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First discovery of *Promimomys* (Arvicolidae) in East Asia

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Abstract ***Promimomys asiaticus* sp. nov., the first known species of the genus in East Asia, is described. The material was collected from the early Pliocene cave deposit in Dajushan Hill, Huainan, Anhui Province. *Promimomys* was first found in Europe and considered as the ancestor of the family Arvicolidae. The new species from China is distinct from the type species, *P. cor*, and other known species in its thicker enamel of uniform thickness, simple anterior loop of m1, and blunt, salient angles. It is more primitive than other known species in Europe and North America and also more primitive than *Mimomys bilikeensis* of early Pliocene of Inner Mongolia. It is thus the earliest and the most primitive arvicolid rodent known. The discovery of *Promimomys asiaticus* sp. nov. is significant to the study on the origin and the phylogeny of arvicolids, and to the discussion of the intercontinental dispersal events of arvicolids.**

Keywords: Huainan, Anhui, early Pliocene, *Promimomys*.

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The family Arvicolidae is one of the groups that evolves most rapidly among rodents. This highly diversified group consists of many genera and species and is widely distributed in frigid or temperate grassland of Palaearctic and Nearctic realms. The primitive genus *Promimomys* of Arvicolidae was found in the Pliocene of Europe and North America a long time ago, but it has not been reported in East Asia so far. During an expedition conducted by investigators from the Institute of Vertebrate Palaeontology and Palaeoanthropology (IVPP), the Museum of Anhui Province, and the Cultural Relic and Archeology Institute of Anhui Province we have found a Neogene site of cave deposit with abundant vertebrate fossils in Huainan area, where a mandible of *Promimomys* was collected.

The locality yielding the specimen of *Promimomys* is named Xindong (New Cave) and is located on the southwest slope of Dajushan Hill, Bagongshan District, Huainan (117°01′49″E, 32°35′47″N). It is a water-eroded cave developed in the Ordovician limestone. The deposit is strongly consolidated by abundant calcitic cementation and consists of chocolate-brown clayey breccia, red-brown sandy mudstone with small amount of breccia, sandstones with small amount of breccia, and red-brown sandstone with gravels and sandy mudstone. The deposit can be divided into 5 lithological layers, with a visible thickness of about 16 m.

Several excavations have been carried out on Xindong Cave and large amount of vertebrate fossils were collected. Preliminary study has identified more than 40 species of vertebrates, belonging to 38 genera, 20 family, 12 orders (or classes), such as Chelonia, Aves, Insectivora, Scandentia, Chiroptera, Rodentia, Carnivora, Perissodactyla, and Artiodactyla. This fauna is named *Promimomys* fauna (to be published in another paper). *Pannonictis* and *Paramachairodus* that are associated with *Promimomys* in this fauna were only found in the Pliocene of Eurasia. Furthermore, some carnivores, such as *Nyctereutes* cf. *tingi*, *Martes* cf. *zdanskyi*, *Meles* cf. *taxipater*, were also only found in Gaozhuang Formation (Pliocene) in Yushe and early Pliocene Bilike in Inner Mongolia. But it is interesting to note that all the above species appear smaller in size and more primitive in morphological characters, compared to known species elsewhere. Therefore, the age of Xindong Cave deposit with *Promimomys* is probably somewhat earlier than the early Pliocene Bilike site in Inner Mongolia.

Our analysis indicates that the *Promimomys* fauna contains more grassland-adapted members of Palaearctic realm, such as *Promimomys*, *Kowalskia*, *Allorattus*, and *Huaxiamys*, but it also contains some forest-adapted members of Oriental realm, such as *Palacotupaia*, *Pliopentalagus*, *Brachyrhizomys*, and *Herpestes*, which suggests that the landscape is a mixed forest-grassland environment with both southern and northern elements in contact with each other.

1 Specimen description

Arvicolidae Gray, 1821

***Promimomys* Kretzoi, 1955**

Type species *Promimomys cor* Kretzoi, 1955

***Promimomys asiaticus* sp. nov.**

Holotype A right mandible with incisor and m1 and m2 (IVPP V14006)

Locality and horizon Bagongshan, Huainan, Anhui, the third layer of Xindong Cave deposit

Age Early Pliocene

Etymology The species is the first described *Promimomys* in Asia.

Diagnosis Middle-sized; mental foramen anteriorly positioned; the tip of incisor is higher than the occlusal surface of lower molars; the incisor deflecting to the labial side at the processus angularis notch; the thick enamel band lacking differentiation; sinuous line is slightly undulant; simple anterior loop of m1 lacking enamel islet and additional folds; the apexes of LRA3 and BRA2 opposite to each other; the front wall of T2 conspicuously curving backwards.

Measurements Mandible: length of diastema 3.10 mm, height of mandible (at the anterior root of m1 on

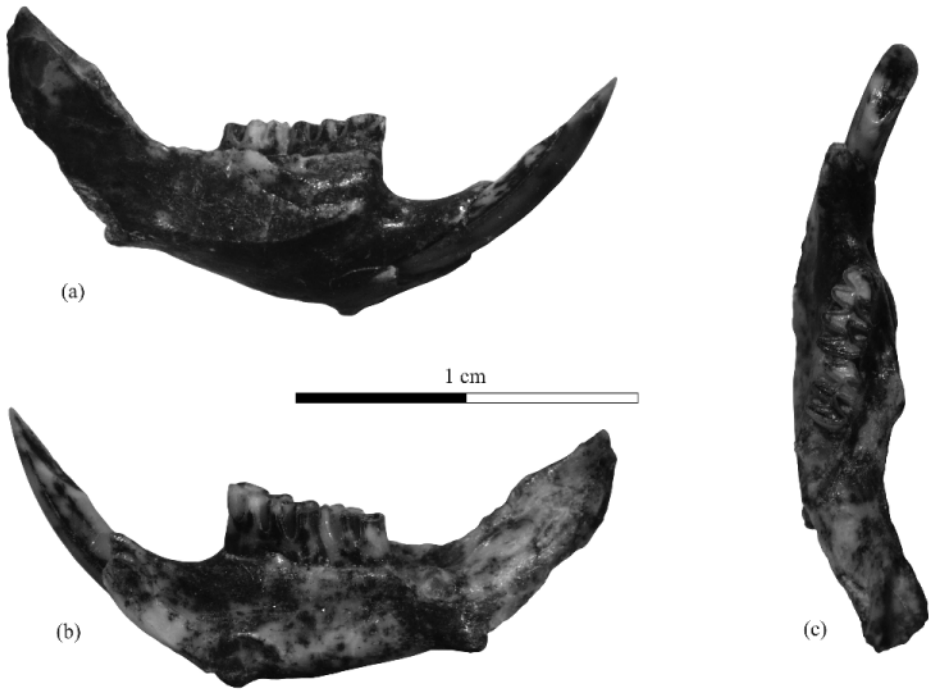

Fig. 1. *Promimomys asiaticus* sp. nov. Mandible (V14006): (a) Buccal view; (b) lingual view; (c) occlusal view.

lingual side) 3.80 mm; length of m1—m3 alveolus 6.40 mm; m1: length 2.72 mm, width 1.57 mm, anterior loop 0.9 mm, E_b 0.31 mm; average thickness of enamel band 0.13 mm; m2: length 1.57 mm, width 1.41 mm (methods of measurement after refs. [1,2]).

Description Nomenclatures for the occlusal surface of cheek teeth follow that in ref. [2], and the term "dentine isthmus" is introduced. The term "ACC" of Zheng (1986) is changed to "anterior loop" according to Zheng et al.[3] and Kakwamura[4], and also the present paper, because the ACC of *Promimomys* is very simple.

The specimen probably represents a mature individual, instead of an old one, because of its less worn molars, the well-developed, and forwardly located mandibular symphysis, less developed upper crest of masseter muscle, small holes in the temporal fossa, and deep alveolus of m3.

The mandible is strong and arc-shaped; the coronoid, condyloid and angular processes are all broken. The maximal height of the horizontal branch lies between the front root of the m1 and the elevated mandibular symphysis. The diastema is shorter than half of lower alveolar length of cheek teeth (6.40 mm) and conspicuously curves upwards. From the labial view, the mental foramen is big and lies lower and more forward on the labial side of diastema before m1. The horizontal ramus swells outwards. The upper crest for the insertion of the masseter muscle has a typical "arvicoline groove" and ascends smoothly backwards and upwards. The lower crest for the masseter muscle is prominent, the anterior tip of which is expanded, while the posterior one extends backwards and downwards above the notch of processus angularis. The upper and lower crests of the masseter muscle meet with each other below the anterior root of the m1 by an acute angle. The masseteric fossa extending backwards broadly (this is unclear), is broad and deep; the surface is smooth. The ascending process starts from the posterior edge of the anterior loop of m1 and covers the posterior half of m2. In lingual view, the area of symphysis is very large and saddle-shaped, the posterior tip of which forms a broad and large elevation. It stops right below the posterior loop of the m1; the lingual surface of the anterior and posterior parts of the horizontal ramus is a little concave and decorated by several foramina; the mandibular foramen is large and long-oval shaped, lies above the m3, and extends upwards. In dorsal view, the temporal fossa between lower dentition and ascending ramus is broad and deep, and there are at least 6 small foramina aligned nearly in a line. The angle between the midline of lower dentition and horizontal ramus is very narrow.

The tip of lower incisor is very sharp and higher than occlusal surface of lower dentition; the transverse section of the lower incisor is triangular in outline (its diameter is between 1.20 and 1.30 mm). It extends backwards and turns from the lingual to labial side until it reaches the lower part of the condyloid process and forms the notch of incisor that is higher than the tip of incisor (Fig. 1).

The lower cheek teeth are brachydont, the enamel

band of which is thick and undifferentiated. There is no cement in the reentrant fold of molars. The salient angles are blunt. All the molars have two roots.

Anterior edge of anterior loop of m1 is broken. There are 3 triangles between anterior and posterior loop (T1—T3), so there are 4 salient angles (LSA1—4) and 3 reentrant folds (LRA1—3) on lingual side, and 3 salient angles (BSA1—3) and 2 reentrant folds (BRA1 and BRA2) on labial side. The anterior loop is obliquely elliptical in shape, and is simple, i.e. there are no enamel islet, *Mimomys* angle, and additional folds. The lingual salient angles are stronger than the labial ones. LSA4 is more blunt than BSA3, and the posterior walls are nearly in the same line. Both walls of LSA3 and LSA2 are nearly isosceles. The anterior walls of LSA3, LSA2 and LSA1 are perpendicular to the long axis of m1. The anterior walls of BSA2 and BSA1 are conspicuously curved backwards. Lingual reentrant folds are broader and deeper. The apices of LRA2 and BRA2 are nearly opposite to each other and those of LRA3 and LRA2 exceed the longitudinal midline of m1. is1 and is3 are closed, and is2 is more open, which leads to the confluence of T1 and T2. The is4 is nearly closed and connects to T3 and anterior loop. Sinuousa line of both lingual and labial sides is undulant (Fig. 2).

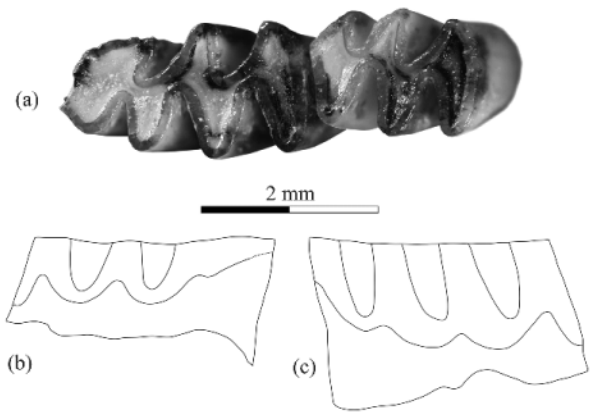

Fig. 2. *Promimomys asiaticus* sp. nov. m1 and m2 (V14006): (a) occlusal view; (b) labial view of sinuousa line of m1; (c) lingual view of sinuousa line of m1.

There are 4 triangles before posterior loop, and 3 salient angles and 2 reentrant folds on lingual and labial sides respectively. Triangles of lingual side are stronger than those of labial side. The apices of BRAs lie before those of LRAs, which leads to the wide confluences of triangles.

2 Comparison and remark

During the late Cenozoic, arvicolids evolved and dispersed rapidly to form a highly diversified and widely distributed group. However, controversies exist about its classification of both living and fossil species. The validity of the genus *Promimomys* was once controversial. This genus was first proposed by Kretzoi[5] in 1955 on the basis of materials found in the early Pliocene cave deposit of the locality Csarnóta 2 in Hungary. Because there was only a fragment of left mandible with m1 which was worn deeply and this specimen did not come out of the section, several scholars[6,7] thought *Promimomys* was a synonym of *Mimomys*. After comparing the arvicolid material from Teruel Basin in Spain with the type species of *Promimomys*, *P. cor*, Fejfar et al.[8] revised the diagnosis of the genus and proposed a *Microtodon-Promimomys-Mimomys-Arvicola* lineage. Repenning[9] discussed the systematic relationships between *Promimomys* and *Mimomys* after he restudied the arvicolid material of North America. *P. antiquus* described by Zazhigin[10] of the former Soviet Union and early Pliocene species *Aratomys bilikeensis*[11] from Inner Mongolia were revised as *Mimomys antiquus* and *Mimomys bilikeensis* respectively. Therefore the validity of *Promimomys* as the ancestor of *Mimomys* should be accepted because of its conspicuous diagonstic characters, such as brachydonty, simple anterior loop of m1, and lack of a *Mimomys* angle, which distinguish it from *Mimomys*.

The Huainan species is distinguishable from more advanced arvicolid genera such as *Mimomys* and *Arvicola*, and is consistent with the diagnosis of *Promimomys*. For example, molars are brachydont; there is no cement in the reentrant folds; enamel band is undifferentiated and the thickness is moderate; there are 3 triangles between anterior and posterior loops of the m1; anterior loop is simple and has no *Mimomys* angle.

There are four species of *Promimomys* in both Europe and North America so far: *P. cor* Kretzoi, 1955 (type), *P. minus* (Shotwell, 1956), *P. insuliferus* Kowalski, 1958, *P. microdon* Janossy, 1974. Moreover, *Promimomys* was also found in Mugureny of the former Soviet Union, northern part of Kazakhstan and Siberian area, such as *Promimomys* sp. n. 1, *Promimomys* sp. n. 2, *Promimomys* sp. Nov[12]. But comparison between Huainan species and these cannot be carried out, because there is no detailed systematic study on them.

The Huainan species is different from the type specimen of *P. cor* by having larger size (Table 1), more blunt salient angles, thicker enamel band, opposite apices of LRA3 and BRA2 on m1, and narrower is4. Fejfar et al.[8,13] referred to *P. moldavicus* from late Ruscinian (MN15) strata of Vendargues[14] and Canterrane[15] in France, Ptolemais 1 and Kardia[1] in Greece to *P. cor*[13]. The most important differences between *P. cor* from France, Greece and Huainan species lie in that the European species have thinner enamel band on anterior loop of m1; their anterior loop has additional folds and irregular-shaped enamel islet; their apex of LRA2 on m1 extends forwards; their salient angles are sharp; their apex of BRA2 lies before that of LRA2 on m2 (while on m2 of

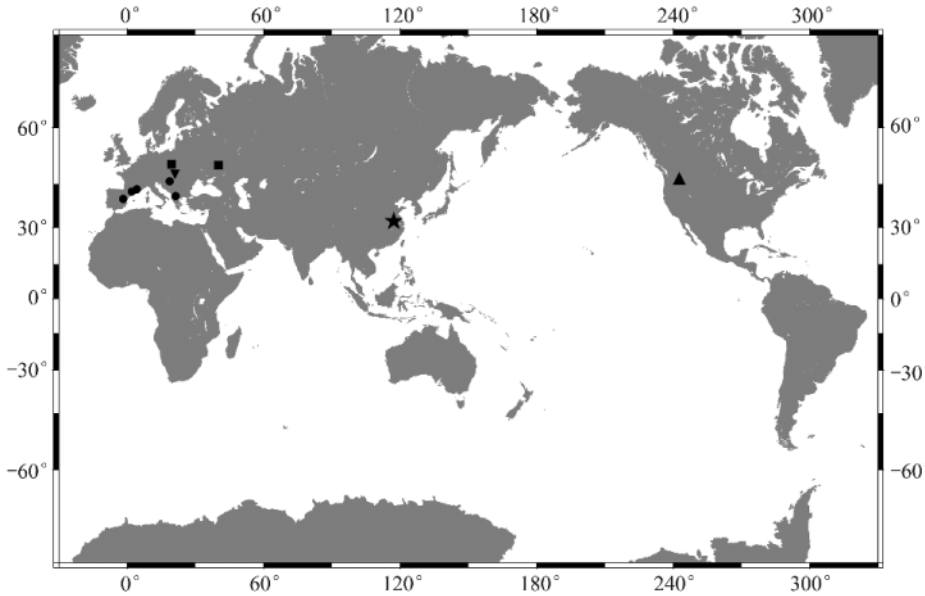

Fig. 3. Worldwide distribution of the genus *Promimomys*. ●, *P. cor*; ■, *P. insuliferus*; ▼, *P. microdon*; ▲, P. *minus*; ★, *P. asiaticus* sp. nov.

Table 1 Size Comparison between *P. asiaticus* sp. nov. and other species of *Promimomys*

Species	Locality	L				W			
		N	min	*M*	max	*N*	min	*M*	max
	Csarnóta 2, Hungary	1		2.90		1		1.60	
	Ptolemais 1, Greece	21	2.38	2.60	3.00	26	1.09	1.30	1.50
	Kardia, Greece	9	2.40	2.62	2.81	11	1.03	1.30	1.46
P. cor	La Gloria 4, Spain	2	2.56	2.59	2.62	2	1.22	1.30	1.37
	Celadas 9, Spain	2	3.10	3.13	3.15	2	1.58	1.60	1.63
	Vendargues, France	?	2.36	2.48	2.82				
	Canterrane, France	1		2.54					
P. minus	Mckay, U.S.A.	1		1.90		1		1.10	
	Christmas Valley, U.S.A.	49	2.14	2.50	2.97				
	Podlesice, Poland	15	1.91	2.43	2.65	15	1.04	1.20	1.30
P. insuliferus	Antipovka, U.S.S.R	5	2.25	2.37	2.55	6	1.0	1.16	1.3
	Chugunovka, U.S.S.R	5	2.2	2.35	2.5	5	1.1	1.37	1.6
?*P. microdon*	Osztramos Loc.9, Hungary	1		?1.82			1	?2.02	
P. asiaticus sp. nov.	Huainan, China	1		2.72			1	1.57	

Huainan species the opposite is true), and their m1 has a third small root between the two roots. *P. cor* from France and Greece is more advanced than Huainan species because its m1 has a third deuterogenic root and anterior loop of m1 has additional folds.

Another species, *P. insuliferus*, was first proposed by Kowalski in 1958 based on materials from Podlesice in Poland, and it is a widely distributed species. In addition to Podlesice, the species was also found in Vendargues, Canterrane in France (Michaux, 1971, 1976)[14,15] and Olkhon, Antipovka, Chugunovka in Russia, but its age and systematic position are still controversial. Kretzoi (1959) referred it to *Polonomys*, while Agadjanian and Kowalski[6] and Fejfar et al.[13] thought that it should be referred to *Prosomys*, but several European and American scholars insisted that *Polonomys* and *Prosomys* were just subgenera of *Promimomys*, and they had no apparent differences. For convenience and practicality in classification, we adopt Kowalski's opinion, and regard it as a representative species of Middle Ruscinian (MN14, b) in Europe. Compared with Huainan species, this species has the following differences: The mental foramen of mandible lies more backwards; the tip of lower incisor is lower; the salient angles are more sharp, which makes the triangles look more slim; the enamel band thickness of anterior loop on m1 is thinner; the enamel islet is quite well developed on anterior loop and extends a long way along the crown, which can reach 1/3—1/2 height of the unworn crown (Huainan species has no enamel islet); the posterior walls of BRA2 and BRA2 on m1 are straight (curved

backwards on Huainan species); is3 and is4 of m1 are less closed.

P. microdon is a doubtful species. Janossy[16] established two species based on limited material from the cave deposit of northern Hungary (Osztramos 9, middle Pliocene), namely, *P. microdon* and *Mimomys silasensis*. *P. microdon* was based on only one right m1 (Inv. No. V. 74. 3) whose anterior loop was completely broken. The measurement data in the paper were obviously estimates. According to the plate and the original description, the labial sinuousa line of m1 is very steep, and the enamel band is very thin, which shows that it is probably an old individual of *M. silasensis*.

P. minus (Shotwell, 1956) was found in Mckay[17], Umatilla County and Christmas Valley[18], Lake County in Oregon of USA. Compared with it, Huainan species has nearly the same size; but the enamel band of the former is not even and well-differentiated, and its salient angles are sharper; the anterior wall of T2 does not tend to be curved backwards on m1 of *P. minus*; is3 on m1, is1 and is3 on m2 are less closed than Huainan species; the position of the apex of BRA2 is more forward compared with that of LRA2 on m2 of *P. minus*.

The above comparison shows that Huainan species is obviously (I do not see the obvious difference between the new species and the one from Csarnóta 2, Hungary) different from European and American *Promimomys* species on the characters of both mandible and molars, so that it should represent a new species of the genus.

Promimomys is mostly found from the Ruscinian strata, and European scholars usually regard it as a typical representative of terrestrial biostratigraphic zonation of Europe in the Early Pliocene, namely, MN14[19—22]. Some *Promimomys* materials were reported in Mugureny area near the upper reach of Kogilnik River in the former Soviet Union, and they were more primitive than *P. insuliferus*, the age of which is 5.8 Ma based on paleomagnetic data; moreover, the age of *Promimomys* from Novaya Stanitsa area is 5.5 Ma (also based on paleomagnetic data[8,12,23]). But all these specimens have not yet been described, so that it is impossible for us to know how their morphological characters and paleomagnetic age fit each other. Furthermore, some eastern European scholars usually confused *Promimomys* with *Mimomys*, so we still consider *Promimomys* as a typical representative of MN14.

Based upon the comparison and discussion above, we consider the evolutionary trend of *Promimomys* molars as follows: the enamel band gradually becomes thinner and better differentiated; the salient angles turn from blunt to sharp; anterior loop of m1 tends to become more complicated; m1 first has no enamel islet and then islet appears; the number of roots increases. The type species, *P. cor*, has more apomorphic characters, such as differentiated enamel band and additional folds on anterior loop of m1, and the third small root on labial side of m1, which shows that it is more advanced than *Promimomys asiaticus* sp. nov.; another species *P. insuliferus* has more sharp salient angles, slimmer triangles, thinner enamel band on anterior loop of m1, and well-developed and long enamel islet, which makes it also more advanced than Huainan species; the enamel band of *Promimomys asiaticus* sp. nov. is thick and undifferentiated, and the salient angles are blunt, and there is no islet on the anterior loop of m1, which shows that Huainan species is more primitive than *P. minus*. Thus we can conclude that *Promimomys asiaticus* sp. nov. probably represents a more primitive species among all of the known species according to the molar morphology.

Until now, the Early Pliocene species *Mimomys* (*Aratomys*) *bilikeensis*[9,11] from Bilike, Inner Mongolia is the most primitive arvicolid in China. It apparently has more advanced characters than *Promimomys asiaticus* sp. nov., such as more hyposodont molars, steeper labial linea sinuosa, more complicated anterior loop with prism fold and *Mimomys* angle of m1. Therefore, *Promimomys asiaticus* sp. nov. should be the most primitive arvicolid in China, the age of which ought to be earlier than *Mimomys* (*Aratomys*) *bilikeensis* and is probably early Early Pliocene (MN14, a).

Promimomys asiaticus is the fisrt record of the genus in East Asia, which undoubtedly will be beneficial to the discussion of the phylogeny, origin and dispersal events of arvicolids. Repenning[18] thought *Promimomy*s to be the ancestor of all arvicolids and it was probably closely related to the lophodont cricetid *Microtodon* Miller, 1927, after he studied morphology of arvicolids molars and mandibles[18]. Fejfar et al.[8] also proposed the *Microtodon-Promimomys-Mimomys-Arvicolia* lineage. Even though most species were found in Europe (Fig. 3), there is no transitional form between *Microtodon* and *Promimomys*. The latest *Promimomys* in Europe came from the late MN15 (3.6 Ma, based on paleomegnetic data), while the earliest descendant of *Promimomys* in China is from the MN14 (such as *Mimomys bilikeensis* from Inner Mongolia, about 4.0 Ma)[9,11]. Furthermore, there are abundant specimens of *Mocrotodon atavus* (Schlosser, 1924[24]) from the Late Miocene Ertemte fauna and Harr Obo fauna in North China, which shows that early forms of *Promimomys* evolved from their ancestor probably in East Asia.

According to the studies made by paleontologists of both United States and China, there are a total of 11 dispersal events within the last 6.7 million years. Repenning called the former 10 Event 1—10, every one of which was characterized by the widespread dispersal of mammals[21,25]. He thought the first appearance of *Promimomys* in Europe was later than that in North America, and *P. minus* of North America evolved from its ancestor in East Asia and then immigrated into North America through

Bering Strait, which was the result of "Event 1" (*Promimomys* dispersal event)[21,24]. The pattern of both north and south zoogeographical regions in China has begun to be formed since Miocene[26], during which there was no natural barrier such as rivers and mountains between South and North China. At that time, there was a transitional region where both south and north type animals lived together because of the influence of natural climate. The locality of *P. asiaticus* sp. nov. lies in the east part of the region. This species is a result of *Promimomys* dispersal event of Late Cenozoic, and it was probably a native species of East Asia but not immigrated from Europe. In other words, the inference of Repenning (1987) is reasonable, that is, the origin center of Arvicolidae should be East Asia, not Europe or North America.

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