

The type material and the enamel structure of *Villanyia exilis* KRETZOI, 1956 (Arvicolidae, Rodentia)

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Received: 24 November 2008

Accepted: 20 January 2009

MAYHEW D. F. The type material and the enamel structure of *Villanyia exilis* KRETZOI, 1956 (Arvicolidae, Rodentia). *Acta zoologica cracoviensia*, **52A**(1-2): 81-94.

Abstract. Re-examination of the two teeth constituting the original type and genotype material of *Villanyia exilis* KRETZOI, 1956 from Villány-5, Hungary, indicates that subsequently published descriptions need revision. The tooth selected as the lectotype of *Villanyia exilis* by RABEDER (1981) is considered here to belong to *Clethrionomys kretzoi* (KOWALSKI, 1958). The second specimen, with morphology in accordance with the original description of Kretzoi, is considered to represent the characters of *Villanyia exilis*. In order to stabilise the nomenclature in accordance with current usage an application has been made to the International Commission on Zoological Nomenclature. The fine structure of the enamel of *Villanyia exilis* as defined above is described for the first time, based on a tooth from the Late Villanyian of Osztramos-3, Hungary. It demonstrates a simple grade of arvicolid evolution. This enamel type differs substantially from the enamel structure of material from Rebiełice Królewskie, Poland, which was originally identified as *Mimomys (Villanyia) exilis* by KOWALSKI (1960), but considered here to be referable to the genus *Borsodia*. The generic name *Villanyia* has been applied widely in the literature to various other taxa, mainly species of extinct rooted lagurine voles which are currently referred to the genus *Borsodia* (JÁNOSSY & VAN DER MEULEN, 1975). It is proposed to limit the use of the genus name *Villanyia* to the latest part of a lineage of uncertain origin which became extinct close to the Villanyian/Biharian boundary.

Key words: Voles, Pliocene, Pleistocene, taxonomy, evolution, Europe, enamel structure.

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I. INTRODUCTION

The new genus and species *Villanyia exilis* was described from Villány-5, Hungary, by KRETZOI (1956) on the basis of two lower first molars. The description was brief with no illustrations. The first illustrations of the two specimens were provided by RABEDER (1981), who designated one of the teeth as the lectotype of *V. exilis* and the other the holotype of a new species *Cseria ultima*.

TERZEA (1991) described abundant material of *V. exilis* from Betfia-XIII and demonstrated that the morphology of the lower first molar corresponded not to the specimen from Villány-5 selected

as the lectotype by RABEDER (1981), but to the other specimen. She figured this second specimen as being the “lectotype”. Subsequent authors have adopted the description of TERZEA (1991) as the correct definition of the characters of *V. exilis*. Since the original description, the genus name *Villanyia* has also been widely used in the literature for a diversity of taxa. Various authors referred teeth from a number of Pliocene and Pleistocene localities to *V. exilis* (e.g. KOWALSKI 1960, from Rębielice Królewskie, Poland). Some of these referrals were made on unclear grounds, and require reassessment on the basis of recent knowledge.

During a visit to the Hungarian Geological Institute, Budapest the type material was cleaned and re-examined. This revealed discrepancies in respect of previously published descriptions. As there is no material other than the type of *V. exilis* known from Villány-5, a tooth of *V. exilis* found in the samples from the fissure filling Osztramos-3, Hungary (considered close in age to Villány-5) was studied to investigate the enamel structure (Schmelzmuster). This enables a broader discussion of the definition of *Villanyia* and its place in the Arvicolidae. Finally, this enamel structure is compared with that of a tooth from the assemblage from Rębielice Królewskie, Poland, previously identified as *Mimomys (Villanyia) exilis*, but considered here to be in fact referable to *Borsodia*.

A b b r e v i a t i o n s:

PAS – Institute of Systematics & Evolution of Animals, Polish Academy of Sciences, Kraków;

GIH – Hungarian Geological Institute, Budapest;

NHMUS – Hungarian Natural History Museum, Budapest.

II. SYSTEMATIC SECTION: REDESCRIPTION OF TYPE MATERIAL

The terminology follows RABEDER (1981) and TESAKOV (2004). Crown height and enamel free area heights are measured perpendicular to the wear surface. The base of the crown is considered to be the base of the enamel of the posterior labial re-entrant fold. Measurements are in mm.

Genus *Villanyia* KRETZOI, 1956

1956 *Villanyia exilis* gen. et sp. nov. (*partim*) – KRETZOI: 118.

1960 *nec Villanyia exilis* – KOWALSKI: 184 figs 6 a-f, 7 a-d. (= *Borsodia*)

1965 *nec Mimomys (Villanyia) sp.* – ALEXANDROVA: 101, 106, fig. 13 a,b.

1970 *Mimomys (Villanyia) sp. (partim)* – SUKHOV: 61, plate 8, figs 108-110. (assigned with some reservation).

1970 *nec Mimomys (Villanyia) praehungaricus* – SUKHOV: plate 10, figs 131-143 (a mixture of species, some specimens *Borsodia*).

1976 *nec Villanyia* – ALEXANDROVA: 46 *et ff.* (= *Borsodia*).

1977 *Villanyia (partim)* – GROMOV & POLYAKOV: 215 *et ff.* (only type, rest are lagurids referable to *Borsodia*).

1980 *nec Villanyia* – ZAZHIGIN: 98 *et ff.* (all species described as *Villanyia* appear to be *Borsodia*).

1981 *Cseria proopsia* – RABEDER: 56.

1981 *Cseria opsia* – RABEDER: 59.

1991 *nec Villanyia kowalskii* – TERZEA: 91 (= *Borsodia*).

1991 *nec Villanyia veterior* – TERZEA: 91 (= *Borsodia*).

1994 *nec Villanyia* – REKOVETS: fig. 31 etc.

2001 *Villanyia* – KOWALSKI: 291.

2005 *nec Villanyia* – ERBAJEVA: 58 *et ff.* (*Villanyia eleonorae* and *Villanyia klochnevi* = *Borsodia*).

2006 *nec Villanyia* – ERBAJEVA et al.: 115 *et ff.* (= *Borsodia*).

2008 *nec Villanyia fangchangensis* – ZHANG et al.: 165 (considered referable to tribe Clethrionomyini).

***Villanyia exilis* KRETZOI, 1956**

- 1956 *Villanyia exilis* – KRETZOI: 188 (*partim*).
 1960 *nec Mimomys (Villanyia) exilis* – KOWALSKI: 184, figs 6 a-f, 7 a-d. (= *Borsodia*).
 1976 *nec Villanyia exilis* – ALEXANDROVA: 59 (= *Borsodia*).
 1980 *nec Villanyia (Villanyia) exilis* – ZAZHIGIN: 103, pl. 18 figs 4-6, pl. 20, figs 1-3.
 1981 *nec Villanyia exilis* – RABEDER: 63, fig. 44/1 a,b. (= *Clethrionomys*).
 1981 *Cseria ultima* – RABEDER: 63, fig. 44/2 a,b.
 1983 *Villanyia exilis* – FEJFAR & HORÁČEK: pl. X, fig. 1.
 1986 *Mimomys exilis* – JÁNOSSY: 36.
 1990 *Villanyia exilis* – MAUL: tab. 11.
 1991 *Villanyia exilis* – TERZEA: 92.
 1991 *Villanyia paraexilis* – TERZEA: 101.
 1994 *Villanyia exilis* – SALA et al.: pl. I, figs 7-9.
 1998 *Villanyia exilis* – NADACHOWSKI: tab. 1 etc. (Kamyk, Kadzielnia 1 (*partim*), Kielniki 3B).
 2001 *Villanyia exilis* – KOWALSKI: 291.
 2001 *Villanyia exilis (partim)* – REKOVETS and DEMA.
 2004 *Villanyia exilis (partim)* – DEMA and REKOVETS.
 2007 *Villanyia exilis* – MAUL and MARKOVA: section 3.16.

M a t e r i a l. Specimen GIH V-12702 Vt95 #2, m1 (dext.) from Villány-5.

F i g u r e s. Fig. 1 a-c.

M e a s u r e m e n t s. Crown height (CH) = 1.20; Length of wear surface (L) = 2.13; Width of wear surface (W) = 0.85; Anterosinuid (ASD) = 0.78; Hyposinuid (HSD) = 0.75; Hyposinulid (HSLD) = 0.35; Hyposinuid/Hyposinulid index (HH-index) = 0.82; Relative anteroconid length (A/L) = 45%.

D e s c r i p t i o n. This is a very small tooth, with a relatively low crown, and very low enamel free areas. The anterior loop is relatively long, corresponding precisely to KRETZOI's description "high" when viewed with the occlusal surface axis orientated vertically. There is a slight trace of a *Mimomys* ridge visible on the labial side, although this is not clearly to be seen in the occlusal view. The angles are rounded, the lingual re-entrant angles especially so. On the occlusal surface, T2 and T3 are very broadly confluent. They are separated from T1, which is confluent with the posterior loop. There is no trace of crown cement. The enamel is thick relative to the size of the tooth, and is similar in thickness on the anterior and posterior margins of the triangles. The posterior enamel is worn more, giving the impression of being thinner than the anterior enamel. However, as demonstrated in section III, it is actually thicker.

D i s c u s s i o n. This tooth is similar to the description and drawing of RABEDER (1981, p. 63, Abb. 44, fig. 2.), although slightly wider, and with T2 and T3 slightly more confluent. This tooth corresponds to the original type description of *V. exilis* by KRETZOI (1956) as already recognised by TERZEA (1991, p. 91, last paragraph) in her thorough description of *Villanyia* from the Betfia-XIII, Roumania, fissure deposit. The interpretation of this material is considered later in the general discussion.

RABEDER (1981, p. 63) selected this tooth as the holotype and only specimen of a new species *Cseria ultima*, in view of the similarity to other material assigned to *Cseria*. Later however, CARLS and RABEDER (1988, p. 213) withdrew this, stating: "the separation of the lectotype described as *Cseria ultima* RABEDER, 1981 does not seem to be justified". The name *Villanyia exilis* KRETZOI, 1956 has priority over *Cseria ultima* RABEDER, 1981.

Genus *Clethrionomys* TILESIIUS, 1850

Note: Current proposals (CARLETON et al. 2003; CARLETON and MUSSEY 2005) would make *Clethrionomys* TILESIIUS, 1850 a junior synonym of *Myodes* PALLAS, 1811. However, currently the genus name *Clethrionomys* is still in widespread use. As the present paper concerns *Villanyia*, in order not to confuse different nomenclature issues, *Clethrionomys* is used here on the understanding that revision to *Myodes* may be made in future.

Clethrionomys kretzoi (KOWALSKI, 1958)

1958 *Dolomys kretzoi* – KOWALSKI: 27, fig. 15.

1981 *Villanyia exilis* – RABEDER: 63, fig. 1.

1981 *Clethrionomys kretzoi* – RABEDER: 257.

1988 *Clethrionomys kretzoi* – CARLS and RABEDER: 148.

1996 *Clethrionomys kretzoi* – TESAKOV: 542.

1998 *Clethrionomys kretzoi* – TESAKOV: 112.

M a t e r i a l. Specimen GIH V-12702 Vt95 #1 m1 (dext.) from Villány-5.

F i g u r e s. Fig. 1 d-f.

M e a s u r e m e n t s. Crown height (CH) = 2.83; Length of wear surface (L) = 2.10; Basal length (BL) = 2.25; Width of wear surface (W) = 0.76; Anterosinuid (ASD) = 2.35; Hyposinuid (HSD) = 2.15; Hyposinulid (HSLD) = 2.41; Relative anteroconid length (A/L) 43%.

D e s c r i p t i o n. This is a relatively high crowned tooth. It is damaged, probably by digestion by a predator. The enamel crown is completely formed, roots are just beginning to form. The dentine triangles on the wear surface are broadly communicating. The enamel appears approximately equally thick on anterior and posterior sides of the triangles. The anteroconid has prominent external triangles, and a well defined, slightly angular, anterior loop. The BSA3 is directed backwards. The tips of BRA1 and BRA2 curve anteriorly.

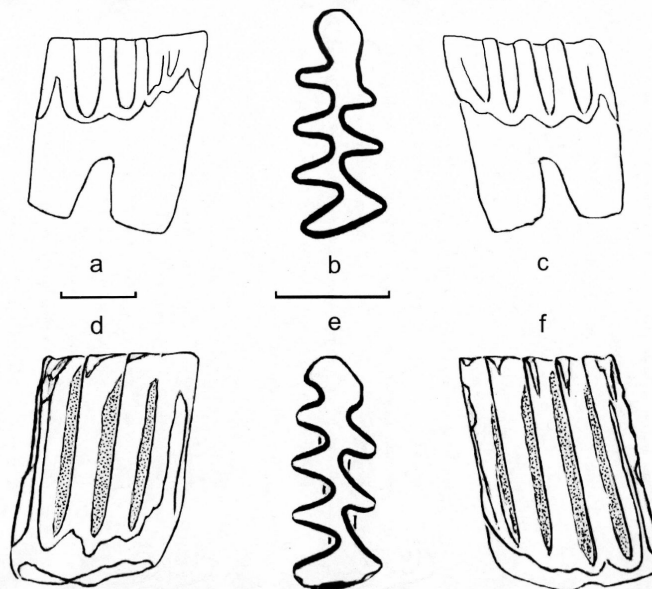


Fig. 1. a-c – GIH V-12702 Vt95 # 2 lower right m1 *Villanyia exilis* KRETZOI, 1956; d-f – GIH V-12702 Vt95 # 1: lower right m1 *Clethrionomys kretzoi* (KOWALSKI, 1958). Scale mark 1 mm.

Thorough cleaning of the tooth (removal of wax) and study under alcohol and acetone indicates that the anterior and posterior enamel free areas are high. The anterosinuid extends at least 2.35 mm but appears not to reach the wear surface. The hyposinuid is at least 2.15 mm high: the rest of the back of the tooth is damaged so the true height cannot be determined. The hyposinuid appears to be closed at a height of 2.41 mm. Crown cementum was visible in most of the re-entrants. These observations differ substantially from those of previous authors.

D i s c u s s i o n. This tooth was redescribed and first figured by RABEDER (1981, Abb. 44, fig. 1), who selected it as the lectotype of *V. exilis*. However, he recorded the enamel free areas as low, whereas they are high, and he found crown cement to be absent, whereas it is present. This changes the interpretation of the tooth. Furthermore, this tooth does not correspond well to the type description of KRETZOI (1956) viz. (translation from German original) “The characters of *Mimomys* and *Prometheomys* combined in a very small-sized type (m1 – length 2.0-2.1 mm), with confluent prism pairs and wide rounded re-entrant angles behind the high *Mimomys* anterior loop (without fold or islet)”. As is obvious from the illustrations given here, this description applies much more accurately to specimen Vt95#2.

The configuration of the tooth Vt95#1 is unusual and clearly it does not belong to the same taxon as Vt95#2. It has been attempted to locate similar teeth in the literature and in museum collections. The closest found have been *Ungaromys dehmi* CARLS & RABEDER, 1988 (observed in Ozstramos-3 material, NHMUS collection) and “*Dolomys*” *kretzoii* KOWALSKI, 1958 (currently referred to *Clethrionomys* see below) from the type locality Kadzielnia, Poland (PAS collection, type and topotype material seen) and from Ozstramos-3 (NHMUS collection).

Compared with *U. dehmi* from Ozstramos-3, Vt95 #1 differs in having more rounded lingual re-entrant angles, and a larger more rounded and posteriorly directed BSA3. BRA 1 and BRA2 are more forwardly directed and crown cement is present (considered absent in *Ungaromys*). In lateral view the lower first molar of *U. dehmi* has a leading edge which is concave, whereas in Vt95#1 it is almost straight. In *U. dehmi* the enamel free areas (especially the hyposinuid) are lower than in Vt95#1.

C. kretzoii is abundant in the assemblage from Ozstramos-3. Vt95#1 falls within the range of size and morphology of this sample.

Compared with the type of “*Dolomys*” *kretzoii* from Kadzielnia, Vt95#1 differs in occlusal view in having a smaller, less rounded, anterior lobe. However, this may be at least partly due to damage and dissolution of enamel in Vt95 #1 at the top of the tooth, seen by the greater basal length. Further, the confluence between T1 and T2 is less in Vt95 #1 and between T2 and T3 greater in Vt95 #1. The overall configuration of re-entrant folds and salient angles (allowing for damage) is quite similar. The type material of “*Dolomys*” *kretzoii* consists of a fragmentary mandible with m1 and m2. The overall height of the enamel free areas of the m1 cannot be determined accurately. However, it appears that all do not reach the wear surface. Two isolated m1 provide information on the heights of the dentine tracts (Table I).

Table I

Measurements of “*Dolomys*” *kretzoii* KOWALSKI, 1958 from type locality Kadzielnia, Poland

Specimen	CH	L	W	ASD	HSD	HSLD	RAL
Type: PAS ISEZ MF/40/1	1.72	2.20	0.86	1.19	1.20	1.20	48%
NHMUS Kretzoi colln #1	2.94	2.05	0.91	2.21	2.22	2.13	49%
NHMUS Kretzoi colln #2	2.36	2.27	0.94	1.81	2.05	1.67	47%

The overall size of these teeth agrees with Vt95 #1, and the heights of the enamel free areas are slightly lower.

"*Dolomys*" *kretzoi* is currently considered to belong to the genus *Clethrionomys*. Abundant material referred to *C. kretzoi* has been described by CARLS and RABEDER (1988). The overall similarity in appearance of Vt95#1 to *Clethrionomys* has also previously independently been noted by TERZEA (1991, p. 91) and by TESAKOV (2004, p. 173). The new details observed, i.e. high enamel free areas, and presence of some crown cement, strongly support this allocation. The relatively confluent triangles and small amount of crown cement are characteristic of teeth of a young animal. Following the scheme of TESAKOV (1996) the tooth can be assigned to *C. kretzoi*.

However, it can be noted that from Villány-5, another *Clethrionomys* species (*C. solus* KRETZOI, 1956, later renamed *C. intrans* KRETZOI, 1958) is recorded. The type lower first molar of *C. solus* (GIH V12703 Vt96) is of different appearance to *C. kretzoi* from Kadzielnia. It has rounded, more typically *Clethrionomys*-like salient and re-entrant angles, and is larger. This might imply that either two species of *Clethrionomys* coexisted, or that the Villány-5 assemblage is heterogeneous in geological age, or that there is a high degree of variability in *C. kretzoi* (see CARLS and RABEDER 1988).

In view of the above information and conclusions about the type material of *V. exilis* KRETZOI, 1956, and as the proposals of RABEDER (1981) have not been followed by subsequent authors, an application has been made to the International Commission for Zoological Nomenclature to consider void taxonomic acts between the original publication and TERZEA (1991) in the interests of stability.

III. FINE STRUCTURE ("SCHMELZMUSTER") OF THE ENAMEL OF *VILLANYIA EXILIS* FROM OSZTRAMOS-3, HUNGARY

VON KOENIGSWALD (1980, p. 60-61) described the enamel fine structure of three teeth said to belong to *Villanyia*. The first was of *V. steklovi* ZAZHIGIN, 1980 from Beteke, northern Kazakhstan. Currently this species is referred to the genus *Borsodia* (TESAKOV 2004). The second came according to the text description from Rebielice, Poland (incorrectly labelled in the figure 62 as coming from Węże, Poland). Following examination of the Rebielice material, this is considered to belong to *Borsodia*. The third tooth was from Kizikha, Western Siberia, Russia, and is considered to be an advanced *Borsodia* species. Therefore it is concluded that the fine structure of the enamel of *V. exilis*, as defined here, has not been previously documented.

A lower first molar considered to belong to *V. exilis* was selected by the author for study by SEM from previously unidentified material from the locality Osztramos-3, Hungary (collection of Hungarian Natural History Museum, locality here considered to be somewhat older than Villány-5). The tooth was prepared according to the method of VON KOENIGSWALD (1980) using 2n HCL for 5 seconds to etch the enamel, and examined using the SEM facility of Naturalis, Leiden. The enamel pattern studied was approximately 1.5 mm above the crown base. The description below follows the terminology of VON KOENIGSWALD (1980, 1997).

The enamel pattern of *V. exilis* (see Fig. 2) appears relatively simple, lacking the very clear differentiation of enamel types usually seen in Gelasian and Early Pleistocene *Mimomys* or *Borsodia* species. In occlusal section mainly radial enamel is to be seen. There are very small patches of discrete lamellar enamel (= uniserial Hunter-Schreger bands, HSB) in the salient angles (Fig. 2B, 2E). On the lingual side, the anterior enamel of the triangles and posterior loop ("leading edge") consists of two layers of radial enamel: an external layer and an internal layer in which the prisms are orientated more obliquely (ca. 45 degrees) to the surface with little interprismatic substance (Fig. 2C). The anterior enamel of the buccal part of the posterior loop and T2 consists of a single layer of radial enamel in which the great majority of the crystallites are orientated perpendicularly to the occlusal plane with little interprismatic substance. The rear margin of the posterior loop appears to consist

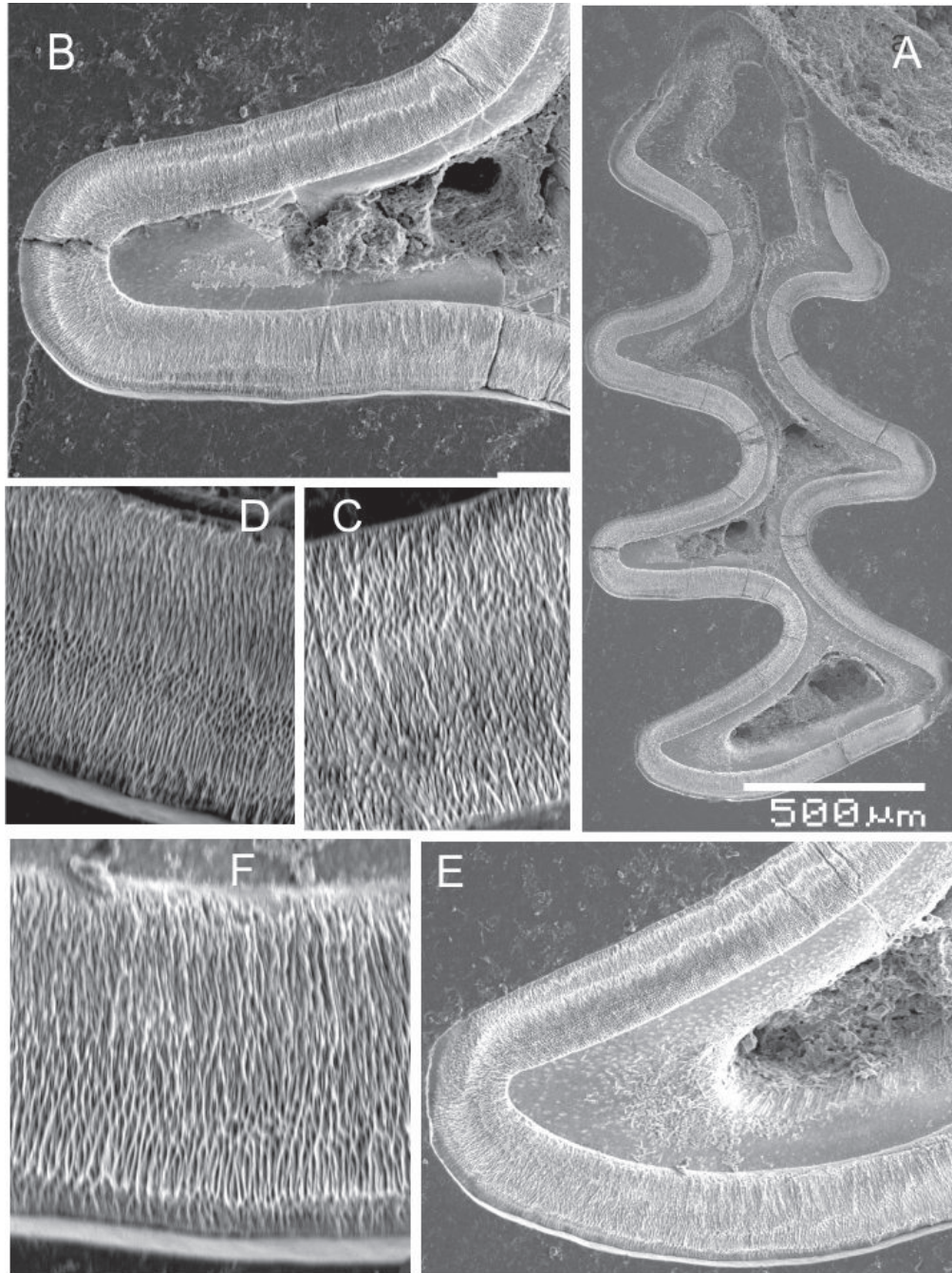


Fig. 2. Enamel fine structure of *Villanyia exilis* from Osztramosz-3, Hungary. Material: lower m1, NHMUS Budapest. A – whole tooth in cross section approximately 1.5 mm above crown base: the enamel consists almost entirely of various layers of radial enamel; B – second lingual salient angle demonstrating enamel thicker on the posterior margin; C – enlargement of radial enamel on anterior face of second lingual salient angle; D – enlargement of radial enamel on the posterior face of the second lingual salient angle; E – posterior loop with radial enamel and very limited development of lamellar enamel at the salient angle; F – enlargement of enamel of posterior loop to show concentric layers of radial enamel. (SEM Naturalis, Leiden).

only of radial enamel. The rear margins (“trailing edge”) of the lingual triangles consist of radial enamel orientated into concentric layers by small changes in the direction of the crystallites. The rear margin of the buccal salients consists of radial enamel with towards the rear side a small area of change in orientation of the crystallites which, although very limited in extent, could be possibly considered primitive tangential enamel.

The ground section as used for the SEM photographs (Fig. 2A) shows that the enamel is slightly differentiated, with the posterior enamel of T1, T2 and T3 being about 10% thicker than the anterior. This result is of interest, because photographs of the wear surface of the same tooth before preparation gave the appearance of the enamel being slightly thicker on the anterior margins of the triangles. It suggests that only preparation of ground sections allows objective comparisons of this feature in arvicolid. The small degree of differentiation observed, and the simplicity of the enamel structure, is in accordance with previous descriptions (e.g. TERZEA 1991) considering the enamel undifferentiated.

The relatively simple pattern described here separates *V. exilis* from most other arvicolids dating from the Late Villanyian/Early Biharian, which have by then acquired more diverse enamel configurations including clear tangential and lamellar enamel on the leading and trailing faces of the triangles. Broadly similar simple enamel configurations have been described by VON KOENIGSWALD (1980) in primitive arvicolids including *Ungaromys*, *Stachomys*, *Ellobius* and particularly *Prometheomys*. Particularly interesting is the lack of tangential enamel in *V. exilis* except possibly for small areas on the buccal salients.

A photograph of a similar enamel pattern in a tooth from Stranzendorf-F, Austria, was described under the name *Cseria opsia* by RABEDER (1981, pl. 10, fig. 4). This has radial enamel, with no tangential enamel, and only small areas of lamellar enamel. It appears to differ from the m1 of *V. exilis* from Osztramos-3 in that the enamel is shown as much thicker on the leading edge, but this is due mainly to the image concerning the BSA1 of the upper M2, where the relative thickness is atypical (RABEDER, pers. comm.) The definition of the species *C. opsia* (RABEDER 1981, p. 59) states “enamel not or only weakly differentiated”. TESAKOV (2004) proposed that the species *Cseria opsia* and *Cseria proopsia* may belong instead to the genus *Villanyia*. The study of RABEDER (1981) and examination of the original material from Stranzendorf, Austria, on which the taxa *Cseria opsia* and *Cseria proopsia* were based support this. Therefore they are provisionally included in the synonymy of *Villanyia* given in section II.

IV. FINE STRUCTURE (“SCHMELZMUSTER”) OF THE ENAMEL OF “*MIMOMYS (VILLANYIA) EXILIS*” FROM REBIELICE (= *BORSODIA*)

A lower first molar from the assemblage from Rebielice (collection PAS) originally referred to *Mimomys (Villanyia) exilis* by KOWALSKI (1960) has been examined. The enamel pattern (Fig. 3) consists largely of radial enamel. Discrete lamellar enamel extends around the salient angles as a layer between inner and outer radial enamel and extends some way along the anterior enamel. Significant areas of incipient tangential enamel occur at the back of the posterior loop and on the rear margins of the lingual triangles and the lingual side of the anterior loop. In this lower first molar the enamel is 5-10% thicker on the anterior margins of the triangles. This description is in accordance with that of VON KOENIGSWALD (1980 p. 60-61, fig. 62, under the name “*V. exilis*”), and is considered here to document a very early stage of evolution of the genus *Borsodia*. Similar material has been described from Ripa Skortselskaya as *Borsodia* cf. *steklovi* (ZAZHIGIN, 1980) by TESAKOV (2004). As noted above, the enamel differentiation in *Villanyia exilis* is also rather small, but in the opposite sense.

The material from Deutsch Altenburg described by RABEDER (1981) under the name *Cseria carnuntina* appears very similar to *Borsodia* from Rebielice. The relationship between *Borsodia* from Rebielice and *V. exilis* requires further clarification.

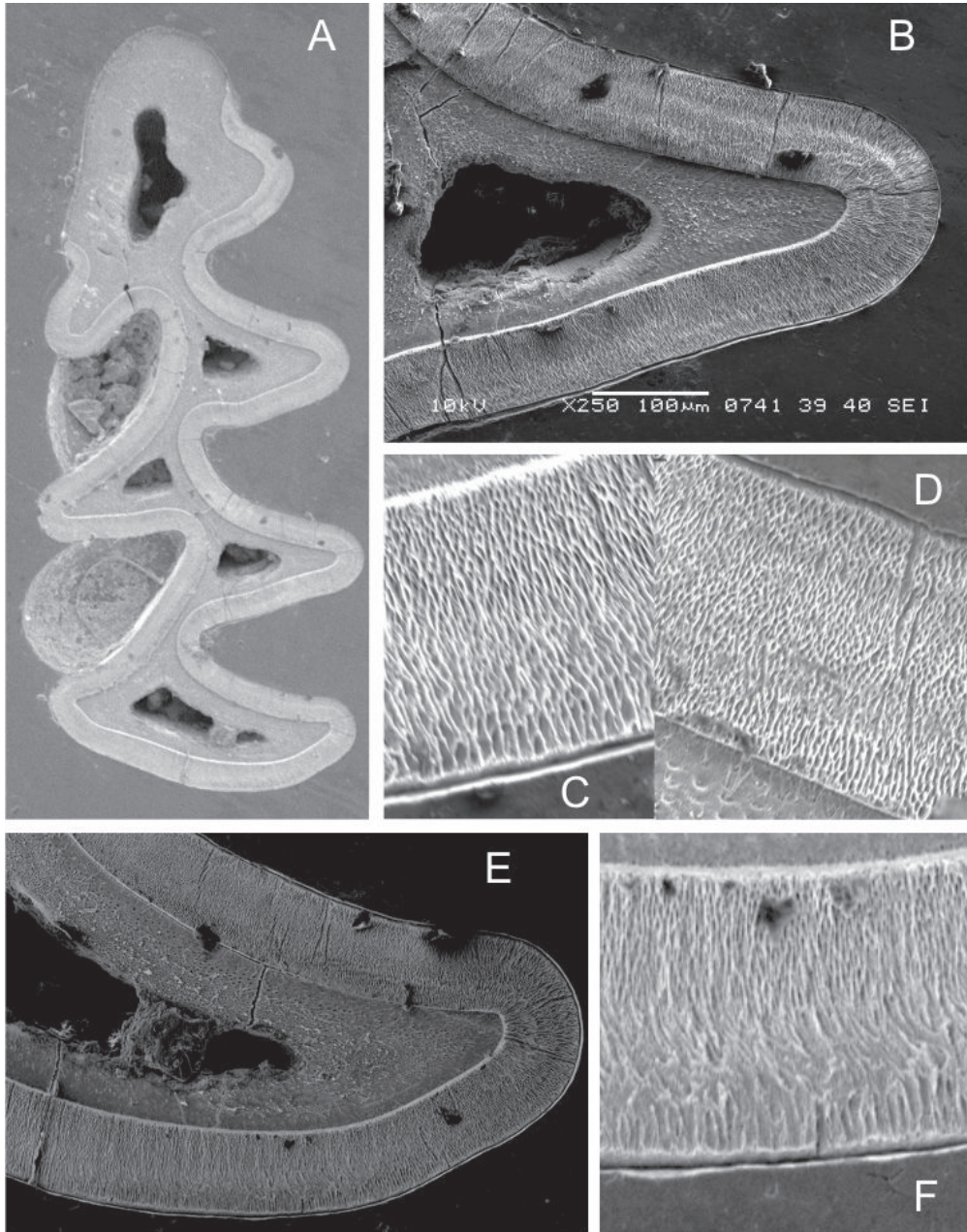


Fig. 3. The enamel fine structure of *Borsodia* from Rebielice Królewskie 1, Poland (previously known under *Mimomys* (*Villanyia*) *exilis*). Material: lower m1, PAS Kraków. A – whole tooth in cross section ca 1.5 mm above crown base: the enamel consist mainly of radial enamel with weak development of primitive tangential enamel on the posterior margins of the lingual salients and the posterior loop, and some lamellar enamel at the salients and anterior margins; B – second lingual salient angle demonstrating unequal (reverse differentiated) enamel thickness; C – enlargement of posterior enamel of second lingual salient, consisting of an internal layer of radial enamel and an external layer of primitive tangential enamel; D – enlargement of anterior enamel on second salient angle consisting of radial enamel; E – posterior loop with weak development of lamellar enamel at the salient angle and primitive tangential enamel on the posterior side; F – enlargement of posterior loop rear enamel demonstrating an internal layer of radial enamel and an external layer of primitive tangential enamel. (SEM Naturalis, Leiden).

V. GENERAL DISCUSSION

Since the original brief description, lacking an illustration and type designation, there has been unclarity about the definition and the affinities of *V. exilis*. Assemblages found at various localities particularly in the Eastern European countries have been described in the literature as containing various species of the genus *Villanyia*: e.g. by KOWALSKI (1960, material from Rebielice identified as *Mimomys (Villanyia) exilis* followed by e.g. ALEXANDROVA (1965), SUKHOV (1970), GROMOV and POLYAKOV (1977), ZAZHIGIN (1980), TERZEA (1991), REKOVETS (1994), REKOVETS and DEMA (2001) and ERBAJEVA (2005). This approach was also followed by ZHANG et al. (2008). However, in view of the new information presented here concerning the genotype material, much of the material called *Villanyia* in these publications seems better separated into the extinct lagurine vole genus *Borsodia* (JÁNOSSY & VAN DER MEULEN, 1975).

Several publications have described material which appears to be the same taxon as the tooth (VT95#2) taken here to represent *V. exilis*. For example, FEJFAR and HORÁČEK (1983, pl. X, fig. 1) illustrated a lower first molar from Včelare 3, Slovakia. SALA et al. (1994) illustrate specimens from the fissure filling of Rivoli Veronese, Italy. *V. exilis* is also recorded from Kadzielnia and Kamyk, Poland (NADACHOWSKI 1998): examination of this material confirms that teeth in approximately the same stage of wear are very similar in morphology to VT95#2. Further, *V. exilis* has been described from level 11d of Kozarnika Cave, Bulgaria (POPOV & MARINSKA 2007). From Hungary, as well as the single tooth from Villány-5, *V. exilis* is recorded (JÁNOSSY 1986) as present in the assemblage from Osztramos-3 (collection NHMUS Budapest): further material from this locality including a maxilla and several mandibles was determined recently by the author whilst in Budapest.

The publication of TERZEA (1991) on *Villanyia* from Betfia-XIII describes to modern standards relatively abundant material which clearly belongs to the same species as Vt 95#2. All the teeth in the dentition are described, so her work is the best reference point for *V. exilis*: however, the conclusions require some comments. TERZEA (1991) separated *V. exilis* from Betfia-XIII as a distinct temporal subspecies, *V. exilis crisiensis*, said to be more primitive than *V. exilis exilis* from Villány-5. However, in a following paper (TERZEA 1996) it was suggested that the fauna of Villány-5 was not later, but earlier, than Betfia-XIII. Therefore separation into (temporal) subspecies is here regarded as abandoned. Fig. 3 C of TERZEA (1991) is stated to be the lectotype of *V. exilis* (“d’après RABEDER, 1981, fig. 44/2”). However, this drawing is actually RABEDER’s type of *Cseria ultima*, and the figure legend can be understood only in relation to the comments of TERZEA (1991 p. 91, last paragraph) concerning change of lectotype.

TERZEA (1991) also described the new species *V. paraexilis* from Betfia-XIII, the new species *V. kowalskii* from Rebielice Królewskie and proposed to use the name *V. veterior* KRETZOI, 1969 for a second supposed species from this locality. The lectotypes from Rebielice were designated by reference to figures from KOWALSKI (1960). According to her analysis of *Villanyia* there were two parallel lineages through the Late Pliocene and Early Pleistocene, an idea suggested originally by KOWALSKI (1960) in view of observed variability. The lineage *V. kowalskii-V. paraexilis* was supposed to be more primitive, and the other *V. veterior-V. exilis* was supposed to be more progressive.

Now *V. exilis crisiensis* from Betfia-XIII is described as lacking a *Mimomys* fold on the anterior loop of the lower m1, whereas in *V. paraexilis* also from Betfia-XIII this fold is supposed to be present. However, on VT95#2 *V. exilis* from Villány-5, there is actually a slight indication of the *Mimomys* fold on the side of the tooth, i.e. it is not absent. Therefore it is considered more probable that the presence or absence of a *Mimomys* fold, or its persistence in the crown, is not a sufficient character to justify recognising two coexistent species of *Villanyia*. A similar situation is known from the large *Mimomys* from West Runton, UK, split by HINTON (1926) into *M. majori*, *M. intermedius*, and *M. savini* using a similar approach, but currently treated by most workers as a single species with variability in this character. *V. paraexilis* TERZEA, 1991 is therefore considered a junior synonym of *V. exilis* KRETZOI, 1956.

Examination of the original material from Rebielice assigned to *Mimomys* (*Villanyia*) *exilis* by KOWALSKI (1960) (and to *V. kowalskii* and *V. veterior* by TERZEA 1991), as well as further material from this locality (PAS collection), indicates high variability in respect of the *Mimomys* ridge and configuration of the anterior loop. These teeth are of small size and have enamel thicker on the leading edges, apparently not noticed by previous authors. The dentine of the triangles of the m1 is hardly confluent even in worn teeth. The enamel free areas are very low. The angles are pointed. There is no crown cement. It is considered probable that these teeth represent a very early stage in the evolution of *Borsodia*, similar to *Borsodia* cf. *steklovi* (ZAZHIGIN, 1980) from Ripa Skortsel'skaya as described in TESAKOV (2004). In particular the upper first molars demonstrate a typical *Borsodia* morphology. This may imply that the locality Rebielice 1 is somewhat older than previously realised. However, further work is needed to clarify this, and indeed how many different taxa are present in the fauna.

The very limited material from Kadzielnia (PAS collection) previously considered to belong to *Villanyia* includes teeth with closed dentine fields, resembling *Borsodia*, as well as other teeth with confluent dentine fields and apparently undifferentiated enamel which resemble *V. exilis*. The material appears to be heterogeneous.

A single worn tooth from Kamyk (PAS collection) has confluent dentine fields and an enamel configuration as in *V. exilis*. The material described from Betfia-XIII (TERZEA 1991) is indistinguishable from that seen by the author from Ozstramos-3.

From Russia, the genus *Villanyia* (as defined here) is known from the Urals (unpublished, TESAKOV, pers. comm.). Some teeth described as *Villanyia* from Akkulaevo (SUKHOV 1970, tab. 8, figs. 108-110) and from Simbugino (SUKHOV 1977, tab. 51, figs. 11, 12) appear to be attributable to this genus. TESAKOV (2004) lists these occurrences under the name *V. veterior*, and records early *Borsodia* species from the same deposits.

Recently the genus name *Villanyia* has been used broadly to include the subgenera *Villanyia*, *Borsodia*, *Cseria*, *Kulundomys* and *Shamaromys* covering several lines of arvicolid evolution (REKOVETS & DEMA 2001; DEMA & REKOVETS 2004). This proposal seems to extend the definition of *Villanyia* (a genus based on a late Early Pleistocene single tooth, of unusually simple structure) too widely in morphology and time. Synapomorphies uniting these five diverse subgenera are not obvious, and the heterogeneity of the type material of *V. exilis* as demonstrated here was apparently not recognised.

A similar broad view of the genus *Villanyia* has been proposed in a redefinition by ZHANG et al. (2008), but this was not based on direct observation of the genotype material or reference to the important work of TERZEA (1991). Their new species *Villanyia fanchangensis* is considered on the basis of their illustrations to be probably referable to the clade of Clethrionomine voles. The mandible of "*V. fanchangensis*" differs markedly from that of *V. exilis* from Ozstramos-3 (pers. obs.).

The origin and relationships of "*V. exilis*" have been debated in the literature, but this discussion has frequently been based on other fossil assemblages which are considered here to belong to the extinct lagurid vole genus *Borsodia*. The dentition of *V. exilis* from Villány-5, Ozstramos-3 and Betfia XIII is relatively low crowned and primitive, with confluences in the dentine fields and simple enamel structure. It has therefore been thought to be a burrowing species, possibly related to recent genera *Ellobius*, *Prometheomys* or *Hyperacrius*. RABEDER (1981) and CARLS and RABEDER (1988) suggested a relationship with *Cseria* and/or *Ungaromys*. As conceived here, *Villanyia* is distinct in morphology from *Borsodia*, and restricted to a single lineage commencing in the Early Villanyian and most prominently represented in East European faunas of the later part of the Villanyian and earliest Biharian. The distribution of this form appears to have been restricted mainly to East Europe. It was of small size, and possibly of burrowing habit. The earliest representatives appear to be from Simbugino, and the latest occurrence at Kamyk.

VI. CONCLUSIONS

It is proposed that, of the original 2 types, Specimen #2 is considered the genotype and type of *V. exilis* KRETZOI, 1956, and specimen #1 is identified as *C. kretzoi* (KOWALSKI, 1958). It is proposed that taxonomic acts subsequent to the original publication and prior to TERZEA (1991) are discarded in the interests of stability. A proposal to this effect is submitted to the International Commission on Zoological Nomenclature.

Much of the material previously identified in the literature as *Villanyia* is considered to belong to other taxa, notably *Borsodia*. It is proposed that the genus *Villanyia* should be restricted to the later part of an isolated lineage which evolved rather little during the Late Pliocene and Early Pleistocene.

The enamel structure of *V. exilis*, described here for the first time on the basis of a tooth from Osztramos-3, Hungary, consists largely of radial enamel, with very little tangential or lamellar enamel. This is the primitive arvicolid condition, although secondary simplification cannot be ruled out. This enamel pattern differs substantially from that of a tooth from Rebielice, Poland, from the assemblage described as *Mimomys (Villanyia) exilis* by KOWALSKI (1960), and here referred to *Borsodia* sp.

A c k n o w l e d g e m e n t s. I thank Prof. Laszlo KORDOS (Hungarian Geological Institute, Budapest) and Prof. Adam NADACHOWSKI (Polish Academy of Sciences, Kraków) for access to collections in their care, hospitality, and essential discussions. I am grateful to Dr. Mihaly GASPARIK and the management of the Hungarian National Natural History Museum for hosting my visits and providing material for analysis. Part of this work was supported by a travel grant under the EEC Synthesys program. SEM facilities were provided by Naturalis, Leiden. I thank Dr. Alexey TESAKOV (Geological Institute, Academy of Sciences, Moscow) for generously providing additional information and for discussions, Dr. Lutz MAUL for valuable comments on the manuscript, and Dr. Lars VAN DEN HOEK OSTENDE (Naturalis, Leiden), Dr. Federica MARCOLINI (University of Rome) and Dr. Francien DIELEMAN for assistance and advice.

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