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# A new species of the extinct vole *Villanyia* from Renzidong Cave, Anhui, East China, with discussion on related species from China and Transbaikalia

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# Abstract

A new species of extinct vole with rooted cementless molars is described on the basis of abundant remains from the Early Pleistocene (= Late Pliocene) sediments of Renzidong Cave. Among the extinct cementless voles, distinction between *Villanyia* and *Borsodia* is recommended to determine the generic allocation of the new species. The comparison of diagnostic characters of these two genera obtained by this study indicates that the new species belongs to *Villanyia*, and the species is named as *V. fanchangensis*. The provided revision of the Chinese and Transbaikalian species of *Villanyia* and *Borsodia* has revealed that the species of *Villanyia* were distributed in southern China during the Late Pliocene, and in Transbaikalia during the Middle Pliocene. In China, *Villanyia* was replaced by *Borsodia* in the earliest Pleistocene, while in Transbaikalia it was replaced by *Borsodia* in the Late Pliocene. (© 2007 Published by Elsevier Ltd.)

## 1. Introduction

The fossil locality of Renzidong Cave is situated near the south bank of the Yangtze River in Fanchang County of Anhui Province, China (Fig. 1). The sediments of the cave have yielded numerous mammalian remains in association with artifacts, and are assigned to the time interval between 2.0 and 2.4 Ma by the faunal data (Jin et al., 2000). This interval falls into the Early Pleistocene in the chronological sense generally accepted in China, but in the Late Pliocene in the geological time scale by Gradstein et al. (2004). In this paper, Early or Lower Pleistocene means the usage in Chinese sense, in which the Plio-Pleistocene boundary is determined at ca. 2.6 Ma.

The remains from the sediments include thousands of bones and teeth of extinct voles close to *Mimomys* and *Villanyia*. The vole remains can be easily classified into three forms by clear differences in size and patterns of the molars, as shown in Fig. 2. Unfortunately, their systematic studies have not been published yet, although Zhang (2004) described in detail the ontogenetic changes of the molars in one form of the three. Following Zhang's work, this paper presents the results of a systematic study on the same form that is referable to a new species of the genus *Villanyia*. In addition to the detailed description of the new species, recommendation on the distinction between *Villanyia* and *Borsodia* is presented, due to previous ambiguous applications. The replacement of *Villanyia* by *Borsodia* in China and Transbaikalia is discussed.

#### 2. Geological and faunal settings

According to Jin et al. (2000), the sediments of Renzidong Cave can be divided lithologically into 8 layers. Among them, the first 7 layers with a total thickness of about 15 m comprise the upper part of the sediments, which is composed mainly of brown to reddish brown mud or sandy mud with limestone breccia. This part yielded abundant mammalian remains including the vole remains described here. The eighth layer with a thickness more than

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15 m comprises the lower part, which is composed mainly of gray sandy mud, sand and rounded gravel. This part contains few mammalian remains.

Jin et al. (2000) listed more than 67 forms of mammals from this site. They include both Palaearctic (35.8%) and Oriental (34.4%) faunal elements. The remaining 29.9% of the mammalian species are widespread in Eurasia. The



Fig. 1. Fossil localities of *Villanyia* and its allied genus *Borsodia* in China and Transbaikalia.  $\bullet$ , *V. fanchangensis*,  $\blacktriangle$ , *V. hengduanshanensis*,  $\blacktriangledown$ , *V. eleonorae* and *V.* ex. gr. eleonorae,  $\bigcirc$ , *B. chinensis*,  $\triangle$ , *B. klochnevi*.

present zoogeographic boundary between the Palaearctic and Oriental Regions is far to the north of Renzidong Cave. Thus, Jin et al. (2000) concluded that a cooling event at the beginning of the Pleistocene caused southward migration of the Palaearctic elements.

# 3. Method and terminology

The vole remains were collected mainly by fine-mesh screening of the sediments. The terminology and measuring method adopted here follow those generally used for detailed descriptions and measurements of prismatic molars of voles. They are shown in Fig. 2, where molars of the three forms from Renzidong Cave are illustrated. The HH-index (Carls and Rabeder, 1988) is calculated as  $\sqrt{Hsd^2 + Hsld^2}$ . The enamel band (Schmelzband) differentiation quotient (SDQ; Heinrich, 1978) is calculated as the average of W<sub>p</sub> (width of the posterior enamel band)/W<sub>a</sub> (width of the anterior enamel band) \*100 measured in all the triangles, a part of the anteroconid complex, and the posterior loop of M<sub>1</sub>.

# 4. Systematic description

Family Arvicolidae Gray, 1821 Genus Villanyia Kretzoi, 1956

Synonym:

Villanyia Kretzoi, 1956. Geologica Hungerica, Series Palaeontologica, 27, 188

*Villanyia* Kretzoi; Gromov and Polyakov (1977). Fauna of the USSR, Mammals, 3 (8), 312–321. (in part)

*Villanyia* Kretzoi; Zazhigin (1980). Transactions of the Academy of Science, USSR, 339, 98–108. (in part)

*Borsodia* Jánossy and van der Meulen; Tesakov (1993). Quaternary International 19, 41–45. (in part)

*Villanyia* Kretzoi; Kowalski (2001). Folia Quaternaria 72, 291–292.



Fig. 2. Molars of the three forms of the extinct voles from Renzidong Cave, and the terminology and measuring method adopted here. 1: Left  $M_1$  of the first form described here as *Villanyia fanchangensis*, sp. nov. (V13991.54, 1-1: occlusal view, 1-2: lingual view, 1-3: buccal view) 2: Left  $M^3$  of the same form as 1 (V13991.1304 in occlusal view) 3: Left  $M_1$  (unnumbered) of the second form originally assigned to *Cromeromys* cf. *gansunicus* by Jin et al. (2000) in occlusal view, 4: Left  $M_1$  (unnumbered) of the third form originally assigned to *Mimomys* cf. *peii* by Jin et al. (2000) in occlusal view. AC: anterior cap, ACC: anteroconid complex, AL: anterior loop, BRA: buccal re-entrant angle, BSA: buccal salient angle, EI: enamel island, Hsd: height of hyposinuid, Hsld: height of hyposinulid, IF: islet fold, *L*: length of crown,  $L_a$ : length of anteroconid complex, LRA: lingual re-entrant angle, LSA: lingual salient angle, MA: *Mimomys* angle, PF: prism fold, PL: posterior loop, SL: sinuous line, T: triangle, *W*: width of crown,  $W_a$ : width of anterior enamel band,  $W_p$ : width of posterior enamel band.

*Borsodia* Jánossy and van der Meulen; Kowalski (2001). Folia Quaternaria 72, 284–287. (in part)

Type species: Villanyia exilis Kretzoi, 1956

Included species: Villanyia petenyii (Mehely, 1914) including "Mimomys praehungaricus Schevtschenko, 1965" and "Mimomys tanaitica Schevtschenko, 1965"; Villanyia eleonorae Erbajeva, 1976; Villanyia novoasovica (Topachevsky and Scorik, 1977); Villanyia steklovi Zazhigin, 1980; Villanyia betekensis Zazhigin, 1980; Villanyia hengduanshanensis (Zong, 1987); Villanyia fanchangensis, sp. nov.

Chronological range: Middle to Late Pliocene

Amended diagnosis: Rooted vole with cementless molars;  $M^1$  with three roots;  $M^2$  with three roots in primitive species, but with two roots in advanced species;  $M^3$  with one or two enamel islands, of which the anterior one tends to be reduced in advanced species; posterior loop of  $M^3$  short and broad; no enamel island on  $M_1$ ; *Mimomys* angle usually present; enamel band differentiation quotient (SDQ) close to or more than 100; posterior root of  $M_2$  sits on the incisor in primitive species, but slides to its buccal side in advanced species.

Differential diagnosis: Villanyia differs from the genus Borsodia

- by having in M<sup>1</sup> three roots in contrast to two in *Borsodia*;
- by three or two roots in  $M^2$ ;
- by one or two enamel islands in M<sup>3</sup>, and no island in *Borsodia*;
- by undifferentiated or negatively differentiated enamel band of the teeth (SDQ equal to or >100), in *Borsodia*, enamel band differentiation is positive or *Microtus*-type (SDQ<100).

# 4.1. Remarks

The distinction between Villanyia and Borsodia has been obscure. Previously, several related species have been included in these two genera (Kretzoi, 1956; Gromov and Polyakov, 1977; Zazhigin, 1980; Tesakov, 1993; Kowalski, 2001). Jánossy and van der Meulen (1975) proposed Borsodia as a subgenus of Mimomys with the diagnosis: "A group of *Mimomys* species with molars which lack crown-cementum and in which the enamel at the occlusal surface is thicker at the anterior side of the triangles in the lower molars and thicker at the posterior sides in the upper molars". From this definition, the genus Borsodia has distinctive morphological features. Villanvia represents a different genus, some species of which gave rise to Borsodia (Tesakov, 1993). These two genera have distinct morphological features and represent different evolutionary stages. The included species of Villanyia is based on our amended diagnosis and the descriptions or revisions given by Gromov and Polyakov (1977), Zazhigin (1980), Kowalski (2001), Jánossy and van der Meulen (1975), and Tesakov (1993). Other related species, such as Villanyia klochnevi Erbajeva, 1998, etc., are re-referred to *Borsodia* (see the Discussion below).



Fig. 3. Molars of *Villanyia fanchangensis*, sp. nov. from Renzidong Cave  $(M^1: 1-2, M^2: 3-4, M^3: 5-13, M_1: 14-22, M_2: 23-24, M_3: 25-26)$  and *Borsodia chinensis* from Majuangou-III (27-31). 1: V13991.861, 2: V13991.971, 3: V13991.1039, 4: V13991.1161, 5: V13991.1245, 6: V13991.1234, 7: V13991.1284, 8: V13991.1302, 9: V13991.1304, 10: V13991.1274, 11: V13991.1321, 12: V13991.1337, 13: V13991.1351, 14: V13991.52, 15: V13991.54, 16: V13991.196, 17: V13991.200, 18: V13991.287, 19: V13991.289, 20: V13991.297, 21: V13991.425, 22: V13991.458, 23: V13991.520, 24: V13991.586, 25: V13991.744, 26: V13991.754, 27-31: unnumbered, inv: drawing of the molar is inverted.



Fig. 4. Mandibles of *Villanyia fanchangensis*, sp. nov. from Renzidong Cave. 1: V13991 (holotype), 2–4: V13991.1–V13991.3.

Synonym: Borsodia sp.; Jin et al. (2000). Acta Anthropologica Sinica, 19 (suppl), 190.

*Holotype*: Left mandible with I and  $M_1$  to  $M_3$  (V13991). *Hypodigm*: 1 premaxilla–maxilla with left incisor and  $M^1$ , and with right incisor,  $M^1$  and  $M^2$  (V13991.8); 213 isolated  $M^1$  (V13991.825–V13991.1037); 189 isolated  $M^2$  (V13991.1038–V13991.1226); 133 isolated  $M^3$  (V13991.1227–V13991.1359); 3 right mandibles with I and  $M_1$  to  $M_3$  (V13991.1–V13991.3); 2 right mandibles with  $M_1$ ,  $M_2$  and  $M_3$  (V13991.4, 13991.5); 1 left mandible with  $M_1$  and  $M_2$  (V13991.7); 1 right mandible with  $M_1$  (V13991.6); 461 isolated  $M_1$  (V13991.9–V13991.469); 261 isolated  $M_2$  (V13991.470–V13991.730); 94 isolated  $M_3$  (V13991.731–V13991.824).

*Respository*: All the specimens are stored in the Institute of Vertebrate Paleontology and Paleonthropology, Chinese Academy of Sciences, Beijing.

Name derivation: Fanchang—the county of the fossil site. Locality and horizon: Renzidong Cave, a limestone quarry on the southern slope of Lailishan Hill, Suncun, Fanchang Country, Anhui Province (31°5′ 23″ N, 118°5′ 46″E; Fig. 1); Layers 3 and 4.

*Geological age*:Early Pleistocene (possibly between 2.0–2.4 Ma).

*Diagnosis*:Medium-sized species with three roots in  $M^1$ and two roots in  $M^2$  and  $M^3$ ;  $M^1$  and  $M^2$  without "lagurine" structure;  $M^3$  with two enamel islands, two or three salient angles and one or two re-entrant angles on the lingual side, two or three salient angles and re-entrant angles on its buccal side, anterior loop broadly confluent with T2, isthmus between T2 and T3 narrow or closed; anterior cap of  $M_1$  simple in shape, isthmus between the anterior cap and T5 showing a clear constriction, anteroconid complex of  $M_1$  having neither enamel island, islet fold, *Mimomys* ridge nor prism fold, T4 and T5 of  $M_1$ broadly confluent with each other; in  $M_2$  and  $M_3$ , T1 and T3 broadly confluent with T2 and T4, respectively; both roots of  $M_2$  slides to the buccal side of the incisor; both roots of  $M_3$  sits on the incisor.

# 4.2. Description

*Premaxilla–maxilla and upper incisor*: This part is preserved in only one specimen (V13991.8). The incisive foramen is slender, 4.2 mm in length and about 0.5 mm in width. It begins on the level of the posterior margin of the upper incisor alveola and ends close to the anterior margin of the alveolus of  $M^1$ . The upper incisor is triangular in cross section, and has no groove on enamel surface.

 $M^1$  and  $M^2$ : The occlusal patterns of  $M^1$  and  $M^2$  comprise four and three alternating triangles, respectively. LRA2 is normal in shape, and shows the same feature as the other re-entrant folds. The "lagurine" structure is not observed there. In young individuals, the anterior wall of T3 is nearly parallel to the posterior wall of T2, so that T3 and T2 form a parallelogram together (1 and 3 in Fig. 3). In adult individuals such feature is not observed. The deepness of both lingual and buccal re-entrant angles are the same. In lingual and buccal views, the sinuous line ascends very high on both sides of the anterior loop and on the buccal side of T4, in comparison with the line on the other parts. Additionally only in M<sup>1</sup>, the line also ascends high on the lingual side of T1.

 $M^3$ : The pattern of  $M^3$  shows more conspicuous variation than those of  $M^1$  and  $M^2$ . It comprises two alternating triangles (T2 and T3) between the anterior and posterior loops.

The anterior loop has an enamel island except in young and aged individuals. In young individuals, BRA1 deeply penetrates lingually into the central part of the crown (5–7 in Fig. 3). The lingual part of BRA1 becomes the island by the advance of wear, where its buccal part remains as a shallow fold (8 and 9 in Fig. 3). Moreover in aged individuals, the island disappears, so that the anterior loop is broadly confluent with T2 (10–13 in Fig. 3). BRA1 is also shallow in these individuals. The anterior wall of the anterior loop is slightly concave. LSA2 is more robust than and not as acute as BSA1. LRA2 is broad, and is the deepest in all the re-entrant angels. BSA2 is relatively delicate and well-pointed. BRA2 is much shallower than LRA2, but developed. The isthmus between T2 and T3 is narrow or closed. T3 and the posterior loop are confluent with each other, and form a large dentine field that accommodates the posterior enamel island. This island is formed by the isolation of the lingual part of BRA3, as observed in a very young individual (5 in Fig. 3). The island disappears by wear in very old individuals (12 and 13 in Fig. 3), where the island in the anterior loop was already extinguished. Thus no island is seen in these individuals. LSA3 is well developed, but LRA3 is shallow and indistinct. BSA3 is well developed in 66% of the examined specimens, but it is indistinct or absent in the remaining specimens. BRA3 is sometimes observed, but shallow.

In lingual and buccal views, the sinuous line ascends very high on both sides of the anterior loop and on the buccal side of the posterior loop, in comparison with the line on the other parts.

Mandible and lower incisor: The mental foramen is small, and situated somewhat anteriorly of  $M_1$ . The lower masseteric crest is stout, and starts posterodorsally from about 0.5 mm behind the mental foramen. The crest is slightly convex ventrally, and extends to the lower margin of the angular process. The upper masseteric crest runs parallel to the anterior edge of the ascending ramus, and connects to the lower masseteric crest by an acute angle. The anterior edge of the ascending ramus ascends beside the posterior loop of  $M_1$ . The internal temporal fossa between the ramus and the alveoli of the molars is broad and shallow, and elongates anteroposteriorly. The lower incisor with a triangular section passes by the lingual sides of the roots of  $M_1$  and  $M_2$ , and it is overlain by the roots of  $M_3$ .

 $M_1$ : The occlusal pattern of  $M_1$  comprises five triangles between the anterior cap and posterior loop. The anterior cap is simple, shows a round or elliptical shape, and is relatively short anteroposteriorly. It has no enamel island. The buccal wall of the anterior cap is smooth in almost all the specimens, but weak BSA4 is observed in few specimens (about 1.3% of the examined specimens; 15 in Fig. 3). LRA4 and BRA3 are generally well developed, but shallower than the other lingual and buccal re-entrant angles, respectively. In few specimens, however, LRA4 and BRA3 are weak or absent (17 and 21 in Fig. 3). The isthmus between the anterior cap and T5 is broad, but shows a clear constriction in the anteroconid complex. T5 and T4 is opposite in position and completely confluent with each other to form a single dentine field which elongates obliquely to the transverse axis of the crown. The anterior wall of T4 has no Mimomys angle in almost all the specimens, but a feeble salient angle, possibly a degenerate *Mimomys* angle, is observed in few specimens (about 1.3%; 22 in Fig. 3). The isthmus between T4 and T3 is narrow or closed. T3, T2 and T1 are alternate in position. The isthmus between T3 and T2 is narrow, while that between T2 and T1 is broad, and these triangles are generally confluent with each other. The isthmus between T1 and the posterior loop is generally closed. The posterior margin of the posterior loop is slightly convex posteriorly.

Table 1 Measurements of the molars of *Villanyia fanchangensis*, sp. nov. (in mm except SDQ)

Element	Parameter	п	Mean (min-max)
$M^1$	L	125	2.20 (1.84-2.46)
	W	125	1.21 (0.78–1.46)
M <sup>2</sup>	L	125	1.70 (1.53–1.89)
	W	125	1.07 (0.84–1.24)
M <sup>3</sup>	L	125	1.48 (1.18–1.72)
	W	125	0.85 (0.63-1.06)
M <sub>1</sub>	L	125	2.50 (2.11-3.03)
	W	125	1.12 (0.91–1.41)
	$L_{a}$	125	1.07 (0.85-1.26)
	SDQ	125	122 (98–154)
	HH	45	4.56 (3.78-5.09)
M <sub>2</sub>	L	125	1.57 (1.38-1.88)
	W	125	1.00 (0.68–1.24)
M <sub>3</sub>	L	94	1.30 (1.08-1.59)
	W	94	0.77 (0.58–1.05)

Abbreviations: *n*: number of specimens; *L*: length; *W*: width; *L*<sub>a</sub>: length of anteroconid complex; SDQ: enamel band (Schmelzband) Differentiation Quotient, see Heinrich, 1978; HH: HH-index, see Carls and Rabeder, 1988.

In lingual and buccal views, the sinuous line ascends very high on the buccal side of the anterior cap and both sides of the posterior loop in comparison with the line on the other parts (1-2 and 1-3 in Fig. 2).

 $M_2$  and  $M_3$ : The occlusal patterns of these molars comprise three dentine fields. T4 and T3 are opposite in position, and completely confluent with each other to form the lozenge-shaped anterior field. T2 and T1 are also opposite, and confluent to form the middle field with a more transversely elongated lozenge-shape. The isthmuses between the anterior and middle fields and that between the middle field and posterior loop are closed. The lingual reentrant angles are deeper than the buccal ones. In lingual and buccal views, the sinuous line ascends very high on both sides of the anterior field and posterior loop in comparison with the line on the other parts.

The measurements of the molars are given in Table 1. The mean of SDQ is 122, which indicates that the enamel differentiation is assignable to the negative type or *Mimomys* type.

#### 4.3. Comparison and taxonomic position

The specimens described above are compared with the known species of *Villanyia* listed in "Included species".

On the basis of the descriptions and figures given by Kowalski (1960), Gromov and Polyakov (1977) and Zazhigin (1980), *V. exilis* differs from new species by the enamel differentiation and morphology of  $M^3$ ,  $M_1$  and  $M_2$ . The anterior enamel island of  $M^3$  is mostly absent and possibly disappears earlier in *V. exilis*. The *Mimomys* angle is usually present and the isthmus between the anterior cap and T5 is less constricted in *V. exilis*. T1 and T2 are alternating and separated from each other in  $M_2$  of *V. exilis*.

The description and figure of *V. petenyii* given by Zazhigin (1980) show clear differences from the present specimens. In *V. petenyii*,  $M^3$  has only one island (posterior enamel island), and  $M_1$  has the *Mimomys* angle. Furthermore, the posterior root of  $M_2$  stands on the incisor in *V. petenyii*.

*V. eleonorae* differs from the new species by having in some  $M^2$  three roots, and only posterior enamel island in  $M^3$ . The *Mimomys* angle of  $M_1$  is usually present, and the isthmus between the anterior cap and T5 is less constricted in *V. eleonorae* than in *Villanyia fanchangensis* sp. nov

The isthmus between T1 and T2 is closed in  $M_2$  of *V. eleonorae. V. steklovi* differs from the new species by having in  $M^2$  three roots and by its posterior root of  $M_2$  which stands on the incisor and *V. beketensis* differs by having only the posterior enamel island in  $M^3$  (Zazhigin, 1980).

V. novoasovica and V. hengduanshanensis differ from the present specimens in having the Mimomys angle in  $M_1$  (Zong, 1987; Tesakov, 1993).

Thus, the new species *V. fanchangensis* differs from all known species.

## 5. Discussion

All the related localities of *Villanyia* and *Borsodia* from both China and Transbaikalia are shown in Fig. 1. In China, the genus *Borsodia* is represented by only one species, i.e. *B. chinensis*. Reexamination of the specimens of *B. chinensis* from the Nihewan Basin, Linxi and Jingou, found that the specimens had the differential characters of *Borsodia* given in "Systematic description", and were easily distinguishable from *V. fanchangensis* described here. In spite of these two species having nearly the same size (Fig. 3, Table 2), *Borsodia* differs by having in M<sup>1</sup> and M<sup>2</sup> the "lagurine structure" in LRA2 (30 in Fig. 3); M<sub>1</sub> has a longer anteroconid complex, and its posterior loop has a slightly concave posterior margin (27 in Fig. 3); in all lower molars triangles are more alternating and the isthmus between T1 and T2 are narrow or closed (27–29 in Fig. 3). These observations indicate that the generic allocation of *chinensis* to *Borsodia* is undoubted, and *B. chinensis* is greatly different from *V. fanchangensis* in morphology.

As for the Transbaikalian species V. klochnevi Erbajeva, 1998 from the Late Pliocene sediments (MN17) of Klochnevo and Zasukhino in Transbaikalia (Erbajeva, 1998), we re-refer it to *Borsodia* because of: the *Microtus*type or positive differentiation of enamel band;  $M^1$  with two roots;  $M^3$  without enamel island; and posterior loop of  $M^3$  long and slender like in *B. chinensis*. These characters clearly restrict *klochnevi* to *Borsodia* on the basis of the differential diagnosis given above and the diagnosis given by Jánossy and van der Meulen (1975).

The Plio-Pleistocene biostratigraphic succession of small mammals of Transbaikalia was established by Erbajeva and Alexeeva (2000) and Alexeeva and Erbajeva (2005). According to them, the first appearance of Borsodia is B. klochnevi (formerly V. klochnevi) from the Late Pliocene locality Klochnevo I-1. Then it was replaced by the Early Pleistocene species B. chinensis laguriformes from Dodogol 1 (Erbajeva, 1973). Erbajeva (1998) stated that B. klochnevi differed from B. chinensis laquiformes in having slightly shorter lower teeth, in the considerably weaker development of the "lagurus angle" on M<sup>1</sup> and M<sup>2</sup> and in having thicker enamel band on the posterior borders of the lower teeth and on the anterior borders of the upper teeth. B. klochnevi was a transitional form between V. eleonorae and B. chinensis laguriformes. Whereas in China, as mentioned above, Borsodia was represented only by B. chinensis, which was reported from Early Pleistocene sediments of Xiashagou and Majuangou-III in the Nihewan Basin of Hebei Province (Kormos, 1934; Zheng and Li, 1986; Cai and Li, 2003),

Table 2

Measurements of  $M_1$  of Borsodia chinensis comparing with Villanyia fanchangensis, sp. nov. (in mm except SDQ). Abbreviations as in Table 1

Species	Locality	Parameter	Ν	Mean (min-max)
V. fanchangensis, sp. nov.	Renzidong cave	L	125	2.50 (2.11-3.03)
	-	$L_{\mathrm{a}}$	125	1.07 (0.85-1.26)
		SDQ	125	122(98–154)
B. chinensis	Xiashagou (type locality)	L	1	2.68
		$L_{\mathrm{a}}$	1	1.28
		SDQ	1	66
	Majuangou-III	L	20	2.52 (2.33-2.66)
		$L_{\mathrm{a}}$	20	1.22 (1.11–1.33)
		SDQ	20	67
	Jingou	L	1	2.64
	C C	$L_{\mathrm{a}}$	1	1.24
		SDQ	1	62
	Linxi	L	1	2.73
		$L_{\mathrm{a}}$	1	1.25
		SDQ	1	73

Linxi in Inner Mongolia (geological age unknown; Zheng and Li, 1986), Early Middle Pleistocene (?) sediments of Jingou in Heshui County of Gansu Province (Zheng, 1976; Zheng and Li, 1986), and Early Pleistocene (?) sediments of Gonghe in Qinghai Province (Zheng et al., 1985; Zheng and Li, 1986). Among these localities, Majuangou-III in the Nihewan Basin was dated magnetostratigraphically by Zhu et al. (2004) at 1.66 Ma, which is the most definitive external age control of *B. chinensis*.

In China, there is no equivalent between *Borsodia* and Villanvia like B. klochnevi. Besides V. fanchangensis sp. nov., another Villanvia species V. henaduanshanensis from the Early Pleistocene (?) sediments of Diging, Yunnan Province (Zong, 1987) was represented by scarce materials (one mandible with  $M_{1-2}$ , probably missing) and the age is uncertain. As indicated above, V. fanchangensis shows great differences from *B. chinensis*, so it seems that the transition from Villanvia to Borsodia cannot be concluded on the basis of these two species in China. The Transbaikalian species V. eleonorae from Beregovava and V. cf. eleonorae from Udunga were regarded as of the Middle Pliocene age, MN16b and MN16a respectively (Erbajeva, 1976; Erbajeva and Alexeeva, 2000; Erbajeva et al., 2003, 2006). Compared with V. fanchangensis, V. eleonorae has some more primitive features indeed, such as sometimes 3 roots in  $M^2$ ; *Mimomys*-angle in  $M_1$ , etc., which seems affirmative for the assignment of the Early Pleistocene age of V. fanchangensis.

Thus, *B. chinensis* was distributed in both North China and Transbaikalia during the Early Pleistocene; however, during the Late Pliocene, *V. fanchangensis* occurred in the southern part of China at Renzidong, and *B. klochnevi* occurred in Transbaikalia as a concurrent species; up to now, no *Villanyia* species older than *V. fanchangensis* has been discovered in China. Further detailed joint studies on related species of arvicolids from both Transbaikalia and China are eagerly expected to solve further phylogeny and correlation problems.

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