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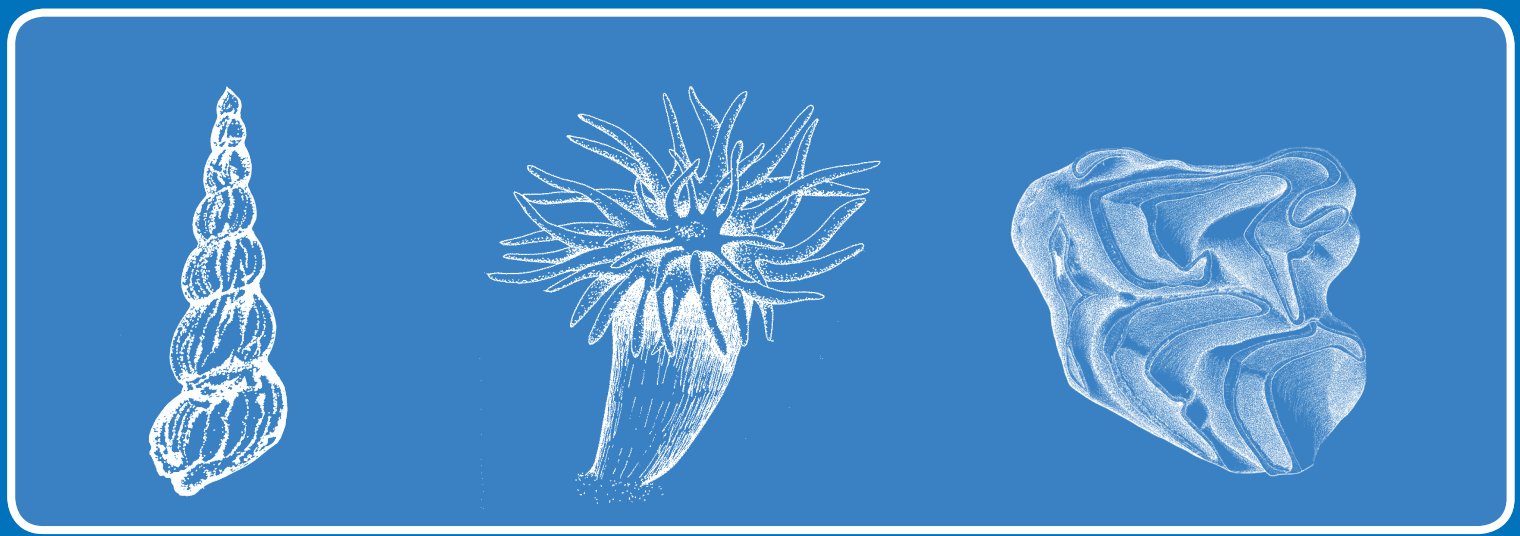

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Cover illustrations: (from left to right) Shell of the gastropod *Loxonema regium* De Koninck from the Carboniferous of Belgium (redrawn from De Koninck 1881); Solitary coral *Caninia* sp. from the Carboniferous of England (redrawn from Ramsbottom in McKerrow 1978); Tooth of the rare ruminant *Orygotherium escheri* von Meyer from the Miocene of Germany (after Rössner & Mörs 2001). **Back cover:** Atrium of the Munich Palaeontological Museum, view from the main entrance.

Umschlagbilder: (von links nach rechts) Gehäuse der Schnecke *Loxonema regium* De Koninck aus dem Karbon von Belgien (neu gezeichnet nach De Koninck 1881); Solitärkoralle *Caninia* sp. aus dem Karbon von England (neu gezeichnet nach Ramsbottom in McKerrow 1978); Zahn des seltenen Wiederkäuers *Orygotherium escheri* von Meyer aus dem Miozän von Deutschland (nach Rössner & Mörs 2001). **Rückseite:** Lichthof des Paläontologischen Museums München, Blick vom Haupteingang.

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Note on the morphological variability of *Keramidomys thaleri* (Eomyidae, Mammalia) from Puttenhausen (North Alpine Foreland Basin, Germany)

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Abstract

The morphological variability within the large sample of *Keramidomys* teeth from Puttenhausen (Bavaria, OSM C+D) is described. The teeth are assignable to *K. thaleri*, a species that is especially well known from the Fossillagerstätte Sandelzhausen, which is stratigraphically and geographically close to the Puttenhausen site. The two samples represent by far the richest record of the genus in the German part of the North Alpine Foreland Basin.

Key words: Miocene, Rodentia, Bavaria, Upper Freshwater Molasse

Zusammenfassung

Die morphologische Variabilität innerhalb des reichhaltigen Materials von *Keramidomys*-Zähnen aus Puttenhausen (Bayern, OSM C+D) wird beschrieben. Die Zähne gehören zu *K. thaleri*, eine Art, die vor allem aus der stratigraphisch und geographisch Puttenhausen nahstehenden Fossillagerstätte Sandelzhausen sehr gut bekannt ist. Die Molarsammlungen aus Sandelzhausen und Puttenhausen sind die bei weitem besten und umfangreichsten Vorkommen der Gattung *Keramidomys* aus dem deutschen Teil des Nordalpinen Vorlandbeckens.

Schlüsselswörter: Miozän, Rodentia, Bayern, Obere Süßwassermolasse.

1. Introduction

The tooth genus *Keramidomys* belongs to one of the smallest mammals ever, and generally is a relatively rare element in the faunas. However, the genus is well represented in the rodent faunas from Obergänserndorf (more than 540 teeth; see Daxner-Höck 1998) and Sandelzhausen (more than 250 teeth; see Mein 2009). The latter locality has recently been studied intensively (Rössner & Göhlich 2009, 2010). Another large sample of *Keramidomys* teeth has been excavated from the locality Puttenhausen, which is both geographically and stratigraphically close to Sandelzhausen (Fahlbusch & Wu 1981). However, the material from Puttenhausen has not been analyzed in detail to date. In this paper, the morphological variability within the tooth sample from Puttenhausen is described and compared to the material from Sandelzhausen.

The locality Puttenhausen is located north of the town Puttenhausen, approximately 3.5 km south of the city of Mainburg, Bavaria. The section comprises an 18 m-thick succession of fine grained alluvial deposits that includes at least six red-colored palaeosols rich in vertebrate remains (Abdul Aziz et al. 2008). The *Keramidomys* sample has been collected from the lowermost palaeosol ("Puttenhausen classic layer"). The fauna from Puttenhausen is predominantly composed of small mammals (e.g. Fahlbusch & Wu 1981; Wu 1982, 1990; Ziegler & Fahlbusch 1986; Ziegler 2000, 2005; Rössner & Heissig 1999) and lower vertebrates (Abdul Aziz et al. 2008), but large mammals are fairly well represented as well (Eronen & Rössner 2007).

Based on the local biostratigraphic scale, the 'Puttenhausen classic' layer (abbreviated PUT cl.) correlates to the unit OSM C+D (see Abdul Aziz et al. 2008: 120–122), and paleomagnetic studies suggest a correlation to chron C5Cn.2n, at 16.4 Ma (Abdul Aziz et al. 2008, in press). The fauna is slightly older than that reported from Sandelzhausen.

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Table 1: Occurrence of *Keramidomys* Hartenberger, 1967 in the German part of the North Alpine Foreland Basin. L*M*: Length of the m1 in the main *Megacricetodon* lineage; n.p. = not indicated.

Locality	Correlation	L*M*	number of teeth	species	Reference
Gallenbach 2b	OSM F	Absent	n.i.	*K.* sp.	Heissig 1989
Unterzolling 1a	OSM F	Absent	n.i.	to be reviewed	Heissig 1989
Giesseltshausen 1a	OSM F	n.i.	n.i.	to be reviewed	Heissig 1989
Unterneul 1a	late OSM E	Absent	n.i.	*K.* sp.	Heissig 1989
Edelbeuren-Maurerkopf	OSM E	2.26 (1 m1)	2	probably *K. thaleri*	Sach 1999
Furth 460	OSM E	2.21 (1 m1)	n.i.	probably *K. thaleri*	Abdul-Aziz et al. 2008
Untereichen-Altenstadt 565m	early OSM E	2.09	35	*K. thaleri*	Prieto et al. 2009
Oggenhof	late OSM C+D	1.89	1	probably *K. thaleri*	Fahlbusch 1975
Massendorf	OSM C+D	Absent	15	probably *K. thaleri*	Schötz 1979
Oggenhausen 2	OSM C+D	1.91	1	probably *K. thaleri*	Böttcher et al. 2009
Sandelzhausen	late OSM C+D	1.91	261	*K. thaleri*	Mein 2009
Puttenhausen E	late OSM C+D	n.i.	n.i.	probably *K. thaleri*	Abdul-Aziz et al. 2008
Buchtenbach 1b	late OSM C+D	1.91	in prep.	*K. thaleri*	Abdul-Aziz et al. in press
Puttenhausen B-D	OSM C+D	n.i.	n.i.	*K. thaleri*	Abdul-Aziz et al. 2008
Puttenhausen cl.	OSM C+D	1.86	258	*K. thaleri*	this paper
Gisseltshausen 1b	OSM C+D	1.86	n.p	to be reviewed	Heissig 1989
Engelwies 1	early OSM C+D	1.75 (all layers)	2	probably *K. thaleri*	Ziegler 1995
Engelwies 3	early OSM C+D	1.75 (all layers)	1	probably *K. thaleri*	Ziegler 1995
Schellenfeld 3	early OSM C+D	1.74 (all layers)	1	undetermi-nated	Ziegler 1995
Roßhaupten	early OSM C+D	1.74	2	probably *K. thaleri*	Fahlbusch 1975
Niedereichbach	late OSM B	1.68 (1 m1)	2	probably *K. thaleri*	Schötz 1979
Adelschlag	late OSM B?	no m1	7	*K. thaleri*	Fahlbusch 1975
Langenmoosen	OSM B	1.66	2	probably *K. thaleri*	Fahlbusch 1975
Pöttmes	OSM B	1.65 (1 m1)	3	probably *K. thaleri*	Fahlbusch 1975
Eitensheim	earliest OSM B?	1.55 (1 m1)	4	to be re-viewed	Fahlbusch 1975
Gündlkofen	unknown	Absent	1	*K.* sp.	Fahlbusch 1975
Undorf	unknown	Absent	1	probably *K. thaleri*	Fahlbusch 1975

1.1 *Keramidomys* in the German part of the North Alpine Foreland Basin.

A species related to *K. mohleri* has been recorded for younger German deposits (Fahlbusch 1975; Prieto 2007; Seehuber 2009), but the samples are in need of a revision based on the most recent taxonomic considerations by Daxner-Höck & Höck (2009), among other authors. Earlier reports of the genus, which are of interest with regard to the results presented in this study, are listed in Table 1. However, uncertainties usually remain with regard to the precise affinities of these samples due to either the limited number of specimens available or

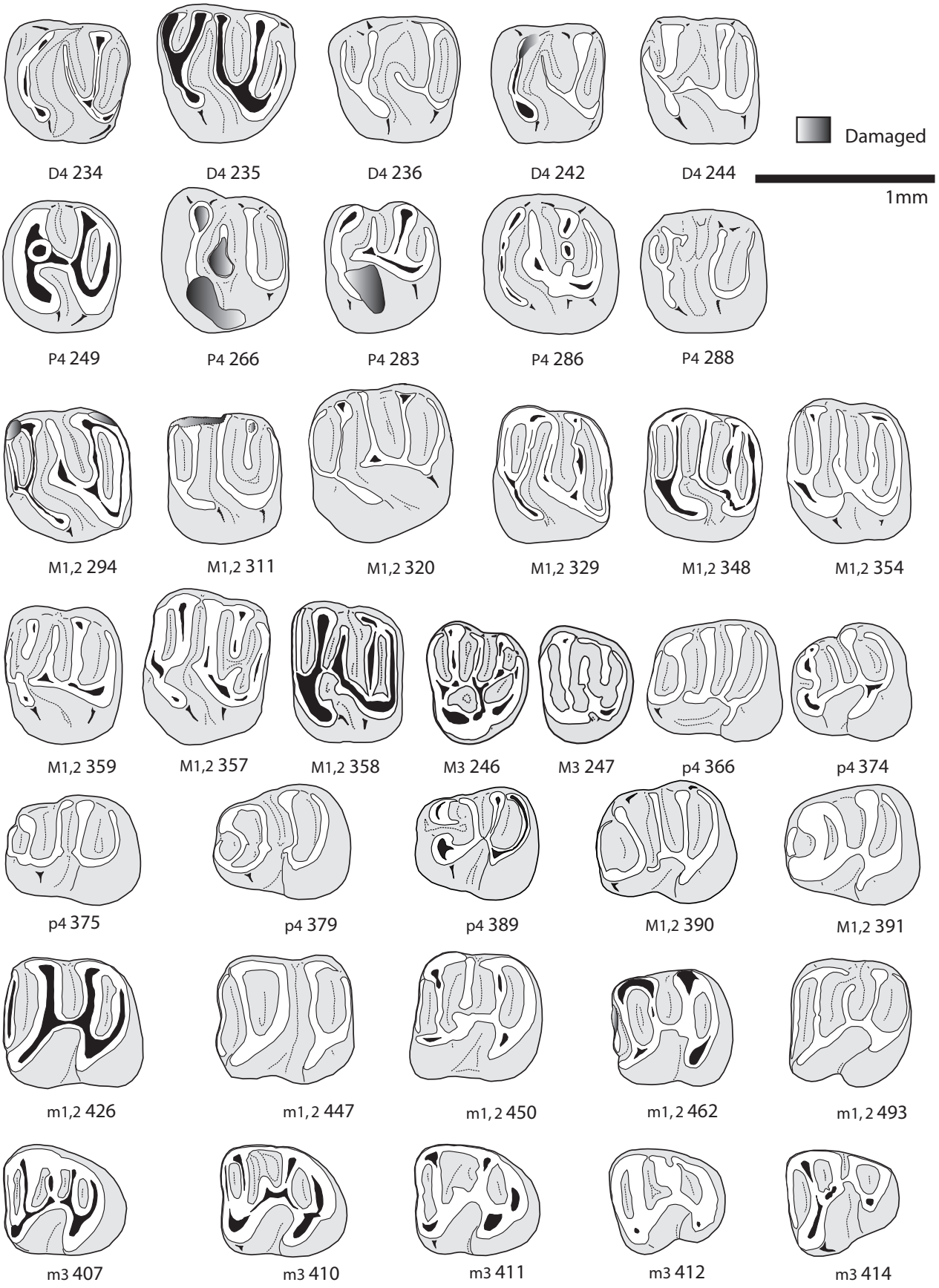


Figure 1: *Keramidomys thaleri* Hugueney & Mein, 1967 from the 'Puttenhausen classic' layer. Note that only the last part of the accession number is given for each tooth directly in the figure; this last part is consistently preceded by BSPG 1979 XVI. Reversed teeth: 234, 236, 242, 249, 266, 329, 348, 389, 390, 391, 447, 450, 412, 414.

the still widespread cherishing of the synonymy *K. thaleri-K. carpathicus* in Germany (see details in Mein 2009). Comparisons with the Swiss part of the Molasse basin are difficult as well because Bolliger (1992), Kälin (1993), and Kälin & Kempf (2009) also have adopted the *K. thaleri-K. carpathicus* synonymy. The earliest evidence of the genus *Keramidomys* in Bavaria has been reported from near the Ottnangian/Karpatian boundary (base of the OSM B; Abdul-Aziz et al. in press). This evidence is somewhat younger than the record of this genus from Franzensbad (Fejfar 1974).

2. Material and methods

The teeth are kept in the Bavarian State Collection for Paleontology and Geology at Munich (*Bayerische Stattssammlung für Paläontologie und Geologie*, abbreviated BSPG), Germany, under accession number 1979 XVI *x*. Because of the uncertainties with regard to the discrimination between the two first lower and upper molars (for details, see Mein 2009), I have chosen not to distinguish between M1/m1 and M2/m2 in the fossils from Puttenhnausen. Also, the labial connections of the crests and conules are not considered because this character changes with tooth wear.

The following damaged, corroded or senile teeth are not included in the morphological analysis: D4: BSPG 1979 XVI 243, 241 and 238; P4: BSPG 1979 XVI 263, 267, 281; M1,2: BSPG 1979 XVI 350, 314; p/4: BSPG 1979 XVI 364, 367, 369, 370, 392, m1,2: BSPG 1979 XVI 416, 417, 425, 468, 474, 476, 478, 480, 488; m3: 400, 404.

As only a single lower premolar has been discovered, this dental element has not been studied.

All teeth are illustrated as left ones; right molars are reversed. To make the text easier to read, only the last part of the accession numbers referring to the individual teeth are given in Figure 1 and in the description. This last part of the accession number is consistently preceded by BSPG 1979 XVI.

3. Systematic paleontology

Rodentia Bodwich, 1821
Eomyidae Deperet & Douxami, 1902

Keramidomys Hartenberger, 1967

Type species: *Keramidomys pertesunatoi* Hartenberger, 1967

Other species included in *Keramidomys*: *K. carpathicus* (Schaub & Zapfe, 1953), *K. thaleri* Hugueney & Mein, 1968, *K. anwilensis* Engesser, 1972, *K. mohleri* Engesser, 1972, *K. reductus* Bolliger, 1992, *K. fahlbuschi* Qiu, 1996, *K. ermannorum* Daxner-Höck & Höck, 2009.

Keramidomys thaleri Hugueney & Mein, 1968
Fig. 1

1981 *Keramidomys carpathicus* Fahlbusch & Wu: 117
2009 *Keramidomys* Mein: tab. 1

Original diagnosis: Hugueney & Mein (1968); for a translation of the diagnosis to English and comments, refer to Mein (2009).

Type locality: Vieux-Collonges (France)

Age of the type locality: Middle Miocene, MN 5

4. Variability of the characters in the upper check teeth

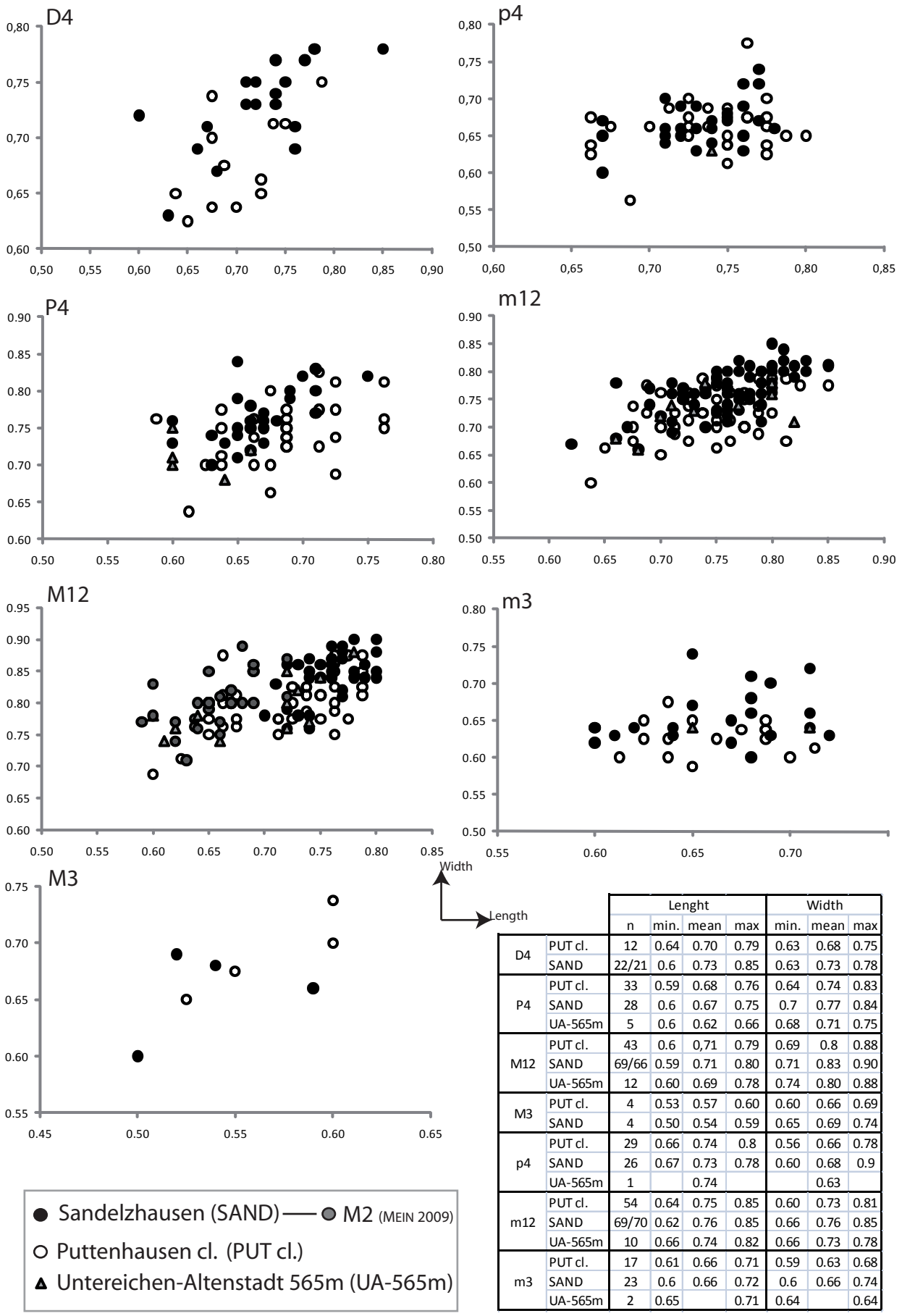
D4: 10 teeth. The anteroloph is generally well developed (6 teeth, e.g. 235, 236, 244), although it may be very short (3, e. g. 234) or absent (1, 242). The longitudinal crest does not merge with the protoloph in all D4 (e.g. 235), but may connect to the protocone (e.g. 244). If connected to the protocone, the connection is weak. The mesoloph reaches the labial border in three teeth (e.g. 235), it is long in one premolar (234), extends to half of the syncline in three others (e.g. 242), and in still two others is shorter (e.g. 244). In one D4, the longitudinal crest cannot be distinguished from the mesoloph (236).

P4: 37 teeth. The anteroloph is absent in all but two (e.g. 288) teeth; if present, the anteroloph is short. The longitudinal crest usually is interrupted (5, e. g. 286), but may also be directed towards the protoloph (22, e.g. 283). The connection is present in 9 teeth (e.g. 249). The mesoloph generally is of medium length (17, e.g. 266), or somewhat shorter (3 teeth), but may also be long (16, e.g. 283, 286).The crest is absent in one P4 (288). The metaloph is interrupted in one P4 (286).

M1,2: 68 teeth. The anteroloph is always present. The longitudinal crest is interrupted in all but seven specimens. The connection may be well defined (e.g. 358) or very low; it divides the second syncline (e.g. 348). On one molar, the longitudinal crest connects to the protocone (354). In high M1,2, the longitudinal crest tends to merge with the protocone (spur on the longitudinal crest), and one tooth possesses a complete longitudinal crest plus a spur (358). The mesoloph is usually long (52 M1,2, e.g. 320), but may also be connected to the base of the paracone (16, e.g. 329, 358). The metaloph may be interrupted or at least constricted at its connection with the longitudinal crest (6, e.g. 311, 357). Similarly, the protoloph is interrupted in one tooth (359).

M3: 4 teeth. The molars have five transversal crests. The mesoloph extends to the border of the crown in all M3 but one (247, synclines full of sediment). The metaloph is interrupted in one tooth (247). The longitudinal crest is interrupted in three M3, but the M3 246 has narrow junction between proto- and mesoloph. In the same tooth, Meta-and posteroloph are connected by a short transversal crest. The protoloph does not connect to the anteroloph in one M3 (247), but to the protocone in this case.

p4: 29 teeth. The anterolophid is well developed and connects to the metaconid (26, e.g. 366). It rarely stands isolated (391) or is even absent (4, e.g. 374, 389). In most p4 (25 teeth), the longitudinal crest is continuous, although the connection just reaches the base of the protoconid (366, 390); it may also show a superficial notch in juvenile premolars (379). The mesolophid is always well developed, very variable with regard to the labial connections.



		Lenght				Width		
		n	min.	mean	max	min.	mean	max
D4	PUT cl.	12	0.64	0.70	0.79	0.63	0.68	0.75
	SAND	22/21	0.6	0.73	0.85	0.63	0.73	0.78
P4	PUT cl.	33	0.59	0.68	0.76	0.64	0.74	0.83
	SAND	28	0.6	0.67	0.75	0.7	0.77	0.84
	UA-565m	5	0.6	0.62	0.66	0.68	0.71	0.75
M12	PUT cl.	43	0.6	0,71	0.79	0.69	0.8	0.88
	SAND	69/66	0.59	0.71	0.80	0.71	0.83	0.90
	UA-565m	12	0.60	0.69	0.78	0.74	0.80	0.88
M3	PUT cl.	4	0.53	0.57	0.60	0.60	0.66	0.69
	SAND	4	0.50	0.54	0.59	0.65	0.69	0.74
p4	PUT cl.	29	0.66	0.74	0.8	0.56	0.66	0.78
	SAND	26	0.67	0.73	0.78	0.60	0.68	0.9
	UA-565m	1		0.74			0.63	
m12	PUT cl.	54	0.64	0.75	0.85	0.60	0.73	0.81
	SAND	69/70	0.62	0.76	0.85	0.66	0.76	0.85
	UA-565m	10	0.66	0.74	0.82	0.66	0.73	0.78
m3	PUT cl.	17	0.61	0.66	0.71	0.59	0.63	0.68
	SAND	23	0.6	0.66	0.72	0.6	0.66	0.74
	UA-565m	2	0.65		0.71	0.64		0.64

Figure 2: Measurements of *Keramidomys thaleri* Hugueney & Mein, 1967 from Puttenhausen, Sandelzhausen (based on data in Mein 2009), and Untereichen-Altenstadt 565m (based on data in Prieto et al. 2009).

m1,2: 72 teeth. The anterolophid is well developed (e.g 426). The longitudinal crest is interrupted in one molar (447). The mesolophid usually connects to the base of the metaconid, and a constriction/superficial interruption occurs at the base of the crest in five teeth (e.g. 450). The mesolophid of the m1,2 493 is somewhat shorter.

m3: 18 teeth. In the most common morphotype, the m3 possesses five complete transversal crests (15, e.g. 407). The m3 410 and 411 possess a short mesolophid, and the crest is fused with the hypolophid in specimen 412. The mesolophid may also be interrupted near to the longitudinal crest. The longitudinal crest is displaced labially in one tooth (414).

5. Comparison with Sandelzhausen

Since the m3 /M3 are usually characterized by five tranversal crests and the (pre)molars even more commonly have long mesoloph(id)s, the tooth assemblage from Puttenhausen is ascribed to *K. thaleri* as defined by Daxner-Höck (1998) and Mein (2009), but *contra* Fahlbusch (1975). The measurements of the teeth from the 'Puttenhausen classic' layer and Sandelzhausen are given in Figure 2. The two samples overlap in tooth size, although the D4 from Sandelzhausen are somewhat wider. Bias due to differences in the measurement methodologies used can be ruled out because of the squarish to rectangular shape of the teeth.

Regarding tooth morphology, the samples from the 'Puttenhausen classic' layer and Sandelzhausen are very similar, and only a few minor differences have been observed noticed: the mesoloph of D4 and P4 from Puttenhausen is more often shorter than that in teeth from Sandelzhausen, and the P4 possesses a shorter longitudinal crest, although this crest clearly tends to connect to the protoloph. Moreover, p4 usually shows an isolated/absent anterolophid in specimens from Puttenhausen. In addition, a single m1,2 from Puttenhausen possesses an interrupted longitudinal crest, a morphotype not recorded for Sandelzhausen. Unfortunately, this comparison does not shed new light on evolutionary trends within the *Keramidomys* lineage, due possibly to the short stratigraphic distance between the two localities.

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