

河北泥河湾“*Pliopentalagus nihewanensis*” 分类地位的再思考¹⁾

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摘要:自20世纪60年代,欧亚大陆晚新生代地层中陆续发现了p3由5个主要褶沟组成的兔类化石,并先后建立了上新五褶兔(*Pliopentalagus* Gureev et Konkova, 1964)和三裂齿兔(*Trischizolagus* Radulesco et Samson, 1967)两属。

近年,在中国安徽淮南大居山新生代晚期不同时代的洞穴、裂隙堆积物中发现了保存相当完整,数量颇多的上新五褶兔的材料。笔者在研究大居山新洞早上新世的上新五褶兔时,将其与欧亚大陆该属内的已知种和三裂齿兔的各种进行了详细比较,发现产自河北省阳原县泥河湾盆地晚上新世稻地组的*Pliopentalagus nihewanensis* Cai, 1989被指定为上新五褶兔值得商榷。*Pliopentalagus nihewanensis*的材料仅有1枚p3(GMC V 2008-1)和两枚中间颊齿(p4或m1, GMC V 2008-2及m2, V 2008-3)。正型标本p3的中前褶沟(AR)中央、后外褶沟和后内褶沟后壁釉质层具有小褶曲,这些形态确实与上新五褶兔的特征有些相似。但褶曲的发育程度明显比上新五褶兔的弱;另外,其齿冠舌侧后缘向后内突出,后外褶沟和后内褶沟较平直并近与齿纵轴垂直,后外褶沟与后内褶沟深度相近等而与上新五褶兔也有所不同。褶沟的釉质层在两枚中间颊齿中较平直,与上新五褶兔显然也有较大的区别。就该p3而言,可以认为它属于一枚釉质构造极简单的上新五褶兔的前臼齿,也可以认为是釉质构造很复杂的三裂齿兔的p3。研究表明,在上新五褶兔和三裂齿兔的系统演化过程中,其颊齿褶沟釉质层的构造有越来越复杂的趋向。作为上新世较晚期的“*Pliopentalagus nihewanensis*”的p3,指定为上新五褶兔显然有悖于该属釉质构造在地史中越来越复杂的演化事实,而指定为三裂齿兔则正好与该属釉质构造的演化趋势相符(Averianov and Tesakov, 1997)。另外,从共生动物群和动物的生活习性看,安徽淮南发现的上新五褶兔与大量现代东洋界特有的类型共生(如Tupaïidae、Platacanthomyidae等),上新五褶兔的后裔——现生的日本琉球奄美黑兔(*Pentalagus*)的栖息地为温暖、湿润的多山环境;而目前发现的三裂齿兔共生动物群所指示的是干凉的稀树草原环境,与上新五褶兔的生态环境有所不同。含“*Pliopentalagus nihewanensis*”的晚上新世稻地动物群主要由典型的古北界属种(如*Mesosiphneus paratingi*、*Mimomys orientalis*、*Germanomys cf. G. weileri*、*Chardinomys nihewanicus*及*Ochotona* spp.等)组成,而未见典型的东洋界成员。这种温带相对干旱的草原环境,显然与中国发现的上新五褶兔及其后裔的生存环境很不一样。因此,笔者认为“泥河湾上新五褶兔”应归入三裂齿兔属,正名泥河湾三裂齿兔*Trischizolagus nihewanensis* (Cai, 1989)。种征订正为:p3具有较复杂的形态构造;中前褶沟具衍生的中央小褶曲,后外褶沟和后内褶沟后壁釉质层褶曲相对发育。该种以这些基本特征而不同于欧亚大陆的已知种(如*T. dumitrescuae*、*T. mirificus*等),它可能代表该属的一个进步类型。

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RECONSIDERATION OF THE GENERIC ASSIGNMENT OF “*PLIOPENTALAGUS NIHEWANENSIS*” FROM THE LATE PLIOCENE OF HEBEI, CHINA

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Abstract “*Pliopentalagus nihewanensis*” was described by Cai (1989), based on an isolated p3 and two isolated lower molariform teeth from the bottom of the “Nihewan beds” of Hebei Province, China. Detailed re-examination of the original specimens and comparisons with other species of the genus and *Trischizolagus* suggest: 1) the holotype (p3) alone can be interpreted as a species of the genus *Pliopentalagus* having p3 with least complicated enamel pattern. But, this hypothesis violates an evolutionary trend of the genus that the enamel pattern becomes more complicated through time. On the other hands, 2) the holotype can also be interpreted as a species of the genus *Trischizolagus* having p3 with most complicated enamel pattern. This hypothesis fits on an evolutionary trend of the genus that enamel pattern becomes more complicated through time (Averianov and Tesakov, 1997), 3) the associated fauna which is indicative of a dry and cool environment also suggests that the holotype may not belong to the genus *Pliopentalagus*. Therefore, we conclude that generic assignment of this taxon should be *Trischizolagus*, and *T. nihewanensis* is characterized by p3 with most complicated enamel pattern within the genus.

Key words Nihewan (Hebei, China), Late Pliocene, Daodi fauna, *Pliopentalagus*, *Trischizolagus*

1 Introduction

“*Pliopentalagus nihewanensis*” was described by Cai (1989), based on three isolated lower teeth from the lower part of the Daodi Formation of Yangyuan and Yuxian, Hebei Province, China. The fauna associated with “*P. nihewanensis*”, called Daodi fauna (Cai, 1987), is correlated to the late Pliocene, comparable to MN16 of European mammal ages. During the course of studying the abundant fossils of *Pliopentalagus* spp. from three different-age deposits, in Huainan, Anhui Province, we recognized that “*P. nihewanensis*” does not fit well on the evolutionary trend and phylogeny that we tentatively established (Tomida and Jin, 2002; Jin, 2004). Therefore, we re-examined the original material of the species, and reached a conclusion that this taxon most likely belongs to the genus *Trischizolagus* rather than *Pliopentalagus*, based on the morphology of the teeth and the character of the fauna associated with this taxon. We re-describe and illustrate the original specimens and discuss their generic identifications below.

Terminology of tooth structure followed White (1991, Fig. 1), in addition to EL for the enamel lake. Measurements were made by the scale of stereo microscope (Wild M5), and illustrations were made by making fair copies of camera lucida drawings (which were made by Y. T.) using computer illustrator (Graphics tablet, Wacom Co. Ltd.).

2 Re-description of original specimens

The original specimens of “*Pliopentalagus nihewanensis*” described by Cai (1989) are

stored at the Geological Museum of China in Beijing, currently in charge of Dr. Lu Liwu of the museum.

The left p3 (GMC V 2008-1, holotype) is an isolated tooth, with both occlusal and base sides broken off, so that almost no original occlusal surface is preserved. In addition, all surfaces except for the base broken surface are covered by evaporated gold for SEM, and therefore, it is in some part extremely difficult to observe and to draw the enamel pattern. The enamel pattern in occlusal view (Fig. 1A) was compared with that of base view (Fig. 1B), and it was made sure that the pattern was correct. General enamel pattern is similar to the figure in Cai (1989), but the detail of enamel crenulations and thickness is different.

General outline of V 2008-1 in occlusal view is trapezoidal. Although the positions of thickened enamel and presence of all 5 reentrant angles are basically same as in those of *Pliopentalagus* spp., the detail of each reentrant angle differs. PER reaches slightly over one half of the tooth width, while PIR reaches about 40%; crenulations of TN and thin enamel of PIR are rather weak; AER is short and simple; AIR is very shallowly incised with no crenulation, and it is not present in the base view (Fig. 1B); AR is rather short but consisting of two folds. The measurements are 3.46 mm in length and 3.06 mm in width. Cai (1989) mentioned the measurements in the text as 2.8 mm and 2.6 mm, respectively, while his figure 3 measures approximately 3.6 mm and 3.1 mm, respectively. If Cai's measurements in the text were correct, it had been an extremely small individual as *Pliopentalagus*, but it actually is a medium sized species and individual.

Two other teeth referred to “*P. nihewanensis*” by Cai (1989) are left p4 or m1 (GMC V 2008-2) and left m2 (GMC V 2008-3).

We agree with him on the identification of the tooth positions. Preservation of V 2008-2 is rather poor, as it is weathered as a whole, but much of the occlusal surface is preserved. Although most of the enamel surrounding the tooth is missing, the area that was originally covered by enamel is visible on the side walls of the tooth; antero-external, postero-external, and posterior surfaces; and the enamel connecting the trigonid and talonid lingually is preserved near the bottom of the tooth. Thus, the dotted lines indicating the positions of missing enamel are more or less accurate (Fig. 1C). General morphology is typical of most leporine taxa. Important point to mention is that the thin enamel of anterior edge of talonid is only weakly crenulated. Measurements of the occlusal surface are 3.09 mm in length and 3.25 mm in width, as currently preserved (Fig. 1C).

V 2008-3 is very poorly preserved, much worse than V 2008-2. The tooth body curves posteriorly rather strongly, suggesting the tooth position to be m2.

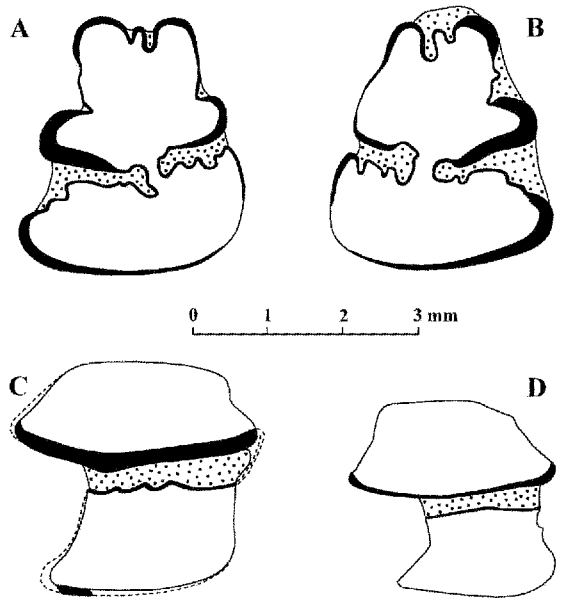


Fig. 1 *Trischizolagus nihewanensis* and Leporidae gen. et sp. indet.

A, B. *T. nihewanensis* (Cai, 1989), holotype (GMC V 2008-1), p3 in occlusal (A) and base (B) views; C. Leporidae gen. et sp. indet., p4 or m1 (GMC V 2008-2) in occlusal view; D. Leporidae gen. et sp. indet., m2 (GMC V 2008-3) in occlusal view

The periphery of the tooth, including enamel and dentine, is entirely chipped (or shaved) off probably by weathering, and so the outline of enamel on the occlusal surface cannot be estimated. But, it is still clear that the thin enamel on the anterior edge of talonid is smooth without any crenulations. Measurements of the occlusal surface are 2.66 mm in length and 2.78 mm in width, as currently preserved (Fig. 1D).

3 Discussion

3.1 Morphological aspect

Tomida and Jin (2002) tentatively recognized three successive species of *Pliopentalagus* from Anhui Province, China, and Jin (2004) described the oldest one of them, *P. huainanensis*. *P. huainanensis* is the oldest (latest Miocene; MN 13) known species of the genus, but it already has p3 with TN and EL (counting as another form of PIR) enamel rather strongly crenulated, and deep AIR. Two other species from Anhui (species B and C of Tomida and Jin, 2002; correlated probably to MN14 and 15) have p3's showing the same characters but in stronger degree, and deeper and/or more complicated AER. *P. progressivus* from the latest Pliocene or earliest Pleistocene of Henan, China (Liu and Zheng, 1997) is the largest known species of the genus so far. Its p3 has deep but single AR, deep AER, deep and complicated AIR, and strongly crenulated TN and posterior wall of PIR. *P. dietrichi* (Fejfar, 1961; Daxner and Fejfar, 1967) and *P. moldaviensis* (Gureef and Konkova in Gureev, 1964) are similar species from Europe, and their p3's share following characters: deep two-folded AR, deep AIR, somewhat deep and complicated AER in some specimens, and TN and thin enamel of PIR with strong crenulations.

Comparing with these species, p3 of "*P. nihewanensis*" differs in 1) PER extends over one half of the width of the tooth (while it extends less than one half, and PER and PIR (or EL) are about the same depth in other species), 2) enamel crenulations of TN and posterior wall of PIR much simpler, 3) AIR much shallower or possibly not present, and 4) AER somewhat simpler and shallower, in addition to 5) the trapezoidal outline being formed by expansion of posterointernal corner of the tooth (while somewhat curved-oval in majority of individuals of other species). The fact that AR consists of two small reentrant angles is same as in majority of individuals of other species, but 6) it is rather shallower.

On the other hands, comparing p3 of "*P. nihewanensis*" with that of *Trischizolagus dumitrescuae*, most advanced species of the genus (Radulesco and Samson, 1967; Averianov, 1995; Averianov and Tesakov, 1997), following similarities can be pointed out: 1) general outline in occlusal view is trapezoidal, 2) all five reentrant angles present (PIR may be EL in some cases), 3) PER usually deeper than PIR, 4) AIR very shallow or absent, 5) generally shallow and simple AER, and 6) shallow AR. However, "*P. nihewanensis*" differs from *T. dumitrescuae*: 1) AR is clearly 2-folded in the former, while it is almost always single and simple in the latter (exceptional examples are Figs. 4j, 4q, 5k of Averianov and Tesakov (1997), which can be interpreted as a primitive stage of 2-folded); and 2) TN and posterior wall of PIR are crenulated in certain degree in the former, while they are smooth in majority of the latter, although they are weakly crenulated in some cases.

Fossils of *Trischizolagus* spp. are also known from China recently. They are from Bilike, Nei Mongol (Inner Mongolia) (Qiu and Storch, 2000; early Pliocene, correlated to MN14), Yushe, Shanxi (unpublished; Wu Wenyu (pers. comm., May, 2005); upper Gaozhuang, MN 14), and Leijiahe, Gansu (Zheng and Zhang, 2001; mainly early Pliocene, correlated to MN 14 and 15). Of these, only *T. mirificus* has been described (Qiu and Storch, 2000), and it is more primitive than *T. dumitrescuae*. Material from Yushe and Leijiahe has not been described yet, but p3's from these localities are comparable to *T. dumitrescuae* from Europe

and show similar characters mentioned above, including some p3's with weak crenulations on TN and posterior enamel of PIR, and some specimens show deeper AR (Wu (pers. comm., May, 2005); Zheng Shaohua (pers. comm., May, 2005)).

Summing up the above discussion, p3 of “*P. nihewanensis*” can be interpreted as a species of *Pliopentalagus* whose p3 with simplest enamel pattern, or a species of *Trischizolagus* whose p3 with most complicated enamel pattern, based on the morphology alone. But, majority of characters indicates that the latter case is more probable.

In terms of the molariform lower teeth (V 2008-2, 3), they strongly differ from all other species of the genus *Pliopentalagus*, in having the very weakly crenulated or non-crenulated enamel of the anterior border of talonid. Based on this character alone, it is clear that these teeth do not belong to *Pliopentalagus*. That part of enamel is strongly crenulated or folded in all other species of the genus. They can be almost any taxon with smooth or very weakly-crenulated enamel of the anterior border of talonid in lower molariform teeth.

If all three teeth were collected from the same locality, it may be probable that all three belong to a same taxon. However, because they were collected from all different localities, their taxonomic identifications should be considered independently.

3.2 Faunal aspect

The small mammal fauna (= Daodi fauna) associated with “*P. nihewanensis*” can be compiled from Cai (1987), Cai and Qiu (1993) and Cai et al. (2004). Among them, the abundance of *Mesosiphneus paratingi*, *Mimomys orientalis*, *Germanomys* cf. *G. weileri*, *Chardinomys nihewanicus*, *Ochotona* spp. and *Trischizolagus* sp. is indicative of rather dry and cool climate, or Palaeartic realm.

On the other hand, although the mammal faunas associated with *P. huainanensis* and *P.* spp. B and C from Anhui have not been published, they include *Hipposideros*, *Palacotupaia*, *Brachyrhizomys*, *Hystrix*, *Herpestes* which are indicative of rather warm and humid climate, or Oriental realm, although they also include *Kowalskia*, *Allorattus*, and *Huaxiamys* which are indicative of presence of some grasslands (Jin and Zhang, 2005).

The small mammal fauna associated with *Trischizolagus mirificus* is described by Qiu and Storch (2000). According to them, the diversity and abundance of Cricetidae and Dipodidae and the presence of *Prosiphneus*, *Ochotona* and *Atlantoxerus* indicate a temperate environment of steppe or grassland, although some other elements indicate presence of some local forests; and they are indicative of Palaeartic realm, as a whole. The faunas associated with *Trischizolagus* spp. similar to *T. dumitrescuae* from Yushe (Flynn et al., 1997) and Leijiahe (Zheng and Zhang, 2001) are indicative of dry climate, or Palaeartic realm, although the former includes some members of Oriental realm, indicating some mixture of both environments.

In general, among the terrestrial faunas of the Late Miocene to Pleistocene in northern China (Palaeartic realm, north of Qin Ling Mountains), as the age becomes more recent, they include more taxa indicative of dryer climate. So, Daodi fauna is more likely to include rabbit(s) adapted to dry and cool environment.

Summing up the above discussion on the associated faunas, “*P. nihewanensis*” and *Trischizolagus* spp. from China are associated with the faunas indicative of dry and cool climate, or Palaeartic realm, while faunas associated with other species of *Pliopentalagus*, at least in China, are indicative of rather warm and humid climate, or Oriental realm. These facts suggest that “*P. nihewanensis*” is unusual as a species of *Pliopentalagus* to appear in northern China, or Palaeartic realm.

4 Conclusion

Based on the discussions above, we conclude as follows:

1) Holotype (V 2008-1) alone can be interpreted as a species of the genus *Pliopentalagus* with p3 having least complicated enamel pattern. But, in this case, one of the evolutionary trends of the genus, that enamel pattern becomes more complicated through time, is violated.

2) Holotype (V 2008-1) alone can also be interpreted as a species of the genus *Trischizolagus* with p3 having most complicated enamel pattern. In this case, this taxon fits with one of the evolutionary trends of the genus that enamel pattern becomes more complicated through time (Averianov and Tesakov, 1997). Because the Daodi fauna is younger (MN16) than *T. dumitrescuae* (mainly MN 14 and 15), it is more probable to include a species with p3 having more complicated enamel pattern.

3) Considering the associated fauna, plus 2) above, we believe that the holotype should belong to the genus *Trischizolagus*, and *T. nihewanensis* is characterized by p3 with most complicated enamel pattern within the genus.

4) Molariform teeth (V 2008-2, 3) do not belong to the genus *Pliopentalagus*. Although they might belong to the genus *Trischizolagus*, there is no evidence to prove it, and they should be interpreted as Family Leporidae gen. et sp. indet.

5) At least in China, *Pliopentalagus* is restricted to Oriental realm (south of Qin Ling Mountains), while *Trischizolagus* is restricted to Palearctic realm (north of Qin Ling Mountains) in distribution.

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