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Arvicola mosbachensis (SCHMIDTGEN 1911) of Mosbach 2: a basic sample for the early evolution of the genus and a reference for further biostratigraphical studies

With 6 Text-figures, 2 Tables and 5 Plates

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Abstract

Arvicola materials from Mosbach 2, including the types of *A. mosbachensis* housed at the Forschungsinstitut Senckenberg Frankfurt am Main, are described. Six specimens display incipient root development. This population is therefore one of the oldest of the genus *Arvicola*. This is confirmed by SDQ and tooth length values indicating a primitive evolutionary stage. The age of the population correlates with either Cromer Interglacial III or IV.

The type material of *Arvicola cantianus* consists of a few fragmentary molars only. This scarce material does not permit a clear assessment of the most significant features in middle Pleistocene populations, rootless molars with negative enamel differentiation, and is not clearly distinguishable from either *Mimomys savini* or *Arvicola terrestris*. We therefore propose to restrict the name *A. cantianus* to the type material. All other middle Pleistocene *Arvicola* finds should be referred to *A. mosbachensis*.

Key words: Mammalia, Rodentia, *Arvicola*, Middle Pleistocene, phylogeny, taxonomy.

Kurzfassung

[*Arvicola mosbachensis* (SCHMIDTGEN 1911) von Mosbach 2: grundlegendes Material für das Verständnis der frühen Evolution der Gattung *Arvicola* und ein Richtmaß für weitere biostratigraphische Untersuchungen.] — Die im Forschungsinstitut Senckenberg in Frankfurt am Main aufbewahrten *Arvicola* Reste von Mosbach 2, einschließlich des Typusmaterials von *A. mosbachensis*, werden beschrieben. Die an sechs Exemplaren zu beobachtende beginnende Wurzelbildung belegt, daß es sich hierbei um eine der ältesten *Arvicola* Population handelt. Die SDQ-Werte sowie die Zahnlängen verweisen ebenfalls auf ein primitives Evolutionsniveau. Das Alter der Population kann mit dem Cromer Interglazial III oder IV korreliert werden.

Das Typusmaterial von *Arvicola cantianus* besteht nur aus wenigen fragmentarischen Molaren. Hierbei kann die Ausbildung der für die taxonomische Zuordnung der mittelpleistozänen *Arvicola* Funde wichtigen Merkmale, Wurzellosigkeit der Molaren und negative Schmelzdifferenzierung, nicht eindeutig festgestellt werden. Das Material ist somit weder von *Mimomys savini* noch von *Arvicola terrestris* eindeutig abgrenzbar. Daher wird vorgeschlagen, die Verwendung des Namens *A. cantianus* auf das Typus Material zu beschränken. Alle anderen mittelpleistozänen *Arvicola* Funde sollten zu *A. mosbachensis* gestellt werden.

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Contents

Introduction

Finds of the *Mimomys savini – Arvicola* lineage are used extensively in the biostratigraphic subdivision of the Pleistocene in Eurasia (e. g. JÁNOSSY 1969; KOENIGSWALD 1973; FEJFAR & HEINRICH 1980; ZAZHIGIN 1980; KOLFSCHOTEN 1990; KOENIGSWALD & KOLFSCHOTEN 1996). One of the reasons is that these voles are widespread and often numerous. The other reason is that the main characters that distinguish evolutionary stages – the presence or lack of roots, and relative enamel thickness of the posterior to the anterior cutting edges of the molars – can be clearly defined.

The ancestor of *Arvicola* LACÉPÈDE 1799, *Mimomys savini* HINTON 1910 (e. g. CHALINE 1972; AGADZHANYAN 1983; KOENIGSWALD & TOBIEN 1987; KOENIGSWALD & KOLFSCHOTEN 1996), already possesses hypsodont but still rooted molars. The increasing hypsodonty eventually leads to the loss of roots. Another tendency relates to changes in the relative thickness of the enamel cutting edges. Contrary to the situation in *Mimomys savini*, and in ancient *Arvicola*, in most of the recent Eurasian populations of *Arvicola* the enamel walls are thinner in the posterior edges of the lower molars and in the anterior edges of the upper ones. In addition, the occlusal surface patterns of the M/1 change somewhat with time, and the length of this tooth also increases.

All features are, however, variable within populations. On the basis of their different developmental degree in recent populations within the whole distribution range (RÖTTGER 1987) one can therefore also expect regional differences in the fossil record. The evolution of these features can be safely assessed only by statistical evaluation and further biostratigraphic studies require well-defined samples.

Consequently, the present situation where the poorly preserved type material of *Arvicola cantianus* (HINTON 1910) from Ingress Vale, Kent, England, is considered as the reference for the ancestral stage of the genus is not satisfactory. On the other hand, the well known German locality of Mosbach 2 has been providing an increasingly rich material of *Arvicola*, re-examination of which now enables us to suggest a much better reference for this early stage of the evolution of water voles of the genus *Arvicola*. In this article a rather large *Arvicola*-sample from Mosbach 2 is documented and its biostratigraphic and taxonomic implications discussed.

The Mosbach Sands

The so-called Mosbach Sands are fluviatile sediments of the rivers Main and Rhine, and are excavated industrially in the eastern part of Wiesbaden. On lithological and palaeontological grounds they can be subdivided into two parts of different stratigraphic age, Mosbach 1 and 2:

– Mosbach 1 ("Grobes Mosbach")
This section is dominated by coarse clastic sediments. In superimposed fine-granular sediments a palaeomagnetic reversal was recorded and interpreted as the Jaramillo Event (see BRÜNING 1978 and KOENIGSWALD & TOBIEN 1987). Thus, the fauna of Mosbach 1 is older than the base of this reversal. *Arvicola*-remains have not been recorded in that section.

– Mosbach 2 ("Graues Mosbach")
Sediments of the "Graues Mosbach" of 13 m thickness discordantly overlay the sediments of Mosbach 1. Within this sediment body several discordances suggest the existence of different fluviatile sequences. BRÜNING (1978) established a subdivision of the "Graues Mosbach" into Mosbach 2 and 3 (see also KOENIGSWALD & TOBIEN 1987). However, according to sedimentological and faunal investigations this subdivision is less likely.

The majority of small mammal remains including all *Arvicola* finds originate from Mosbach 2. The more recently collected remains from the area of the "Abbaufeld Ostfelder" (BAHLO & MALEC 1969, ANDRES 1971, and specimens collected by TH. KELLER) originate from medium grained to coarse sands of brown ochre to grey colour with frequently interstratificated fine gravels, but occasionally occurred also in greyish green medium to fine grained sands. *Arvicola* finds are known from all major parts of the Mosbach 2 profile.

Small mammal fauna composition and environment

We considered the complete materials housed at the Forschungsinstitut Senckenberg, Frankfurt am Main, and at the Naturhistorisches Museum/Landessammlungen für Naturkunde, Mainz, including previously published specimens (SCHMIDTGEN 1911; HELLER 1933; 1969, BAHLO & MALEC 1969; KOENIGSWALD & TOBIEN 1987) as well as newly collected stratified specimens (TH. KELLER, Landesamt für Denkmalpflege Hessen, Wiesbaden). The numbers of specimens in tab. 1 are based on all available dental and postcranial elements of *Desmana*, soricids, *Sciurus*, and *Lepus*; on humeri of *Talpa*; on P/4 of *Trogontherium* and *Castor*; and on M/1 of arvicolids. General overviews of the Mosbach mammalian faunas are provided by KAHLKE (1961), BRÜNING (1978) and KOENIGSWALD & TOBIEN (1987).

The striking predominance of *Arvicola* and the occurrence and abundance of beavers and desmans strongly suggest varied freshwater bodies such as rivers, abandoned river courses, and ponds with dense vegetation cover along the waters edge, and at least some patchy riparian forest. Among shrews, *Drepanosorex* and neomyines are also assumed to have been semiaquatic. On the other hand, the absence of typical forest species such as glirids and *Apodemus*, which would predominate in forested environments, suggests rather open conditions at least in the area of accumulation of the micromammal remains. Thus, we conclude a vast well-watered plain as the local Mosbach paleoenvironment.

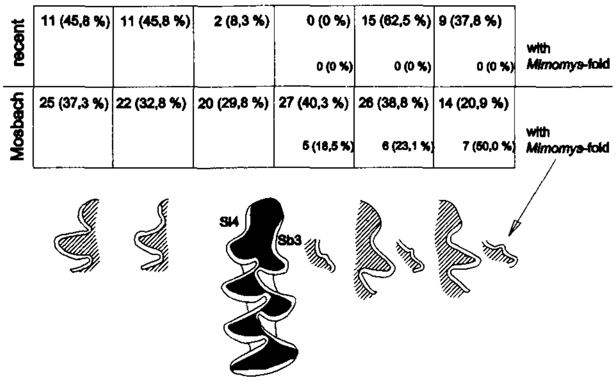
The composition of the micromammal fauna as represented in our samples generally resembles temperate present-day faunas of the same latitudes. The occurrence of *Lemmus* seems to contradict this assessment but the genus is known to be present in various kinds of early and middle Pleistocene ecosystems. Thus, temperate conditions for the Mosbach environment are most likely, although any more detailed climatic assessment is impossible due to our still poor understanding of relevant faunal characters during these periods.

Arvicola mosbachensis from Mosbach 2

The initial small sample of water voles from Mosbach was described by SCHMIDTGEN (1911) as *Microtus mosbachensis*. Later, both the type material and additional new material were referred to several species of *Arvicola*, including *Arvicola mosbachensis* (HELLER 1933, 1969). Even today, further remains are being collected. A large sample of material excavated from this site is now preserved at the Forschungsinstitut Senckenberg Frankfurt am Main. It consists of 102 sufficiently well preserved M/1, 23 M3/, and more than 150 other molars or fragments thereof. Among this material are the type specimens of *Arvicola mosbachensis*: one left mandible with M/1 and M/2 (SMF 74/4835, holotype: pl. 1 fig. 1) and 18 isolated molars (SMF 74/4836-53, paratypes: pl. 1 figs 2, 3, 5, 6). The catalogue numbers of the other M/1 and M3/ which are included in the present analyses, are SMF 99/1543-662. Many of the specimens were collected under stratigraphical control from the Mosbach profile.

Tab. 1. Fossil site Mosbach 2, numbers of specimens of small mammal remains (basing on all available elemts in *Desmana*, soricids, *Sciurus*, and *Lepus*, on humeri in *Talpa*; on P/4 in *Trogontherium* and *Castor*, and on M/1 in arvicolidis). *Microtus arvalinus* = Microtus nivaloides, and *Microtus ratticepoides* = M. nivalinus according to REKOVETS & NADACHOWSKI (1995).

	M/1	other elements
Talpa ex gr. *fossilis*		67
Talpa minor		4
Desmana moschata		13
Sorcidae indet.		3
Sorex sp.		1
Drepanosorex savini		1
Neomyini indet.		2
Sciurus		1
Castor fiber		52
Trogontherium cuvieri		57
Lemmus sp.	4	
Clethrionomys acrorhiza	9	
Pliomys episcopalis	2	
Arvicola mosbachensis	456	
Microtus nivaloides	20	
Microtus hintoni	6	
Microtus nivalinus	1	
Lepus sp.		10



Text-fig. 1. Developmental degrees of Sl4 and Sb3 (forming an angle less than 90°, approximately 90°, and larger than 90°) of M/1, fossil specimens from Mosbach 2 and recent specimens of *Arvicola terrestris*.

The cheek teeth are hypsodont. Synclines are normally filled with crown cement which may be lacking in corroded specimens. Occasionally parts of the dentine are eroded. With the exception of two mandibular fragments, the molars are isolated. Most specimens are pictured in plates 1-5.

As is typical for *Arvicola*, the majority of molars have no trace of roots. Two M/1, however, (i. e. 2% of all M/1) and four M3/ (10% of all M3/) display different degrees of incipient roots. This is never seen in modern *Arvicola* teeth and contradicts the rootless condition commonly assumed for that sample (SCHMIDTGEN 1911; HELLER 1933, 1969). Similar stages of root development have been recently documented in *Arvicola* teeth of the localities Gura Dobrogei 4, Casian Cave, Romania (RADULESCU & SAMSON 1993), and Isernia, Italy (KOENIGSWALD & KOLFSCHOTEN 1996).

The mesial anteroconid complex (ACC) of the M/1 has synclines Sl4 and Sb3 developed to different degrees (text-fig. 1); in some specimens an additional anticline Ab4 is more or less conspicuous. The *Mimomys*-fold (= *Mimomys*-Kante) occurs in 27% of all specimens with preserved ACC. Compared with recent *Arvicola terrestris* (LINNAEUS 1758), the frequent occurrence of the *Mimomys*-Kante in the material from Mosbach, as well as the more shallow Sl4 and Sb3, indicate a rather primitive state of the ACC.

The occlusal surface of the M3/ is typical for *Arvicola*: three lingual and three buccal anticlines are divided by two synclines on each side. Additional synclines are developed on both sides to various extent. Usually, a confluence broader than in recent *Arvicola terrestris* is to be seen between the triangles T3 and T4.

All the molars of Mosbach 2 are smaller than in modern *Arvicola terrestris*. The measurements of the M/1 are documented in tab. 2. The mean length of the M3/ is 2.18 mm (min = 2.04 mm, max = 2.31 mm, n = 7, sd = 0.086).

As already mentioned, *Mimomys savini* and the early forms of *Arvicola* have thicker posterior edges than anterior ones on the lower molars; it is the reverse on upper molars.

Tab. 2. M/1 measurements of several middle and late Pleistocene populations of *Arvicola*: length, SDQ (the relative thickness of the posterior cutting edges of all anticlines expressed as a percentage of the corresponding anterior cutting edges), SZQV (the relative thickness of the anterior cutting edges of all anticlines expressed as a percentage of the occlusal length of the tooth), SZQH (the relative thickness of the posterior cutting edges of all anticlines expressed as a percentage of the occlusal length of the tooth):

Locality	Taxon	M_1 length [mm]						SDQ						SZQV						SZQH					
		n	min	x	max	Sx	sd	n	min	x	max	Sx	sd	n	min	x	max	Sx	sd	n	min	x	max	Sx	sd
Euerwanger Bühl	*Arvicola terrestris*	27	3,70	4,092	4,44	0,032	0,164	27	74,91	83,029	94,52	0,809	4,206	27	2,01	2,338	2,67	0,030	0,156	27	1,66	1,933	2,52	0,033	0,170
Burgtonna 2	*Arvicola terrestris*	41	3,40	3,762	4,42	0,034	0,214	40	76,34	99,651	116,95	1,466	9,275	40	1,44	1,879	2,32	0,035	0,217	41	1,54	1,854	2,35	0,032	0,200
Stuttgart-Untertürkheim	*Arvicola mosbachensis*	37	3,40	3,808	4,24	0,037	0,225	37	88,41	101,188	130,00	1,528	9,294	37	1,57	1,925	2,35	0,032	0,197	37	1,66	1,930	2,32	0,023	0,142
Petersbuch 1	*Arvicola mosbachensis*	10	3,50	3,651	4,00	0,050	0,159	11	107,87	126,157	146,40	3,730	12,383	10	1,40	1,744	2,11	0,086	0,272	10	1,93	2,184	2,59	0,064	0,203
Bilzingsleben 2	*Arvicola mosbachensis*	9	3,40	3,584	3,88	0,061	0,182	9	122,43	132,102	146,19	3,184	9,551	9	1,35	1,749	2,12	0,085	0,255	9	1,97	2,333	2,75	0,091	0,272
Miesenheim 1	*Arvicola mosbachensis*	9	3,40	3,482	3,60	0,027	0,082	9	123,32	140,620	155,26	3,382	10,147	9	1,48	1,706	2,04	0,078	0,235	9	2,12	2,365	2,69	0,067	0,199
Mosbach 2	*Arvicola mosbachensis*	44	3,06	3,254	3,50	0,017	0,115	45	117,60	133,340	159,27	1,728	11,593	44	1,46	1,949	2,44	0,045	0,297	44	1,90	2,555	3,13	0,042	0,281
Voigtstedt	*Mimomys savini*	16	3,30	3,528	3,71	0,038	0,153	10	121,60	139,090	165,94	3,218	11,136	10	1,80	2,130	2,44	0,074	0,233	10	2,49	3,017	3,53	0,095	0,299

The primitive differentiation has been defined as 'negative' and evolves into a 'positive' one (MARTIN 1987). The percent relation of the posterior to the anterior cutting edges in M/1 is expressed by the parameter SDQ (Schmelzband-Differentierungs-Quotient) which was devised by HEINRICH (1978; for details see also HEINRICH 1982). Another index (SZQ, see HEINRICH 1982) concerns the enamel thickness relative to the length of the tooth. In contrast to the modern *Arvicola terrestris*, the enamel differentiation is negative in all lower cheek teeth and positive in all upper ones (for M/1 see tab. 2).

Chronological implications and discussion

The *Arvicola* population of Mosbach 2 has been compared with *Arvicola* remains from other German localities. Some of the features described above provide a suggestion of the relative order of the populations.

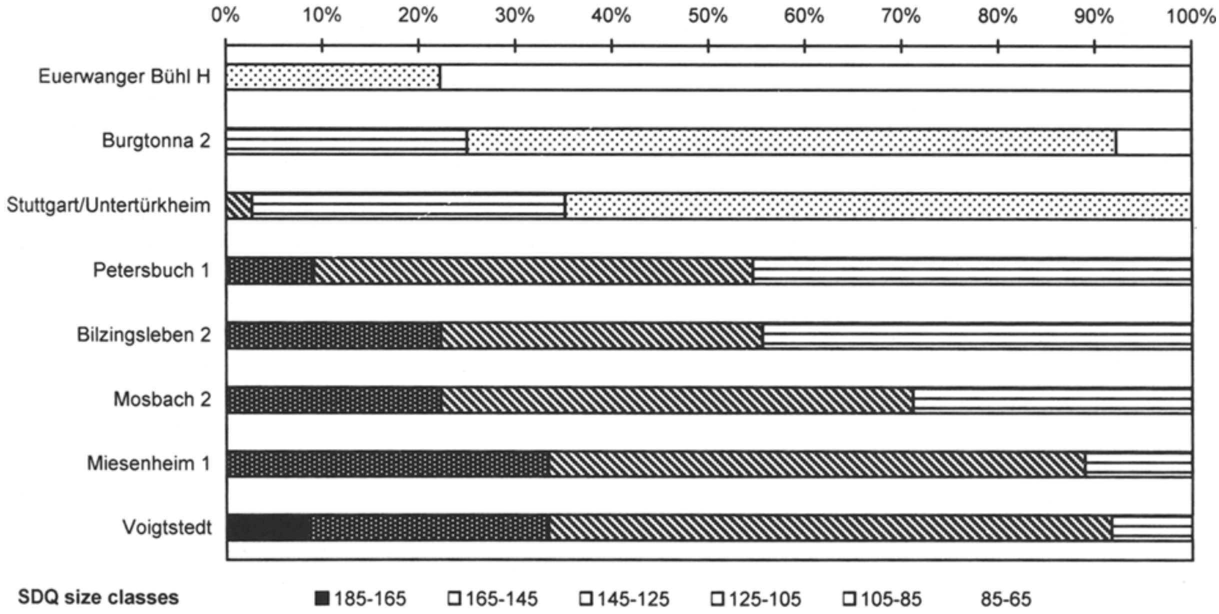
All the *Arvicola* populations mentioned in tab. 2 are completely rootless with the exception of Mosbach 2. According to this character, Mosbach 2 is the oldest *Arvicola* fauna and therefore appears even older than Miesenheim 1 where the absence of roots was established in a sample of more than 150 specimens (KOLFSCHOTEN, in litt.).

A general and rather consistent decrease of the SDQ has been documented for numerous middle and late Pleistocene water vole populations in Europe (HEINRICH 1982, 1987; KOLFSCHOTEN 1990; REKOVETS 1994). If we consider the percentages of specimens belonging in six classes of SDQ, Voigtstedt, Miesenheim 1, Mosbach 2, Bilzingsleben 2, Petersbuch 1, Stuttgart/Untertürkheim, Burgtonna 2, and Euerwanger Bühl H, a chronological succession may be observed (text-fig. 2). A similar succession can be seen when average values are considered for each population but with an inversion between Voigtstedt and Miesenheim 1 (text-fig. 3).

According to the M/1 length, the localities mentioned above can be ordered in the same way as according to the SDQ index, with the same exception: as for the root character, Mosbach 2 appears older than Miesenheim 1 (text-fig. 4). This compares well with the SZQH ratios (tab. 2). The ACC morphology shows less incised synclines in comparison to recent *Arvicola terrestris* but no clear comparison with other localities is possible so far.

In summary, according to the presence of incipient roots in some specimens, as well as M/1 length, SDQ, and SZQH, Mosbach 2 is older than Bilzingsleben, Petersbuch, Stuttgart/Untertürkheim, Burgtonna 2, and Euerwanger Bühl H. This is also in agreement with the species composition of these faunas: in Mosbach 2 there are taxa (*Talpa minor, Trogontherium, Pliomys*) which disappear during the later part of the middle Pleistocene but which still occur in the older faunas of this period (text-fig. 5). Beside Mosbach 2, Miesenheim 1 is the only other site with the co-occurrence of these taxa. Three characters (roots, M/1-length, SZQH) favour an older age for Mosbach 2 than Miesenheim. One, the SDQ places Mosbach 2 as younger.

Still it is not clear which character has the greatest biostratigraphic value. The transition to rootless molars is an irreversible process, and therefore this character seems to provide the strongest argument. Without doubt, the *Mimomys savini* population from Voigtstedt, with a domination of rooted molars, is older than all *Arvicola* faunas. Mosbach 2,



Text-fig. 2. SDQ size classes of M/1 of several fossil populations of *Arvicola*. Vertical bars indicate the maximum possible age range.

the only locality where incipient root creation could be observed, should be the next youngest fauna and older than Miesenheim 1. When comparing the two latter populations, there is no reason to interpret the differences in this feature as evidence for different age structures of the populations since more than 150 molars are known from both localities. The older age of Mosbach 2 is in agreement with the smaller size of M/1 and the larger values of SZQH. The M/1 from Voigtstedt are a little larger in comparison to those from Mosbach, but this concerns the rooted specimens only. Rootless M/1 from this site are of similar size (x = 3.27 mm, min = 3.00 mm, max = 3.65 mm, n = 21).

On the other hand, an older age for Miesenheim 1 could be inferred from the higher SDQ values in comparison to Mosbach. However, geographical clines have been observed in recent populations within Europe (RÖTTGER 1987). Even in various places in Germany, the mean values already differ considerably (between 78 and 85 – FRAHNERT 1991). This is the same difference of SDQ values as that between Miesenheim and Mosbach (140 to 133). Another argument is that despite Voigtstedt being clearly older than Miesenheim, it has smaller SDQ values. For biochronological correlations, more data are necessary to estimate the geographic variability of these features.

KOENIGSWALD & KOLFSCHOTEN (1996) place the first appearance dates of *Arvicola* in Europe in the Cromer Interglacial III. By several arguments they refer Miesenheim to Interglacial IV. Mosbach 2 should therefore be placed in one of these two interglacials.

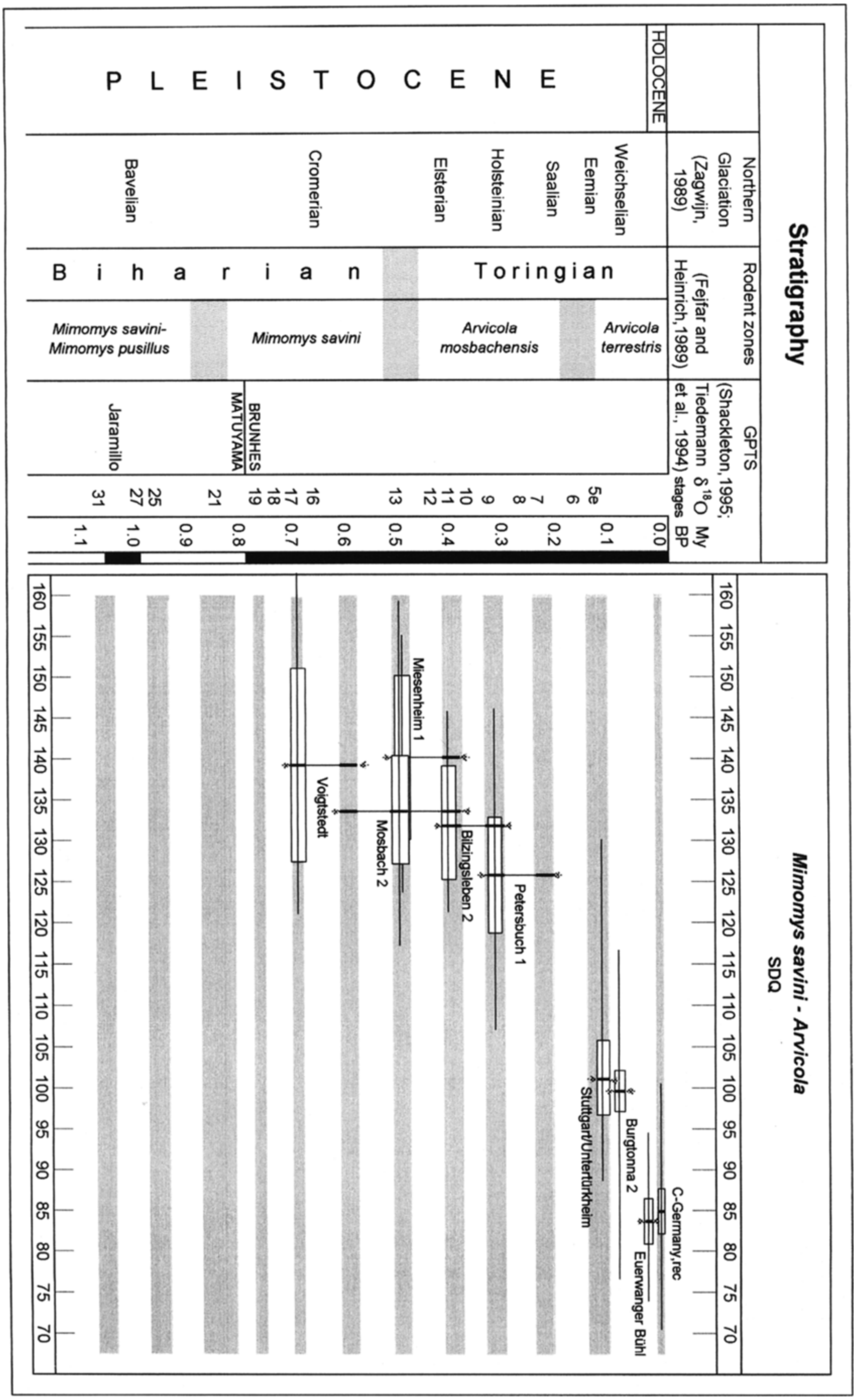
Taxonomic comments on early Middle Pleistocene *Arvicola* remains

The current taxonomic expression of the three main levels of the successive evolution are: *Mimomys savini* with roots and negative enamel differentiation, *Arvicola cantianus* without roots and negative enamel differentiation, and *Arvicola terrestris* without roots and with positive enamel differentiation (KOENIGSWALD 1973; HEINRICH 1982; KOENIGSWALD & KOLFSCHOTEN 1996).

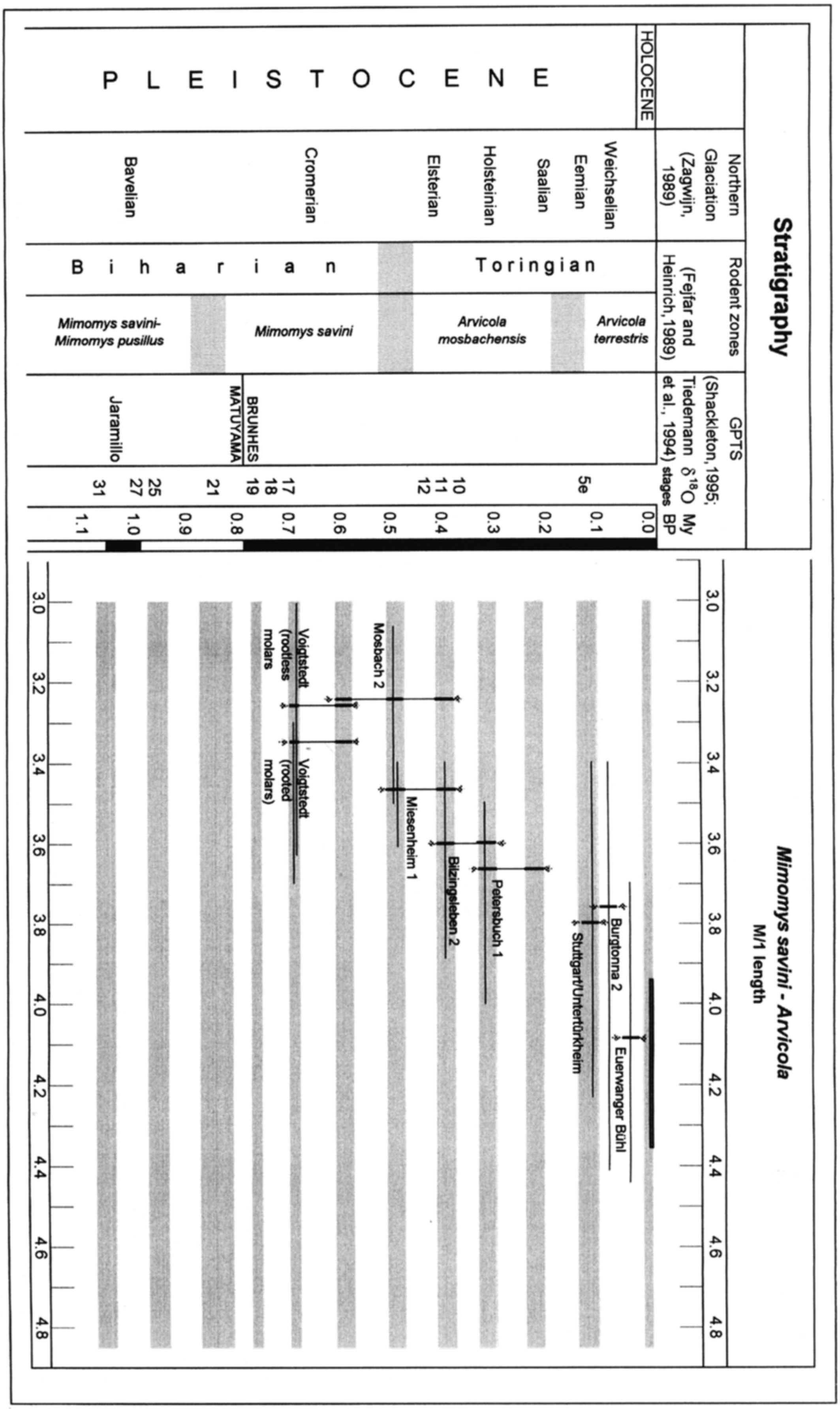
Several middle Pleistocene *Arvicola* species with negative enamel differentiation have been previously described: *Arvicola mosbachensis* (SCHMIDTGEN 1911), *A. greeni* HINTON 1926, *A. praeceptor* HINTON 1926, *A. bactonensis* HINTON 1926, *A. weinheimensis* HELLER 1952, and *A. moenana* HELLER 1969. However, they are now usually considered as partially different morphotypes of a single species, one which, for reasons of priority, has been named *Arvicola cantianus* (HINTON 1910) with the type locality Ingress Vale, Kent.

However, there is a problem with the type specimens of *Arvicola cantianus* since these finds are not clearly referable to one of the three successive species mentioned. Only two fragmentary M/1 one M1/, and one M3/ are known from this site (HINTON 1926). Because there are also rootless specimens in the population of *Mimomys savini* from Přezletice, the single molars from Ingress Vale cannot be referred without doubt either to *Arvicola* or to *Mimomys*. Moreover, according to the SDQ values (120 measured on 4 anticlines of the type specimen, and 115 measured on 3 anticlines of another M/1) the two M/1 can be referred to middle as well as to late Pleistocene forms of both types of enamel differentiation. Because the M/1 are incomplete, and their lengths can be only estimated to around 3.5 mm, this measurement also refers the finds to either the middle or to the late Pleistocene species. Thus, even in crucial features, the character states are not clearly recognisable in these specimens, and a clear distinction is impossible. This taxon is therefore not suitable as a reference (a nomen dubium).

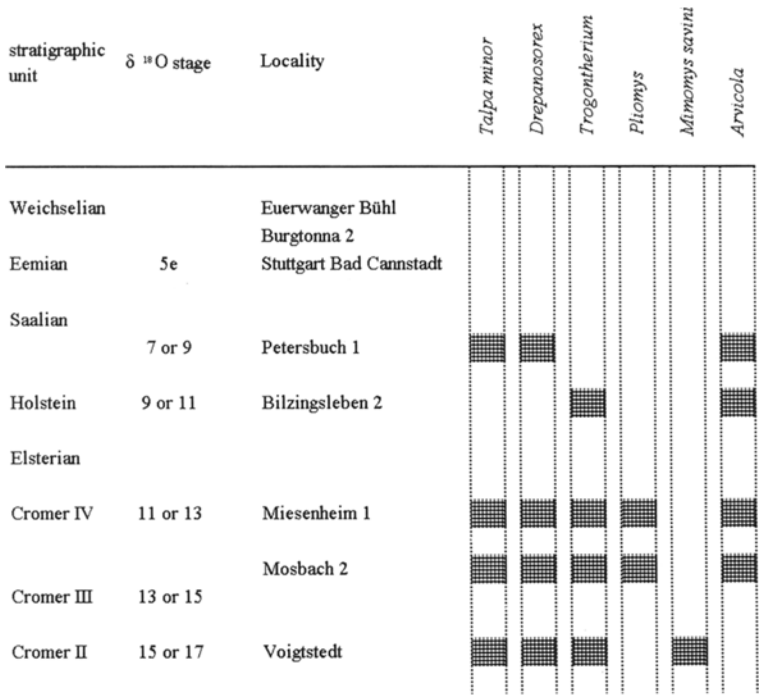
Moreover, with increasing knowledge about middle Pleistocene *Arvicola* populations, a more detailed subdivision is necessary. The Ingress Vale specimens do not provide any possibility of comparison with other populations, neither for detailed relative chronology nor for geographical clines. The-



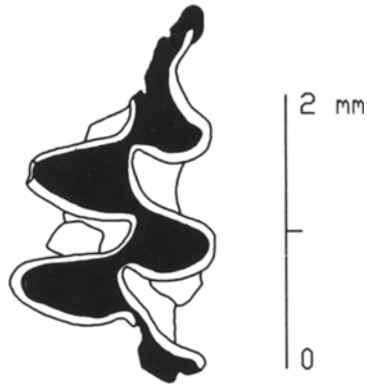
Text-fig. 3.
SDQ (mean values, variation and confidence interval) and SDQ size classes of M/1 of several fossil populations of *Arvicola* and recent populations of *Arvicola terrestris*. Vertical bars indicate the maximum possible age range.



Text-fig. 4.
M/1 length (mean values, variation) of several fossil populations of *Arvicola* and recent specimens of *Arvicola terrestris*. Vertical bars indicate the maximum possible age range.



Text-fig. 5. Stratigraphic range of some Pleistocene small mammal taxa (after KOLFSCHOTEN 1990, and KOENIGSWALD & KOLFSCHOTEN 1996).



Text-fig. 6. *Arvicola cantianus* (HINTON 1910), holotype. Brit. Mus. natur. Hist. [BMNH] London, catalogue number M 48392.

se things are of importance in answering the question of whether the transition *M. savini* – *Arvicola* occurred everywhere in Europe at about the same time (it did probably not). In addition, the influence of possible migrations must be considered. The types of A. *cantianus* cannot be used for these kinds of investigations.

Because it is impossible to assess clearly diagnostic stages in these features, we propose to restrict the name *Arvicola cantianus* (HINTON 1910) to the material of Ingress Vale. For all other middle Pleistocene finds with negative enamel differentiation the name *Arvicola mosbachensis* (SCHMIDTGEN 1911) is available and should be applied. For the Mosbach population these features can be assessed with sufficient confidence because the sample is large, and has the added advantage of a rich accompanying mammalian fauna.

We do not support the use of subspecific names as proposed by KOLFSCHOTEN (1990). In addition to all the problems with chrono-subspecies discussed elsewhere (REMANE 1985), there is no practical advantage in the relegation of former species to subspecific rank. If regional differences of data in penecontemporaneous fossil sites are referred to different races, it will be impossible then to subordinate geographical defined subspecies under biostratigraphically defined ones.

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References

AGADZHANYAN, A. K. (1983): Eine altertümliche *Arvicola* (Rodentia, Mammalia) aus dem Mittelpleistozän der Russischen Ebene. – Schriftenr. geol. Wiss., **19/20**: 9-29, 7 text-figs, 5 tabs; Berlin.

ANDRES, W. (1971): Sedimentologische und morphoskopische Untersuchungen eines Fundprofiles aus den pleistozänen Mosbacher Sanden bei Wiesbaden-Bieberich. – Mainzer naturwiss. Arch., **10**: 101-112, 8 text-figs; Mainz.

BAHLO, E. & MALEC, F. (1969): Insectivoren (Mammalia) aus den oberen Mosbacher Sanden (Mittelpleistozän) bei Wiesbaden-Biebrich/Hessen. – Mainzer naturwiss. Arch., **8**: 56-76, 5 text-figs, 6 tabs, 2 pls; Mainz.

BRÜNING, H. (1978): Zur Untergliederung der Mosbacher Terrassenabfolge und zum klimatischen Stellenwert der Mosbacher Tierwelt im Rahmen des Cromer-Komplexes. – Mainzer naturwiss. Arch., **16**: 143-190, 12 text-figs, 3 tabs; Mainz.

CHALINE, J. (1972): Les rongeurs du Pleistocène moyen et supérieur de France. – Cah. Paléont., CNRS: 410 p., 72 text-figs, 3 tabs, 17 pls; Paris.

FEJFAR, O. & HEINRICH, W.-D. (1980): Zur biostratigraphischen Abgrenzung und Gliederung des kontinentalen Quartärs in Europa anhand von Arvicoliden (Mammalia, Rodentia). – Èas. Mineral. Geol., **25**: 185-189, 1 text-fig.; Praha.

FEJFAR, O. & HEINRICH, W.-D. (1989): Muroid Rodent Biochronology of the Neogene and Quaternary in Europe. – In: E. H. LINDSAY, V. FAHLBUSCH & P. MEIN [Eds], European Neogene

Mammal Chronology: 91-116, 5 text-figs; New York, London (Plenum Press).

FRAHNERT, S. (1991): Zur Variabilität der Schmelzbandbreiten rezenter Schermäuse, *Arvicola terrestris* (Rodentia, Mammalia), im zentralen Mitteleuropa. – Säugetierkundl. Inform., **3**: 235-247, 13 text-figs, 5 tabs; Jena.

HEINRICH, W.-D. (1978): Zur biometrischen Erfassung eines Evolutionstrends bei Arvicola (Rodentia, Mammalia) aus dem Pleistozän Thüringens. – Säugetierkundl. Inform., **2**: 3-21, 5 text-figs; Berlin.

HEINRICH, W.-D. (1982): Zur Evolution und Biostratigraphie von *Arvicola* (Rodentia, Mammalia) im Pleistozän Europas. – Z. geol. Wiss., **10**: 683-735, 26 text-figs, 3 tabs; Berlin.

HEINRICH, W.-D. (1987): Neue Ergebnisse zur Evolution und Biostratigraphie von *Arvicola* (Rodentia, Mammalia) im Quartär Europas. – Z. geol. Wiss., **15**: 389-406, 9 text-figs; Berlin.

HELLER, F. (1933): Die Wühlmäuse der Mosbacher Sande. – Notizbl. Ver. Erdkde. u. hess. geol. L.-Anst., **1931/1932**: 108-116, 1 pl.; Darmstadt.

HELLER, F. (1969): Eine Kleinsäugerfauna aus den Mittleren Mosbacher Sanden bei Biebrich-Wiesbaden. – Mainzer naturwiss. Arch., **8**: 25-55, 3 text-figs, 2 pls; Mainz.

HINTON, M. A. C. (1910): A preliminary account of the British fossil voles and lemmings; with some remarks on the Pleistocene climate and geography. – Proc. Geologists' Assoc., **21**: 489-507, 1 tab.; London.

HINTON, M. A. C. (1926): Monograph of the voles and lemmings (Microtinae) living and extinct. – 488 p., 110 text-figs, 56 tabs, 15 pls; London (Brit. Mus. natur. Hist.).

JÁNOSSY, D. (1969): Stratigraphische Auswertung der europäischen mittelpleistozänen Wirbeltierfaunen. Teil I. – Ber. dt. Ges. geol. Wiss., (A) **14**: 367-438, 8 text-figs; Berlin.

KAHLKE, H.-D. (1961): Revision der Säugetierfaunen der klassischen deutschen Pleistozän-Fundstellen von Süßenborn, Mosbach und Taubach. – Geologie, **10**: 493-532, 7 pls; Berlin.

KOENIGSWALD, W. VON (1973): Veränderungen in der Kleinsäugerfauna von Mitteleuropa zwischen Cromer und Eem (Pleistozän). – Eiszeitalter u. Gegenwart, **23/24**: 159-167, 2 text-figs; Öhringen.

KOENIGSWALD, W. VON & KOLFSCHOTEN, T. VAN (1996): The *Mimomys-Arvicola* boundary and the enamel thickness quotient (SDQ) of *Arvicola* as stratigraphic markers in the Middle Pleistocene. – In: Ch. TURNER [Ed.], The Early Middle Pleistocene in Europe: 211-226, 7 text-figs; Rotterdam (A. A. Balkema).

KOENIGSWALD, W. VON & TOBIEN H. (1987): Bemerkungen zur Altersstellung der pleistozänen Mosbach-Sande. – Geol. Jb. Hessen, **115**: 227-237, 2 text-figs, 1 tab.; Wiesbaden.

KOLFSCHOTEN, T. VAN (1990): The evolution of the mammal fauna in The Netherlands and the middle Rhine Area (Western Germany) during the late Middle Pleistocene. – Meded. Rijks Geol. Dienst., **43**: 1-69, 27 text-figs, 11 tabs; Haarlem.

MARTIN, R. A. (1987): Notes on the classifications and evolution of some North American fossil *Microtus* (Mammalia, Rodentia). – J. Vertebrate Paleont., **7**: 270-283, 7 text-figs, 2 tabs; Lawrence/ Kan.

RADULESCU, C. & SAMSON, P.-M. (1993): Dental morphology of the *Mimomys/Arvicola* transition forms. – Theoret. and applied Karstology, **6**: 199-206, 1 text-fig., 1 tab.; Bucuresti.

REKOVETS, L. I. (1994): Melkie mlekopitayushchie antropogena yuga vostochnoj Evropy. [Small mammals of the Anthropogene of Eastern Europe.] – 370 p., 73 text-figs, 36 tabs; Kiev (Naukova dumka). – [In Russian.]

REKOVETS, L. I. & NADACHOWSKI, A. (1995): Pleistocene voles (Arvicolidae) of the Ukraine. – Paleontologia i Evolució, **28/29**: 145-245, 76 text-figs, 47 tabs; Sabadell.

REMANE, J. (1985): Der Artbegriff in Zoologie, Phylogenetik und Biostratigraphie. – Paläont. Z., **59**: 171-182; Stuttgart.

RÖTTGER, U. (1987): Schmelzbandbreiten an Molaren von Schermäusen (*Arvicola* LACÉPÈDE, 1799). – Bonner zool. Beitr., **38**: 95-105, 7 text-figs, 2 tabs; Bonn.

SCHMIDTGEN, O. (1911): Über Reste von Wühlmäusen aus dem Mosbacher Sand. – Notizbl. Ver. Erdkde. u. Großherzogl. geol. L.-Anst., 4. Folge, **32**: 185-193, 3 text-figs, 1 tab.; Darmstadt.

SHACKLETON, N. J. (1995): New data on the evolution of Pliocene Climatic Variability. – In: E. S. VRBA, G. H. DENTO, T. C. PARTRIDGE & L. H. BURCKLE [Eds], Paleoclimate and Evolution, with Emphasis on Human Origins: 242-248, 3 text-figs, 3 tabs; New Haven, London (Yale Press).

TIEDEMANN, R., SARNTHEIN, M. & SHACKLETON, N. J. (1994): Astronomic timescale for the Pliocene Atlantic $\delta^{18}O$ and dust flux records of Ocean Drilling Program site 659. – Paleoceanogr., **9**: 619-638, 112 text-figs, 3 tabs; Washington/D.C.

ZAGWIJN, W. H. (1989): The Netherlands during the Tertiary and the Quaternary: A case history of Coastal Lowland evolution. – Geol. Mijnbouw, **68**: 107-120, 27 text-figs; Dordrecht.

ZAZHIGIN, V. S. (1980): Gryzuny pozdengo Pliotsena i Antropogena yuga zapadnoj Sibiri. [Rodents of the Pliocene and Anthropogene of Southwestern Siberia.] – 156 p., 39 text-figs, 12 tabs; Moskva (Nauka). – [In Russian.]

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Plate 1

Figs 1-10. *Arvicola mosbachensis* (SCHMIDTGEN 1911). – Mosbach 2.
' = drawing reversed, b = buccal view, c = basal view, d = distal view, m = mesial view, all other views are occlusal.

1. SMF 74/4835. – M/1, Holotype.
2. SMF 74/4843. – M/1, Paratype.
3. SMF 74/4835. – M/1, Paratype.
4. SMF 99/1543. – M/1.
5. SMF 74/4841. – M3/, Paratype.
6. SMF 74/4842. – M/1, Paratype.
7. SMF 99/1544. – M/1.
8. SMF 99/1545. – M3/.
9. SMF 99/1546. – M3/.
10. SMF 99/1547. – M3/.

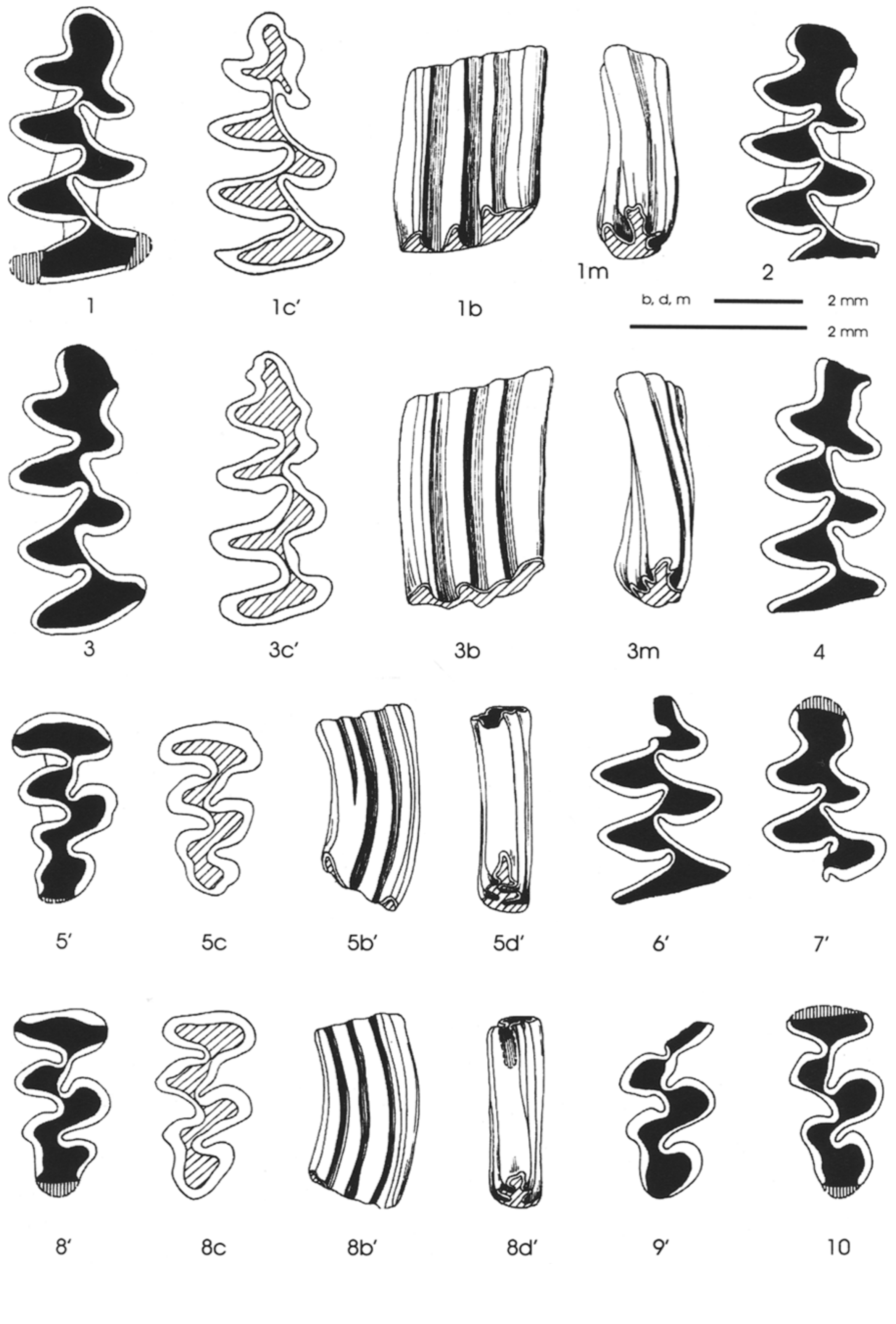

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Plate 2

Figs 11-35. *Arvicola mosbachensis* (SCHMIDTGEN 1911). – Mosbach 2.
' = drawing reversed, b = buccal view, m = mesial view, all other views are occlusal.

11. SMF 99/1548. – M/1.
12. SMF 99/1549. – M/1.
13. SMF 99/1550. – M/1.
14. SMF 99/1551. – M/1.
15. SMF 99/1552. – M/1.
16. SMF 99/1553. – M/1.
17. SMF 99/1554. – M/1.
18. SMF 99/1555. – M/1.
19. SMF 99/1556. – M/1.
20. SMF 99/1557. – M/1.
21. SMF 99/1558. – M/1.
22. SMF 99/1559. – M/1.
23. SMF 99/1560. – M/1.
24. SMF 99/1561. – M/1.
25. SMF 99/1562. – M/1.
26. SMF 99/1563. – M/1.
27. SMF 99/1564. – M/1.
28. SMF 99/1565. – M/1.
29. SMF 99/1566. – M/1.
30. SMF 99/1567. – M/1.
31. SMF 99/1568. – M/1.
32. SMF 99/1569. – M/1.
33. SMF 99/1570. – M/1.
34. SMF 99/1571. – M/1.
35. SMF 99/1572. – M/1.

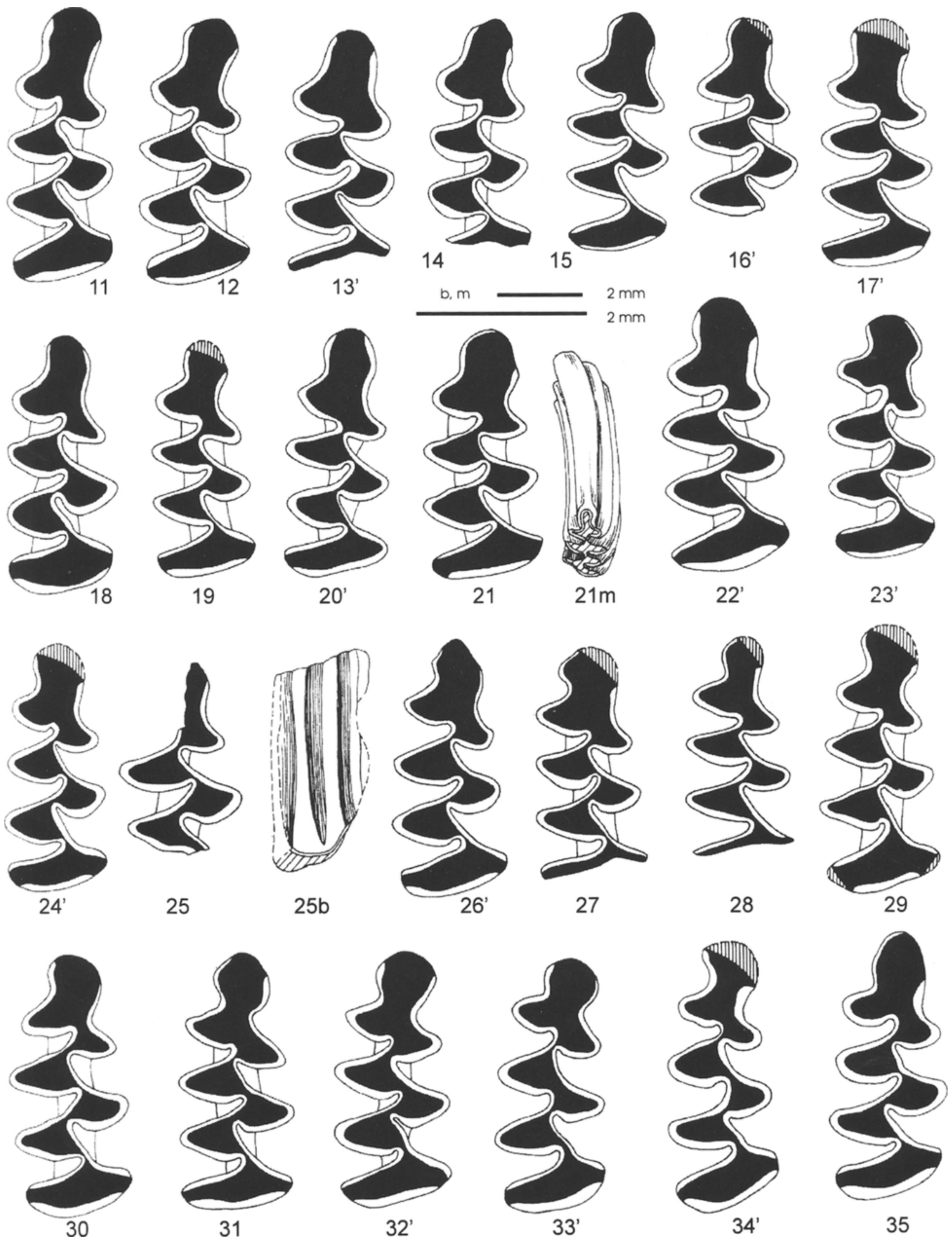

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Plate 3

Figs 36-57. *Arvicola mosbachensis* (SCHMIDTGEN 1911). – Mosbach 2.
' = drawing reversed, b= buccal view, c = basal view, l = lingual view, m = mesial view, all other views are occlusal.

36. SMF 99/1573. – M/1.
37. SMF 99/1574. – M/1.
38. SMF 99/1575. – M/1.
39. SMF 99/1576. – M/1.
40. SMF 99/1577. – M/1.
41. SMF 99/1578. – M/1.
42. SMF 99/1579. – M/1.
43. SMF 99/1580. – M/1.
44. SMF 99/1581. – M/1.
45. SMF 99/1582. – M/1.
46. SMF 99/1583. – M/1.
47. SMF 99/1584. – M/1.
48. SMF 99/1585. – M/1.
49. SMF 99/1586. – M/1.
50. SMF 99/1587. – M/1.
51. SMF 99/1588. – M/1.
52. SMF 99/1589. – M/1.
53. SMF 99/1590. – M/1.
54. SMF 99/1591. – M/1.
55. SMF 99/1592. – M/1.
56. SMF 99/1593. – M/1.
57. SMF 99/1594. – M/1.

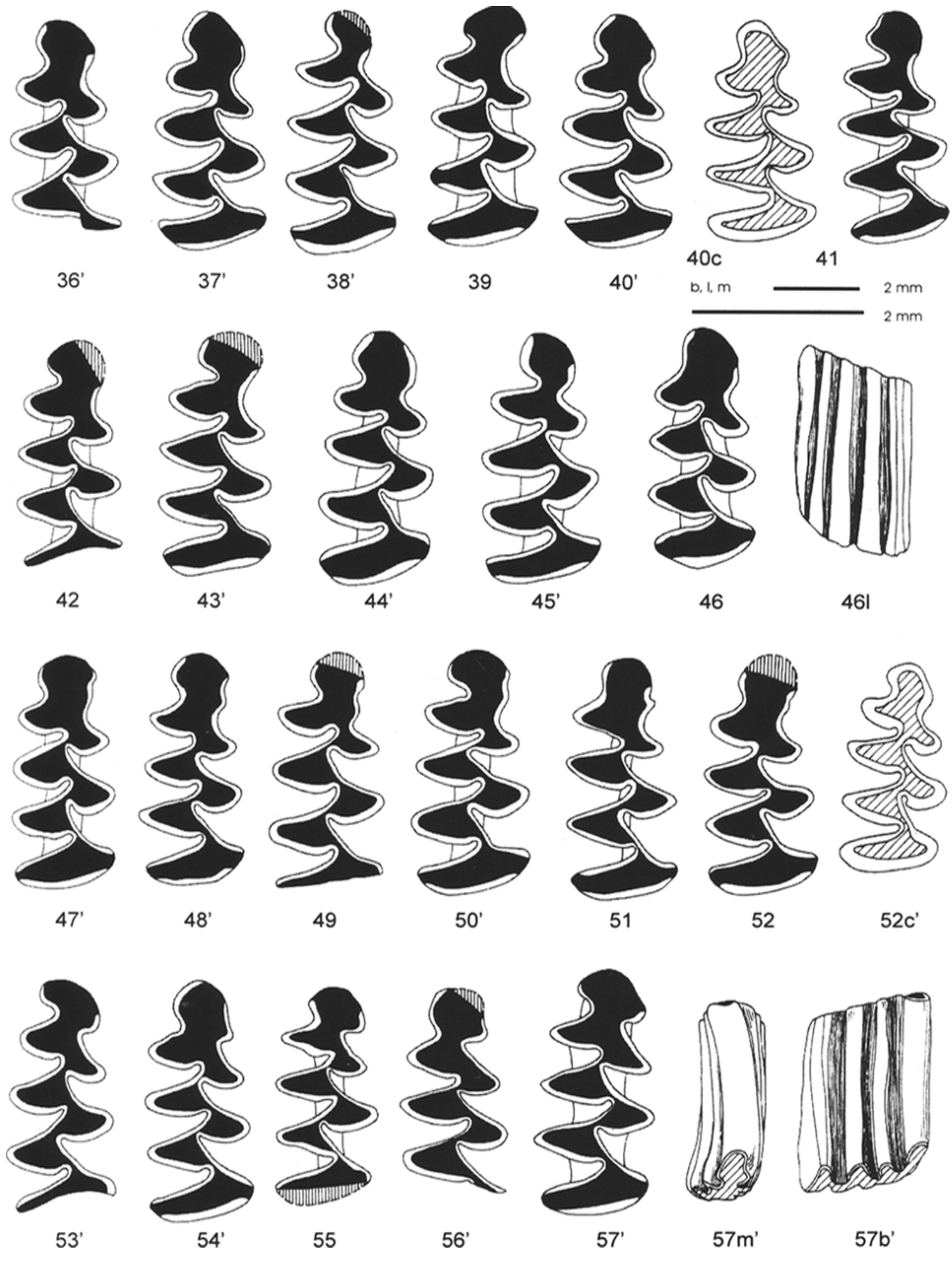

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Plate 4

Figs 58-73. *Arvicola mosbachensis* (SCHMIDTGEN 1911). – Mosbach 2.
' = drawing reversed, b = buccal view, c = basal view, all other views are occlusal.

58. SMF 99/1595. – M/1.
59. SMF 99/1596. – M/1.
60. SMF 99/1597. – M/1.
61. SMF 99/1598. – M/1.
62. SMF 99/1599. – M/1.
63. SMF 99/1600. – M/1.
64. SMF 99/1601. – M/1.
65. SMF 99/1602. – M/1.
66. SMF 99/1603. – M/1.
67. SMF 99/1604. – M/1.
68. SMF 99/1605. – M/1.
69. SMF 99/1606. – M/1.
70. SMF 99/1607. – M/1.
71. SMF 99/1608. – M/1.
72. SMF 99/1609. – M/1.
73. SMF 99/1610. – M/1.

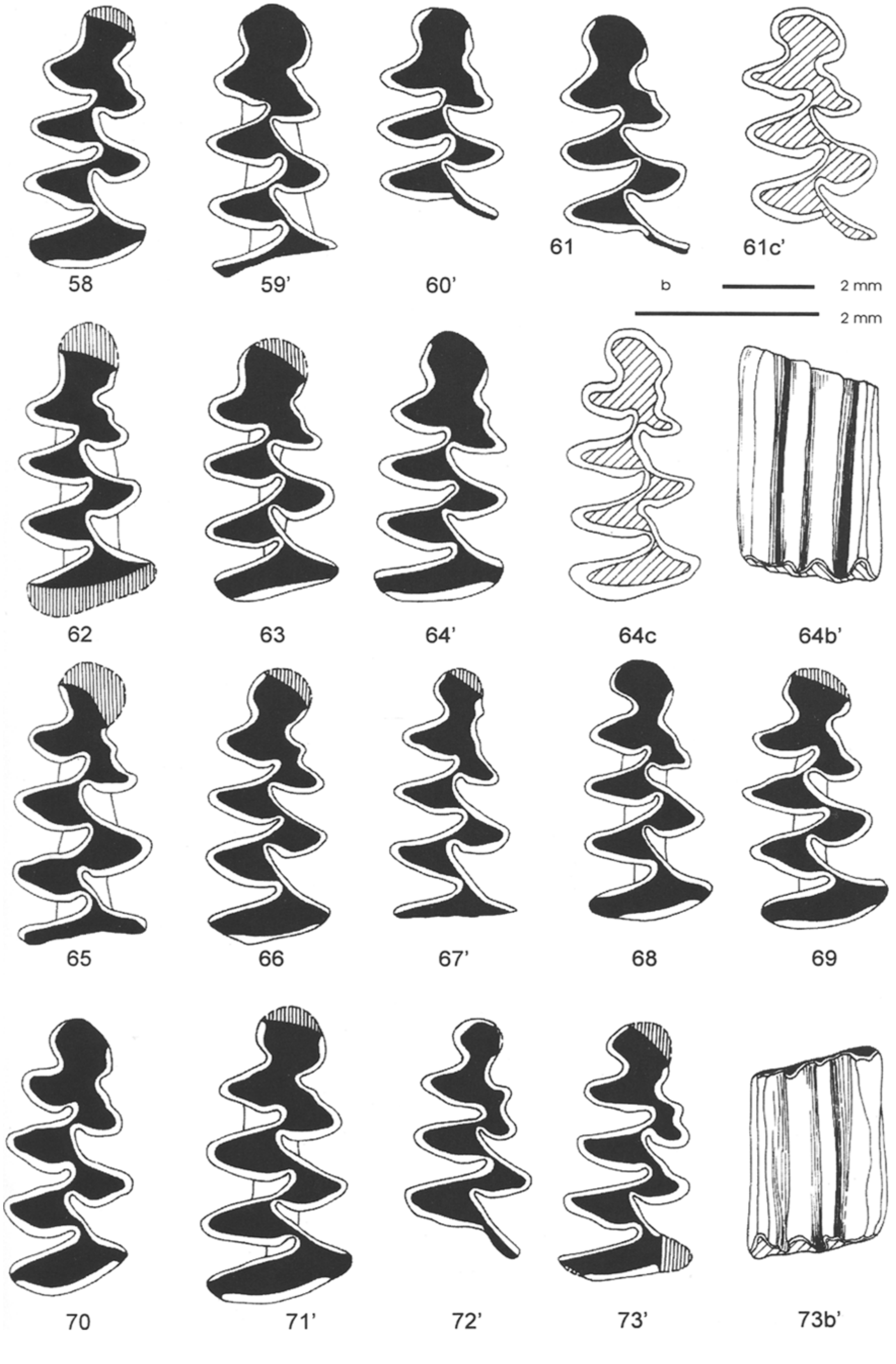

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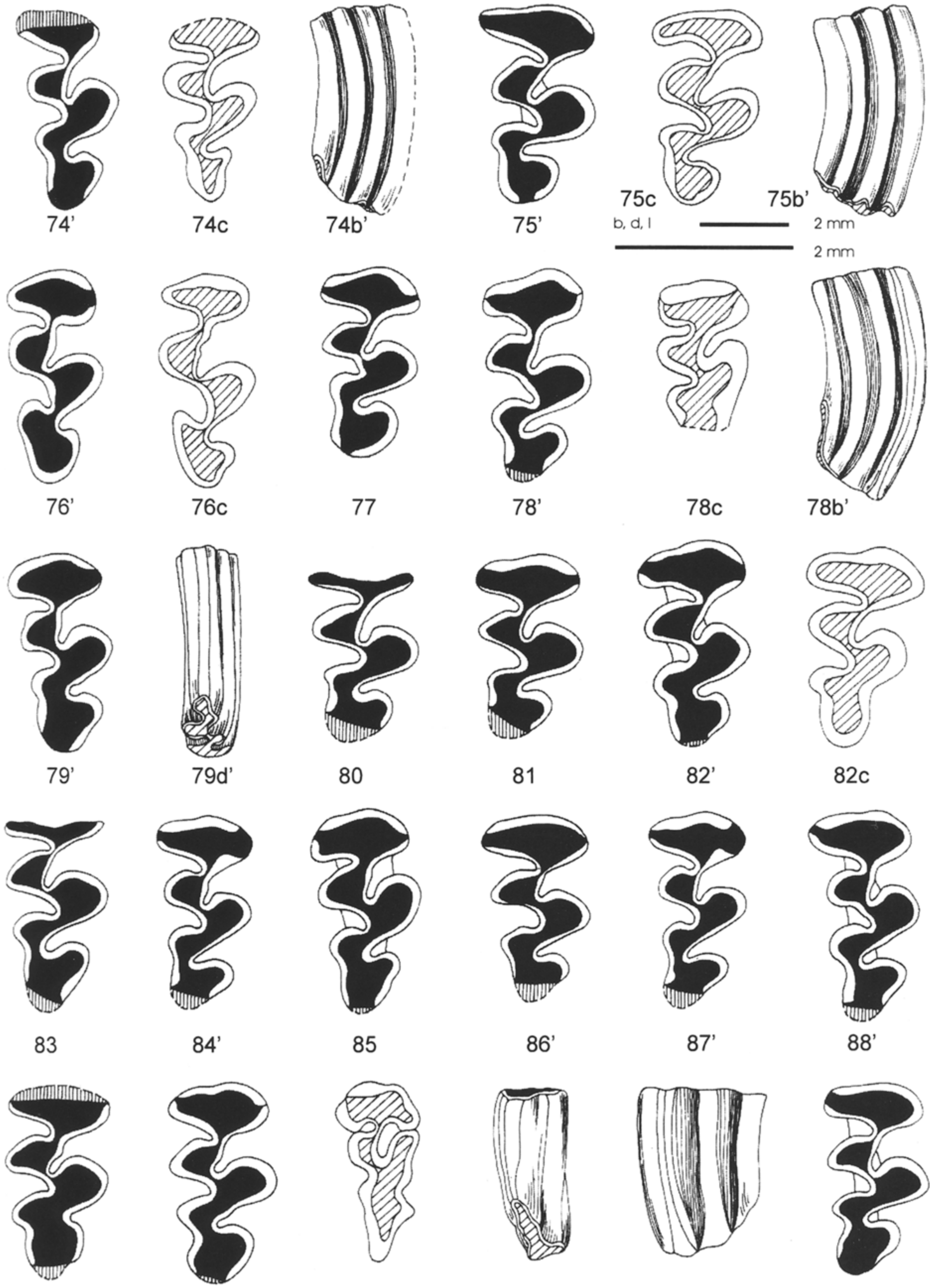
Plate 5

Figs 74-91. *Arvicola mosbachensis* (SCHMIDTGEN 1911). – Mosbach 2.
' = drawing reversed, b = buccal view, c = basal view, d = distal view, l = lingual view, all other views are occlusal.

74. SMF 99/1611. – M3/.
75. SMF 99/1612. – M3/.
76. SMF 99/1613. – M3/.
77. SMF 99/1614. – M3/.
78. SMF 99/1615. – M3/.
79. SMF 99/1616. – M3/.
80. SMF 99/1617. – M3/.
81. SMF 99/1618. – M3/.
82. SMF 99/1619. – M3/.
83. SMF 99/1620. – M3/.
84. SMF 99/1621. – M3/.
85. SMF 99/1622. – M3/.
86. SMF 99/1623. – M3/.
87. SMF 99/1624. – M3/.
88. SMF 99/1625. – M3/.
89. SMF 99/1626. – M3/.
90. SMF 99/1627. – M3/.
91. SMF 99/1628. – M3/.



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