	50-55	0.50	2;5;4;1	2	6	0.43	3;9;5;1	2	6	0.43	2;7;4;2	2	6	0.48	2;7;8;2	1	6	0.43	2;7;5;1	1	6
C. skinneri 11.2-10.5	?60	0.50	5;5;2;1	2	1	0.35	3;7;4;1	2	1	0.41	1;8;5;1	1	1	0.45	1;5;6;1	1	1	0.39	1;6;5;1	1	1
C. matthewi 11.1-10	40-45	0.49	3;8;6;2	2	4	0.44	6;8;6;2	3	4	0.45	2;7;4;1	3	4	0.53	2;8;6;1	1	4	0.47	3;7;5;1	1	4
C. occidentale; XMas 11.1-10	50-66	0.52	6;8;5;3	2	7	0.45	5;10;8;2	2	8	0.45	6;9;7;2	3	7	0.48	4;8;7;2	2	8	0.44	4;8;6;2	2	8

M1 (fig. 3K and tab. 1; NHMW 2008z0062/003) is at or even below the lower range of adult wear (about 65 %). It shows a somewhat diminished plication count (4;9;8;2) at the anterior border of the prefossette and posterior border of the postfossette, at least, and the apparently single pli caballin might have been double in earlier wear. The protocone is ovate; the hypoconal groove simple. Another M1 (NHMW 2008z0062/0011) is missing the lingual part of the tooth, but was in earlier wear (40 %; tab. 1). The plication count (6;9;9;1) is compatible with this stage of wear, possibly except for the posterior border of the postfossette. Table 2 shows a combined plication count of 5;9;9;2 for these specimens.

A similarly incomplete M2 (NHMW 2008z0062/002), and in a similar stage of wear (tab. 1), shows a plication count of 4;9;6;1.

R e s u l t s : The upper cheek tooth dentition of the limited *Hippotherium* sample from Atzelsdorf suggests that the unworn MSTHT ranged from about 45-50 mm in P2-M2; the protocone was connected to the protoloph at least by 50 % wear in P2; the protocones of all teeth were ovate to semicircular at various stages of wear (never lingually flattened). Except for P2, plis caballin tended to be more complex in premolars than in molars. By about 40 % wear, P4, at least, tended to have slightly more complex fossette plications than M1 or M2. The sole P2 shows that the pre- and postfossettes are confluent labially, rather than being separate, as in the other upper cheek teeth.

As shown in table 1, elements of the lower dentition range in wear stage from about 70 % to virtually unworn. In the latter case, NHMW 2800z0061/0010, Rm2, is about 50 mm tall at the metaconid. This condition likely reflects the unworn crown heights of the upper and lower cheek teeth, except for the first premolar and the last molar in the series, which would be about 5 mm lower crowned, to judge from other hipparionine taxa (Woodburne 2007). There appears to be little to distinguish the lower teeth preserved here from others referred to *Hippotherium* sp. or *H. primigenium*. Table 1 indicates that, except for p2, protostylids are present on all lower cheek teeth examined after a certain amount of occlusal wear. In the little worn m3s, NHMW 2008z0062/0007 and NHMW 2008z0062/0008, the enamel pattern does not display a protostylid (fig. 4B), but remnants of the structure indicate that this feature would be present after about 20 % wear. Protostylids are generally present in species of *Cormohipparion* where the lower dentition is known (Woodburne 2007), as well as in the Gaiselberg sample (Bernor et al. 1988) of *Hippotherium* sp. and specimens of *H. primigenium* and *H. koenigswaldi* Sondaar, 1961 (Bernor et al. 1997), among others.

Species nomenclature

As shown in fig. 3, the Atzelsdorf *Hippotherium* is similar to the sample from Mariathal and Gaiselberg, especially when similar wear stages are compared (Atzelsdorf and Mariathal P4 at about 40 % wear). Table 2 indicates that the *Hippotherium* sp. samples are comparable in unworn MSTHT values, plis caballin, and general plication complexity. These samples are also different from those of *Hippotherium primigenium* in being overall simpler and less complex, as also summarized above and in Woodburne (2007). The Atzelsdorf material adds to these comparisons and is consistent with them. Although the evidence is suggestive of a single species of *Hippotherium* being represented

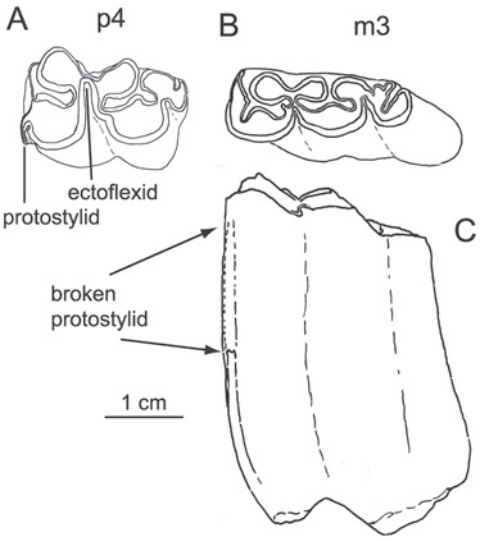

Fig. 4. Lower cheek teeth of *Hippotherium* sp. from Atzelsdorf. **A**. Occlusal view of NHMW 2008z0062/0009, Lm1. **B**. Occlusal view (reversed) of NHMW 2008z0062/0008, Rm3. **C**. Labial view (reversed) of **B**. Scale bar equals 1 cm.

in the samples from Atzelsdorf, Gaiselberg, Mariathal, and Inzersdorf, this taxon is not formally named here. One reason for caution is the small size of the samples from Atzelsdorf, Gaiselberg, and Inzersdorf. An intriguing aspect of the morphology of P2 is the connection of the protocone to the protoloph in relatively early wear in the Atzelsdorf sample (as compared with its continual isolation until latest wear in P3; tab. 1, fig. 3), and the similarity in that regard to the single specimen of *Cormohipparion* sp. from California (fig. 3L). As indicated above, one of fifteen specimens of P2 in the sample from Mariathal shows an otherwise unusual connection of the protocone and protoloph at about 49 % wear. Whereas this clearly is an isolated occurrence in the Mariathal sample (and also does not occur in the three P2s from Gaiselberg), the frequency of such a connection in the Atzelsdorf (and *Cormohipparion* sp.) populations is unknown. The presence of this morphology being recorded in the only known P2s of these two samples might appear to be representative, rather than due to happenstance, but this cannot be determined at the present time. It also cannot be determined now whether, with better samples, this and other features of the Atzelsdorf and *Cormohipparion* sp. populations, such as the broadly open P2 pre- and postfossette confluence, could result in their being recognized at a specific level distinct from the samples from Mariathal, Gaiselberg, and Inzersdorf. At this time, the evidence promotes caution in assuming that all five of these samples represent a single paleospecies. Similarly, caution prevents a formal specific designation for the material here allocated as *Hippotherium* sp. relative to that allocated to *Hippotherium primigenium*.

Comparisons with other samples

Table 2 summarizes dental parameters of a number of species samples of *Hippotherium* and *Cormohiparion*, from WOODBURNE (2007) and fig. 3 illustrates representative upper cheek teeth from Gaiselberg, Mariathal, and Höwenegg. Except for the senile P4 (fig.

3I), all of these specimens are in adult wear (about 45 % wear) and show isolated protocones in P2 as well as the other cheek teeth. The protocones are ovate in shape, which is the norm for these samples, and in that context the dentition from Mariathal is virtually the same as that from Gaiselberg. As discussed in WOODBURNE (2007) the purported lingually-flattened protocones attributed by BERNOR et al. (1988) to the Gaiselberg sample are, in fact, largely artifacts of ontogenetically young wear stages, and in any case not fundamental to the morphology of that population.

In table 2 it is clear that the HLMD sample from Eppeslheim is the largest for *H. primigenium*, whereas the Mariathal specimens comprise the largest of the Austrian samples. In general the unworn MSTHTs of the upper cheek teeth in the Austrian samples of *Hippotherium* sp. seem to be slightly lower than for *H. primigenium*, but the difference apparently is slight. The pre- and postfossettes are in most cases more complex in adult wear in *H. primigenium* from Höwenegg and Eppelsheim than for the Mariathal or other Austrian samples of *Hippotherium* sp., as is the case also for plis caballin. The following description of the upper cheek teeth from Gaiselberg, Mariathal, Eppelsheim and Höwenegg is based on WOODBURNE (2007).

The Mariathal, Gaiselberg, and Atzelsdorf samples of *Hippotherium* sp. consistently show that the pre- and postfossettes are confluent in P2, although the connection is stronger in the Atzelsdorf and Gaiselberg specimens than in those from Mariathal. Fig. 3B displays the very fine-scale confluence of the pre- and postfossettes in the Mariathal sample, which is consistent in that population. This type of pre- and postfossette confluence also is found in limited numbers of the *Hippotherium primigenium* samples from Eppelsheim, but is absent in those from Höwenegg. In the present context, the open style of pre- and postfossette confluence in the Atzelsdorf and Gaiselberg samples is similar to that seen in *Cormohipparion* sp. (figs 3G, H, and L).

As discussed in WOODBURNE (2007) the sample from Gaiselberg displays unworn upper cheek teeth MSTHTs in the range of 50 mm. P4 and M1 may have been 55 mm tall. P2 is represented by three adult-wear specimens (38 % to 58 % wear), with a mean protocone ratio of 0.56 (demonstrated in specimens to be ovate to slightly flattened lingually; fig. 3G). The mean plication count is 4;10;6;3; there is an average of two plis caballin. The protocone is isolated from the protoloph at least until 58 % wear.

P3, also with an unworn MSTHT of about 50 mm, is represented at Gaiselberg by two adult (29 % and 56 % wear) and two senile teeth (68 % wear). The mean adult protocone ratio is 0.68 (slightly ovate to ovate in specimens); the mean plication count is 6;9;8;3; there is an average of 3 plis caballin. The protocone remains isolated from the protoloph at least to 68 % wear.

In the Gaiselberg P4 (unworn MSTHT about 55 mm.), a single adult tooth (20 % wear) shows a plication count of 6;12;6;?1; a mean protocone ratio of 0.41 (slightly flat lingually); and 3 plis caballin.

M1 (unworn MSTHT about 55 mm – comparable to that of P4) is represented at Gaiselberg by two adult teeth (42 % and 55 % wear), one young individual (18 % wear) and one much older (65 % wear; protocone still isolated). The mean plication count is 4;8;6;2; mean pli caballin count is 2; mean protocone ratio is 0.57 (slightly concave lingually in specimens).

For M2 (unworn MSTHT about 50 mm.), three adult Gaiselberg specimens range from 36 % to 50 % wear, have a mean plication count of 5;11;8;2, a mean protocone ratio of 0.55 (oval to slightly concave lingually in specimens). The protocone is still isolated at 50 % wear. There are 2 plis caballin.

In the Gaiselberg upper cheek teeth, the pli protoconule tends to be a single large loop, but commonly shows one or a few extra plications.

P2 in the Mariathal collection has an unworn MSTHT of about 44 mm. It is represented by ten specimens, of which seven (tab. 2) have an adult morphology, and range from 25 % to 49 % wear. The pre- and postfossettes are confluent labially. The mean protocone index in the adult condition is 0.56 (oval to slightly oval with one specimen with a lingually flat protocone). The Mariathal sample records the P2 protocone being separated from the protoloph to at least 64 % wear (with one exception in ten specimens at 49 % wear). The mean pli caballin count is 3. The mean plication count is 8;9;6;3.

P3 is represented by fifteen Mariathal specimens, of which five show an adult morphology (41 % to 46 % wear; unworn MSTHT about 55 mm.). The ovate to slightly ovate protocone (one juvenile specimen has a lingually flat protocone at 28 % wear) has a mean ratio of 0.60. It is separate from the protoloph until at least 71 % wear. There is a mean of 3 adult plis caballin. The mean plication count is 8;9;6;3.

P4 is represented by 23 specimens at Mariathal, of which fourteen have an adult morphology (39 % to 61 % wear; unworn MSTHT about 56 mm.). The slightly ovate protocone has a mean ratio of 0.51 (tab. 2). One juvenile specimen at 18 % wear; one adult specimen at 27 % wear, and one senile specimen at 68 % wear has a lingually flat protocone. The protocone is separate from the protoloph at least as late as 68 % wear. There is a mean of 2 plis caballin. The mean plication count is 6;13;9;3.

M1 is represented by seventeen Mariathal specimens, of which nine have an adult morphology (range from 22 % to 47 % wear). The unworn MSTHT is about 55 mm. The mean adult protocone ratio is 0.50 (slightly ovate to ovate). Two juvenile specimens (14 % and 19 % wear), and two adult (33 % and 38 % wear) have a lingually flat protocone. The protocone is separate from the protoloph at least as late as 72 % wear. The mean pli caballin count is 3; plication count is 6;11;9;3 (tab. 2).

M2 is represented only by four specimens at Mariathal, none of which is an adult. In juvenile (12 %) wear, the plication count is 4;10;6;6. The protocone ratio (tab. 2) is 0.47 (slightly oval).

In summary, the Gaiselberg and Mariathal *Hippotherium* sp. upper cheek tooth morphology ranges in unworn MSTHT from about 50 – 56 mm (Mariathal P2 likely is 44 mm tall). In P2 the pre- and postfossettes are consistently confluent, and mean plication counts about 6;10;6;3. This is slightly more complex than in the Atzelsdorf material (tab. 2), which also has one less pli caballin (but is based on a single specimen). In P3 (as in all other upper cheek teeth, with minor exception at a given juvenile, adult, or senile wear stage) the pre- and postfossettes are separated; mean plication count is about 7;9;7;3. In P4, the mean plication count was about 6;12;8;3, and also likely comparable to the population represented by the Atzelsdorf single specimen. For M1, the mean plication count likely was about 5;10;8;3, and for M2 about 5;11;8;3.

Specimens of *Hippotherium primigenium* from Eppelsheim at the HLMD indicate that the unworn MSTHT of P2 is about 50 mm, with the mature range of morphology shown between 34 % to 52 % wear. The pre- and postfossettes are confluent in four of twenty-two specimens (18 %), and the protocone, subovate to ovate in shape, remains isolated at or very nearly the base of the crown. The mean plication index of mature wear individuals is 7;11;10;4 (tab. 2), more complex than the Vienna Basin materials. The Höwenegg sample is even more complex and has many more plis caballin (tab. 2).

In P3, the unworn MSTHT is estimated as about 52 mm, with the adult morphology shown at about 23 % to 54 % wear. In the ten adult specimens (of a total of sixteen), the protocone is usually subovate to ovate; the pre- and postfossettes separate, as is the case for all other upper cheek teeth. The protocone connects to the protoloph after about 67 % wear. The mean plication count in adult specimens is 6;10;9;3, slightly more complex than the Vienna Basin sample. There are 3 plis caballin on average. The Höwenegg sample is similar to the Senckenberg collection (below) from Eppelsheim.

P4 apparently had an unworn MSTHT of 55 mm, with the adult morphology displayed within a range of about 31 % to 61 % wear (fourteen of twenty specimens). In this range the mean plication count is 7;12;9;4, comparable to that seen in the Mariathal sample, and possibly slightly more complex than the average of the Vienna Basin samples. The protocone is ovate, with a mean width/length ratio of 0.58. The protocone is isolated to at least 62 % wear. On average there are 3 plis caballin. The Höwenegg sample is more complex than either the HLMD or the Senckenberg material of *H. primigenium* (and had more plis caballin; tab. 2).

M1 had an unworn MSTHT of about 58 mm. The adult morphology is displayed between 33 % to 56 % wear in seven of thirteen specimens. The average plication count is 7;12;9;3, more complex than all but the Inzersdorf specimen (*Hippotherium* sp.) in the Vienna Basin (tab. 2). The mean protocone ratio is 0.60, showing that these are basically slightly ovate to ovate in all but one specimen, where it is slightly concave. The protocone is isolated nearly to the base of the crown with one specimen showing incipient connection to the protoloph at about 86 % wear. There are 3 plis caballin on average. The Höwenegg sample is somewhat more complex and comparable in that respect to the Senckenberg material from Eppelsheim (tab. 2).

M2 had an unworn MSTHT of about 55 mm. In the two adult specimens (of five total), the average plication count is 6;14;10;3, more complex than the Vienna Basin material of *Hippotherium* sp. (tab. 2). The adult morphology is found within a range of 20 % to 50 % wear (based on the two specimens). The mean protocone ratio is 0.52, reflecting its subovate shape, and there is an average of 4 plis caballin. The Höwenegg sample is generally less complex than this material and thereby comparable to the Senckenberg Eppelsheim collection (tab. 2).

The Senckenberg collection of *H. primigenium* upper cheek teeth from Eppelsheim is comparable to that at Darmstadt (tab. 2) except that the unworn P2 MSTHT was somewhat shorter (about 45 mm; and comparable to that of *Hippotherium* sp. from Gaiselberg). The adult morphology of P2 is shown between 27 % to 47 % wear. As in the Darmstadt material, the pre- and postfossettes in P2 are mostly separate (eight of ten specimens). The adult plication count of 7;10;10;3 is generally more complex than in the Vienna Basin materials of *Hippotherium* sp. (tab. 2), especially as regards the opposing

borders of the pre- and postfossettes. The plication complexity of the Senckenberg material of *H. primigenium* from Eppelsheim is comparable to that of the Darmstadt sample and less than that of the Höwenegg sample (tab. 2). The protocone is ovate (mean ratio is 0.67), and there is an average of 2 plis caballin. In general the unworn MSTHT for all cheek teeth of *H. primigenium* in the Höwenegg sample is somewhat lower crowned than teeth in the Darmstadt and Senckenberg collections.

The unworn MSTHT for P3 may have been somewhat taller (58 mm) than in the Darmstadt sample (52 mm), with four specimens having a range of adult morphology from 42 % to 59 % wear. In comparison to other cheek teeth loci both in these and in the Darmstadt collections, this adult wear range for P3 is considered limited. Apparently less worn adult specimens of P3 are not present in the Senckenberg collection, although one juvenile (11 % wear) and one senile (60 % wear) specimen are represented. In the known adult range, the mean plication count is 8;14;11;5, and pli caballins 4, more complex than in any Vienna Basin material as well as for the Darmstadt material and the Höwenegg sample. The protocone is ovate in the four adult teeth (of six total), with a ratio of 0.65.

P4 apparently had an unworn MSTHT of about 56 mm in the Senckenberg collection from Eppelsheim, slightly taller than found in the Darmstadt collection from that location (55 mm). The adult morphology was found in specimens ranging from 30 % to 52 % wear, within which the average plication count was 5;13;10;4 (four of six specimens in the Senckenberg Eppelsheim collection), with a mean of 3 plis caballin (tab. 2). The plication count is slightly higher than in the Darmstadt Eppelsheim sample (except for the anterior border of the prefossette) and less than that of the Höwenegg sample from that location. The protocone is ovate to subovate in outline (mean ratio is 0.87). In all premolars, the protocone still is isolated from the protoloph at about 60 % wear, greater than which specimens are not represented in the Senckenberg Eppelsheim material.

M1 possibly had an unworn MSTHT of about 57 mm, at which figure the protocone remained isolated until about 63 % wear in the Senckenberg Eppelsheim specimens. The adult range appears to have been from 35 % to 53 % wear, with a mean plication count of 8;15;8;5; 4 mean plis caballin (tab. 2). The ovate protocone had an average ratio of 0.72 (four adult of seven teeth total). The plications are more numerous in the Senckenberg Eppelsheim material than in the Darmstadt sample, comparable to the Höwenegg sample, and much more complex than the Vienna Basin materials of *Hippotherium* sp. (tab. 2). The morphology of the sole specimen of *Hippotherium* sp. from Inzersdorf approaches that for *H. primigenium* at Höwenegg (tab. 2).

M2 probably was about as tall as M1, with a likely unworn MSTHT of 57 mm. The ovate protocone (mean ratio of 0.60 in two adult of a total of five specimens in the Senckenberg Eppelsheim collection) was isolated from the protoloph until at least 58 % wear. Within the available adult wear range (37 % to 46 %), the mean plication count was 5;11;8;5; the plication count 3. The plication count is like that of the Vienna Basin sample of *Hippotherium* sp., but somewhat simpler than found in the Darmstadt material and in the Höwenegg sample of *Hippotherium primigenium* (tab. 2).

With most emphasis being attributed to the Mariathal sample in the Vienna Basin and that from Eppelshiem for *H. primigenium*, it appears that *Hippotherium* sp. from the Vienna Basin differs from *H. primigenium* in the consistent confluence between the

pre- and postfossettes in P2 and the generally less complex pre- and postfossette plication counts, the lower number of plis caballin for all upper cheek teeth. The Inzersdorf specimen is considered most like the other Vienna Basin materials, especially in view of it being only a single individual.

Implications for dispersal and the *Hippotherium* Datum

The first stratigraphic occurrence of *Hippotherium*, commonly recorded as *H. primigenium*, defines the beginning of the Vallesian mammal age and MN9 in the Mammal Neogene chronology (MEIN 1975; DAXNER-HÖCK 1996). Fig. 1 indicates that the Czech Republic site of Hovorany is correlated with Pannonian Zone B (HARZHAUSER et al. 2004), but the material assigned to *Hippotherium* from this site has been lost (DAXNER-HÖCK, pers. commun., 2008). For the purposes of this report, the age of the *Hippotherium* Datum in the Pannonian Basin is taken as about 11.1 Ma, with the realization that it could be somewhat older.

WOODBURNE (2007) reviewed species of the North American genus, *Cormohipparion* and considered the relationship of these to the origin of the Old World genus *Hippotherium*. Fig. 5 summarizes the geochronologic range and phyletic relationships of *Cormohipparion* species (all from North America) and a proposed origin of the morphology leading toward *Hippotherium*. Based on possessing a functional dP1 in the adult condition, an unworn upper cheek tooth MSTHT ranging from 50 t 55 mm, and the labial confluence of the P2 pre- and postfossettes, *C. fricki* was suggested as the likely source of the morphology that ultimately was achieved in *Hippotherium*. These traits are lost or less commonly expressed in *C. skinneri*, *C occidentale*, and *C. matthewi*, and neither these taxa nor *C. johnsoni* or *C. merriami* are considered relevant to the present discussion. On the other hand, a single specimen from the Punchbowl Formation of California at about 11.5 Ma shows an increased complexity of fossette border plications that approaches the condition seen in specimens of comparable wear stage of *Hippotherium* sp. from the Vienna Basin (fig. 3), as well as having similarly ovate protocones, overall size and crown height and labially confluent pre- and postfossettes (tab. 2). The connection of the protocone in P2 at an early (about 35 %) wear stage is similar to the condition seen in specimens from Atzelsdorf, but the fact that both instances involve the sole specimen in each sample should be kept in mind. Nevertheless, there is little to disbar the California *Cormohipparion* from a potentially close phyletic association with *Hippotherium* sp. from the Vienna Basin. Pursuit of this possibility could result in an evaluation of the generic status of *Cormohipparion* SKINNER & MACFADDEN, 1977 relative to *Hippotherium* MEYER, 1929, but this is beyond the scope of the present report.

Summary and Conclusions

The Atzelsdorf *Hippotherium* sp. is found to have a cheek tooth morphology comparable to other samples in the Vienna Basin of Pannonian C age. These samples have a generally less derived morphology than those referred to *Hippotherium primigenium* from Eppelshiem and Höwenegg of Germany, compatible with the geologically younger age of that species. Whereas it is likely that the Vienna Basin samples here designated as

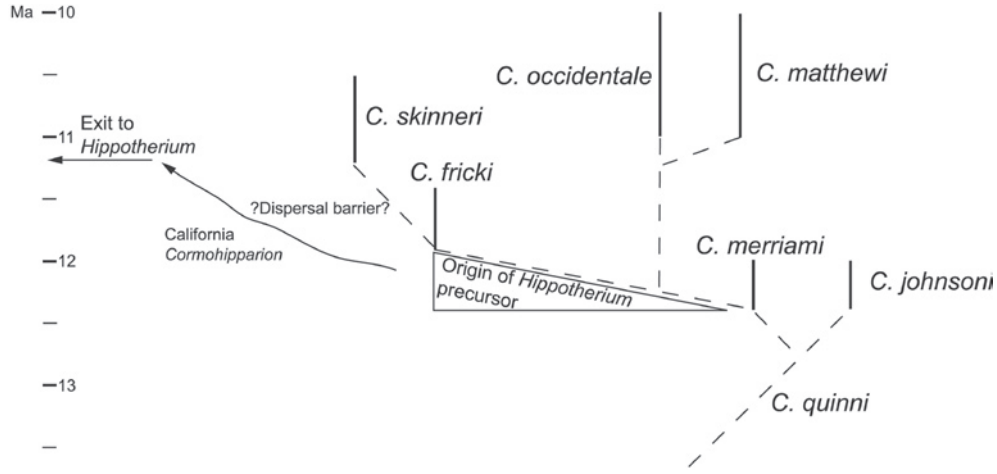

Fig. 5. Speciation in *Cormohipparion* and Origin and Dispersal of *Hippotherium* from North America. Modified from WOODBURNE (2007, fig. 29).

Hippotherium sp. pertain to a single species, formally designating a name for that taxon should await a better sample of dental and cranial morphology than now is available. In any case, the Atzelsdorf *Hippotherium* sp. material supports the proposal by WOODBURNE (2007) that lingually flattened protocones do not characterize the upper cheek tooth dentition in these early hippotheriines; that the presence of such a morphology in some specimens of these samples is due to ontogenetic and interpopulational variation, and is not of phyletic significance. In spite of the intriguing degree of similarity between the Vienna Basin *Hippotherium* sp. and *Cormohipparion* sp. of North America, the present level of phyletic analysis is compatible with the interpretation that, just as *Hippotherium* has not been recognized in North America, neither has *Cormohipparion* been demonstrated as having been present in the Old World, as also discussed in WOODBURNE (2007) and contrary to BERNOR et al. (2003). In the present context there appears to have been only a single dispersal event from North America to the Old World. Whereas the population represented by *Cormohipparion* sp. from California existed about 11.5 Ma, the earliest record of the *Hippotherium* Datum in the Old World is considered to be about 11.2 Ma old (Hovorany). The apparent lapse of about 0.3 my. may be filled when more evidence is developed on either side of the ancient Bering Straits.

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