A Preliminary Revision of the Extinct Voles of *Mimomys* and its Allies from China and the Adjacent Area with Emphasis on *Villanyia* and *Borsodia*

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Abstract

*Mimomys* and its allies constitute a group of extinct voles with rooted molars, which is important for biostratigraphic and evolutionary studies of small mammals. Their remains have commonly occurred from the Pliocene and Early Pleistocene sediments of China and Transbaikalia. They are referred to four genera such as *Promimomys*, *Mimomys*, *Villanyia* and *Borsodia*. Taking controversial taxonomy of these genera into consideration, we have presented a key to the genera and taxonomic notes with the specific composition of each genus in order to clarify the generic distinctions. Among the four genera, we focus on *Villanyia* and *Borsodia* and discuss their chronospatial distributions in China and Transbaikalia. During the later part of the Pliocene, the more archaic genus *Villanyia* was replaced by the more advanced genus *Borsodia*, although *Villanyia* survived somewhat later in southern China than in Transbaikalia.


1. Introduction

Extinct voles of *Mimomys* and its allies constitute a group adapted to grass-eating habits, which distributes mainly in the Holartic Region from the Early Pliocene to the Middle Pleistocene. Reflected by the habits, they are characterized by high-crowned prismatic molars, but still retain roots in the molars. In China, they have commonly occurred from the Pliocene and Early Pleistocene sediments and are considered to have great importance in biostratigraphic and evolutionary studies of small mammals in these periods.

The first recognition of these voles in China was made by Kormos (1934) who allocated the remains already described as "Arvicolidé gen. ind." by Teilhard de Chardin and Piveteau (1930), to *Mimomys*. After this work, the voles were recorded from several localities in northern China (Young, 1935; Research Group for the Huanghe Elephant, 1975; Zheng, 1976; Xue, 1981). On the basis of the knowledge hitherto obtained, Zheng and Li (1986) published a comprehensive revision of the voles from China. This work has greatly advanced the subsequent studies of these voles, and was followed by a number of studies which described remains of the voles from many localities in China (Zong, 1987; Zheng and Cai, 1991; Zheng, 1993; Qiu and Storch, 2000; Qiu et al., 2004; Cai et al., 2008). However, these studies described the remains from each locality, and no comprehensive work on the voles from China has been published since Zheng and Li (1986). Moreover in the previous works, the generic taxonomy of the voles is rather obscure especially in the...
distinction among *Mimomys*, *Villanyia* and *Borsodia*. Thus a new revision on the voles is required on the basis of the data accumulated after Zheng and Li (1986).

Recently, a new species of *Villanyia* was described from southern China by Zhang, Kawamura and Jin (2008) who provided a generic diagnosis of *Villanyia* and its differential characters from *Borsodia*. But they did not describe the distinction among *Mimomys*, *Villanyia* and *Borsodia* sufficiently in order to avoid deviation from the purpose of the paper. Here we present a preliminary revision of *Mimomys* and its allies including their generic distinction and the chronospatial distribution of *Villanyia* and *Borsodia* on the basis of the data already published. A more comprehensive revision of the voles will be published in the near future to include new and unpublished data from several localities in China that are not treated herein. The present paper also emends the chronological confusion in Zhang, Kawamura and Jin (2008), which was caused by the controversies on the age of the Pliocene / Pleistocene boundary (whether ca. 1.8 Ma or ca. 2.6 Ma), because the boundary is strongly related to the chronological comparisons of *Villanyia* and *Borsodia* between China and the adjacent countries.

2. Generic taxonomy with a key

We here define *Mimomys* and its allies as the voles with the following dental characters (Figs. 1–3): The molars are rooted. M³ has one or two triangles between the anterior and posterior loops, while M₁ has three triangles between the anterior loop (usually forming the anteroconid complex) and posterior loop. They comprise four genera: *Promimomys*, *Mimomys*, *Villanyia* and *Borsodia*. A key to the genera is given below.

1. Molars lower in crown height; sinuous line weakly undulated; M³ usually without LRA3 (unknown in China); anterior loop of M₁ small and simple, generally lacking LRA4 and BRA3, and not forming the anteroconid complex. .......... *Promimomys*

2. Molars higher in crown height; sinuous line ascending high aside of the anteroconid complex and posterior loop in M₁; M³ with LRA3; anterior loop of M₁ larger and complicated, with LRA4 and BRA3, and forming the anteroconid complex. ....... 2

3. Cementum developed except in very primitive species; enamel negative type (*Mimomys*-type) in differentiation, or undifferentiated (in primitive species); M₁ and M³ with two or three roots; M³ generally with an enamel island (but two in primitive species, and no island in advanced species); posterior loop of M³ broader; M₁ with the *Mimomys* angle and an enamel island except in advanced species. .......... *Mimomys*

4. Cementum absent; enamel negative type in differentiation or undifferentiated; M₁ with three roots; M³ with two or three roots; M₁ usually with one or two enamel islands; posterior loop broad and short, where the posterior enamel island can be accommodated; M₁ usually with the *Mimomys* angle, but no enamel island. .................. *Villanyia*

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Fig. 1 Schematic diagram showing the buccal views of M₁ of *Mimomys* and its allies. The ontogenetic change from a juvenile individual (j) to an aged individual (a) is also shown.
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Fig. 2 Schematic diagram of M3 of Mimomys and its allies showing their occlusal patterns with terminology and differentiation types in enamel thickness. M3 of Promimomys is unknown in China. AL: anterior loop, BRA: buccal reentrant angle, ei: enamel island, LRA: lingual reentrant angle, PL: posterior loop, T: triangle. BRA, LRA and T are numbered for showing the homology of each part.

Fig. 3 Schematic diagram of M1 of Mimomys and its allies showing their occlusal patterns with terminology and differentiation types in enamel thickness. ACC: anteroconid complex, AL: anterior loop, BRA: buccal reentrant angle, ei: enamel island, LRA: lingual reentrant angle, ma: Mimomys angle, PL: posterior loop, T: triangle. BRA, LRA and T are numbered for showing the homology of each part.

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3. Taxonomic notes on *Promimomys*

The genus *Promimomys* was described by Kretzoi (1955) on the basis of a material with uncertain geological age from Hungary. In China, only one mandible with I1, M1, and M2 is referred to this genus. The mandible was collected from the Lower Pliocene of Xindong Cave, Huainan (Fig. 4), and was named *P. asiaticus* as a new species by Jin and Zhang (2005). Besides this, the following European and North American species are considered to be included in the genus: *P. cor* Kretzoi, 1955; *P. insuliferus* Kowalski, 1958; *P. microdon* Jánossy, 1974; *P. minus* (Shotwell, 1956); *P. moldavicus* (Kormos, 1932). On the other hand, Zazhigin (1980) listed *antiquus*, *baschkirica*, *cor*, *gracilis*, *moldavicus*, *occitanus* and *stehlini* as the members of *Promimomys*, but all of them except *cor* and *moldavicus* are assignable to *Mimomys* in the present treatment.

4. Taxonomic notes on *Mimomys*

The genus *Mimomys* is an extensive genus comprising many species and was established by Forsyth Major (1902) on the basis of remains from the Lower Pleistocene of England. *Aratomys* described by Zazhigin in Gromov and
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Polyakov (1977) and Cromeromys by Zazhigin (1980) are considered to be synonymous with Mimomys. Remains assigned to Mimomys have been recorded from many localities in China (Fig. 4). We examined the literatures describing the remains as well as the remains stored in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences. As the result of the examinations, we recognize the following species as the members of this genus:

Mimomys bilikeensis (Qiu and Storch, 2000)
M. orientalis Young, 1935
M. youhenicus Xue, 1981
M. banchiaicus Zheng et al., 1975
M. gansunicus Zheng, 1976
M. peii Zheng and Li, 1986

Besides these, Zheng and Li (1986) described the remains assigned to M. cf. intermedius and Mimomys sp.

The representative localities yielding these forms are mapped in Fig. 4, and detailed information on each locality is given in Table 1. This figure and table also show Transbaikalian localities.

In regard to European species, we follow a comprehensive review by Kowalski (2001) who listed many species of Mimomys, although he did not treat Villanyian (early Pliocene) species. He included Pitymimomys described by Tesakov (1998) in Mimomys. The species listed by him are considered to have the diagnostic characters of Mimomys mentioned above. On the other hand, Zazhigin (1980) showed a different scheme on the taxonomy of Mimomys, in which European and Siberian species were treated. We include all the species of Promimomys except P. cor and P. moldavicus, and all the species of Cromeromys except "C. newtoni" listed by him, in Mimomys.
Table 1 Detailed information on the representative localities yielding *Mimomys* and its allies in China and Transbaikalia. For location of each locality see Fig. 4.

<table>
<thead>
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<th>Locality</th>
<th>Taxon (partly revised)</th>
<th>Geological age</th>
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<td><em>Borsodia chinensis</em></td>
<td>? Early Pleistocene</td>
<td>Zheng and Li (1986)</td>
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<td>2 Bilike</td>
<td><em>Mimomys bilkeensis</em></td>
<td>Early Pliocene</td>
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<td>and Danangou in the Nihewan Basin</td>
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<td>8 Dongyan, Pinglu</td>
<td><em>Mimomys orientalis</em></td>
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<td>Middle Pliocene</td>
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<td>in the Gonghe Basin</td>
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<td>Late Pliocene (=&quot;Early Pleistocene&quot;)</td>
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<td>13 Xindong Cave, Huainan</td>
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<td>18 Klochénevo I, II</td>
<td><em>Mimomys cf. reidi</em>, <em>M. cf. pusillus</em>, <em>M. pseudintemiadius</em>, <em>Borsodia klochnevi</em></td>
<td>Late Pliocene</td>
<td>Erbajeva (1998), Alexeeva et al. (2001)</td>
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</table>
5. Taxonomic notes on *Villanyia*

The genus *Villanyia* was described by Kretzoi (1956) from Early Pleistocene remains collected from Hungary. Its distinction from *Mimomys* and from *Borsodia* have been controversial. The diagnostic characters given in the key, however, distinguish the following two species described in China as *Villanyia*:

*Villanyia fanchangensis* Zhang, Kawamura and Jin, 2008

*V. hengduanshanensis* (Zong, 1987)

These two species occurred from one locality each in southern China (Fig. 4, Table 1). Moreover *V. hengduanshanensis* is known from only one specimen, although *V. fanchangensis* is represented by abundant specimens.

Using the diagnostic characters, we include the following European and Siberian species in *Villanyia*:


*V. petenyi* (Méhely, 1914); possibly including “*Mimomys prachungaricus*” Schevtschenko, 1965” and “*M. tanaica*” Schevtschenko, 1965.”

*V. eleonorae* Erbajeva, 1976

*V. novoasovica* (Topachevsky and Scorik, 1977)

*V. steklovi* Zazhigin, 1980

*V. betekensis* Zazhigin, 1980

6. Taxonomic notes on *Borsodia*

Jánossy and van der Meulen (1975) first described *Borsodia* as a new subgenus of *Mimomys*, which was characterized by the molars without cementum and with positive-type enamel differentiation. Subsequently, *Borsodia* was often treated as a full genus (Tesakov, 1993; Kowalski, 2001 and others). We adopt the generic treatment of *Borsodia* and consider that it is distinguishable from *Mimomys* and *Villanyia* by using the diagnostic characters given in the key. In China, only one species, *B. chinensis*, is allocated to this genus. “*Mimomys heshuinicus*” Zheng, 1976” is considered to be a synonym of this species (Zheng and Li, 1986). In Transbaikalia, Erbajeva (1973) described “*Mimomys (Villanyia) laguriformes*”, which was subsequently synonymized with “*M. (V.) chinensis*” (= *B. chinensis*) by Zheng and Li (1986). Additionally, *Villanyia gromovi* Erbajeva, 1976 is probably a subspecies of “*M. (V.) laguriformes*” (Gromov and Polyakov, 1977). Thus *V. gromovi* is considered to be included in *B. chinensis*. As shown in Fig. 4 and Table 1, *B. chinensis* is known from several localities in northern China and Transbaikalia.

We regard the positive-type enamel differentiation in the molars as the most important character to distinguish *Borsodia* from the other genera. The following European and Siberian species are considered to be included in *Borsodia* because they have the diagnostic characters in the key:

*Borsodia newtoni* (Forssky Major, 1902); Mayhew and Stuart (1986) included “*Mimomys hungaricus*” Kormos, 1938” in this species. “*Mimomys lagurodontoides*” Schevtschenko, 1965” seems not to belong *Borsodia*, because its M1 usually has the *Mimomys* angle judging from the figures of Schevtschenko (1965).

*B. fejervari* (Kormos, 1934)

*B. arankoides* (Alexandrova, 1976)

*B. prolaguroides* (Zazhigin, 1980)

*B. klochnevi* (Erbajeva, 1998)

The specific compositions of *Borsodia* and *Villanyia* in this paper are considerably different from those in Tesakov (1993) and Kowalski (2001). Among the species listed above, *B. klochnevi* is known from Transbaikalia, and was originally allocated to *Villanyia* (Erbajeva, 1998). Its generic allocation to *Borsodia* was discussed in Zhang, Kawamura and Jin (2008).

7. Chronospatial distribution of *Villanyia* and *Borsodia*

In China and Transbaikalia, the chronospatial distributions of *Villanyia* and *Borsodia* are more limited than that of *Mimomys* (Fig. 4, Table 1). Before discussing their distributions, we emend the chronological confusion having occurred during the publication of Zhang, Kawamura and Jin (2008). In China, the boundary between the Pliocene and Pleistocene is generally placed at ca 2.6 Ma, which is different from the geochronological scheme accepted in other countries (adopting ca 1.8 Ma as the boundary; Fig. 5). In the draft of Zhang, Kawamura and Jin (2008), the usage in the Chinese sense was distinguished as “Early (Lower) Pleistocene” and “Pleistocene” from that in the other scheme. These quotation-marked words mean the Late Pliocene plus Early Pleistocene and the Late Pliocene plus Pleistocene respectively, in the other scheme (Fig. 5). Thus the words Early Pleistocene, Lower Pleistocene and Pleistocene in the following sentences in Zhang, Kawamura and Jin (2008) should be emended as follows:

- In this paper, “Early” or “Lower Pleistocene” means the usage in Chinese sense, ... in page 163.
- A cooling event at the beginning of the “Pleistocene” caused southward migration of the Palaearctic elements. in page 164.
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Transbaikalia
Northern China
Southern China

Borsodia chinensis
Borsodia chinensis
Borsodia chinensis

Villanyia fanchangensis
Villanyia eleonorae

Fig. 5 Chronospatial distribution of Villanyia and Borsodia in China and the adjacent area. Note that two schemes on geological age are shown for the difference in the Pliocene / Pleistocene boundary. In China, the boundary is generally placed at ca. 2.6 Ma. In this sense, we use “Early Pleistocene” for the late Pliocene plus the Early Pleistocene in another scheme. (1): chronological division adopted here (boundary ages mainly by Gradstein et al., 2004), (2): chronological division generally used in China, (3): mammal biozones and units in Europe (boundary ages by Steininger et al., 1996). Transbaikalian species redrawn from Bazorov et al. (1976) and Erbajeva (1998).

• which seems affirmative for the assignment of the “Early Pleistocene” age of V. fanchangensis.’ in page 169.

In China and Transbaikalia, Villanyia occurred from Late Pliocene sediments of Renzidong Cave (V. fanchangensis; Zhang, Kawamura and Jin, 2008), “Early Pleistocene” (?) sediments of Nixi (V. hengduanshanensis; Zong, 1987), the Middle Pliocene (MN16b) of Beregovaya (V. eleonorae; Erbajeva and Alexeeva, 2000) and the Middle Pliocene (MN16a) of Tologoi 1.1 and Udunga (V. cf. eleonorae or V. ex. gr. eleonorae; Alexeeva et al., 2001, Erbajeva et al., 2003). Among the localities, Tologoi 1.1 and Udunga are the earliest in geological age; Beregovaya is next; and Renzidong Cave is the latest, although Nixi is uncertain in age. Thus V. eleonorae is earlier than V. fanchangensis (Fig. 5). The descriptions of V. eleonorae by Erbajeva (1976) and Bazorov et al. (1976) permit us its morphological comparison with V. fanchangensis. M² of V. eleonorae sometimes has three roots, while the same tooth of V. fanchangensis always has two roots. M₁ of V. eleonorae often has the Mimomys angle, but the same tooth of V. fanchangensis usually lacks the angle (Fig. 5). These differences suggest that V. eleonorae is more primitive than V. fanchangensis. In M³, however, V. eleonorae has the posterior enamel island easily disappeared by wear and lacks an anterior one. In V. fanchangensis, both of the islands appear more frequently (Fig. 5). This character suggests that V. eleonorae is more advanced than V. fanchangensis. V. eleonorae is considered to be a sister species of V. fanchangensis, although the phylogenetic relationship between them is still unclear, owing to the scarcity of the information on Villanyia in China.

As shown in Fig. 5, it is inferred that Villanyia inhabited Transbaikalia in the Middle Pliocene, but its distribution to China in this period is still unknown. In the Late Pliocene, it was already replaced by Borsodia in Transbaikalia, but still survived in southern China. Even in southern China, Villanyia was absent in the Early Pleistocene fauna.

In regard to Borsodia, we recognize the two species, B. klochnevi and B. chinensis, in Transbaikalia and China (Fig. 4, Table 1). B. klochnevi occurs from the Late Pliocene sediments (MN17) of Klochnevo (I-1 and II-1) and Zasukhino I in Transbaikalia (Erbajeva, 1998). B. chinensis is known from many localities in China and Transbaikalia, which are dated to the Early Pleistocene (Table 1). Thus B. klochnevi is earlier than B. chinensis.
(Fig. 5). Erbajeva (1998) pointed out that *B. klochnevi* had several morphological characters intermediate between *V. eleonorae* and *V. chinensis*, and stated “*Villanyia klochnevi* (= *B. klochnevi*) n. sp. is considered to be transition form between the archaic species *Villanyia eleonorae* and advanced species *Borsodia laguriformes* (= *B. chinensis*).” This statement is coincident with the chronological order of the three species (Fig. 5). Thus it is likely that the three species represent a single evolutionary lineage, in which *Borsodia* originated from *Villanyia*.

In Europe, *Borsodia* (*B. newtoni*, *B. fejervari* and *B. arankoides* as its components) ranges from early Villanyian to early Biharian (Kowalski, 2001). In western Siberia, *B. prolaguroides* was recorded from the Eopleistocene (=Villanyian) by Zazhigin (1980). In Transbaikalia, *B. klochnevi* is dated to MN17 (late Villanyian) as mentioned above. If the early Villanyian occurrences of *Borsodia* in Europe are reliable, *Borsodia* first appeared in Europe, and then spread eastward to Transbaikalia and China. If *Villanyia eleonorae*, *B. klochnevi* and *B. chinensis* form a single evolutionary lineage as mentioned above, *Villanyia* gave rise to *Borsodia* in Transbaikalia then spread vice versa. At any rate, more chronological and taxonomical data are required to clarify the origin and evolution of *Borsodia*.

As shown in Fig. 5, *Borsodia* appeared in Transbaikalia in the Late Pliocene, then its distribution expanded to northern China in the Early Pleistocene. *Borsodia* survived at least at 1.36 Ma in northern China (Zhang, Kawamura and Cai, 2008).

8. Conclusion

*Mimomys* and its allies from China and Transbaikalia comprise four genera such as *Promimomys*, *Mimomys*, *Villanyia* and *Borsodia*. These genera are distinguishable from each other by the molar characters given in the key. Among the genera, *Promimomys* is known by the only species *P. asiaticus* from the Lower Pliocene of China. *Mimomys* is more diversified and has a longer chronological range from the Early Pliocene to Early Pleistocene. It consists of *M. bilikeensis*, *M. orientalis*, *M. yadohensis*, *M. banchiaonicus*, *M. gansunicus*, *M. peii* and several other forms in this area. The taxonomic positions of *Villanyia* and *Borsodia* have been controversial not only in China but also in other countries. We consider that the following species belong to *Villanyia*: *V. exilis*, *V. petenyii*, *V. eleonorae*, *V. novoasovica*, *V. steklovi*, *V. betekensts*, *V. fanchangensis* and *V. hengduanshanensis*. We also refer the following species to *Borsodia*: *B. newtoni*, *B. fejervaryi*, *B. arankoides*, *B. prolaguroides*, *B. klochnevi* and *B. chinensis*.

Among the species of *Villanyia*, *V. eleonorae* and *V. fanchangensis* are known from the Middle Pliocene of Transbaikalia and from the Upper Pliocene of southern China, respectively (Fig. 5). Among the species of *Borsodia*, *B. klochnevi* and *B. chinensis* are recorded from the Upper Pliocene of Transbaikalia, and from the Lower Pleistocene of Transbaikalia and northern China, respectively.

These records illustrate the chronospace distributions of *Villanyia* and *Borsodia* in China and Transbaikalia. In the Middle Pliocene, *Villanyia* was distributed in Transbaikalia, where it was replaced by *Borsodia* in the Late Pliocene. In southern China, however, *Villanyia* still survived in the Late Pliocene. In the Early Pleistocene, *Villanyia* was already extinguished from China, but *Borsodia* was distributed from Transbaikalia to northern China. These changes can be interpreted as the replacement of the more archaic genus (*Villanyia*) by the more advanced one (*Borsodia*) during the later part of the Pliocene.

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