第47卷 第1期
2009年1月
古 脊 椎 动 物 学 报
VERTEBRATA PALASIATICA
pp.53－71
figs.1－5

安徽上新五褶兔两新种及淮南上新五褶兔化石[1)]

富田幸光[1] 金昌柱[2]

(1 日本国立科学博物馆地质与古生物部 东京 169－0073)

(2 中国科学院古脊椎动物与古人类研究所,脊椎动物进化系统学重点实验室 北京 100044)

摘要:近年,作者在安徽淮南大居山陆续发现了数量很多的上新五褶兔化石,其中包括保存较完整的数十个头骨及上百个下颌骨,均产自新洞、无名洞及铁四局洞穴、裂隙堆积,分别记述为大居山上新五褶兔 *Pliopentalagus dajushanensis* sp. nov. 和安徽上新五褶兔 *Pl. anhuiensis* sp. nov. 两新种。

淮南地区的晚新生代洞穴和裂隙堆积十分发育,其中常含有丰富的脊椎动物化石,而且在时、空分布上有一定的规律。区内洞穴和裂隙堆积垂直分布至少有6个水平层,最高的第6层海拔高度为160 m(如大居山老洞),第5层(如大居山新洞、无名洞)及第4层(如大居山铁四局洞穴)的海拔高度分别为130 m和90 m,属于新近纪,常含有丰富的上新五褶兔化石;第3层为第四纪早期(如大居山西裂隙),未见上新五褶兔,代之出现丝绸兔(*Sericolagus* sp.),第2层为中更新世(如大顶山西裂隙),出现野兔(*Lepus* sp.)。

迄今为止,安徽淮南地区共发现了3种上新五褶兔化石,即淮南上新五褶兔 *Pl. huainanensis* (金昌柱,2004)、大居山上新五褶兔 *Pl. dajushanensis* sp. nov. 及安徽上新五褶兔 *Pl. anhuiensis* sp. nov.,至少涉及了3个不同地质时期的动物群:一为 *Pl. huainanensis*, *Kowalskia neimengensis*, *Adcrocuta eximia* 等代表的老洞晚中新世动物群,二为 *Pl. dajushanensis* sp. nov. 和 *Promimomys asiaticus* 等代表的新洞早上新世动物群,三为 *Pl. anhuiensis* sp. nov. 和 *Kowalskia yinanensis* 所代表的晚上新世动物群。淮南地区发现的3种上新五褶兔地史分布较连续,演化特征明显,它们构成上新五褶兔连续的进化系列。从晚中新世至晚上新世,淮南大居山上新五褶兔体型从小变大;p3较原始的釉岛状后内褶沟逐渐向舌侧开放(晚中新世种 *Pl. huainanensis* 的后内褶沟均为釉岛状,早上新世种 *Pl. dajushanensis* 为83.9%,晚上新世种 *Pl. anhuiensis* 为33.3%);p4－m2的前外褶沟逐渐退化,其下跟座舌侧的釉质层越来越变细。

依性状分析,安徽发现的3种上新五褶兔化石与日本琉球奄美黑兔(*Pentalagus furnessi*)具有密切的亲缘关系,但从日本奄美黑兔的p4－m2完全缺失前外褶沟、颊齿褶沟釉质层的褶曲异常复杂等衍生性状看,上新五褶兔和奄美黑兔的系统演化关系较为复杂,尚有待发现更多早更新世的材料进一步探讨。

关键词:安徽淮南,上新世,上新五褶兔

中图法分类号:Q915.873 **文献标识码**:A **文章编号**:1000－3118(2009)01－0053－19

---

1)国家重点基础研究发展规划项目(编号:2006CB806400)、中国科学院知识创新工程重要方向项目(编号:KZCX2－YW－106)、日本学术振兴会科学研究费补助金(C)(No. 14540441,18540464)和日本国立科学博物馆(综合研究)资助。

收稿日期:2008－09－09

TWO NEW SPECIES OF *PLIOPENTALAGUS* (LEPORIDAE, LAGOMORPHA) FROM THE PLIOCENE OF ANHUI PROVINCE, CHINA, WITH A REVISION OF *PL. HUAINANENSIS*

Yukimitsu TOMIDA[1] JIN Chang-Zhu[2]

(1 *Department of Geology and Paleontology*, *National Museum of Nature and Science* 3-23-1 Hyakunin-cho, Shinjuku, Tokyo 169-0073, Japan y-tomida@kahaku.go.jp)

(2 *Laboratory of Evolutionary Systematics of Vertebrates*, *Institute of Vertebrate Paleontology and Paleoanthropology*, *Chinese Academy of Sciences* Beijing 100044, China)

Abstract Abundant fossil material of the genus *Pliopentlagus* from three localities representing the late Late Miocene through Late Pliocene in Auhui Province, China, are studied in morphological and statistical detail. Three species are recognized: *Pl. huainanensis*, *Pl. dajushanensis* sp. nov., and *Pl. anhuiensis* sp. nov., in decreasing age. Although a number of characters overlap among those species, if the specimens from each locality are treated statistically as populations, three species can be distinguished. Further, when they are arranged by their geologic age, they clearly show that average size increases, the ratio of EL in p3 decreases, the ratio of AER in p4-m2 decreases, the ratio of thin enamel band on the lingual face of the talonid in p4-m2 decreases, and the relative length of the palatal bridge decreases. Thus, these three species can be interpreted to represent a gradually evolving sympatric lineage, from the late Late Miocene through Late Pliocene. These three species of *Pliopentalagus* seem to have gradually evolved toward *Pentalagus*, but at least one character contradicts this idea, and the phylogenetic relationship between *Pliopentalagus* and *Pentalagus* may not be so simple.

Key words Huainan, Anhui; Pliocene; *Pliopentalagus*

1 Introduction

Abundant fossils of the genus *Pliopentalagus* were found and collected from deposits of four different caves, namely Laodong, Xindong, Wuming, and Tiesiju. They are located in the same general area (Dajushan Hill) but at different altitudes, hence representing different geologic ages: higher altitude deposits being older in geologic age. Tomida and Jin (2002) reported preliminary study of those fossils, but they treated the specimens from Wuming and Tiesiju together, assuming them to be similar in geologic age. Later, the fossils from each locality were treated separately, and detailed and comparative studies of the fossils from all four caves were carried out. As a result, it became clear that the populations from Wuming and Tiesiju show differences in detailed morphology, ratio of certain characters, and size, and therefore, they should be treated separately. We recognized three different species that change gradually through time. The most primitive species of the genus (*Pl. huainanensis*) from Laodong Cave was described by Jin (2004), and we describe two new younger species below. During the course of these detailed studies, it was recognized that *Pl. huainanensis* had to be revised, so an emended diagnosis and emended description are also given in this paper.

2 Method

Descriptions and measurements are made based on mature or supposed-to-be mature individuals in this paper, and characters of sub-adults and juveniles will be described in a separate paper. Classification of the specimens into adult, sub-adult, and juvenile groups must be somewhat arbitrary, and we used the following criteria: "sub-adult" is obviously smaller than the majority of larger specimens (which are "adult"), and juvenile is extremely small and/or p3 or P2 is almost unworn or not worn at all. These categories are applicable in most cases, but there are a few specimens that are difficult to differentiate between adult and sub-adult among the lower jaws from Xindong Cave and two skull fragments from Tiesiju. In these cases, we judged overall features of each specimen somewhat arbitrarily. Several skull specimens are known from Xindong Cave and Tiesiju localities, but they will be described in detail in a separate paper. Specimens described in this paper are stored at IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences), and specimen numbers start with V.

Measurements of the skull, mandible, and dentition were made following Averianov et al. (2000), using a digital caliper (Mitutoyo CD-20C), with the help of a stereomicroscope for smaller measurements. Measurements of the teeth were made using the scale of the stereomicroscope (Wild M5), with each tooth set vertically as much as possible. Illustration of the occlusal surface of each tooth is also made after setting it vertically as much as possible, so that the total length of the full dentition in illustrations may not be exactly the same as that of full dentition in direct measurement. Pencil line drawings were made using camera lucida (by Y T), and then the final illustrations were completed using computer illustrating soft (Adobe Illustrator CS2) based on those pencil drawings.

There is a small reentrant at the antero-external corner of the trigonid of p4-m2 in some specimens described in this paper. We call this an antero-external reentrant (AER), and the ratio of its presence in the total sample is important in recognition of the species. There are three variations in morphology of AER: 1) rather deep and filled with cement (e. g., m2 of Fig. 3A), 2) shallow but still filled with cement (e. g., m1 of Fig. 3A), and 3) enamel inflected but no cement filling (e. g., p4 of Fig. 3A). We considered the former two cases as displaying AER, but not the third case. For the terminology of p3 and P2, we follow White and Morgan (1995) with slight modifications. For p3: AER, antero-external reentrant; AR, anterior reentrant; AIR, antero-internal reentrant; EL, enamel lake; PER, postero-external reentrant; PIR, postero-internal reentrant; TH, thick enamel in PER and PIR or EL; TN, thin enamel in PER and PIR or EL; for P2: EAR, external anterior reentrant; IAR, internal anterior reentrant; MAR, main anterior reentrant.

3 Geologic setting and ages of the localities

Three localities that yielded lagomorph fossils described in this paper are located on the Dajushan Hill in Bagongshan District, about 15 km west of Huainan City, Anhui Province, China (Fig. 1). Dajushan Hill is composed of a thick limestone body of Ordovician age. Three localities are named Laodong Cave, Xindong Cave, and Tiesiju Cave, and they are water-eroded caves developed in the Dajushan limestones. Laodong Cave is located at the highest in altitude, while Tiesiju Cave is located lowest among three localities, indicating that Laodong is oldest and Tiesiju is youngest in geologic age, because Dajushan Hill is being uplifted, and newer caves have developed lower on the hillside.

Laodong Cave locality It is located a few tens of meters North of Xindong Cave, whose GPS data are given below, and about 160 meters above sea level. The sediments in the cave are composed of grayish sandy mud and brownish muddy sands consolidated by calcareous cement, and can be divided into eight layers. *Pliopentalagus* fossils were obtained from the layers 4 and 5. See Jin (2004) and Jin et al. (1999) for more details on the sediments.

Laodong Cave locality yielded remains of a hamster, *Kowalskia neimengensis*, which was originally described from Ertemte and Harr Obo in Nei Mongol (Inner Mongolia)(Wu, 1991). It has been known only from those localities, which are correlated to the latest Miocene (Qiu et al., 2006). Laodong locality also yielded remains of a bone-cracking hyaenid, *Adcrocuta eximia*, which also indicates the later part of the Late Miocene (Tseng et al., 2008). In addition, Laodong Cave is located about 30 meters higher in altitude than Xindong Cave, which is early

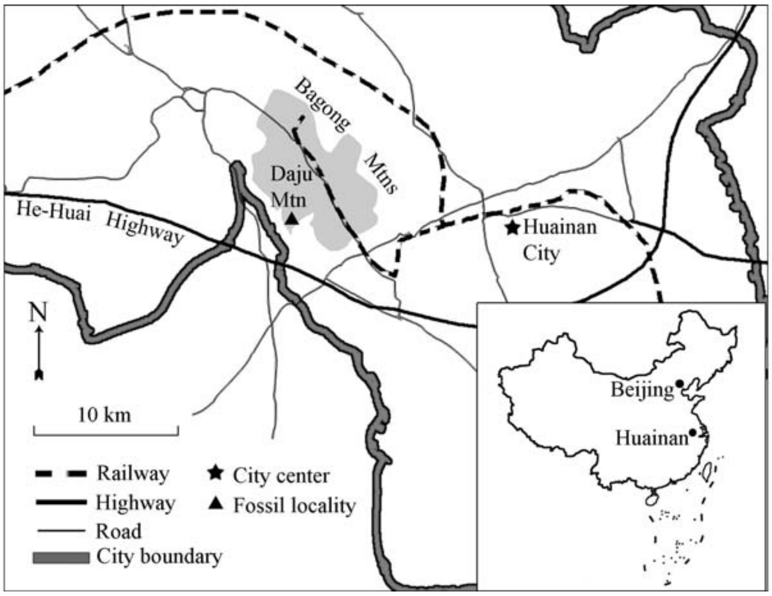

Fig. 1 Local area map of Huainan, with the three localities are of Dajushan Hill (Daju Mtn), part of Bagong Mountains west of Huainan City, Anhui Province (Map after Tseng et al., 2008)

Early Pliocene in age (see below). Thus, the age of Laodong Cave deposits is estimated to be late Late Miocene.

Xindong Cave locality It is located at 32°35′47″N, 117°01′49″ E by GPS and about 130 meters above sea level. The sediments are strongly consolidated by abundant calcitic cementation and consist of chocolate-brown clayey breccia, reddish brown sandy mudstone with small amounts of breccia, and reddish brown sandstone with gravels and sandy mudstone. The deposits can be divided into 5 lithological layers, with a thickness of about 16 meters (Jin and Zhang, 2005). Although named as Xindong "Cave", the deposits may be fissure fillings because the limestone wall is rather smooth and nearly vertical at least on one side, and it seems likely that the duration of sediment filling was a rather short period of time. The *Pliopentalagus* fossils were obtained from various layers of the deposits.

Large amounts of vertebrate fossils have been collected from this locality, and over 40 species of vertebrates have been identified with preliminary studies. *Promimomys asiaticus* is one of them and is more primitive than European species (Jin and Zhang, 2005). The genus is limited to MN14 in Europe, which is early Early Pliocene (Fejfar et al., 1997). The presence of *P. asiaticus* is indicative of its geologic age somewhat older than the Early Pliocene Bilike site in Nei Mongol, China, where no *Promimomys* is known but *Mimomys* is known (Jin and Zhang, 2005; Qiu et al., 2006). Thus, the age of Xindong Cave deposits is probably early part of the Early Pliocene.

Tiesiju Cave locality It is located about 200 ~ 300 meters north of Xindong Cave and about 90 meters above sea level. The sediments are reddish mud and muddy sand with some limestone breccia, consolidated by calcitic cementation, and are divided into five layers. The *Pliopentalagus* remains were scattered in various layers. A total of 18 taxa of mammals have been identified, including *Kowalskia yinanensis*, which was originally described from Shandong Province (Zheng, 1984). It is the largest species of the genus known in East Asia, possesses advanced characters, and correlates to the Late Pliocene. Therefore, the age of Tiesiju Cave deposits is estimated as Late Pliocene.

4 Systematic paleontology

Order Lagomorpha Brandt, 1885
Family Leporidae Gray, 1821
Subfamily Leporinae Trouessart, 1880
Genus *Pliopentalagus* Gureev & Konkova, 1964

Type species *Pliopentalagus moldaviensis* Gureev & Konkova, 1964 (in Gureev, 1964), p. 129.

Emended diagnosis Body size small to medium; diastema of lower jaw short; lower incisor terminates more anteriorly than *Hypolagus*; enamel crenulations of reentrants on cheek teeth complicated; p3 has all five reentrants (counting EL as a modification of PIR); TN of PER and PIR or EL thin and well crenulated; PIR in p3 is always isolated as an EL in primitive species, and the ratio of the presence of EL decreases in advanced species; p4–m2 with posterior enamel wall of external reentrant fold well and deeply crenulated but not as deep as in *Pentalagus*, and with small AER in a majority of the population in primitive species; the length of palatal bridge relatively long in primitive species and becomes shorter in advanced species; P3–M2 with internal reentrant fold deep and enamel crenulations of both anterior and posterior walls deep and heavy but less than in *Pentalagus*.

Included species In addition to the genotype, the following species are included: *Pl. dietrichi* (Fejfar, 1961); *Pl. progressivus* Liu & Zheng, 1997; *Pl. huainanensis* Jin, 2004; *Pl. dajushanensis* sp. nov. and *Pl. anhuiensis* sp. nov. (both described below); *Pl. agilis* (Russell and Harris, 1986), which will be discussed elsewhere (but, see Tomida and Jin, 2004). *Pl. nihewanensis* Cai, 1989 is excluded from the genus (Tomida and Jin, 2005).

Pliopentalagus huainanensis Jin, 2004

(Fig. 2; Tables 1–4)

Holotype A partial left mandible with i2, p3–m1 (V 10817.1; for m2 and m3, see discussion below).

Paratypes One left and two right fragmentary mandibles with p3–m3, p3–m2, and p4–m2 (V 10817.2–4, respectively); two left and two right fragmentary maxillae with P2–M2, P2–M2, P3–M3, and P3–M2 (V 10818.1–4, respectively); isolated left lower incisor (V 10818.6); isolated left M2 (V 10818.8) (currently, this M2 is mistakenly fixed at the position of right P3 of V 10818.3). P2 of V 10818.4, isolated I2 (V 10818.5), and isolated i2 (V 10818.7), which were included in Jin (2004), are currently missing.

Referred specimens Each of right and left fragmentary mandibles with p3–m3 and p3–m3 (V 10817.5–6, respectively).

Type locality and geologic age Laodong cave locality of the Dajushan Hill Limestone Quarries, Huainan, Anhui Province, China (Fig. 1). Late Late Miocene (see “ages of locality” section above).

Emended diagnosis Small-sized (but not the smallest) species of the genus. Lower incisor tends to terminate beneath the trigonid of p3; PIR of p3 always forms the enamel lake (100% of the population), and its posterior wall is heavily crenulated (but somewhat less than later species); p4–m2 with small but clear AER in about 70% of the specimens.

Measurements See Tables 1–4.

Emended description The diastema of the mandible is relatively short, and it is somewhat shorter than the alveolar length of p3–m3. No specimen can provide both measurements on the same individual in the available specimens, but the diastema length can be estimated as 15.4 mm (tip of the dentary is only slightly broken) on V 10817.6, which provides alveolar length of p3–m3 as 16.84 mm. Therefore, mandibular diastema index (diastema L / (diastema L + alveolar L)) is approx. 0.48, which is nearly equal to or only slightly larger than *Pentalagus* (ca. 0.45 ~ 0.47) and *Caprolagus* (ca. 0.43 ~ 0.46) but is much smaller than *Pronolagus* (ca. 0.57 ~ 0.61) (based on the measurements made by YT on the specimens stored at The Natural History Museum in London). Posterior end of the lower incisor forms a tubercle on the lingual face of dentary and terminates beneath the trigonid of p3 in three specimens, and slightly anterior to p3 (beneath the diastema) in one specimen (V 10817.6).

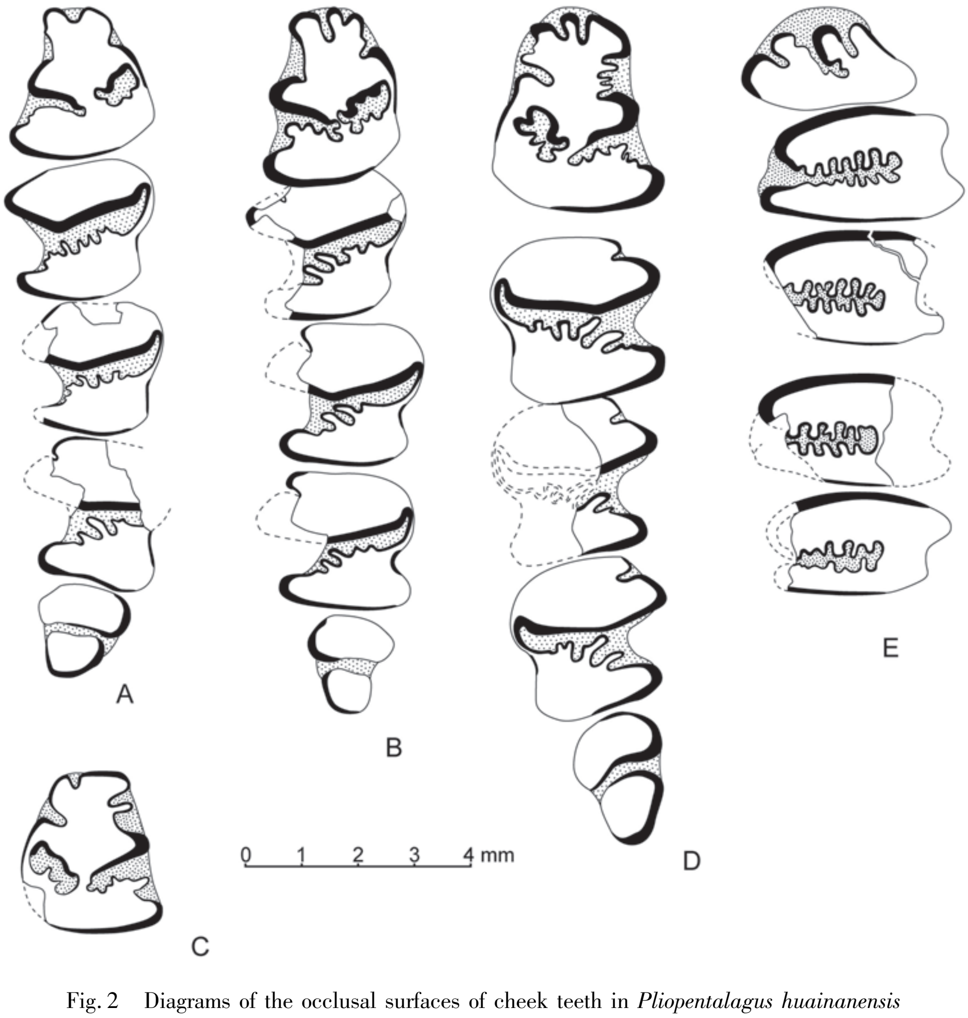

Fig. 2 Diagrams of the occlusal surfaces of cheek teeth in *Pliopentalagus huainanensis*
A. left p3–m3 (holotype, V 10817.1); B. left p3–m3 (V 10817.2); C. right p3 (V 10817.3); D. right p3–m3 (V 10817.5); E. left P2–M2 (V 10818.1)

In the lower dentition, the incisor is relatively curved and similar to that of *Pentalagus*. The p3 has four reentrants (AR, AER, AIR, and PER) and an EL at the position of PIR on the occlusal surface. All the reentrants and EL are filled with cement. The AR varies in morphology from a single shallow fold (Fig. 2A, C) to two relatively deep folds (Fig. 2B, D). The AER is a wide and shallow reentrant in general, but in some cases it shows deeply crenulated enamel (Fig. 2D). The AIR similarly varies from a simple shallow reentrant to a rather wide and partly deep fold. The PER is the largest reentrant angle and extends lingually but somewhat posteriorly and approximately half way across the p3 talonid. The thick enamel of anterior wall

(TH) is rather smooth and extends to posterior end of AER, forming a large curvature. The thin enamel of posterior wall (TN) is well crenulated in general (except for the holotype, in which it is much less crenulated). The PIR is represented by EL in all five known specimens. It looks somewhat antero-posteriorly compressed rectangular in outline, and aligned antero-lingual to postero-buccally. The TH and TN are both irregularly crenulated, but TN is more crenulated. The angle between the long axes of PER and EL is approximately 100 to 140 degrees. The dentine bridge between trigonid and talonid varies in width; the PER and EL are nearly connected in V 10817.2 (Fig. 2B). The thick enamel of the posterior face of the p3 becomes thinner gradually and terminates at about 1/3 way from the lingual edge.

The p4–m2 are similar to each other in morphology, and p4 tends to be the largest among them, although the difference is not much. The trigonid and talonid are separated by a wide and deep external reentrant fold that almost reaches the lingual edge of the tooth. The thick enamel forms the anterior wall of this fold and bends somewhat sharply at a point approximately 1/3 way across the trigonid. It further extends to but becomes thinner at the antero-buccal face of the trigonid and disappears at a point approximately 1/3 way across the trigonid. Small but clear AER filled with cement is present at the antero-buccal face of the trigonid, just before the termination of the enamel, in about 70% of the specimens (Table 1). AER is variable in the specimens available, either present in all three teeth (see Fig. 2B,D) or absent from all three teeth (V 10817.6), but this observation may be modified when more specimens are available. The thin enamel of posterior wall of the external reentrant fold is rather deeply crenulated or undulated, but it is still much less than in *Pentalagus*. This undulation pattern is similar among p4–m2 within the same individual, becoming slightly simpler toward m2. This enamel becomes thicker rapidly at the postero-buccal corner of the tooth, continues to and becomes thinner gradually at the posterior face, and terminates somewhere between a point approximately 2/3 way across the talonid and a point slightly buccal to the postero-lingual corner of the tooth. Although not very clear, there is a thin enamel band on the lingual face near the antero-lingual corner of the talonid in all p4–m2. The trigonid width is about 20% to 30% wider than talonid in average.

Table 1　Comparisons of the presence of EL in p3 and AER in p4–m2, among *Pentalagus furnessi*, *Pliopentalagus anhuiensis* sp. nov., *Pl. dajushanensis* sp. nov., and *Pl. huananensis*

Locality	Taxa	Enamel lake		AER p4		AER m1		AER m2		AER p4–m2	
		n	%	n	%	n	%	n	%	n	%
Amami Island	*Pentalagus furnessi*	22	18.2	42	0.0	43	0.0	42	0.0	127	0.0
Tiesiju	*Pliopentalagus anhuiensis*	6	33.3	8	25.0	8	25.0	8	37.5	24	29.2
Xindong	*Pliopentalagus dajushanensis*	31	83.9	39	48.7	41	75.6	39	71.8	119	65.5
Laodong	*Pliopentalagus huainanensis*	5	100	6	66.7	5	60.0	5	80.0	17	70.6*

* including an isolated tooth with unidentified tooth position (currently at the position of m2 of the "holotype"; see text for detail).

The morphology of m3 is typical for leporines. It is much smaller than other teeth (Table 2), and its body curves strongly postero-ventrally. Trigonid and talonid are completely separated and are connected by cement. Trigonid is laterally widened oval in outline in occlusal view, and the enamel covering varies from buccal 1/3 to nearly 2/3 of the circumference. Talonid is smaller than trigonid and is nearly circular or a rounded triangle in outline, and the buccal enamel covering varies from 1/2 to over 2/3 of the circumference, always thickest in buccal face.

The specimen V 10818.1 (fig. 3 of Jin, 2004) is the only specimen from Laodong Cave locality that preserves the palatal bridge, and its length is 8.21 mm. The anterior edge of the palatal bridge is lingual to the midpoint of P2, while the posterior edge is lingual to the midpoint of M1. Although Jin (2004:244) estimated the width between lingual sides of left and right P4s (alveoli) as 9.8 mm, a new estimate is obtained as 10.17 mm. But, in order to compare with other taxa, we estimated the "width" (= distance) between lingual edges of the alveoli of left and right P3s (which is "C5" of Averianov et al. 2000; P3 is located at about midpoint of palatal bridge length in most leporines) as 9.67 mm. Thus, the length/width ratio of palatal bridge is estimated as 0.85, which is the largest among three species of *Pliopentalagus* from Huainan area (Table 4). The length of palatal bridge relative to the length of P2–M3 alveoli is also largest among them. Comparing the length/width ratio of palatal bridge with other taxa, it is larger in *Pentalagus* (1.02 in average of seven skulls), is somewhat smaller in *Caprolagus* (0.70 and 0.74 in two skulls), and is much smaller in *Bunolagus* (0.47 in the type specimen).

Table 2 Measurements of the lower teeth of adult specimens of *Pliopentalagus huainanensis*, *Pl. dajushanensis* sp. nov., and *Pl. anhuiensis* sp. nov. (mm)

		Length				Width				Talonid width			
		Mean	SD	OR	N	Mean	SD	OR	N	Mean	SD	OR	N
Pl. huainanensis	i2	2.16			1	2.81			1				
	p3	3.26	0.325	2.85～3.61	5	2.75	0.241	2.57～3.12	5				
	p4	2.80		2.54～2.94	4	2.97	0.174	2.72～3.15	5	2.45	0.188	2.32～2.78	5
	m1	2.63	0.136	2.47～2.80	6	2.83	0.198	2.63～3.09	5	2.17	0.116	2.01～2.29	5
	m2	2.63		2.44～2.75	3	2.89		2.78～2.97	3	2.33		2.29～2.35	4
	m3	1.91		1.76～2.13	4	1.67		1.55～1.79	4	1.07		0.96～1.18	4
Pl. dajushanensis	i2	2.48	0.193	2.20～2.69	10	2.94	0.301	2.38～3.53	10				
	p3	3.62	0.263	3.19～4.11	26	2.96	0.270	2.44～3.40	24				
	p4	2.89	0.194	2.54～3.31	34	3.21	0.209	2.78～3.68	24	2.66	0.178	2.23～3.09	27
	m1	2.83	0.168	2.51～3.12	30	3.11	0.230	2.75～3.62	24	2.39	0.180	2.01～2.75	22
	m2	2.79	0.196	2.38～3.12	26	3.03	0.203	2.57～3.40	25	2.33	0.202	1.86～2.63	20
	m3	1.88	0.161	1.70～2.20	11	1.67	0.066	1.55～1.79	11	1.06	0.110	0.90～1.24	9
Pl. anhuiensis	i2	2.66			1	3.49			1				
	p3	3.86	0.099	3.73～4.01	6	3.13	0.099	3.01～3.28	5				
	p4	2.98	0.073	2.82～3.06	8	3.45	0.18	3.15～3.65	8	2.76	0.093	2.72～2.94	7
	m1	2.94	0.135	2.75～3.15	8	3.28	0.165	3.00～3.49	8	2.50	0.147	2.35～2.75	6
	m2	2.93	0.102	2.81～3.12	7	3.23	0.105	3.12～3.36	5	2.47		2.41～2.54	4
	m3	2.04		1.89～2.16	4	1.82		1.61～1.92	4	1.18		0.99～1.24	4

In the upper dentition, P2 is known in two specimens (V 10818.1–2; Fig. 2E). The tooth column of P2 curves antero-dorsally, then further curves postero-dorsally toward the base of the tooth. P2 is oval in outline in occlusal view, and the anterior face swells more compared to the posterior. There are three reentrant folds on the anterior face, EAR, MAR, and IAR, all of which are filled with cement, and cement further develops on the anterior face of the tooth. MAR is deepest, extends postero-buccaly about 2/3 across the tooth length, and the enamel walls are crenulated. EAR and IAR are both shallow, extend postero-buccaly about 1/3 of the tooth length, and the enamel walls are without crenulations. Thick enamel covers lingual corner of the tooth and anterior ends of the dentine peninsulas between reentrants, while moderately thick enamel covers antero-buccal corner.

P3 to M2 are quite similar in morphology, and the outline in occlusal view is typical to that of other leporines. Each tooth has a deep internal reentrant fold located slightly posterior to the midline of the tooth, reaching about 2/3～3/4 way across the tooth width, but tends to be shallower toward the posterior tooth. Secondary folds of enamel (= enamel crenulations) are deep and heavy, but not as deep as in *Pentalagus*. The depth of the enamel crenulations tends to be somewhat deeper on the anterior wall than posterior, and the crenulations of the posterior wall tend to be somewhat simpler toward the posterior tooth, especially in M2 (Fig. 2E). The width of anterior part of the tooth is narrower than posterior in P3 and P4, is about the same in M1, and is wider than posterior in M2. Thick enamel is present at the antero-lingual corner of the tooth, continues to the anterior face of the tooth, and quickly becomes thinner and disappears at a point about 10% ~20% of the tooth width from the antero-buccal corner. Thick enamel is also present at the postero-lingual corner of the tooth, continues to the posterior face of the tooth, but becomes thinner gradually, and disappears at a point about 15% ~25% of the tooth width from the postero-buccal corner.

Table 3　Measurements of the upper teeth of adult specimens of *Pliopentalagus huainanensis*, *Pl. dajushanensis* sp. nov., and *Pl. anhuiensis* sp. nov.　(mm)

		Length				Width, anterior				Width, posterior		
		Mean	SD	OR	N	Mean	SD	OR	N	Mean	OR	N
Pl. huainanensis	I2											
	I3											
	P2	1.65		1.55 ~1.75	2	3.36		3.28 ~3.43	2			
	P3	2.21		2.13 ~2.29	3	3.48		3.29 ~3.67	3	4.15	3.87 ~4.45	3
	P4	2.15		2.04 ~2.26	4	3.93		3.80 ~4.00	3	4.05	3.77 ~4.22	4
	M1	2.10		1.98 ~2.16	4	3.81		3.74 ~3.87	2	3.92	3.80 ~4.03	2
	M2	1.97	0.069	1.86 ~2.04	5	3.48		3.35 ~3.61	2	2.81		1
	M3	0.74			1	1.70			1			
Pl. dajushanensis	I2	2.03	0.065	1.95 ~2.10	5	2.95	0.213	2.75 ~3.25	5			
	I3	0.94	0.086	0.84 ~1.05	5	1.50	0.188	1.24 ~1.67	5			
	P2	1.73	0.090	1.58 ~1.89	11	3.68	0.202	3.42 ~4.19	11			
	P3	2.37	0.160	2.10 ~2.63	23	4.60	0.300	4.19 ~5.09	19			
	P4	2.39	0.148	2.13 ~2.63	27	4.36	0.207	4.06 ~4.83	26			
	M1	2.25	0.125	2.01 ~2.44	26	4.01	0.218	3.80 ~4.45	22			
	M2	2.21	0.103	1.95 ~2.29	20	3.72	0.229	3.29 ~3.93	11			
	M3	0.90	0.080	0.80 ~1.02	9	1.60	0.169	1.30 ~1.89	10			
*Pl. anhuiensis**	I2	2.11			1	2.91			1			
	I3	1.10			1	1.52			1			
	P2	1.58			1							
	P3	2.11		2.01 ~2.20	2	4.25			1			
	P4	2.21		2.16 ~2.26	2	4.25			1			
	M1	2.13		2.10 ~2.16	2	4.12			1			
	M2	1.95		1.89 ~2.01	2	3.74			1			
	M3	0.87			1	1.27			1			

* The specimens measured here may be considered to be subadults (see text for detail).

M3 is known in only one specimen (V 10818.3). It is a very small tooth, about 40% of M2 in length and width, and is oval in outline in occlusal view. Thick enamel covers lingual half of the anterior face, continues to lingual face, and becomes thinner and disappears at a point 1/3 way across the tooth width on the posterior face.

Discussion　Although the holotype (V 10817.1) is considered to be an adult, it is the smallest of the available specimens from Laodong Cave. In addition, the specimen is a composite (not composed of a single left mandible with full dentition). As seen in Fig. 2A (see also fig. 2 of Jin, 2004), m3 is from the right side, as indicated by position of the thick enamel, which should be on the buccal side and on the same side as the thick enamel of p4–m2. Also, m2 is aberrantly larger than m1 and still somewhat larger than p4. The size of these teeth are p4

> m1 > m2 in *Pliopentalagus* in general (see Table 2, especially *Pl. dajushanensis* with a large population). The crenulation patterns of posterior enamel walls of the external reentrant fold in p4–m2 are quite similar to each other within the same individual as described above (e.g., Figs. 2B,D, 3A–E), but that of m2 in the "holotype" is not similar to those of p4 and m1 (which are alike). These points (size and enamel pattern) together strongly suggest that m2 of the "holotype" is also not the same individual as p3–m1. This probably happened when a preparator applied plaster to the mandible and added two isolated teeth. Thus, it is considered that the holotype consists of left mandible fragment with i1 and p3–m1. The newly defined holotype has p4 and m1 without AER, but the majority (about 70%; Table 1) of the specimens of *Pl. huainanensis* has p4 and m1 with AER. Thus, the holotype is not the most typical specimen of the population. Among the rest of the specimens, V 10817.2 (Fig. 2B) is the best one representing and exhibiting the diagnostic characters of the species. It is impossible to change the holotype, and so V 10817.2 is the most important paratype (being from the same locality).

Table 4 Length and width (distance between lingual edges of left and right P3 alveoli) of the palatal bridge, alveolar length of P2–M3, the length/width ratio of palatal bridge, and ratio between palatal bridge length and alveolar length of P2–M3 in *Pliopentalagus huainanensis*, *Pl. dajushanensis* sp. nov., *Pl. anhuiensis* sp. nov., and *Pentalagus furnessi* (mm)

	L of palatal bridge (C4)	Dist. of P3s alveoli (C5)	Alveolar L of P2–M3 (C10)	Ratio C4/C5 in average	Ratio C4/C10 in average
Pl. huainanensis (n = 1)	8.21	9.67*	15.48	0.85	0.53
Pl. dajushanensis (n = 9)					
Average	7.95	10.77	16.14	0.74	0.49
Minimum	7.48	9.89	14.97		
Maximum	8.96	11.29	16.97		
SD	0.481	0.464	0.728		
Pl. anhuiensis (n = 2)					
Average	5.85	9.35	14.55	0.63	0.40
Minimum	5.69	8.99	14.49		
Maximum	6.01	9.71	14.60		
Pentalagus furnessi (n = 7)					
Average	12.13	11.84	18.10	1.02	0.67
Minimum	10.60	10.93	17.81		
Maximum	12.90	12.54	18.47		
SD	0.810	0.579	0.293		

* estimated value.

After Jin (2004), two mandibles were added to the collection: right and left mandible fragments with p3–m3 (V 10817.5, Fig. 2D; V 10817.6, respectively). Table 2 includes their measurements, but the "m2" of the "holotype" may not be m2, so its measurement is not reflected in Table 2. The state of AER for this tooth is reflected in Table 1. The m3 of the "holotype" is included in Table 2, because although it is not the same individual as the holotype, it is an m3 and is from the same locality. All the teeth were measured again for this study, and so the results may not be exactly the same as those by Jin (2004).

Width of the palatal bridge is estimated by the distance from the midline of the palatal bridge to the lingual edge of P3 alveolus (P4 in Jin, 2004) multiplied by two. The midline of the palatal bridge can be defined by the medial protuberance of the anterior edge and a small projection on the posterior edge (Table 4). The illustration of Jin's (2004) fig. 3A is about 3 times, and fig. 3B is about 7.3 times, so the scales are both wrong.

Pliopentalagus dajushanensis sp. nov.

(Figs. 3-4; Tables 1-4)

Holotype A fragmentary left mandible with p3-m3 (V 14180.3).

Paratypes Four left fragmentary mandibles with p3-m2, p3-m3, p3-m2, and i2-m2 (V 14180.1, 2, 15 and 17, respectively); four right fragmentary mandibles with p3-m2, m1-m3, i2-m3, and p4-m3 (V 14180.5, 10, 16 and 23, respectively); right and left mandibles with p3-m3 and p3-m2 that are sliced in the plastic matrix (V 14180.4 and 6, respectively); six posterior partial skulls with no tooth, right P2-M2 + left P3-M1, left and right P3-M3, right M1-2 + left P3-M3, right P2-M1 + left P2-M2, and right P2-M3 (V 14181.1, 3, 5, 8, 10, 11, respectively); two anterior partial skulls with right I2-3, P3-4, M2 + left P3-M3 and full dentition (V 14181.6, 9, respectively); palate with right P3-M2 + left P2-M2 (V 14181.12); right maxilla with P2-M2 (V 14181.17).

Referred specimens 31 left or right fragmentary mandibles with full or partial dentitions (V 14180.7-9, 11-14, 18-22, 24-39, 56-58); two fragmentary skulls with no tooth and right P4-M2 (V 14181.2, 4, respectively); three palates with right and left P3-M1, right P4-M2 + left P2-M1, and left P3-M2 (V 14181.13, 20, and 22, respectively); six right or left maxillae with some teeth (V 14181.14-16, 18, 19, 21, respectively); two snouts with right I2-3 and right I2-3 + left I2 (V 14181.23 and 24, respectively). Some postcranial material is known from this locality, but curation is not completed, so they are not listed here.

Type locality and geologic age Xindong cave locality of the Dajushan Limestone Quarries, Huainan, Anhui Province, China (Fig. 1); Early Pliocene (see "Geologic setting and ages of locality" above).

Etymology From Dajushan, the peak of the limestone hill where a number of small limestone quarries and the Xindong cave locality are located.

Diagnosis Slightly larger (5% ~10%) on average than *Pl. huainanensis*, but slightly smaller (3% ~7%) on average than *Pl. anhuiensis* in tooth measurements; terminating point of the lower incisor tends to be more posterior than *Pl. huainanensis*; ratio of EL in p3 about 80% of the population; p4-m2 with AER in about 65% of the teeth; AR of p3 tends to be deeper and somewhat more complicated than *Pl. huainanensis*; palatal bridge shorter than *Pl. huainanensis* but longer than *Pl. anhuiensis*.

Measurements See Tables 1-4.

Description The diastema of the mandible is relatively short, and it is slightly shorter than the alveolar length of p3-m3; but it is somewhat longer than in *Pl. huainanensis*. The mandibular diastema index can be calculated directly on 6 specimens, and it ranges from 0.471 to 0.516 (0.487 on average). Lower incisor terminates beneath the trigonid of p3 in about 2/3 of the specimens, beneath the talonid of p3 in about 1/3 of the specimens, rarely terminating anterior to p3.

The morphology of the lower dentition is very similar among *Pl. huainanensis*, *Pl. dajushanensis*, and *Pl. anhuiensis*, and therefore, only the differences will be noted below. The lower dentition is slightly larger (3.2% ~11.0% in length and width of p3 to m2) in average than *Pl. huainanensis* (Table 2). In p3, 5 specimens have PIR, while 26 specimens have EL; ratio of EL is 83.9%, compared to 100% in *Pl. huainanensis* (Table 1). AR is deeper and more complicated (Fig. 3A-D) than in *Pl. huainanensis* in a majority of the specimens, and no specimen shows AR as shallow and simple as the holotype of *Pl. huainanensis* (Fig. 2A). The enamel crenulations of TN of PER and EL or PIR also tends to be somewhat more complicated. One specimen has p3 with PER and PIR connected, so that the trigonid and talonid are separated (Fig. 3F).

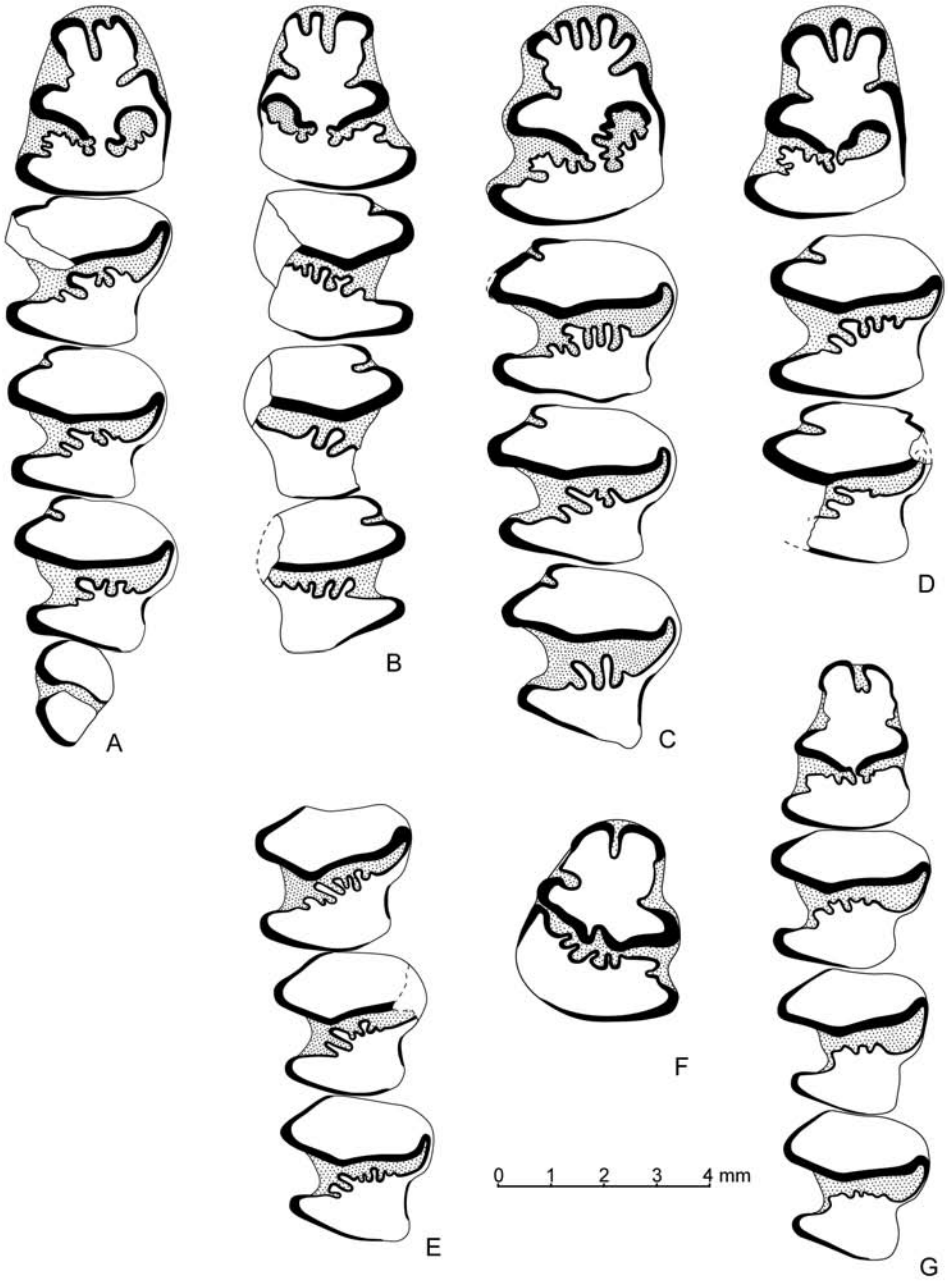

Fig. 3 Diagrams of the occlusal surfaces (or cross sections in C and F) of lower cheek teeth in *Pliopentalagus dajushanensis* sp. nov.
A. left p3-m3 (holotype, V 14180.3); B. right p3-m2 (V 14180.5); C. left p3-m2 (V 14180.6); D. left p3-m1 (V 14180.17); E. left p4-m2 (V 14180.1); F. right p3 (V 14180.4); G. left p3-m2 (V 14180.15)

As in *Pl. huainanensis*, p4-m2 are similar to each other in morphology, and it is clearer that p4 tends to be the largest while m2 tends to be smallest among them, although the difference is not much (Table 2). In p4–m2, AER is not necessarily present or absent in all three teeth of the same individual: it varies from present in all three teeth to none (compare the figures of Fig. 3), but on average, the ratio of the presence of AER is lowest in p4 (ca. 49%) and highest in m1 (ca. 76%), and about 65% in all teeth (Table 1). The thin enamel band on the lingual face near the antero-lingual corner of the talonid in p4–m2 is present in most (about 3/4) of the specimens (Fig. 3A,C–E), while it is not present in other specimens (Fig. 3B,G). Its thickness and length in occulusal view varies among the specimens, and it is almost connected to the enamel on the distal face of the tooth in one specimen (V 14180.19). One specimen (Fig. 3D) has m1 with short and kinked enamel band on the antero-internal part of the trigonid. Other than its somewhat larger size on average (Table 2), m3 is very similar to that of *Pl. huaianensis* in morphology, and nothing can be added in descriptive terms.

Among the specimens from the Xindong Cave locality, both length of the palatal bridge and width between alveoli of left and right P3s are available on 9 individuals. The ratio of length/width of palatal bridge on average is 0.738, and the length of palatal bridge relative to length of P2–M3 alveoli is 0.493, both indices smaller than in *Pl. huainanensis* but larger than in *Pl. anhuiensis* (Table 4). The anterior edge of the palatal bridge is lingual to the midpoint of P2, while the posterior edge is lingual to the border between P4 and M1. Thus, the palatal bridge is shorter than in *Pl. huainanensis*.

The first upper incisor (I2)(Fig. 4E,F) is rounded rectangular (although more rounded on buccal side), with ratio of about 2:3, in cross section, and has a groove on the anterior surface without cement filling. The groove is a wide V shape in cross section, and the apex of the groove locates somewhat medial than the midpoint of the tooth width (about 40% ~45% across the tooth width from the lingual edge). Relatively thin enamel covers the anterior face and the anterior 1/3 of both medial and lateral sides. The second incisor (I3)(Fig. 4F) is much smaller tooth than I2, and is about 1/2 of the latter in length and width. It is oval in cross section, with the middle part of the posterior face somewhat swollen, and thin enamel surrounds the tooth.

The morphology of the upper cheek teeth is also very similar among *Pl. huainanensis*, *Pl. dajushanensis*, and *Pl. anhuiensis*, and therefore, only the differences will be described below. The upper cheek teeth are slightly larger (4.8% ~12.2% in length and width of P2 to M2 on average) than *Pl. huainanensis* (Table 3). Total of 11 P2s of 9 individuals are available from Xindong locality. The majority of the specimens are quite similar to *Pl. huainanensis* in morphology, but the depth and enamel crenulations of three anterior reentrant angles vary as follows: some large specimens (likely old individuals) tend to have MAR deeper and a more crenulated enamel wall, and one specimen (Fig. 4A) has EAR with crenulated enamel wall, while smaller specimens (likely young individuals) tend to have MAR with simpler enamel crenulations and shallower EAR and/or IAR (e.g. V 14181.18).

Other than their somewhat larger size (Table 3), P3 to M2 are very similar to those of *Pl. huaianensis* in morphology, and nothing can be added in descriptive terms. Total of 10 M3s of 8 individuals are available from Xindong locality. It is, again, very similar to *Pl. huainanensis* in relative size to M2 and outline in occlusal view, but the enamel covering differs. In a majority of the specimens, thick enamel covers over 2/3 of the anterior face although it becomes thinner buccally; thinner enamel covers about 2/3 of the posterior face, again decreasing buccally. In one specimen (V 14181.5), the enamel reaches around the tooth.

Discussion Although it was mentioned that AER in p4–m2 are present or absent in all three teeth in *Pl. huainanensis*, this observation is limited by the smaller sample than *Pl. dajushanensis*. The depth of AER and/or degree of enamel inflection at the antero-external corner of p4–m2 vary within a single individual in both species of *Pl. dajushanensis* and *Pl. anhuiensis* (described below).

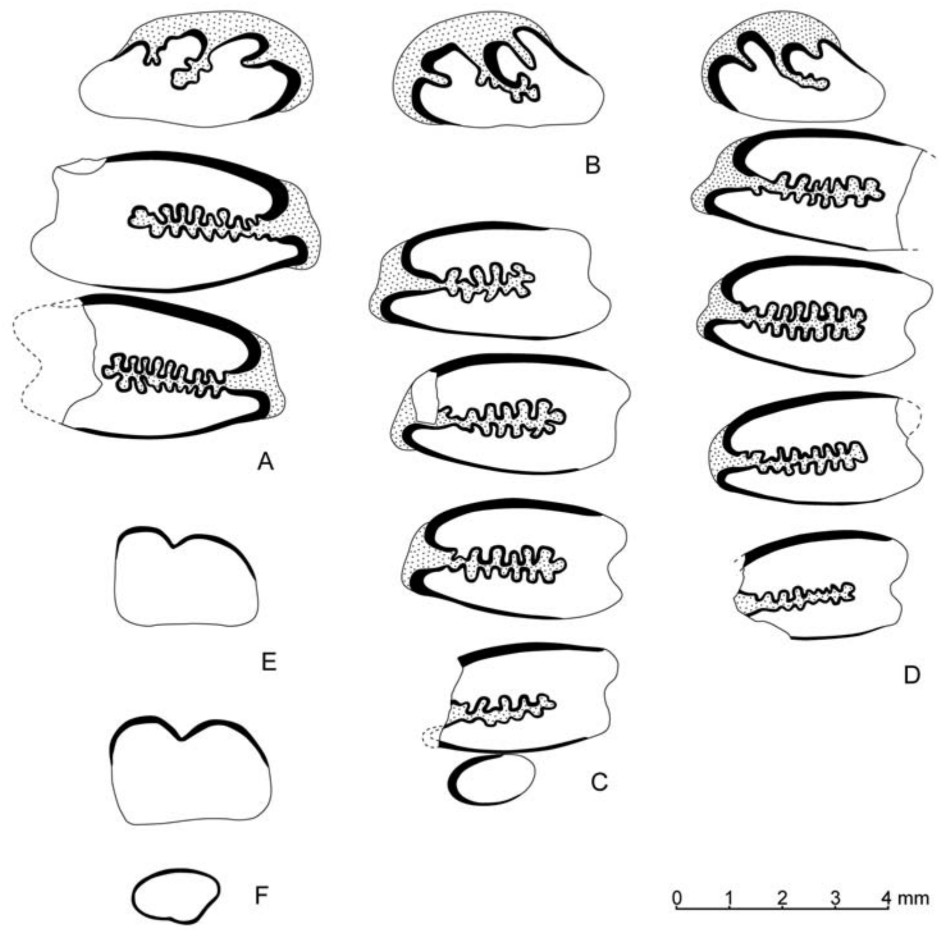

Fig. 4 Diagrams of the occlusal surfaces (or cross section in F) of upper dentitions in *Pliopentalagus dajushanensis* sp. nov.
A. right P2–P4 (V 14181.17); B. left P2 (V 14181.12); C. left P3–M3 (V 14181.8); D. left P2–M2 (V 14181.10); E. left I2 (V 14181.24); F. left I2 and I3 (V 14181.9)

Pliopentalagus anhuiensis sp. nov.

(Fig. 5; Tables 1–4)

Holotype Nearly complete left mandible with p3–m2 (V 15328.1).

Paratypes Seven fragmentary left mandibles with various conditions of tooth preservation (V 15328.2–8); two fragmentary skulls with left I2–3, P2–M3 + roots of right I3 and P2, and left P3–M2 + right P4–M2 (V 15329.1 and 2, respectively).

Type locality and horizon Tiesiju cave locality of the Dajushan Limestone Quarries, Huainan, Anhui Province, China (Fig. 1). Late Pliocene (see "ages of locality" section above for detail).

Etymology From Anhui Province where the locality is located.

Diagnosis Slightly larger (3% ~7%) on average than *Pl. dajushanensis* in tooth measurements; ratio of EL in p3 is about 1/3 of the population; p4–m2 with AER in about 30% of the teeth; palatal bridge shorter than both *Pl. huainanensis* and *Pl. dajushanensis*.

Measurements See Tables 1–4.

Description The diastema of the mandible is relatively short, and it is slightly shorter than the alveolar length of p3–m3. The mandibular diastema index can be calculated directly on 3 specimens, and it ranges 0.482 to 0.488 and is 0.484 on average. Terminating point of the lower incisor tends to be more posterior than *Pl. huainanensis* and about the same condition as *Pl. dajushanensis*.

The morphology of the lower dentition is quite similar among *Pl. huainanensis*, *Pl. dajushanensis*, and *Pl. anhuiensis*, and therefore, again, only the differences are described below. The lower dentition is slightly larger (3.1% ~7.5% in length and width of p3 to m2) on average than *Pl. dajushanensis* and is larger (6.4% ~18.4% in length and width of p3 to m2) on average than *Pl. huainanensis* (Table 2). In p3, four specimens have PIR, while two specimens have EL; ratio of EL is 33.3%, compared to 83.9% in *Pl. dajushanensis* and 100% in *Pl. huainanensis* (Table 1). In p3, AR tends to be deeper and more complicated (Fig. 5A–C) than in *Pl. huainanensis* in a majority of the specimens, but it is similar to *Pl. dajushanensis* in depth and complexity. The enamel crenulations of TN of PER and EL or PIR also tend to be somewhat more complicated than *Pl. huainanensis* but similar to *Pl. dajushanensis*.

As in *Pl. dajushanensis*, p4 tends to be the largest while m2 tends to be smallest among them, although the difference is not much (Table 2). In p4–m2, AER is not present in all 3 teeth in 5 specimens (e.g., Fig. 5A,C), is present in all 3 teeth in one specimen, and is present in 2 teeth (e.g., Fig. 5B) in 2 specimens. In V 15328.3 (Fig. 5B), p4 has an enamel bend at the antero-buccal corner of the trigonid, but it is not filled with cement, and so it is not counted as AER. In the same specimen, m1 and m2 possess typical AER. The ratio of presence of AER in p4, m1, and m2 is 25%, 25%, and 37.5%, respectively and 29.2% in total teeth (Table 1). The thin enamel band on the lingual face near the antero-lingual corner of the talonid in p4–m2 is present in about half of the specimens (e.g., Fig. 5B), while it is not present in other specimens (e.g., Fig. 5A,C). Its length in occlusal view varies among the specimens, and it is continuous with the enamel on the posterior face of the tooth in two specimens (e.g., m2 of V 15328.2). The m3 is similar to the previous two species in general, but the talonid of one specimen (Fig. 5B) possesses enamel around its circumference, although it thins on lingual and anterior faces.

Two specimens (V 15329.1 and 2) are the only known skull elements from the Tiesiju locality. It is very difficult to determine them as adult or subadult. Compared to the subadult specimens of Xindong locality (= *Pl. dajushanensis*), the specimens from Tiesiju are slightly larger than the largest subadult individual of *Pl. dajushanensis* for most measurements (except for the minimum length of the palatal bridge; see below), and some measurements of cheek teeth may be even larger than the smallest adult individual of *Pl. dajushanensis*. If one considers the slightly larger size of the lower dentition in *Pl. anhuiensis* than *Pl. dajushanensis*, these two skulls may be considered to represent large subadults, but they can also be considered to be among the smallest adults.

In either case, size relative to other species may be discussed. The length/width ratio of palatal bridge is 0.626 on average, and the ratio between the length of palatal bridge and length of P2–M3 alveoli is 0.402 on average, both of which are clearly smaller than *Pl. dajushanensis* and are smallest among three species of *Pliopentalagus* from Huainan area (Table 4). The anterior edge of the palatal bridge is lingual to the posterior face of P2, while the posterior edge is lingual to the border between P4 and M1. Thus, the length of the palatal bridge in *Pl. anhuiensis* is shorter than *Pl. dajushanensis*.

Other than the smaller size, both upper incisors (I2 and I3) are very similar to those of *Pl. dajushanensis* in morphology, and nothing can be added in descriptive terms. P2 has 3 reentrants as in other species, but EAR and IAR are very shallow, and MAR is shallower than other species and has no enamel crenulations. Although not described above, these characters

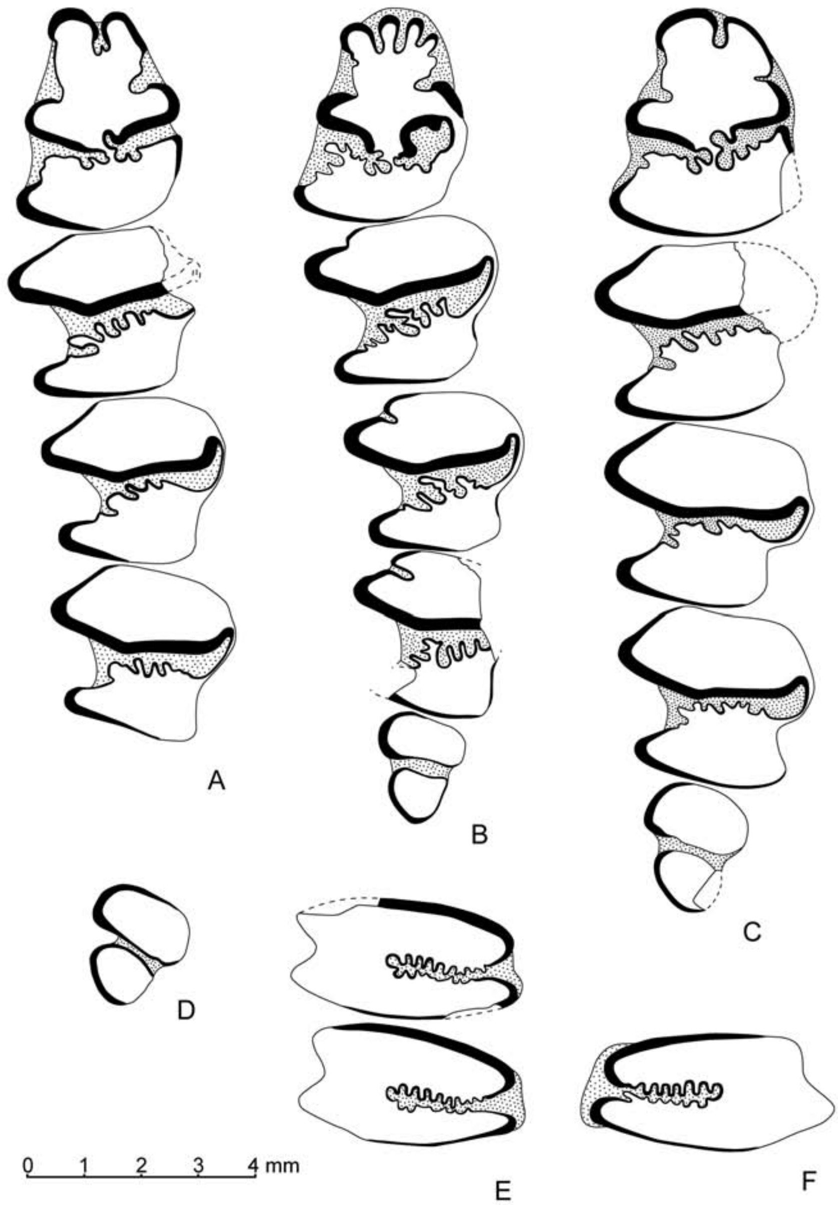

Fig. 5 Diagrams of the occlusal surfaces of lower and upper cheek teeth in *Pliopentalagus anhuiensis* sp. nov.
A. left p3–m2 (holotype, V 15328.1); B. left p3–m3 (V 15328.3); C. left p3–m3 (V 15328.6); D. left m3 (V 15328.4); E. right P4–M1 (V 15329.2); F. left P3 (V 15329.2)

can be observed in subadult specimens of *Pl. dajushanensis*. In P3–M2, their general morphology is also similar to those of the above two species, but the depth of internal reentrant fold is shallower (about 55% ~60% of the tooth width; Fig. 5E,F) and the enamel crenulations of both anterior and posterior walls are shallower than in *Pl. dajushanensis*. Again, this character can be observed in subadult specimens of *Pl. dajushanensis*. Thus, as discussed above, these two skull specimens may be larger subadults.

5 Comparisons

Although *Pl. moldaviensis* (Gureev & Konkova, 1964) is the genotype, it is one of the most poorly known species of the genus. The differences between the genotype and *Pl. dietrichi* (Fejfar, 1961) are not clear, and probably they could be synonymized as Daxner and Fejfar (1967) pointed out, but this is beyond the scope of this paper. In any case, *Pl. moldaviensis* and *Pl. dietrichi* can be distinguished from the three Anhui species described above by having p3 with open PIR (no EL) and p4–m2 without AER; that is, among the specimens of *Pl. dietrichi*, all seven p3s have open PIR, while none of all 24 p4–m2 has AER (Fejfar, 1961; Daxner and Fejfar, 1967). *Pl. progressivus* (Liu and Zheng, 1997) is distinguished from other species of the genus by its largest size (especially in width) and more rounded outline of p3 in occlusal view. *Pl. agilis* (Russell and Harris, 1986) is easily distinguished from other species by its smallest size, but otherwise is similar to *Pl. huainanensis* in general morphology of the dentition, except that the ratio of AER in p4–m2 is only about 11% (Tomida and Jin, 2004). Although a revision of *Pl. agilis* will be published elsewhere, it should be noted that the length/width (at the position of P3) ratio of the palatal bridge in *Pl. agilis* is about 0.95 (measured on fig. 2D of Russell and Harris, 1986), which is larger than *Pl. huainanensis* and is close to *Pentalagus furnessi* (Table 4).

Both *Pronolagus* and *Bunolagus*, living in Africa, have p3 with all five reentrants, but they (except for *Pr. crassicaudatus*) can easily be distinguished from *Pliopentalagus* by having p3–m2 without enamel crenulations in all reentrants. *Pr. crassicaudatus*, however, has p3–m2 with enamel crenulations and p4–m2 with AER in some specimens, which are similar condition in *Pliopentalagus*. However, the former has p3–m2 and P3–M2 with two thick enamel bands nearly crossing the tooth width in each tooth (unlike the latter), and the trigonid and talonid are nearly equal in width in p4–m2 in the former (the trigonid is clearly wider than talonid in the latter). In addition, the former is classified in the genus *Pronolagus* with two other species, based on a number of shared cranial and mandibular characters, which do not appear in *Pliopentalagus* (Tomida and Jin, 2007). Thus, the characters seen in *Pr. crassicaudatus* similar to *Pliopentalagus* (enamel crenulations in p3–m2 and AER in some of p4–m2) should be considered to have evolved independently.

If one considers the extended posterior external reentrant in p3 (*Lepus* type) as the joining of PER and EL, then *Poelagus* (living in Africa), *Caprolagus* (living in South Asia), and "*Pliosiwalagus*" (Patnaik, 2001) can be considered to have 5 reentrants in p3. Because of that fact, they may be related in some way to *Pliopentalagus*, but they can be distinguished from *Pliopentalagus* by that confluence itself. Lopez-Martinez et al. (2007) classifies the 3 genera in Leporinae, and *Pliopentalagus* in Paleolaginae. Either this feature is not an indication of relationship, or the concept of leporid subfamilies may need review.

6 Discussion

Among *Pl. huainanensis*, *Pl. dajushanensis*, and *Pl. anhuiensis*, the variations in size, measurements of various parts, complication of enamel crenulations, and some other characters overlap each other, and therefore, a single mandibular specimen, may be difficult to identify at the species level. But, if the specimens from each locality are treated statistically as populations, those three species can be distinguished by average size, the ratio of EL in p3, ratio of AER in p4–m2, ratio of thin enamel band on the lingual face of the talonid in p4–m2, and relative length of the palatal bridge. Further, when they are arranged by geologic age, it becomes obvious that the average size increases, the ratio of EL in p3 decreases, the ratio of AER in p4–m2 decreases (Table 1), the ratio of thin enamel band on the lingual face of the talonid in p4–m2 decreases (100% → ca 75% → ca 50%, as described above), and the relative length of the palatal bridge decreases (Table 4). Thus, these three species can be interpreted to represent a gradually evolving sympatric lineage, from the late Late Miocene to Late Pliocene.

Comparing these three species of *Pliopentalagus* with *Pentalagus furnessi* (living in Japan), it seems that the size of the cheek teeth becomes larger gradually, crenulations of all reentrant angles in p3 become more complicated, the ratio of EL in p3 becomes smaller (100% → 84% → 33% → 18%), and the ratio of AER in p4–m2 decreases (70% → 65% → 30% → 0%) (Table 1). Thus, as Tomida and Jin (2002, 2004) pointed out, it seems that three species of *Pliopentalagus* continuously and gradually evolve to *Pentalagus furnessi*. However, the length of the palatal bridge (both absolutely and relatively) contradicts the tendency of the above characters; that is, the length of palatal bridge becomes shorter in the younger species among three species of *Pliopentalagus* from Anhui Province, but it is even longer in *Pentalagus furnessi* than the oldest species of *Pliopentalagus*. Furthermore, there is a clear gap in the degree of the depth of enamel crenulations (undulations) in p4–m2 and in P3–M2 between *Pl. anhuiensis* and *Pentalagus furnessi*. Therefore, it can be pointed out that the phylogenetic relationship between *Pliopentalagus* and *Pentalagus* may not be so simple.

Acknowledgements Special thanks are due to Zhang Zhao-Qun and Li Chuan-Kui of Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) for their constructive reviews and useful comments on the manuscript. We thank Lawrence J. Flynn of Harvard University for his comments and English correction of early version of the manuscript. We are grateful to the staffs of excavations carried out by IVPP, the Museum of Auhui Province, and the Cultural Relic and Archaeology Institute of Anhui Province for their efforts in collecting and preparing fossils. We are also grateful to Paula Jenkins, Daphne Hills, and Louise Tomsett of the Department of Mammalogy, the Natural History Museum in London, and Shinichiro Kawada of the Department of Zoology, the National Museum of Nature and Science in Tokyo, for their courtesies and help when YT collected data on the specimens under their care. We gratefully acknowledge Oldrich Fejfar for his translation of Russian paper, Keiko Nagai for her translation of German papers, and Yuri Kimura and Sho Yamamoto for their skill of illustrations (Figures 2 to 5).

References

Averianov A, Abramov A V, Tikhonov A N, 2000. A new species of *Nesolagus* (Lagomorpha, Leporidae) from Vietnam with osteological description. Contrib Zool Inst St Petersburg, **3**: 1–22

Cai B Q(蔡保全), 1989. Fossil lagomorphs from the Late Pliocene of Yangyuan and Yuxian, Hebei. Vert PalAsiat(古脊椎动物学报), **27**(3): 170–181(in Chinese with English summary)

Daxner G, Fejfar O, 1967. Uber die Gattungen *Alilepus* Dice, 1931 und *Pliopentalagus* Gureev, 1964 (Lagomorpha, Mammalia). Ann Naturhist Mus Wien, **71**: 37–55

Fejfar O, 1961. Die Plio-Pleistozanen Wirbeltierfaunen von Hajnacka und Ivanovce (Slowakei), CSR. III. Lagomorpha. Neues Jahrb Geol Paläont, Monatsh, **112**(5): 267–282

Fejfar O, Heinrich W-D, Lindsay E H, 1997. Updating the European Neogene rodent biostratigraphy. Mem Trav RPHE, Inst Montpellier, **21**: 563–565

Gureev A A, 1964. Fauna of the USSR. Mammals, vol. 3, issue 10. Lagomorpha. Akad Nauk SSSR, Zool Inst, Nov Ser, **87**: 1–276(in Russian)

Jin C Z(金昌柱), 2004. Fossil leporids (Mammalia, Lagomorpha) from Huainan, Anhui, China. Vert PalAsiat(古脊椎动物学报), **42**(3): 230–245(in Chinese with English summary)

Jin C Z, Kawamura Y, Taruno H, 1999. Pliocene and early Pleistocene insectivore and rodent faunas from Dajushan, Qipanshan and Haimao in North China and the reconstruction of the faunal succession from the Late Miocene to Middle Pleistocene. J Geosci Osaka City Univ, **42**(1): 1–19

Jin C Z, Zhang Y Q, 2005. First discovery of *Promimomys* (Arvicolidae) in East Asia. Chin Sci Bull, **50**(1): 1–6

Liu L(刘丽萍), Zheng S H(郑绍华), 1997. Note on the Late Cenozoic lagomorphs of Danjiang Reservoir area in Hubei and Henan. Vert PalAsiat(古脊椎动物学报), **35**(2): 130–144(in Chinese with English summary)

Lopez-Martinez N, Likius A, Mackaye H T et al., 2007. A new lagomorph from the Late Miocene of Chad (Central Africa). Rev Espan Paleont, **22**(1): 1–20

Patnaik R, 2001. Late Pliocene micromammals from Tatrot Formation (Upper Siwaliks) exposed near Village Saketi, Himachal Pradesh, India. Palaeontogr Abt A, **261**: 55–81

Qiu Z D(邱铸鼎), Wang X M(王晓鸣), Li Q(李强), 2006. Faunal succession and biochronology of the Miocene through Pliocene in Nei Mongol (Inner Mongolia). Vert PalAsiat(古脊椎动物学报), **44**(2): 164–181

Russell B D, Harris A H, 1986. A new leporine (Lagomorpha: Leporidae) from Wisconsinan deposits of the Chihuahuan Desert. J Mammal, **67**(4): 632–639

Tomida Y, Jin C Z, 2002. Morphological evolution of the Genus *Pliopentalagus* based on the fossil material from Anhui Province, China: a preliminary study. Nat Sci Mus Monogr, **22**: 97–107

Tomida Y, Jin C Z, 2004. *Aztlanolagus* (Lagomorpha, Mammalia) revisited: origin, migration, evolution, and taxonomy. J Vert Paleont, 24(3 Suppl): 121A

Tomida Y, Jin C Z(金昌柱), 2005. Reconsideration of the generic assignment of "*Pliopentalagus nihewanensis*" from the Late Pliocene of Hebei, China. Vert PalAsiat(古脊椎动物学报), **43**(4): 297–303

Tomida Y, Jin C Z, 2007. Extant African leporids, *Caprolagus* and *Pentalagus* revisited: paleontological views on dental and cranial characters. J Vert Paleont, **27**(3 Suppl): 158A

Tseng Z J(曾志杰), Jin C Z(金昌柱), Liu J Y(刘金毅) et al., 2008. Fossil Hyaenidae (Mammalia: Carnivora) from Huainan, Anhui Province, China. Vert PalAsiat(古脊椎动物学报), **46**(2): 133–146

White J A, Morgan N H, 1995. The Leporidae (Mammalia, Lagomorpha) from the Blancan (Pliocene) Taunton Local Fauna of Washington. J Vert Paleont, **15**(2): 366–374

Wu W Y, 1991. The Neogene mammalian faunas of Ertemte and Harr Obo in Inner Mongollia (Nei Mongol), China. –9. Hamsters: Cricetidae (Rodentia). Senckenbergiana lethaea, **71**(3/4): 257–305

Zheng S H(郑绍华), 1984. A new species of *Kowalskia* (Rodentia, Mammalia) of Yinan, Shandong. Vert PalAsiat(古脊椎动物学报), **22**(4): 251–260(in Chinese with English summary)