

A NEW SPECIES OF *KARYDOMYS* (RODENTIA, MAMMALIA) AND A SYSTEMATIC RE-EVALUATION OF THIS RARE EURASIAN MIOCENE HAMSTER

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ABSTRACT. We describe a new species of the rare and enigmatic cricetid genus *Karydomys* from the middle Miocene Ville Formation of the Hambach lignite mine in north-west Germany. The locality Hambach 6C has yielded the first substantial records of *Karydomys* from central Europe. For the first time, all molar positions are well-documented, including the previously unknown m2. The excellent molar material allows us to distinguish *Karydomys wigharti* sp. nov. from the western European species *K. zapfei*. *Karydomys wigharti* predominantly occurs at localities that are correlated with the upper part of the Mammalian Neogene biozone MN 5. The new finds are of palaeobiogeographic significance for the genus *Karydomys*, since Hambach 6C represents the north-westernmost outpost of terrestrial Miocene faunas in Europe. In addition, the locality has yielded the first lower jaws and incisors of the genus. Both the jaw morphology, and the ornamentation and microstructure of the incisor enamel offer new arguments for a systematic classification of *Karydomys* into the subfamily Democricetodontinae. We assume that the scarcity of the two large European *Karydomys* species can be explained by their special adaptation to wet habitats, which are poorly documented in the fossil record.

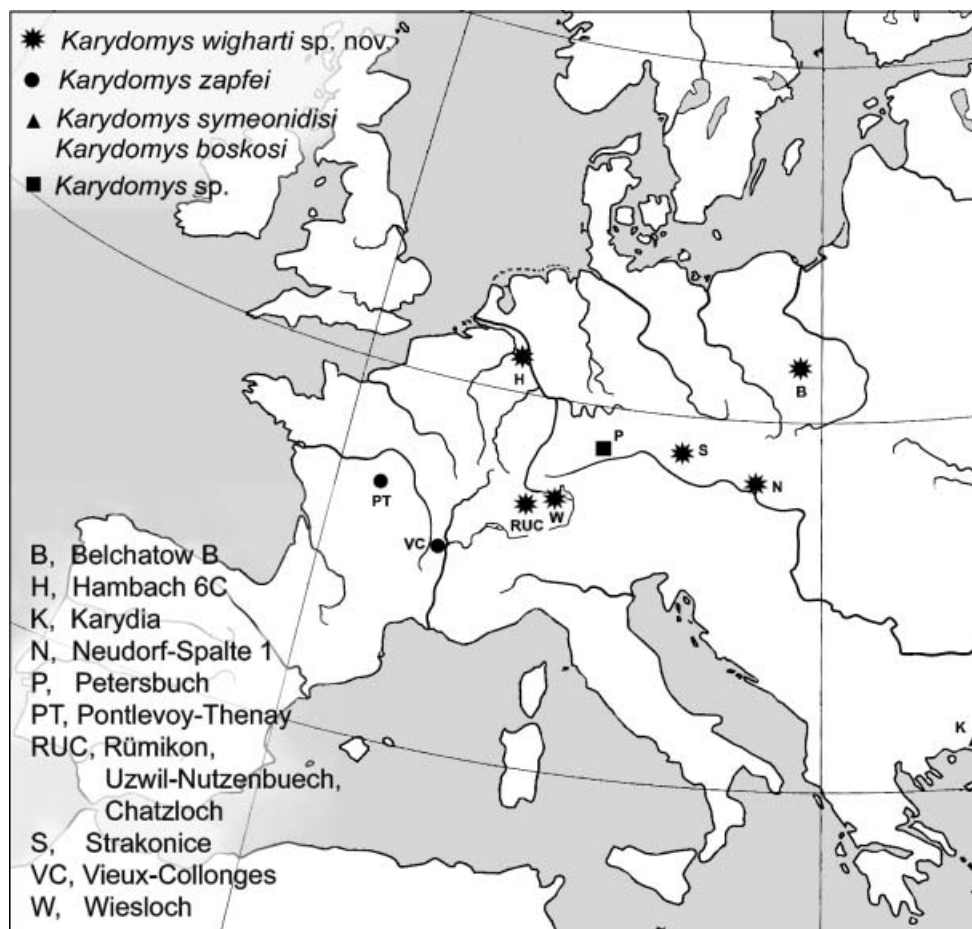
KEY WORDS: Cricetidae, Democricetodontinae, enamel microstructure, palaeoecology, biostratigraphy, Hambach, Germany.

SOME central European localities have sporadically yielded a few isolated molars of a large cricetid (Text-fig. 1). These teeth resemble the scarce material from the French Miocene karstic fissure-fill Vieux-Collonges, which Mein and Freudenthal (1971, 1981) described as *Lartetomys zapfei*. Two decades earlier, a similar tooth had been recovered from the middle Miocene Slovakian fissure-fill Neudorf-Spalte 1 (Devínska Nová Ves). Schaub and Zapfe (1953) described this single cricetid m1 with unusual dental features as a new species of the genus *Cricetodon* without providing a species name. Fejfar (1974, 1990) assigned this molar and two additional m1s from this locality, as well as an M2 from the Bohemian site Strakonice to *L. cf. zapfei*. Fejfar (1974) stated that (1) the few teeth known as *L. (cf.) zapfei* show considerable morphological variation and (2) they are closely related to the genus *Democricetodon*. He also pointed out (3) the early stratigraphical occurrence of *Lartetomys* in Vieux-Collonges.

Fourteen new molars, hitherto the most extensive material of *L. cf. zapfei*, were described by Garapich and Kälin (1999) from Swiss and Polish localities. On the basis of this material they stated that the M1 and M2 of the central European *Lartetomys* are morphologically different from the type material of *L. zapfei* from Vieux-Collonges and, therefore, assigned their material to *L. cf. zapfei*. However, they noticed such obvious morphological differences between the Swiss M3 and the type material that they proposed to assign the M3 of the latter to a different species.

Recently, new *Lartetomys*-like molars have been recovered from the lower Miocene of Greece, Anatolia and Kazakhstan (Theocharopoulos 2000; Kordikova and de Bruijn 2001). On the basis of the rich Greek material, Theocharopoulos (2000) erected the new genus *Karydomys* in which he included the species *K. zapfei*.

The new specimens of *Karydomys* described in this paper were recovered from the middle Miocene of the Hambach lignite mine in western Germany. The importance of the Hambach material is that it represents the first documentation by several specimens of all molar positions of a large *Karydomys*



TEXT-FIG. 1. Map showing the localities that have yielded remains of the European species of *Karydomys*.

species. This is especially remarkable, since the M2 formerly was only represented by two specimens and the m2 was not previously known. The Hambach material offers the possibility of evaluating the morphological and metrical variability in the molars of this central European *Karydomys*. This analysis shows that the new species from Hambach is not identical to *K. zapfei* from Vieux-Collonges but represents a closely related, distinct species. In addition, two lower jaws without molars but with incisors and also isolated lower incisors could be identified, elements that were previously unknown in *Karydomys*. They provide new arguments for the systematic position of this peculiar and rare cricetid on the basis of jaw morphology and incisor enamel microstructure.

The type material of the new species comes from the Lower Rhine Embayment, about 35 km west of Cologne, where the large Hambach open-cast lignite mine of the Rheinbraun AG exposes thick successions of Miocene and Pliocene strata. A well-preserved and rich vertebrate fauna was discovered in a channel fill within the Frimmersdorf seam. The channel fill, horizon 6C in the local lithostratigraphy (Schneider and Thiele 1965), belongs to the Miocene Ville Formation, which contains the Rhenish Main Coal Seam. Along with marine and freshwater fish, amphibians and reptiles, more than 70 mammal species have been identified to date from Hambach 6C (Mörs *et al.* 2000; Ziegler and Mörs 2000; von Koenigswald and Mörs 2001; Rössner and Mörs 2001; Mörs 2002; Hierholzer and Mörs 2003; Klein

and Mörs 2003; Nemetschek and Mörs 2003; Joyce *et al.* 2004). Of special interest is the unusually rich material of *Lanthanotherium*, *Plesiosorex*, *Miopetaurista*, *Myoglis*, *Fahlbuschia*, *Karydomys*, and *Dorcatherium*. In addition, there is evidence of extremely rare mammals, such as *Anchitheriomys*, *Pliopithecus*, and *Orygotherium*.

Based on the rich association of mammalian taxa, including about 30 rodent species (sciurids, petauristids, glirids, eomyids, cricetids, and castorids), this late Orleanian fauna can be correlated with the upper part of the Mammalian Neogene biozone MN 5 (Mörs *et al.* 2000). This means early middle Miocene, and Langhian or Reinbekian according to the stratigraphy of the north-west German Cenozoic, and a numerical age-range of 15.2–16.0 Ma. Aside from its stratigraphical value, the Hambach 6C fauna is of great palaeobiogeographic importance, since it represents the north-westernmost extension of terrestrial Miocene faunas in Europe.

MATERIAL AND METHODS

The material from Hambach 6C represents the most significant sample of the genus *Karydomys* in central and western Europe. It consists of 41 molars, two lower fragmented right jaws without molars but with incisors, and eight isolated lower incisor fragments. The preservation generally ranges from almost unworn to moderately used and the roots are present in most of the molars. There are also some badly preserved and damaged specimens that experienced highly abrasive transportation in running water. All fossils are dark brown to black in colour, owing to the position of the productive horizon within the Rhenish Main Brown Coal Seam. The cricetid material was obtained in part by surface collecting, but mainly by screen washing with a minimum sieve width of 0.5 mm. Dental terminology in the description of molar morphology follows Freudenthal *et al.* (1994). Preparations for enamel microstructure analysis were carried out by the method described in von Koenigswald (1997a) and the specimens were studied under a scanning electron microscope (SEM). The terminology used for the descriptions of the incisor schmelzmuster follows Kalthoff (2000, pp. 12–13). The teeth and mandibles described below are compared to the genera and species listed in Table 1.

TABLE 1. Comparative material.

Species	Locality	Age	Collection	References
<i>Karydomys boskosi</i>	Karydia	MN 4	KRD	Theocharopoulos 2000
<i>Karydomys symeonedisi</i>	Karydia	MN 4	KRD	Theocharopoulos 2000
<i>Karydomys zapfei</i>	Vieux-Collonges	MN 4/5	FSL 65 662, 65 666	Mein and Freudenthal 1971, 1981
<i>Karydomys</i> sp. nov.	Neudorf-Spalte 1	MN 6	SÚÚG 7339-24, 7339-25	Fejfar 1974, 1990; Schaub and Zapfe 1953
<i>Karydomys</i> sp. nov.	Strakonice	MN 5	SÚÚG 7338-4, 7338-13	Fejfar 1974, 1990
<i>Karydomys</i> sp.	Petersbuch 32	MN 6	coll. M. Rummel	unpublished
<i>Karydomys</i> sp.	Petersbuch 54	MN 5	coll. M. Rummel	unpublished
<i>Lartetomys mirabilis</i>	Vieux Collonges	MN 4/5	FSL 65 660, 65 661	Mein and Freudenthal 1971, 1981
<i>Democricetodon crassus</i>	Sansan	MN 6	KOE 2309	Kalthoff 2000
<i>Democricetodon gaillardi</i>	Sansan	MN 6	KOE 2308	Kalthoff 2000
<i>Democricetodon</i> cf. <i>mutilus</i>	Goldberg/Ries	MN 6	KOE 1891	Kalthoff 2000
<i>Democricetodon</i> sp.	Artestilla	MN 4	KOE 1978	Kalthoff 2000
<i>Democricetodon</i> sp.	La Grive M	MN 7/8	KOE 2433	Kalthoff 2000
<i>Democricetodon</i> sp.	Moratilla 2	MN 4	KOE 1982	Kalthoff 2000
<i>Fahlbuschia larteti</i>	La Grive M	MN 7/8	KOE 2304	Kalthoff 2000
<i>Cricetodon albanensis</i>	La Grive M	MN 7/8	KOE 2307	Kalthoff 2000
<i>Cricetodon</i> aff. <i>aureus</i>	Goldberg/Ries	MN 6	KOE 1867	Bruijn and Koenigswald 1994; Kalthoff 2000

Institutional abbreviations. FSL, Faculté des Sciences, Institut de Géologie, Lyon; HaH, Hambach 6C collection, housed in the IPB; IPB, Institute of Palaeontology, University of Bonn, Germany; KOE, enamel collection established by Wighart von Koenigswald, housed in the IPB; KRd, Karydia collection, housed in the University of Athens; SÚÚG, collections of the Czech Geological Survey, Prague.

SYSTEMATIC PALAEOLOGY

Order RODENTIA Bowdich, 1821

Superfamily MUROIDEA Illiger, 1811

Family CRICETIDAE Fischer von Waldheim, 1817

Subfamily DEMOCRICETODONTINAE Mein and Freudenthal, 1971

Genus KARYDOMYS Theocharopoulos, 2000

Type species. *Karydomys symeonidisi* Theocharopoulos, 2000, lower Miocene, Greece.

Karydomys wigharti sp. nov.

Plate 1, figures 1–16; Text-figures 2–6; Tables 2–4

- 1949 *Cricetodon sansaniensis* Lartet; Zapfe, p. 177.
 v.1953 *Cricetodon* nov. sp.; Schaub and Zapfe, p. 192, pl. 2, fig. 7.
 v.1974 *Lartetomys* cf. *zapfei* Mein and Freudenthal, 1971; Fejfar, p. 162, text-figs 22.33, 22.35, pl. 22, figs 4–5.
 v.1990 *Lartetomys* cf. *zapfei*; Fejfar, p. 222.
 .1999 *Lartetomys* cf. *zapfei* Mein and Freudenthal, 1971; Kälin, p. 378, text-fig. 36.5.
 .1999 *Lartetomys* cf. *zapfei* Mein and Freudenthal, 1971; Garapich and Kälin, p. 495, text-figs 1–3, table 3.
 v.2000 '*Lartetomys*' cf. *zapfei* Mein and Freudenthal, 1971; Mörs, von der Hocht and Wutzler, p. 152, text-fig. 6v–w.
 v.2000 *Karydomys zapfei* (Mein and Freudenthal, 1971); Theocharopoulos, p. 73, table 5.
 .2000 *Lartetomys zapfei* Mein and Freudenthal, 1971; Bolliger, p. 11, text-fig. 6c.
 v.2001 *K. zapfei*; Kordikova and de Bruijn, p. 394.
 v.2002 *Karydomys zapfei*; Mörs, p. 182.

Derivation of name. In honour of our teacher, colleague and friend Wighart von Koenigswald.

Holotype. Left upper first molar, IPB-HaH 5297 (Pl. 1, figs 1–3), collected by one of us (TM).

Paratypes. M1 sin. (IPB-HaH 5281, 5304); M1 dext. (IPB-HaH 5291, 5552); M2 sin. (IPB-HaH 5336, 5337, 5570, 5572); M2 dext. (IPB-HaH 5335, 5338, 5341, 5571, 5585, 5586, 5654); M3 sin. (IPB-HaH 5347, 5350, 5613); M3 dext. (IPB-HaH 5173, 5343, 5344, 5346); m1 sin. (IPB-HaH 5002, 5310, 5311, 5318); m1 dext. (IPB-HaH 5309, 5317, 5569); m2 sin. (5362, 5363, 5368, 5605); m2 dext. (IPB-HaH 5355, 5364, 5365, 5594); m3 dext. (IPB-HaH 5374, 5623, 5624); mandible dext. with i (IPB-HaH 6460, 6461); i sin. (IPB-HaH 6462, 6463, 6468, 6470); i dext. (IPB-HaH 6464, 6465, 6467).

Type locality, horizon and age. Hambach open cast lignite mine in the Lower Rhine Embayment, 35 km west of Cologne, Germany. Channel fill in horizon 6C (Schneider and Thiele 1965) within the Frimmersdorf Seam, representing the middle part of the Main Lignite Seam; Ville Formation; middle Miocene, late MN 5.

Diagnosis. Very large democricetodontine; molars with simple tooth pattern; inflated cusps; thick molar enamel; M1 with broad, box-shaped and slightly split anterocone, with usually long mesoloph; M2 with short anterolophule and narrow first synclines, with strong tendency to establish posterior metalophule and small posterosinus; M3 reduced with weak lingual anteroloph, small sinus and weak hypocone; m1 with extremely short anteroconid, with very weak or absent labial posterolophid.

Description

Upper first molar (Pl. 1, figs 1–4; Tables 2–3). Three of five first upper molars (HaH-5281, 5291, 5297) are excellently

TABLE 2. *Karydomys wigharti* sp. nov. Measurements of the upper molars from Hambach 6C (in mm). **, holotype; *, figured specimen

Tooth position	Length × width	Inventory no.
M1 dext. *	3.00 × 2.00	IPB-HaH 5291
M1 dext.	3.04 × 2.00	IPB-HaH 5552
M1 sin.	2.80 × 1.84	IPB-HaH 5281
M1 sin. **	3.00 × 2.04	IPB-HaH 5297
M1 sin.	? × 2.04	IPB-HaH 5304
M2 dext.	2.16 × 1.96	IPB-HaH 5335
M2 dext. *	2.16 × 1.88	IPB-HaH 5338
M2 dext.	? × 1.92	IPB-HaH 5341
M2 dext. *	2.36 × 2.16	IPB-HaH 5571
M2 dext. *	2.20 × 2.00	IPB-HaH 5585
M2 dext.	2.32 × 2.00	IPB-HaH 5586
M2 dext.	damaged	IPB-HaH 5654
M2 sin.	2.20 × 2.00	IPB-HaH 5336
M2 sin.	2.16 × 2.08	IPB-HaH 5337
M2 sin. *	2.28 × 2.00	IPB-HaH 5570
M2 sin. *	2.16 × 1.92	IPB-HaH 5572
M3 dext. *	1.80 × 1.68	IPB-HaH 5173
M3 dext.	1.60 × 1.72	IPB-HaH 5343
M3 dext. *	1.72 × 1.84	IPB-HaH 5344
M3 dext.	1.44 × 1.88	IPB-HaH 5346
M3 sin.	1.56 × 1.82	IPB-HaH 5347
M3 sin. *	1.76 × 1.92	IPB-HaH 5350
M3 sin.	1.80 × 1.76	IPB-HaH 5613

preserved, including the roots. The fourth specimen (HaH-5304) is also well preserved, but the anterocone is broken off. The fifth M1 (HaH-5552) is complete, but heavily worn.

All three well-preserved molars have a short and broad anterocone. Anteriorly, they show a slight splitting, which is also indicated by a shallow depression at the posterior part of the anterocone. This splitting is most pronounced in HaH-5297. The labial portion of the anterocone is higher than the lingual one. The anterolophule is a very short, lingually situated connection between the anterocone and the protocone. In two teeth the small protosinus is lingually open, while it is slightly dammed up in another specimen. The well-developed cingulum between the anterocone and the base of the paracone forms the labial wall of the anterosinus. All five specimens show a well-expressed anterior protolophule that is connected to the paracone. The even more pronounced posterior protolophule joins the entoloph posterior to the protocone. There is an obvious connection between protocone and entoloph in two M1s (HaH-5281, 5304) while this connection is interrupted in two other specimens (HaH-5291, 5297). All molars, however, have an elongated, deep valley between the protocone and paracone, here named 'medial valley'. At the base of the paracone, only one specimen (HaH-5304) shows a very weak posterior paracone spur, which is connected to the mesoloph. The mesoloph is always long and reaches the labial border in three M1s. In HaH-5281 the mesoloph ends slightly in front of this border, and in the fifth molar (HaH-5291) the mesoloph joins the metacone at its base. Between the paracone and the metacone there is a labial wall closing the deep and narrow mesosinus. This wall is best developed in HaH-5297 and includes a very weak mesostyle in HaH-5291 only.

The transverse sinus is markedly deep and narrow. Only one tooth (HaH-5291) shows a strong lingual wall connecting the protocone with the hypocone, while in the other specimens this wall is weak or absent. An entostyle is present in HaH-5304, otherwise it is very small or absent. With the exception of the heavily worn molar, HaH-5552, all other M1s show a well-developed but short metalophule. The short posteroloph is connected to the metalophule and to the metacone, enclosing a small posterosinus.

The maximum width of these brachyodont teeth can be measured at the level of the paracone and protocone. The holotype (IPB-HaH 5297) measures 3.00 mm in length and 2.04 mm in width. All specimens are three-rooted. The anterior root is moderately elongated, while the strong lingual root is markedly elongated. The posterior root is round.

Upper second molar (Pl. 1, figs 5, 7–12; Tables 2–3). Seven right molars and four left molars represent this tooth position. Six of them (HaH-5338, 5570–5572, 5585–5586) are excellently preserved. One M2 (HaH-5335) is only

moderately worn, but the hypocone is broken off. The others are severely worn, and in addition, one of them (HaH-5654) has been rounded by transportation and is slightly damaged.

The development of the anteroloph can only be evaluated in the well-preserved teeth. Here, the labial branch is slightly stronger than the lingual one. The lingual branch of the anteroloph always joins the base of the protocone, while the labial branch joins the paracone base. The anterior synclines are generally narrow. Exceptions are HaH-5570 with a wider labial valley, and HaH-5572 with almost no lingual valley. The anterolophule is situated medially, and is a very short but strong spur towards the protocone. All teeth have well-expressed anterior and posterior protolophules, which, together with the paracone, define the labial side of the deep medial valley. In four teeth the anterior protolophule is more expressed than the posterior protolophule, while in three the two are of equal thickness. A special situation is present in HaH-5571, in which the posterior protolophule does not reach the paracone, but runs directly into the medial valley instead. In none of the M2s is a posterior paracone spur developed. At the labial border of the teeth the mesostyle is elongated and forms a weak ridge damming up the mesosinus. In two molars this ridge is absent. The long mesoloph is well-expressed and runs into the mesostyle at the labial border. However, two specimens (HaH-5337, 5585) have a shorter mesoloph which does not fuse with the mesostyle. In contrast to the M1, the mesoloph in M2 is transverse and not bent posteriorly towards the metacone. The deep sinus is transverse and closed by a lingual wall that is somewhat more expressed than in M1. Only one of the teeth considered (HaH-5570) has a strong entostyle. The posteroloph is always thick, massive and joins the metacone.

The morphology of the metalophule as well as of the posterosinus is highly variable. Therefore, it seems reasonable to describe each tooth separately. The evaluation of these features is, of course, dependent on the state of wear. In HaH-5335 the metalophule is separated into a stronger anterior branch and a weaker posterior branch. Therefore, the posterosinus is divided into two small basins. HaH-5572 shows a strong posterior metalophule from which a very weak anterior branch originates. This spur joins the hypocone. The posterosinus also has two parts and is labially closed by a short posteroloph. The strong posterior metalophule of HaH-5570 joins the posteroloph. The posterior metalophule additionally shows a very weak anterior edge. The posterosinus is a small, deep and labially closed basin. HaH-5571 has a well-developed posterior branch of the metalophule, which shows almost no connection to the metacone. A second robust spur, which originates at the hypocone/entoloph, points towards the metalophule but both are not connected. The posterosinus is identical to that of HaH-5572. The posterior metalophule of HaH-5338 forms a distinct branch turning to the posteroloph. A strong but short anterior spur branches off the posterior metalophule, but does not reach the hypocone/entoloph. The posterosinus is again small and labially closed. Specimen HaH-5585 features a weak posterior metalophule. There is a better developed spur originating at the posteroloph and pointing anteriorly towards the mesoloph. In spite of its considerable length this spur does not join the hypocone/entoloph. The posterosinus is divided into two small basins that are labially dammed up. In HaH-5586 the short and massive posterior metalophule bends backwards and joins the posteroloph. No anterior branch is present. The posterosinus is small and labially closed.

Summing up, two observations can be made: (1) there is a tendency to establish an anterior metalophule branch in addition to the posterior one, and (2) the posterosinus is always labially closed by a short posteroloph that joins the metacone. All M2s are longer than wide. The teeth have three roots of which the lingual one is significantly elongated and broad.

Upper third molar (Pl. 1, figs 6, 13–16; Tables 2–3). Seven M3s are present, three from the left and four from the right side. Four specimens are well-preserved while three specimens are heavily worn.

The labial branch of the anteroloph is well-developed and reaches the paracone. It closes the narrow anterosinus. The reduced lingual anteroloph branch is ledge-shaped and situated close to the anterior base of the protocone. Specimen HaH-5173 is somewhat more elongated and, therefore, shows a wider anterosinus. The protocone and paracone are very massive, while the posterior cones are always small and reduced. Only HaH-5347 features a small

EXPLANATION OF PLATE I

Figs 1–16. Upper molars of *Karydomys wigharti* sp. nov. from Hambach 6C. All SEM micrographs and $\times 18$ except where indicated. 1–3, M1 sin., holotype, HaH-5297. 1, occlusal view. 2, lingual view; $\times 12$. 3, oblique view from posterior; $\times 12$. 4, M1 dext. (inverse), HaH-5291, occlusal view. 5, M2 dext. (inverse), HaH-5585, occlusal view. 6, M3 dext. (inverse), HaH-5173, occlusal view. 7, M2 sin., HaH-5570, occlusal view. 8, M2 dext. (inverse), HaH-5571, occlusal view. 9, M2 sin., HaH-5572, occlusal view. 10–12, M2 dext. (inverse), HaH-5338. 10, occlusal view. 11, lingual view. 12, oblique view from posterior. 13, M3 sin., HaH-5350, occlusal view. 14–16, M3 dext. (inverse); HaH-5344. 14, occlusal view. 15, lingual view; $\times 16$. 16, oblique view from anterior.

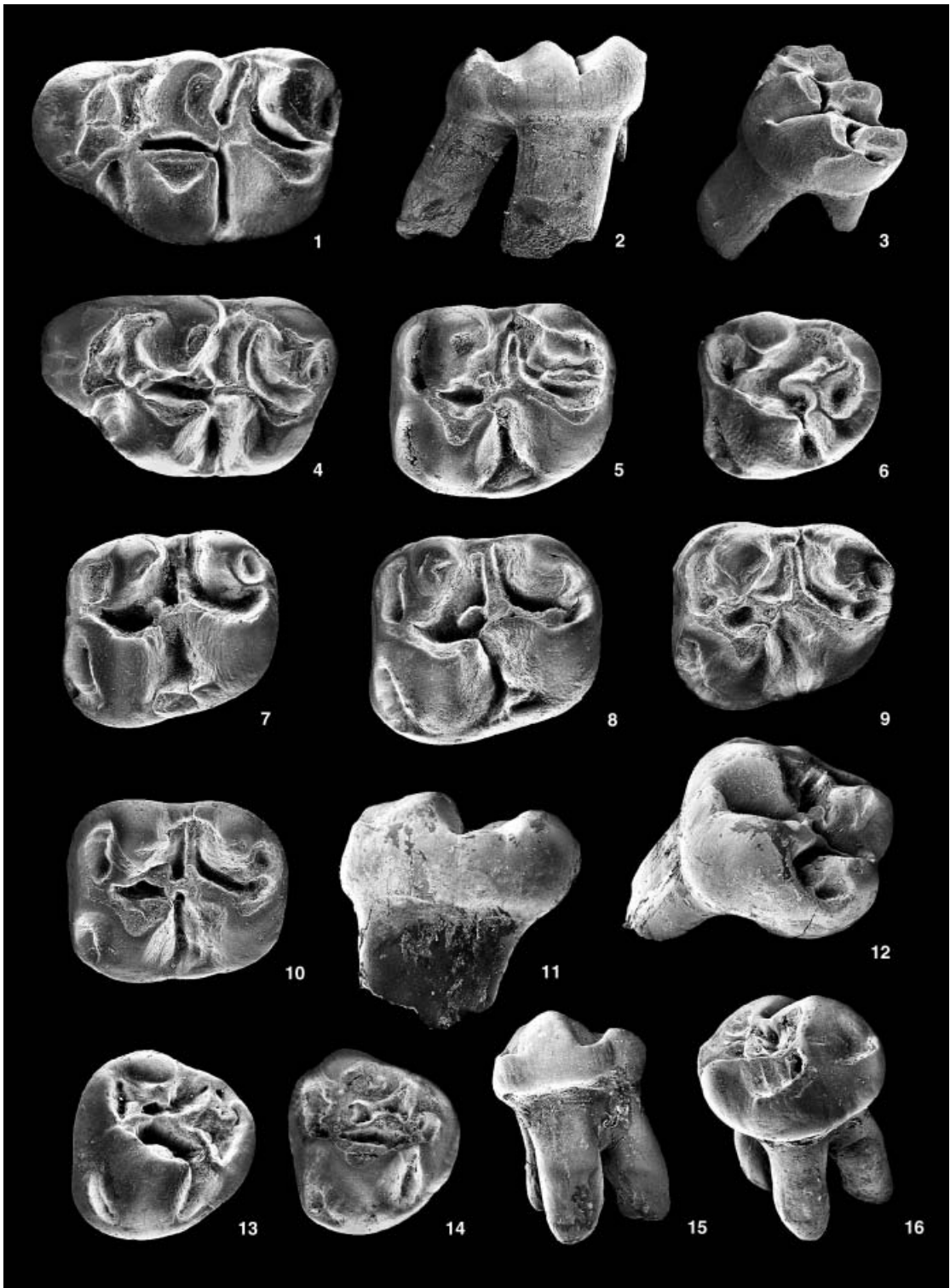


TABLE 3. *Karydomys wigharti* sp. nov. Size ranges of the molars from Hambach 6C (in mm).

	<i>n</i>	min.	max.		<i>n</i>	min.	max.
M1:				m1:			
Length:	4	2.80	3.04	Length:	5	2.36	2.48
Width:	5	1.84	2.04	Width:	6	1.68	1.80
M2:				m2:			
Length:	9	2.16	2.36	Length:	7	2.20	2.52
Width:	10	1.88	2.16	Width:	7	1.80	2.16
M3:				m3:			
Length:	7	1.48	1.80	Length:	3	2.12	2.16
Width:	7	1.68	1.92	Width:	2	1.72	1.80

paracone spur. The small hypocone, best developed in HaH-5344, is attached to the strong posteroloph, while the metacone is included in the posteroloph.

The ridge pattern existing between the four cones is variable. In HaH-5350, 5344 and 5347, a robust axioph originating from the hypocone is directed anteriorly and fuses with the anterolophule and the anterior protolophule. In HaH-5350 there is also a posterior protolophule present, but with no contact to the axioph. A neo-entoloph is always present and best developed and continuous in HaH-5344, while it is slightly interrupted in HaH-5350. This feature cannot be evaluated in HaH-5347. In HaH-5613 the axioph joins the posterior protolophule. The neo-entoloph is present but discontinuous. In HaH-5173 and HaH-5343 the axioph shows no anterior contact. HaH-5343 is so heavily worn that the neo-entoloph is no longer discontinuous and connects the protocone and hypocone. The sinus is always small and narrow. All M3s show a short and very thick metalophule, with the exception of HaH-5344, in which it is very weak.

The M3s have three somewhat oval roots. The anterolabial root is somewhat shorter and weaker than the other two, which are of equal length and thickness. The outline of the M3 is D-shaped and all specimens are of similar width and length. The maximum width can be taken at the level of the paracone-protocone complex.

Lower jaw (Text-fig. 2). Two right mandibles are preserved. Both lack the molars as well as all processi. Specimen HaH-6460 is more complete and shows the anterior part of the corpus mandibulae with all alveoli except the posterior root of the m3. This jaw retains an almost complete incisor. The second specimen (HaH-6461) shows the complete alveolar pattern, but the incisor tip is broken off, as well as the ventral and lingual part of the incisor alveolus.

In occlusal view, the corpus mandibulae is clearly inclined lingually. Therefore, the foramen mentale is not visible in occlusal aspect. The superior masseter crest is weak; the inferior crest is somewhat more expressed. Both crests join without forming a spur (V-shape) below the anterior root of the m1. The slope leading from the tooth row to the diastema is shallow. The foramen mentale is remarkably large and forms a rounded oval which opens labially.

Although the only preserved jaw with complete incisor (HaH-6460) lacks the cheek teeth, it seems that the tip of the incisor may have reached the level of the occlusal surface. The alveolar pattern of both mandibles shows two-rooted molars. This observation fits well with the molar construction. The anterior alveolus of m1 is round and the posterior one is oval. Both alveoli of m2 are oval, but the posterior one is larger and extends somewhat labially. The anterior alveolus of m3 has the oval shape and the size of the anterior alveolus of m2. The posterior alveolus of m3 is round and inclined backwards. The bony walls between the single alveoli are of equal thickness.

Lower first molar (Text-fig. 3A–B; Tables 3–4). Seven specimens, of which four are from the left and three from the right side represent this tooth position. Five m1s are well preserved, one has been heavily worn and one tooth has been much rounded by transportation.

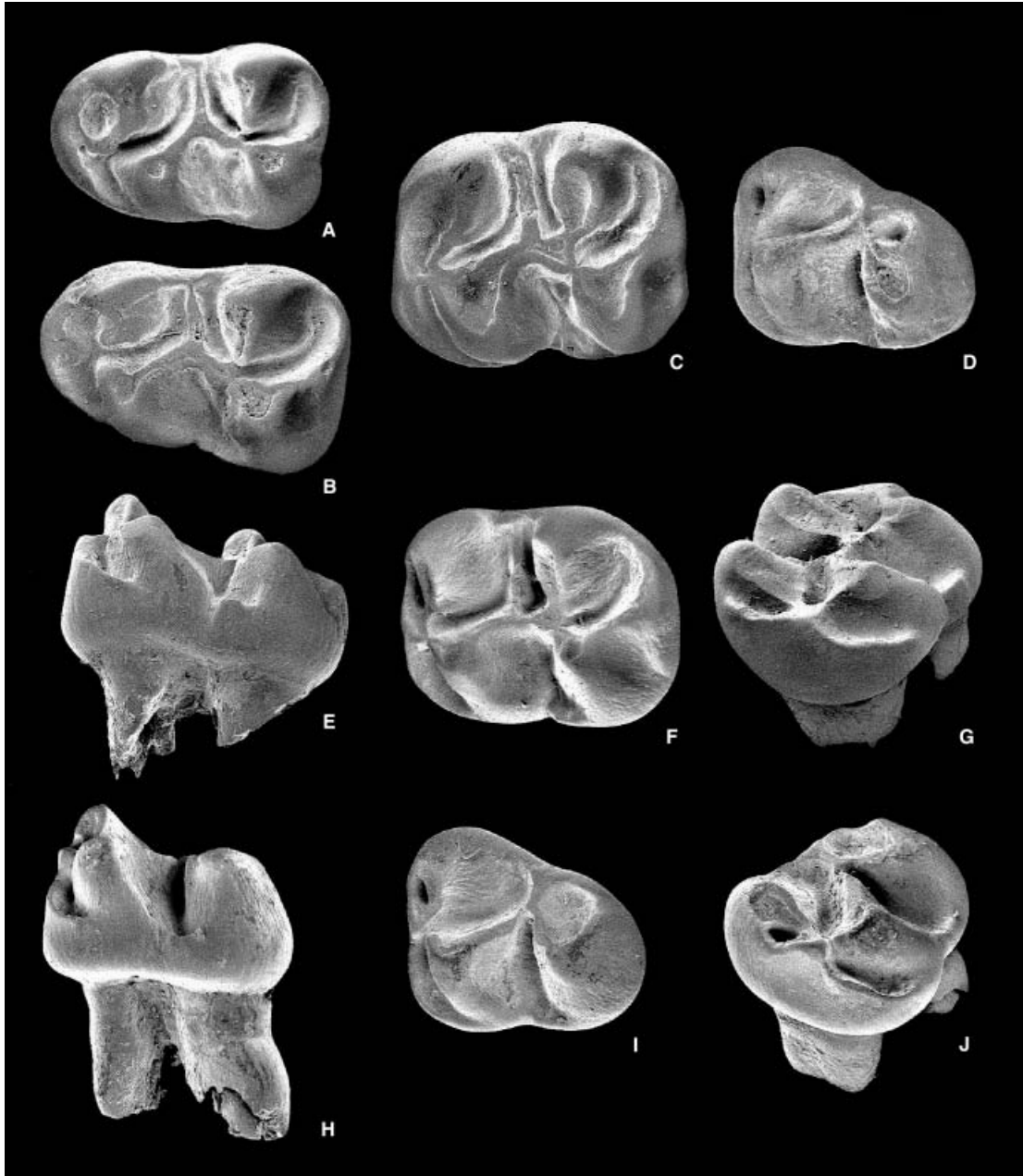
The anterior border of the tooth is short, blunt and semicircular. The anteroconid is also short and flattened. It forms no proper cone but is incorporated into the two branches of the anterolophid. These branches are connected to the protoconid and the metaconid respectively and dam up the narrow protosinusid and anterosinusid. The anterolophid is short and broad, but absent in HaH-5310. In most of the m1s the metalophid is bent anteriorly and is connected to the anterolophid. Only in HaH-5310 is the metalophid not expressed as a ridge but forms a conulid at the metaconid. In all specimens the mesolophid is long and reaches the lingual border of the tooth. The mesolophid is slightly directed towards the anterior. No distinct mesostylid can be detected, but a weak mesostylar ridge always closes the narrow mesosinusid. In only one tooth (HaH-5310) does a strong ridge run from the posterolingual border of the metaconid towards the mesolophid. A short hypolophid, which is bent anteriorly, connects the entoconid and



TEXT-FIG. 2. Lower right jaws with incisors *in situ* of *Karydomys wigharti* sp. nov. from Hambach 6C; $\times 3.7$. A–C, HaH 6460; D–F, HaH 6461. A, D, occlusal view; B, E, lingual view; C, F, labial view.

TABLE 4. *Karydomys wigharti* sp. nov. Measurements of the lower molars from Hambach 6C (in mm). *, figured specimen.

Tooth position	Length \times width	Inventory no.
m1 dext.	2.36 \times 1.76	IPB-HaH 5309
m1 dext.	2.48 \times 1.80	IPB-HaH 5317
m1 dext.	?2.52 \times 1.72	IPB-HaH 5569
m1 sin.	2.44 \times 1.68	IPB-HaH 5002
m1 sin. *	2.40 \times 1.76	IPB-HaH 5310
m1 sin.	2.40 \times 1.68	IPB-HaH 5311
m1 sin.	2.44 \times ?	IPB-HaH 5318
m2 dext. *	2.28 \times 1.96	IPB-HaH 5355
m2 dext.	2.30 \times 2.00	IPB-HaH 5364
m2 dext.	2.24 \times 1.96	IPB-HaH 5365
m2 dext.	2.28 \times ?	IPB-HaH 5594
m2 sin.	2.20 \times 1.80	IPB-HaH 5362
m2 sin.	?2.10 \times ?1.76	IPB-HaH 5363
m2 sin.	2.32 \times 1.96	IPB-HaH 5368
m2 sin. *	2.52 \times 2.16	IPB-HaH 5605
m3 dext.	2.12 \times ?	IPB-HaH 5374
m3 dext. *	2.12 \times 1.72	IPB-HaH 5623
m3 dext. *	2.16 \times 1.80	IPB-HaH 5624



TEXT-FIG. 3. Lower molars of *Karydomys wigharti* sp. nov. from Hambach 6C. All SEM micrographs and $\times 18$. A, m1 sin., HaH-5002. B, m1 sin., HaH-5310. C, m2 sin., HaH-5605. D, m3 dext. (inverse), HaH-5624. E-G, m2 dext. (inverse), HaH-5355. H-J, m3 dext. (inverse), HaH-5623. A-D, F, I, occlusal view; E, H, labial view; G, J, oblique view from anterior.

mesoconid. Three m1s show a well-developed ectomesolophid while it is absent in the remaining four. If present, the ectomesolophid is either of medium length, as in HaH-5318 and 5569, or is long and reaches the lingual border, as in HaH-5309. An ectostylar ridge dams up the sinusid at the labial border of the tooth. The posterolophid runs towards the base of the entoconid and thereby encloses the narrow but relatively long posterosinusid. The m1s show almost no labial posterolophid.

The m1s have two strong roots that are twice as long as the tooth is high. The anterior root is round while the posterior one is more oval. This morphology is in agreement with the configuration of the alveolar pattern in the two jaws. The m1s are longer than wide and the maximum width can be measured at the level of the entoconid-hypoconid complex.

Lower second molar (Text-fig. 3C, E–G; Tables 3–4). Four left and four right lower second molars are preserved. Three of them are in good condition while the other five are heavily worn. Additionally, one of these five has been rounded by transportation (HaH-5362) and one is damaged and lacks most of its labial part (HaH-5594).

In slightly worn teeth both branches of the anterolophid are of equal length. In more heavily worn teeth the labial branch appears to be longer than the lingual one, which then tends to be incorporated by the metaconid. The labial branch of the anterolophid ends at the anterior base of the protoconid. However, in one tooth (HaH-5605) the labial branch is considerably elongated and reaches the protoconid at its labial side, virtually forming a cingulum. The lingual branch encloses a very narrow anterosinusid.

Both the metalophid and the anterolophid are very short and directed anteriorly. They join the anterolophid/anteroconid separately. The mesolophid is usually long and reaches the lingual border (six specimens) but is of medium length in two specimens. It is directed slightly anteriorly. A short and weak ridge closes anterolingual the narrow mesosinusid. There is no distinct mesostylid. The sinusid is also narrow and bent towards the anterior. An ectostylar ridge dams up the labial side of this valley. A true ectostyle is present in HaH-5355 and 5605, but was probably also present in the heavily worn tooth HaH-5364. Only two specimens show a very weak ectomesolophid. In HaH-5364 it is long but not connected to the ectolophid, while in HaH-5605 the ectomesolophid is very short but originates from the ectolophid. The very short and strong hypolophid is slightly bent towards the anterior and merges into the ectolophid/mesoconid. The strong posterolophid, which is attached to the ectoconid, defines the posterior border of the tooth. The long posterolophid encloses a deep and narrow posterosinusid. The less worn teeth show a very weak labial posterolophid, with the exception of HaH-5605, where this feature is somewhat better expressed.

The m2s have two transversely oriented roots of equal length. Both roots show two separated neuritic openings. The anterior root is more or less rectangular, while the posterior root is remarkably much stronger and slightly asymmetrical as a result of its more pronounced labial part. The posterior root is somewhat shifted towards the labial side. This corresponds with the observed alveolar pattern in the jaws. The outline of the m2 is basically rectangular, but the teeth are somewhat narrower between the anterior and posterior pair of conids.

Lower third molar (Text-fig. 3D, H–J; Tables 3–4). All three lower molars are from the right side. Two are in excellent condition while the third is rounded as a result of transportation and therefore damaged anteriorly.

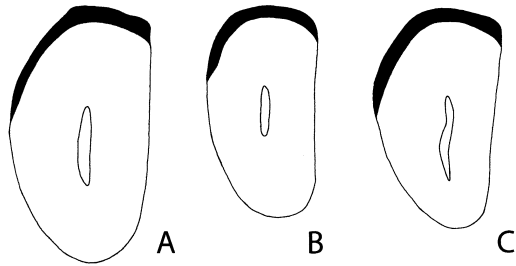
The lingual branch of the anterolophid is very short and joins the metaconid at its anterior border. Thus, the lingual branch encloses a minute but deep anterosinusid. The labial branch is longer and runs towards the labial border. The short and strong metalophid is directed anteriorly.

The transverse sinusid is narrow and deep. It is closed by a weak cingulum. The hypoconid is well-developed in contrast to the entoconid, which is part of the short posterolophid. Together with the short hypolophid, they enclose the posterosinusid, which is deep and funnel-shaped.

The m3s have two roots whose long axes are approximately at right angles to each other. The anterior root is rectangular, transversely oriented and has two neuritic openings. The posterior root is longitudinally oriented, round and directed slightly posteriorly. The terminal part of this root is damaged in all three specimens. The root morphology corresponds to the alveolar pattern of the two preserved jaws.

The teeth are longer than wide, with their maximum width at the level of the protoconid-metaconid complex. Since the posterolingual part of the m3 is markedly reduced, the m3s appear wedge-shaped.

Lower incisor (Text-figs 2, 4). Eight isolated fragments of lower incisors are identical in size and outer enamel ornamentation with the *in situ* incisors of the two jaws. Five come from the left and three from the right side. The enamel band of the lower incisor extends far to the labial side, covering about half of the tooth diameter. In contrast to the unusually thick molar enamel, the incisor enamel is not thickened in comparison to other hamsters. The incisor is oval in cross-section, but shows a distinct flattening of the mesial side. Apart from a very shallow longitudinal edge the outer enamel surface of the lower incisor is smooth. The wear facet of the tip is elongated.



TEXT-FIG. 4. Incisor cross sections of *Karydomys wigharti* sp. nov. showing the oval shape, a distinct flattening of the lingual tooth border, and the relatively labial extension of the enamel band. The shallow longitudinal edge can only be perceived in A. All $\times 16$. A, HaH-6464; B, HaH-6463 (inverse); C, HaH-6470.

Incisor enamel microstructure (Text-fig. 6A, C). Three lower incisors were examined (HaH-6463, 6464, 6470). The Portio interna (PI) consists of Hunter-Schreger-bands (HSB) orientated diagonally relative to the long axis of the tooth. The PI is divided into two layers owing to the changing orientation of the interprismatic matrix (IPM). Starting at the enamel-dentine-junction (EDJ) the apomorphic inner layer of the PI (IPI) shows IPM that is rectangular to the prism direction (Kalthoff 2000, p. 99). In the outer layer of the PI (OPI), the IPM runs parallel to the prisms, representing the more primitive condition. Close to the lateral end of the enamel band, only one layer with parallel-running IPM can be observed. This two-part PI is best seen in the longitudinal section (Text-fig. 6C). The Portio externa (PE) is made up of radial enamel, which fades out towards the outer enamel surface into very thin, prismless enamel (PLEX).

The thickness of the enamel band is uneven. It measures about $90\ \mu\text{m}$ in the centre, but rises to $115\ \mu\text{m}$ at the bend to the lateral side, where a shallow edge ('Kante' *sensu* Kalthoff 2000) is present. All three layers measure about $30\ \mu\text{m}$ each close to the centre and thicken more or less evenly by $5\text{--}10\ \mu\text{m}$ in the range of the shallow edge.

Remarks. *Karydomys wigharti* is the largest cricetid of the Hambach 6C fauna and the second most frequent one. It is represented by two partly fragmented mandibles, 41 molars, and eight lower incisor fragments. Based on characteristic molar features, such as thick enamel layer, typical tooth morphology and size, the cheek teeth can be clearly assigned to *Karydomys* Theocharopoulos, 2000.

Karydomys wigharti differs significantly from *K. symeonidisi* (type species), *K. boskosi* and *K. dzerzhinskii* in its larger size as well as other morphological features. It differs from *K. zapfei*, the only species with which it can be confused, in having (1) larger upper molars; (2) M1 with a broader, box-shaped and slightly split anterocone; (3) M1 usually with a long mesoloph; (4) M2 with a shorter anterolophule and narrower first synclines; (5) M2 with a strong tendency to establish a posterior metalophule and a small posterosinus; (6) more reduced M3 with a weak lingual anteroloph, a small sinus and a weak hypocone; (7) m1 with a very weak or absent labial posterolophid.

The lower incisors, which have not previously been known in *Karydomys*, feature a mesial enamel band of *Democricetodon*-like morphology. Since isolated upper incisors of democricetodontines are difficult to distinguish from those of other rodents of similar size, identification of this tooth position is not possible at present.

The lower jaw of *Karydomys* was also not previously known. The lower jaw of *K. wigharti* resembles the mandibles of *Democricetodon* and *Fahlbuschia*, but not those of *Cricetodon*. The inferior masseter crest is somewhat more expressed as in *Democricetodon* and *Fahlbuschia* but is much less pronounced than in *Cricetodon*. In *Karydomys wigharti* both crests join below the anterior root of the m1, forming a V, just as in *Democricetodon* and *Fahlbuschia*. In contrast, the crests in *Cricetodon* meet below the posterior root of the m1, and the lower crest is continuous anteriorly, forming a prominent spur (Y-shaped). The slope leading from the tooth row to the diastema is somewhat shallower in *Karydomys wigharti* than in *Democricetodon* from Sansan and resembles the morphology of *Fahlbuschia larteti* from La Grive M. The remarkably large foramen mentale of *K. wigharti* opens labially, as in *Democricetodon* and *Fahlbuschia*. *Karydomys wigharti* differs from *Cricetodon*, which shows a small, narrow foramen mentale that opens more anteriorly. The general alveolar pattern of *K. wigharti* with two-rooted molars resembles that of *Democricetodon* and *Fahlbuschia*.

Distribution and stratigraphical range. According to present knowledge, *Karydomys wigharti* is geographically restricted to central Europe and only known from Germany (Hambach 6C), Switzerland

(Chatzloch, Rümikon, Uzwil-Nutzenbuech, Wiesholz), Slovakia (Neudorf-Spalte 1), Czech Republic (Strakonice) and Poland (Bełchatów B). Its stratigraphical range is exceptionally short, being restricted to Mammalian Neogene biozones MN 5 and MN 6 (middle Miocene), which correspond to the transition Orleanian/Astaracian.

SYSTEMATIC POSITION

Assignment to the genus Karydomys

The fairly rich material of *Karydomys wigharti* from Hambach 6C shows the typical features given by Theocharopoulos (2000) in his diagnosis of the genus: inflated cusps; a small posterosinus on M1 and M2; strongly reduced M3 and m3; low and short anteroconid of m1 placed close to the proto- and metaconid. The genus *Karydomys* is characterized by thick molar enamel.

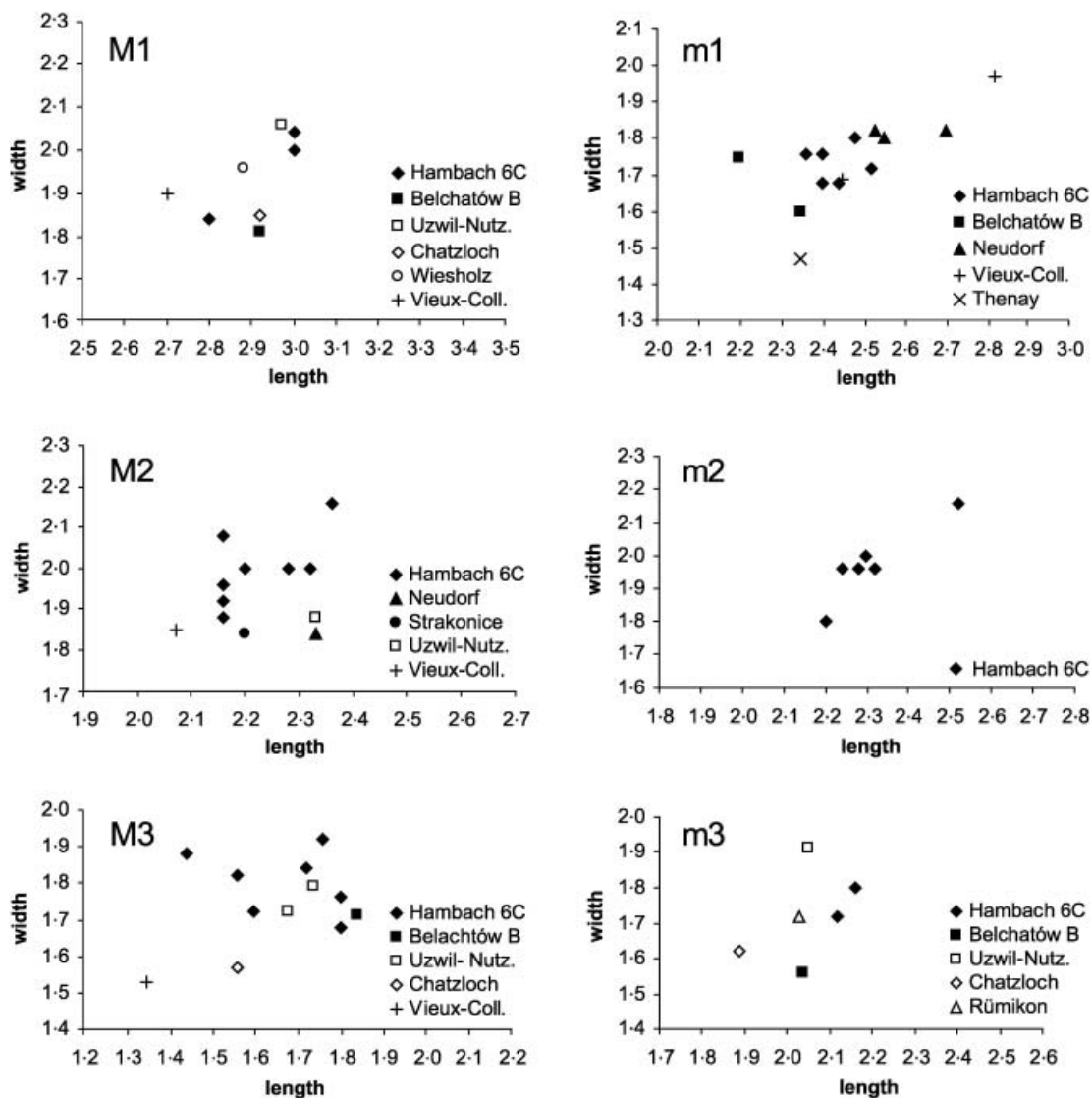
Comparison of K. wigharti with other species of Karydomys

Despite the general similarity there are a number of characteristics separating the five species of *Karydomys*. The early Miocene *K. dzerzhinskii* Kordikova and de Bruijn, 2001 from the Aktau Mountains in south-east Kazakhstan can be clearly distinguished from *K. wigharti* by its much more primitive morphology and significantly smaller molar size. Kordikova and de Bruijn (2001) regarded *K. dzerzhinskii* as the possible ancestor of the type species *K. symeonidisi* Theocharopoulos, 2000 from Karydia in Greece. The M1 of *K. symeonidisi* and also of *K. boskosi* from Karydia feature a discrete and relatively long anterocone (Theocharopoulos 2000). In contrast, this cusp is always shortened and blunt in the stratigraphically younger *K. wigharti*. Another difference from the two Greek species is the general absence of the posterior paracone spur in the M1 and M2 of *K. wigharti*. The mesoloph in the M1 and M2 of *Karydomys* varies from absent to long, but is usually long in *K. wigharti*. In all *Karydomys* species the metalophule is bent posteriorly in M1, while the orientation of the metalophule is still variable in M2. The M1 and M2 of *K. wigharti* generally show a doubled protolophule enclosing a distinct, deep medial valley. The Greek species are not consistent in this feature.

In contrast to *K. symeonidisi*, whose m1s always have a long ectomesolophid, this feature is variable in *K. wigharti*. Like the mesoloph in the upper molars, the mesolophid varies in length in the m1 and m2 in all *Karydomys* species. In other respects the m2 and m3 of *K. wigharti* are morphologically very similar to those of *K. symeonidisi*. In comparison to the two Greek species, *K. wigharti* differs considerably in its larger size.

K. wigharti is characterized by a wide consistency in molar morphology with *K. zapfei*. This was already mentioned by Garapich and Kälin (1999) in their description of Polish and Swiss material of *Lartetomys* cf. *zapfei*, which we attribute here to *K. wigharti*. However, compared to the five molars of *K. zapfei* from the type locality, Vieux-Collonges in France, the material from Hambach 6C shows some more advanced features, indicating a somewhat more derived condition.

The upper molars of *K. wigharti* from Hambach 6C and from the other central European localities are in general larger than the teeth from Vieux-Collonges (Text-fig. 5). The M1s from Hambach 6C, Bełchatów B, Chatzloch and Uzwil-Nutzenbuech (Garapich and Kälin 1999) differ from those of *K. zapfei* in having a broader, box-shaped anterocone, which is slightly split. The anterior part of the M2 from Hambach 6C, Uzwil-Nutzenbuech and Strakonice (Fejfar 1974) is shortened: the antero- and protosinus are narrower than in the M2 from Vieux-Collonges, in which the anterolophule forms a distinct ridge. The posterior part of the M2 from Hambach 6C and Uzwil-Nutzenbuech is characterized by a posterior metalophule and a very small and deep posterosinus. Only one Hambach 6C specimen (HaH-5335) corresponds to the M2 of *K. zapfei*, which has a dominant anterior metalophule and larger posterosinus. The M3s from Hambach 6C, Chatzloch and Uzwil-Nutzenbuech show a higher degree of reduction than those from Vieux-Collonges in featuring a weak lingual anteroloph, a small sinus and a small hypocone. The m1s from Hambach 6C and Neudorf-Spalte 1 (Fejfar 1974) have almost no labial posterolophid which, in contrast, is well-developed in the two molars of *K. zapfei*. It should be mentioned that one m1 from Vieux-Collonges (FSL 65 666) seems to lie outside the size range of *K. zapfei*, as well as of *K. wigharti*. On the other hand, it seems too



TEXT-FIG. 5. Dimensions of upper and lower molars of *Karydomys wigharti* and of *K. zapfei* from different localities.

small to belong to *Lartetomys mirabilis*. The m2 and m3 of *K. wigharti* cannot be compared with *K. zapfei*, since these tooth positions are not known in the latter.

The Hambach 6C material provides the first opportunity to study the variation in the molar morphology and size of middle Miocene species of *Karydomys*. The great morphological variability mentioned by several authors (Fejfar 1974; Garapich and Kälin 1999; Kälin 1999) clearly shows that at least two different species are present in the central and western European material of *Karydomys*. The relatively limited variation in the best-known middle Miocene *Karydomys* population, Hambach 6C, strongly indicates a separate species, presumably restricted to central Europe. The small number of specimens of *K. zapfei* from Vieux-Collonges remains a major problem. This makes it difficult to compare the morphological and size variation in *K. wigharti* with that of the presumably smaller and more primitive *K. zapfei*.

SYSTEMATIC POSITION OF *KARYDOMYS* WITHIN THE CRICETIDAE*Previous knowledge*

Molars. The systematic position of *Karydomys* within the Cricetidae has long been enigmatic for two reasons. Firstly, only a very limited number of isolated molars of *Karydomys* (= *Lartetomys*) *zapfei* and *K. wigharti* were known previously from a few localities in central and western Europe. Secondly, Mein and Freudenthal (1971, 1981) combined in the genus *Lartetomys* two morphologically very different cricetid species on the basis of only seven molars, *L. mirabilis* (two molars) and *K. zapfei* (five molars). Mein and Freudenthal (1971) placed their genus *Lartetomys* in Cricetidae *incertae sedis*, but mentioned that *L. mirabilis* had affinities to *Cricetodon* and *K. zapfei* to *Democricetodon*. In 1981 these authors placed *Lartetomys* in Cricetodontinae *incertae sedis*. Later authors (Fejfar 1974; Garapich and Kälin 1999; Kälin 1999) emphasized that the molar morphology of *K. zapfei* and *K. wigharti* resembles that of the genus *Democricetodon*. Nevertheless, with the limited material known the systematic position of *Karydomys* remained unresolved until Theocharopoulos (2000) classified it as a democricetodontine hamster on the basis of the fairly rich Greek molar material.

New results based on the material from Hambach 6C

Lower jaws. The characteristic mandibular features described in Mein and Freudenthal (1971) show that the lower jaws of *Karydomys wigharti* are most similar to those of *Democricetodon* and *Fahlbuschia*, and differ clearly from those of *Cricetodon*. *Karydomys* and the democricetodontines share the position, shape and size of the foramen mentale, shape and the distinctness of the masseter crests, and shape of the diastema.

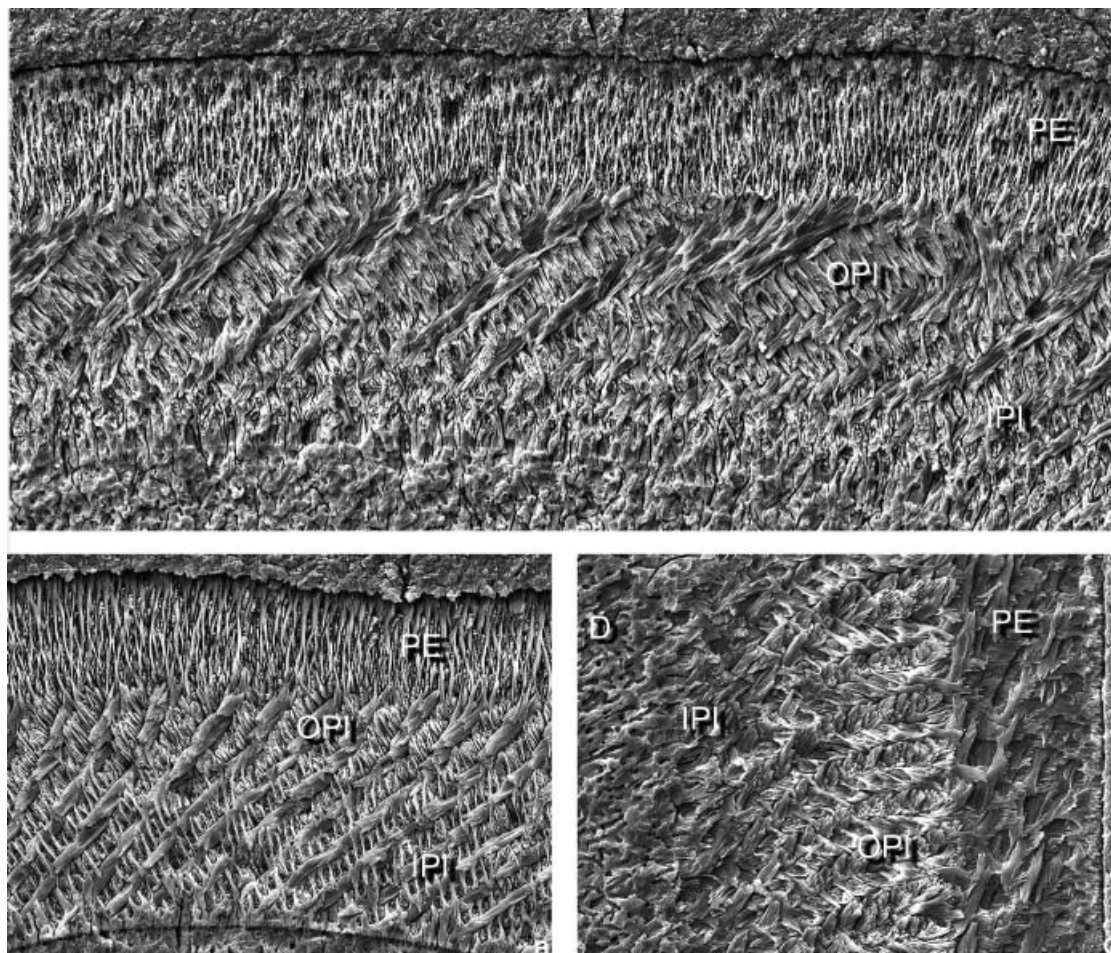
Incisor enamel microstructure (Text-fig. 6). The schmelzmuster of *Karydomys wigharti*, with its diagonally orientated HSB differs from that of *Cricetodon*, which consists of longitudinally oriented HSB. In addition, the more derived schmelzmuster of *Cricetodon* shows narrowly bent HSB, a characteristic feature which is called 'central syncline' (von Koenigswald 1997b; Kalthoff 2000) and is not present in *Karydomys*. In contrast, the schmelzmuster of *Karydomys* resembles that found in different species of *Democricetodon*. *Karydomys* seems to be a little more primitive than the analysed species of *Democricetodon* in the equal thickness of the two PI layers. *Karydomys* also shares a similar schmelzmuster with *Fahlbuschia*, but in this genus the enamel band shows transversely orientated HSB in the mesial part. Since only one unquestionable specimen of *Fahlbuschia*, *F. larteti* (KOE 2304), was available for this study, the above observation has yet to be proved characteristic of the whole genus.

The new finds from Hambach 6C now provide two additional sets of characters for classification that were previously unavailable: jaw morphology and the morphology and enamel microstructure of the lower incisor. Evaluating all three character sets we can now attribute the genus *Karydomys* without any doubt to the Democricetodontinae *sensu* Theocharopoulos (2000) (= Copemyinae Jacobs and Lindsay, 1984).

THE FOSSIL RECORD OF *KARYDOMYS*

The stratigraphically earliest record of the genus *Karydomys* comes from the upper Lower Miocene (MN 4) of Greece and Kazakhstan. *Karydomys dzerzhinskii* from the Aktau Mountains in south-east Kazakhstan is the smallest and probably the most primitive species of the genus (Kordikova and de Bruijn 2001). Two species are known from Karydia in Greece (Text-fig. 1), the smaller *K. boskosi* and the larger type species *K. syeonidisi* (Theocharopoulos 2000). With three known species, *Karydomys* is quite diverse as early as MN 4 without having reached south-western and central Europe.

Only the species *K. zapfei* is known from the lower Middle Miocene of south-west Europe. It is larger and stratigraphically younger than the species from south-east Europe and Kazakhstan. *K. zapfei* is known from the French localities Vieux-Collonges, which is traditionally correlated with MN 4/5, and the MN 5



TEXT-FIG. 6. Incisor enamel microstructure of *Karydomys wigharti* sp. nov. from Hambach 6C (HaH 6463) and of *Democricetodon crassus* from Sansan (KOE 2309). All SEM micrographs; *c.* $\times 600$. A, c, *Karydomys wigharti*. A, transverse section showing the typical schmelzmuster of the democricetodontines, with diagonally orientated Hunter-Schreger-bands (HSB): the Portio interna (PI) consisting of two layers (IPI, inner PI; OPI, outer PI) and the Portio externa (PE) with radial enamel. B, *Democricetodon* exhibits the same schmelzmuster as *Karydomys*, but has a PI with a somewhat thicker inner portion and consequently a thinner outer portion. C, longitudinal section showing the three layers; D, dentine.

reference locality Pont Levoy-Thenay (Mein and Freudenthal 1971, 1981; Ginsburg and Sen 1977; Bruijn *et al.* 1992; Mein 1999). We have to mention here that most of the fissure-filling of Vieux-Collonges is contemporaneous with the Pont Levoy-Thenay deposit. However, there is evidence that besides the MN 4 faunal elements, taxa typical of MN 6 are also mixed in the Vieux-Collonges fissure (K. Heissig, pers. comm. 2003).

A second large species, *K. wigharti*, can be recognized in the middle Miocene of central Europe. In MN 5, it occurs in Hambach 6C and Strakonice (Czech Republic; Fejfar 1974, 1990) while in MN 6 the species is present in Rümikon (Switzerland; Garapich and Kälin 1999) and in Wiesholz (Switzerland; Bolliger 2000). The biostratigraphical settings of Chatzloch and Uzwil-Nutzenbuech are somewhat uncertain, since they have been attributed to MN 5/6 (Garapich and Kälin 1999) or to MN 6 (Uzwil-Nutzenbuech; Kälin

1999). The same is true for Bełchatów B, which has been correlated with MN 5 (Kowalski 1993; Mein 1999) and MN 5/6 (Rzebik-Kowalska 1994; Steininger *et al.* 1996). The fissure of Neudorf-Spalte 1 (Slovakia) is traditionally attributed to MN 6 (Fejfar 1974, 1990; Bruijn *et al.* 1992; Steininger *et al.* 1996). Recently, Mein (1999) also placed Neudorf-Spalte 1 in MN 6 but stated that the faunal composition is older than that of the MN 6 reference locality Sansan. In this context K. Heissig (pers. comm. 2003) mentioned that the fauna from Neudorf-Spalte 1 is not clearly distinguishable from faunas of late MN 5 localities. According to Bernor (*in* Steininger *et al.* 1996, p. 30) Neudorf-Spalte 1 'must predate MN 6 and is correlative therefore with MN 5'.

The presence of *K. wigharti* seems to be an argument for a late MN 5 rather than an MN 6 age for most of the localities. Thus, it coexists with *K. zapfei* in MN 5. Our present knowledge suggests that *K. wigharti* has the largest geographical distribution and consequently the best fossil record of all *Karydomys* species, since it has been reported from Switzerland and Germany to Poland and Slovakia (Text-fig. 1).

PALAEOECOLOGY OF *KARYDOMYS WIGHARTI*

The general scarcity of remains of *K. wigharti* makes it difficult to evaluate its ecological requirements. On the other hand, its astonishing frequency in Hambach 6C and scarcity elsewhere may lead to new ideas about its palaeoecology.

Evidence regarding the autecology of this large hamster comes in two forms in the material. Firstly, the thick molar enamel most probably reflects a crushing function, as already presumed by Garapich and Kälin (1999). However, their conclusion that the thick molar enamel of *K. wigharti* is linked to generally more arid climatic conditions cannot be confirmed for Hambach 6C. Secondly, *K. wigharti* does not exhibit extreme digging adaptations like, for example, living mole rats. Neither the enamel microstructure, nor the ornamentation, nor the cross section of the incisors show any of the features presented by Kalthoff (2000, p. 170). This does not mean, however, that *K. wigharti* was not able to construct subterranean burrows like recent hamsters.

The synecology of *K. wigharti* seems to include special habitat requirements. It is notable that, on the one hand, this hamster is extremely rare in exclusively terrestrial sites. This is true not only for fissure-fills and limnic-fluviatile molasse deposits (e.g. Uzwil-Nutzenbuech) but also for non-paralic lignite deposits (Bełchatów B). On the other hand, *K. wigharti* is also a rare species in a marine-influenced fissure-like Neudorf-Spalte 1.

The only locality in which *K. wigharti* is a dominant faunal element is Hambach 6C. There is further evidence that Hambach 6C represents an exceptional ecology, since it shows a unique faunal composition. Remarkable among the insectivores is the complete absence of *Galerix* in contrast to the abundance of *Lanthanotherium* and *Plesiosorex*. Among the rodents, *Fahlbuschia koenigswaldi* is the most frequent hamster in Hambach 6C and at the same time this is the first record of this species in central Europe. Among the artiodactyls, Hambach 6C is characterized by the occurrence of the extremely rare *Orygotherium escheri* and by the dominance of the otherwise rare *Dorcatherium guntianum*. In contrast, animals that require strictly dry habitats, like tortoises or ochotonids, are very rare (Mörs *et al.* 2000; Mörs 2002; Klein and Mörs 2003).

The only explanation for this unusual faunal association is that Hambach 6C represents an extremely wet habitat. Since the site is situated in the central part of a huge estuarine delta with its paralic coal swamps we must suppose a more or less complete absence of drier areas. This location consequently implies a long distance to the drier backcountry at the margins of the Lower Rhine Embayment. The wet habitat is confirmed by the frequency of semiaquatic mammals, such as the desmanine *Mygalea*, the beavers *Steneofiber* and *Anchitheriomys*, and two species of the tragulid *Dorcatherium* (Mörs *et al.* 2000; Mörs 2002).

Another possible reason for the unusually high frequency of *K. wigharti* in Hambach 6C might be its geographical position (Text-fig. 1). However, this argument is weakened by the fact that Bełchatów B is situated at the same northern latitude but has yielded only a few *Karydomys* remains.

Therefore, the general rarity of *K. wigharti* can only be attributed to specialized ecological requirements in a habitat that is rarely documented in the fossil record. This may also be true of *K. zapfei*.

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