

# 内蒙古依和苏布晚始新世兔形类<sup>1)</sup>

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**摘要:** 记述了内蒙古自治区脑木根乡附近依和苏布地点产出的 4 种兔形类上下颊齿化石。依和苏布位于脑木根乡东南约 18 km 处, 乌兰希热平台北缘, 地理坐标为 N42°36.114', E111°34.596'。依据化石组合, 该点地层年代初步定为晚始新世。4 种兔形类分别是: *Gobiolagus major*, *Hypsimylus yihesubuensis* sp. nov., *Desmatolagus* cf. *D. vetustus* 以及 *Desmatolagus* sp.。

新发现的 *Gobiolagus major* 下颊齿和该种产自沙拉木伦地区乌兰戈楚层的正型标本 (AMNH 26098) 在大小和形态上很相似: 齿冠较低, 侧沟不伸入齿槽, 三角座唇侧较舌侧短; m2 跟座明显大于 m1 跟座; 舌侧有釉质脊连接三角座和跟座。根据个体大小和相对低冠的颊齿, 我们将一块带 P3 ~ M2 的上颌骨归入 *Gobiolagus major*, 成为该种上臼齿的首次记录。上颌骨腭面门齿孔后缘与 P3 前缘齐, 硬腭后缘止于 M1 与 M2 间位置, 无前臼齿孔。P3 ~ M2 均具三齿根, 唇侧两齿根小。P4 非臼齿化, 前后脊完全, 封闭 V 形新月谷。M1 嚼面椭圆状, 舌侧内沟短浅。后脊与舌侧的磨蚀面相连, 其前方的横向谷应为三角座凹。前、后脊唇侧端应分别相当于前、后尖。

*Hypsimylus yihesubuensis* sp. nov. 是继北京长辛店北京种后该属的第 2 个记录。新种较 *H. beijingensis* 大, 齿冠较低, m1 较宽。下颊齿高冠, p4 臼齿化, 稍高于臼齿。下颊齿具有明显的三叶结构, 由下次小尖形成的第三叶强。外侧沟伸入齿槽。依据个体大小, 将一带有 P2 ~ 4 的上颌骨归入该种。上颊齿相对低冠, P2 单根, 齿冠两叶, P3 ~ 4 具三根, P4 显著大于 P3。与北美的 *Megalagus* 标本比较表明这类具高冠齿的动物是一种兔形类, 而不是建属时认为的宽臼齿兽类。其下颊齿明显的第三叶结构是年轻个体的属性。

归入 *Desmatolagus* cf. *D. vetustus* 的标本与 *Desmatolagus vetustus* 的正型相似, 但其个体稍小, 下跟座后缘直与后者不同。*Desmatolagus vetustus* 仍被认为是链兔属最为原始的成员, 它与其他种的差别是具有较多的原始特征, 如颊齿相对低冠、跟座无后褶、无前臼齿孔等。

**关键词:** 内蒙古依和苏布, 晚始新世, 兔形类

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## LAGOMORPHS FROM THE YIHESUBULATE EOCENE OF NEI MONGOL (INNER MONGOLIA)

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**Abstract** Four lagomorphs, *Gobiolagus major*, *Hypsimylus yihesubuensis* sp. nov., *Desmatolagus* cf.

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*D. vetustus*, and *Desmatolagus* sp. from a new late Eocene locality, Yihesubu, Nei Mongol, are described. Upper dental morphology of *Gobiolagus major* is known for the first time. *Hypsimylus yihesubuensis* sp. nov. helps to demonstrate this genus a lagomorph, not a eurymylid. The taxonomic position of *D. vetustus*, the most primitive species of *Desmatolagus*, is reconsidered.

**Key words** Yihesubu, Nei Mongol, Late Eocene, Lagomorph

## 1 Introduction

Early Tertiary lagomorphs, such as *Lushilagus*, *Shamolagus*, *Gobiolagus*, *Desmatolagus* and *Ordolagus*, are common in Asia and represent a main body of evidence for origin and early radiation of the group. Since the report of the Paleogene lagomorphs (Matthew and Granger, 1923), many studies have documented the rich fossil records from the region (Teilhard, 1926; Burke, 1941; Bohlin, 1942; Li, 1965; Sych, 1975; de Muizon, 1977; Huang, 1986, 1987; Tong and Lei, 1987; Qi, 1988; Tong, 1997; Erbajeva, 1999; Meng et al., 1999; Zhang et al., 2001). These taxa are usually considered the basal lagomorphs and are important in understanding the origin and systematics of Lagomorpha (McKenna, 1982). These species are also useful in early Tertiary biostratigraphic divisions and correlations because of their distinctive morphologies and restricted geological distributions (Huang, 1987; Tong et al., 1995; Wang, 1997; Erbajeva and Tyutkova, 1997).

Here we report new material of *Gobiolagus*, *Hypsimylus* and *Desmatolagus* from the locality Yihesubu, Nei Mongol, China. Fossil mammals from the locality were first found in 1992 by Meng Jin. Additional specimens were collected by Meng Jin, Hu Yaoming and Ye Jie in 2000. These new specimens cast new light on the morphology of *Gobiolagus* and *Desmatolagus* and help to illuminate the taxonomic position of *Hypsimylus beijingensis* (Zhai, 1977), a genus and species previously considered a eurymylid.

All specimens reported here are collected from the locality Yihesubu (N42°36.114'; E111°34.596'), about 18 kilometers southeast to the Nomogen village. This locality is at the north rim of the Ulan Shireh platform and is the east extension of the Erden Obo cliff. Other taxa collected from the same locality are preliminarily identified as *Ardynomys* sp., *Pseudocylindrodon* sp., *Lophiomyx* sp., and ? *Ardynia* sp. The fauna is probably late Eocene in age. The specimens are housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing. Specimens compared are mainly from the collections of the American Museum of Natural History (AMNH), New York. We follow Wood (1940) for most of the terminology of the lagomorph dental morphology, and note the inconsistency in terminology used for cheek teeth of lagomorphs. Taxonomy of lagomorphs follows McKenna and Bell (1997).

## 2 Systematics

### Lagomorpha Brandt, 1855

#### Leporidae Fischer de Waldheim, 1817

##### Gobiolagus Burke, 1941

##### *Gobiolagus major* Burke, 1941

**Referred specimens** V 14134, a fragmentary right maxilla with P3 ~ M2; V 14135, a fragmentary right mandible with p4 ~ m2 (Fig. 1).

**Description** The p4 ~ m2 are preserved in the right mandible (V 14135) and increase in size posteriorly (Fig. 1; tooth measurements are in Table 1 ~ 2). The morphologies of the lower cheek teeth are similar to those of the type specimen (AMNH 26098). The lingual surfaces of the teeth are worn in preservation but the tooth morphology is well-preserved. The cheek teeth are semi-hypsodont (or unilaterally hypsodonty of Burke [1941]) and rooted. The hypostridium does not extend into the

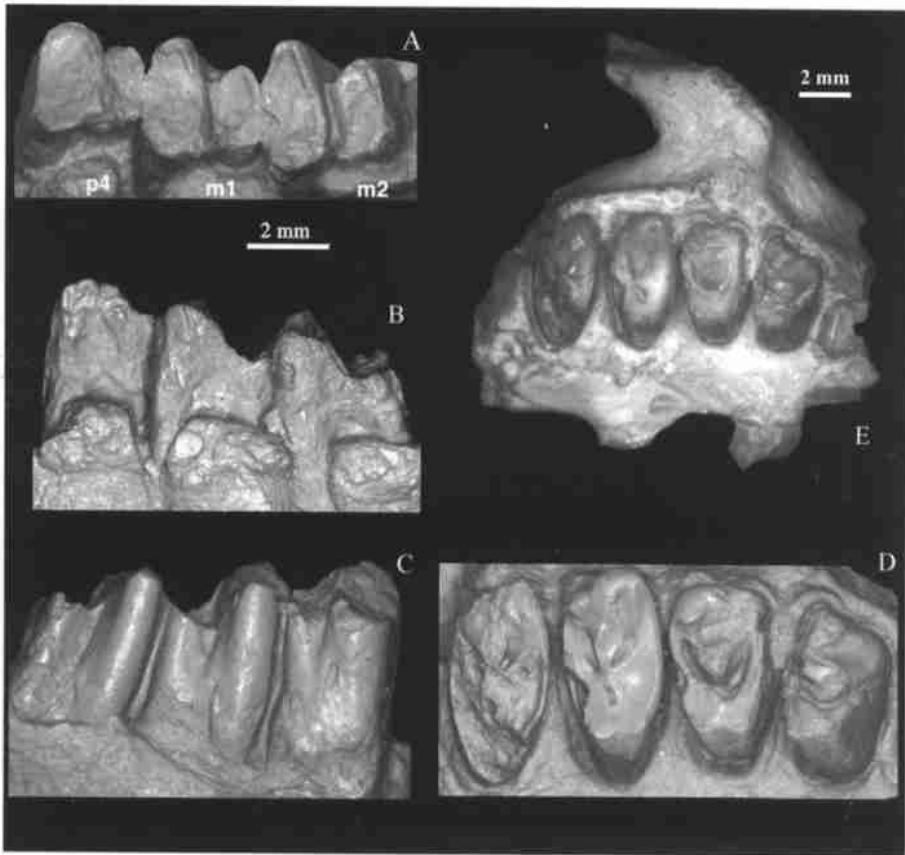


Fig. 1 Upper and lower dentition of *Gobiolaagus major* from late Eocene Yihesubu locality of Nei Mongol, China  
 A ~ C. occlusal, medial and lateral views of right p4~m2 (V 14135); D. occlusal view of right P3~M2  
 (V 14134); E. the maxilla with cheek teeth (V 14134)

alveolus. The trigonid of each cheek tooth is shorter labially than lingually. The posterior wall of the trigonid is formed by thick enamel and does not have a posterior projection. The talonid of p4 is the smallest. The talonid of m2 is significantly larger than that of m1. At the lingual side of each tooth, a nearly vertical enamel ridge connects the posterolingual corner of the trigonid with the anterolingual corner of the talonid. This ridge is a retained portion of the worn talonid. The lateral contour of the talonid is rounded and the enamel thins toward the hypotriid.

The maxilla (V 14134) is considered from the same species because of the unilateral hypsodont teeth that match the lower teeth in size (Fig. 1). All teeth are damaged at various degrees. The zygomatic process is strong, with its posterior margin being lateral to M1. A ventral process is present at the anterior base of the zygoma. Anteromedial to the process is a shallow anteorbital fossa. The ventral portion of the infraorbital foramen is lateral to the alveolus of P2 and has an estimated diameter of 2 mm. From the orbit to the facial region, the infraorbital canal extends anteroventrally. The floor of the orbit is domed and its surface is uneven; ends of cheek teeth roots are exposed. On the ventral side of the palate, the posterior margin of the incisive foramen levels with the anterior edge of P3, and the posterior border of the palate is between M1 and M2. A distinct palatine foramen is medial to the anterior portion of M1 and is located completely within the palatine. There is no premolar foramen.

P2 is not preserved, but the alveolus shows that it has a single root and is not so reduced as in *Desmatolagus*. P3 ~ M2 are rooted, with two small labial roots and a major lingual one. These teeth are unilaterally hypsodont - the lingual crown is much higher than the labial one. The lingual cusp is the largest of three cusps on P3. It has a flat lingual surface and lacks the hypostria. Therefore, the lingual cusp is either a large protocone or a combination of protocone and hypocone, according to Wood (1940). The anteroloph is low and extends to the anterolabial side of the tooth. The posterior crest is strong and extends to the posterior side of the central cusp, but its distal portion was broken. The crescentic valley is shallow, narrow, and in an open V-shape. The central cusp is large; its posterior part was broken. It has an inclined lateral surface and is separated from the labial cusp by a shallow fold that opens anteriorly. The labial cusp is the smallest and lowest one of the tooth.

The lingual surface of P4 is concave, suggesting a shallow hypostria that marks the division of the lingual cusp. The anteroloph and the posterior crest are complete, reaching the anterolabial and posterolabial side of the tooth, respectively. They confine a deep V-shaped crescentic valley. As in the molars, the enamel forming the anteroloph is much thicker than that of the posterior crest. The central cusp is triangular. Its anterolingual and posterolingual surfaces are steep and covered with thin enamel. Its lingual surface is a flat, slope area. Anterolabially, the central cusp sends a low ridge to a small cusp at the anterolabial corner of the tooth. Posterolabially, the central cusp connects with a large posterolabial cusp by a short crest. The lateral surface of the posterolabial cusp is rounded.

M1 is oval in occlusal view (Fig. 1). A shallow hypostria is between the protocone and hypocone on the lingual surface. The lingual outlines of the protocone and hypocone are roughly equal in size, with the hypocone being more lingually positioned. On the occlusal surface, however, the protocone is larger than the hypocone. The lingual half of the crown is a large wear surface, which consists of a large anterior portion and a small posterior portion, separated by a comma shaped fossette of which the tail points posterolabially. The anterior portion of the wear surface is concave and continues laterally as the anteroloph that forms a strong shearing edge walled with thick enamel. The comma shape fossette is presumably the labial portion of a groove that continues with the hypostria. With wear the lingual portion is gone. The inner surface of the fossette is covered with thin enamel. Lateral to the fossette, a widening of the metaloph indicates a transversely elongated metaconule; the metaloph connects lingually with the lingual occlusal surface. Because of the connection, a V-shaped crescentic valley is not formed; instead, two valleys are on the labial half of the tooth. The anterior valley is in reversed L-shape and covered with enamel, which we believe is homologous with the trigon basin of a tribosphenic tooth. The posterior valley is between the metaloph and posteroloph and is narrower and lower than the anterior one. On the labial margin, the ends of the anteroloph and metaloph are homologous with the paracone and metacone, respectively. These cusps are in the form of transverse ridges and fused labially to form the rounded surface of the tooth. The posteroloph that extends from the hypocone ends labially as a small cuspule. M2 was broken, but its general shape is similar to that of M1. M3 is not preserved, but the anterior portion of the alveolus suggests that the reduction of the tooth is moderate.

#### *Hypsimylus* Zhai, 1977

##### *Hypsimylus yihesubuensis* sp. nov.

**Holotype** A fragmentary right lower jaw with erupting p4 and m1 ~ 2 (V 14136) (Fig. 2).

**Referred specimens** V 14137, an isolated right m2; V 14138, a fragmentary right maxilla with P2 ~ 4 (Fig. 2).

**Etymology** Specific name after the locality name.

**Diagnosis** Differs from *H. beijingensis* in being larger and having lower crown and wider m1.

**Description** At the talonid of m1 the mandible measures 9.8 mm deep and 5.6 mm thick

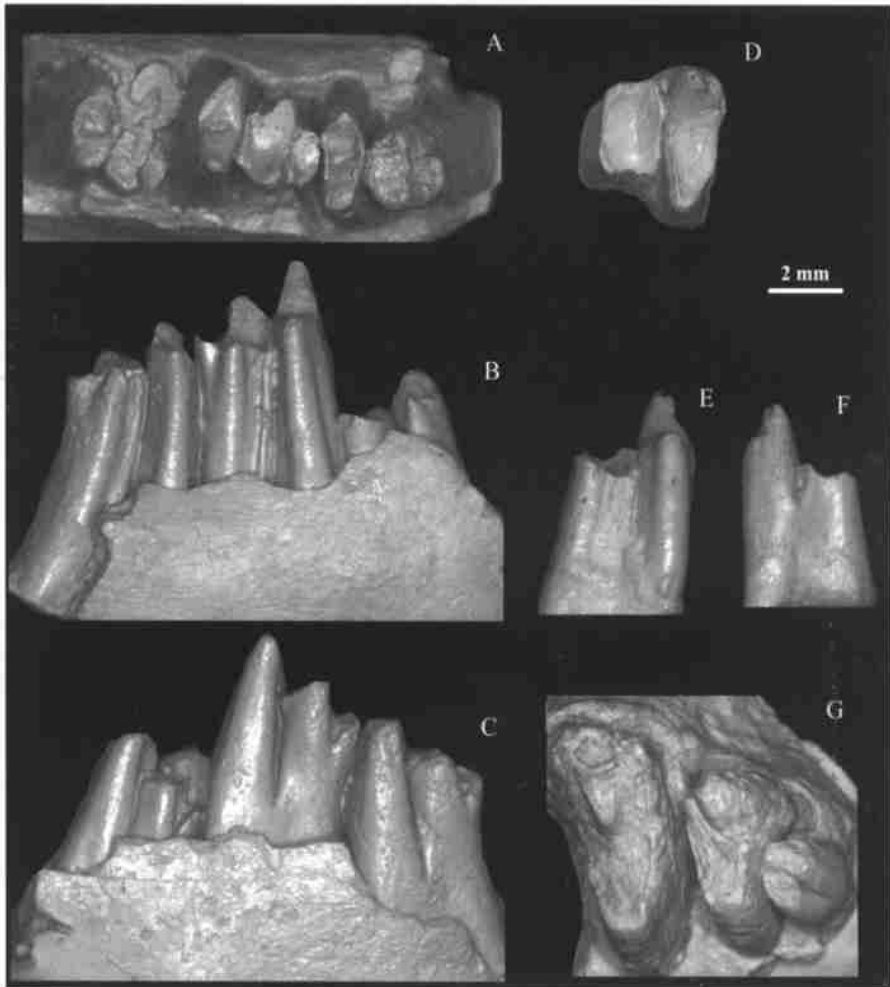


Fig. 2 Teeth of *Hypsimylus yihesubensis* sp. nov. from late Eocene Yihe sublocality of Nei Mongol, China  
A ~ C. occlusal, lateral and medial views of right p4 ~ m2 (V 14136, holotype); D ~ F. occlusal, lateral and  
medial views of a right m2 (V 14137); G. occlusal view of right P2 ~ P4 (V 14138)

(tooth measurements are in Table 1 ~ 2). A mental foramen is below the talonid of p4 on the lateral side of the mandible. One small hole anterior to the foramen and two similar ones on the medial surface of the mandible are probably tooth marks. The masseteric fossa terminates as a blunt knot at the level of the m2 trigonid. The incisor is not preserved, but the posterior end of the alveolus exposed on the lingual surface of the mandible reveals that the incisor extends posteriorly medial to the roots of p4 and m1 and ends at the level of the m1 trigonid.

The lower jaw is from a young individual (Fig. 2). A fragment of the dp4 posterior root is preserved on the lateral side of the erupting p4. The p4 crown is mostly within the mandible, but owing to breakage of the bone the morphology of the tooth is visible. The p4 is molariform and appears to have a higher crown than those of m1 and m2. Nonetheless, the morphologies of these teeth are quite uniform; thus, our description is focused on m1. The tooth is high-crowned and has strong roots - this is uncertain for p4 that is not fully developed. The lingual side of the tooth crown is lower than the labial one. The tooth is broad at crown base and tapers dorsally. After wear, the lingual

part of the trigonid (the metaconid) becomes pointed and is higher than the labial portion (the protoconid). The trigonid is higher but much shorter than the talonid; the latter is characterized by presence of a distinct third lobe, formed by the hypoconulid. Thus, the tooth is trilobate in crown view. On the lateral side of the tooth, the hypostriid, the vertical groove between the protoconid and hypoconid, is wide. The hypostriid extends into the alveolus. Within the hypostriid, several minute enamel ridges run parallel to the columns formed by the protoconid and hypoconid. On the lingual side of the tooth, the internal groove between the columns formed by the metaconid and entoconid is narrow and short; it does not extend into the alveolus. As shown in the lateral or medial view of the tooth, the third lobe flares posterodorsally. A narrow and short groove on the lateral and medial side separates the third lobe from the rest of the talonid, respectively. In crown view, the talonid is about twice the length of the trigonid on V 14136, but this proportion will be changed when the tooth crown gets worn. The talonid is still longer than the trigonid in deeper worn lower tooth (V 14137). The m2 differs from m1 in being more anteriorly inclined and having a slightly shorter crown.

The m2 (V 14137) is associated with the species because of the similar size and comparable morphology. It is larger than *Gobiolagus major*. As in the type specimen, it has a broad hypostriid within which small enamel ridges are present. The talonid of the m2 is rectangular and, although considerably worn, the trigonid and talonid are separated. The talonid is rectangular, wider than long, with the thickest enamel at the posterolateral corner of the tooth.

The maxilla with P2 ~ 4 (V 14138) are associated with V 14136 because of its large size, which is considerably larger than those assigned to *Gobiolagus major*. The posterior edge of the anterior zygomatic root levels with the anterior part of M1. Although the specimen is poorly preserved, the structure of P2 shows that these teeth have not been deeply worn during life; thus the large size of these teeth is not resulted from wear. In addition, the upper teeth are relatively low-crowned, which is consistent with the lower teeth assigned to the same species. The P2 has one root. The crown is bud-like, divided by a narrow groove that extends anteroposteriorly. Thus, the P2 has only two lobes, with the labial lobe larger than lingual one (Fig. 2). A bilobate P2 differs this specimen from the trilobate P2 of North American and Asian early Tertiary lagomorph species where P2 is known (Wood, 1940; Burke, 1941; Li, 1965; Sych, 1975; Huang, 1986, 1987; Tong, 1997). The P3 has one large lingual and two small labial roots. The protocone is anteroposteriorly compressed and lingually extended, and shows no hypostria. The central cusp is relatively lateral compared to that in other early Tertiary lagomorphs. The posterolateral corner of P3 was broken. P4 is much larger than P3 and has three roots. Similar to P3, the protocone of P4 is also anteroposteriorly short but lingually extended. The central cusp is distinct at its lingual side and fades away labially. The labial valley is broad. The outline of either P3 or P4, particularly P3, is more similar to that of the typical tribosphenic therian tooth pattern. In contrast, the P3 and P4 in other early lagomorphs usually have an oval contour. The hypostria is absent on P3 and P4. The lingual root of P4 is so curved that the tip of the root points labially. A similar condition is also true for P3. The M1 alveolus shows that M1 is slightly wider than P4 and has two reduced labial roots and a large lingual one.

### **Ochotonidae Thomas, 1897**

*Desmatolagus* **Matthew et Granger, 1923**

*Desmatolagus* cf. *D. vetustus* **Burke, 1941**

**Referred specimens** V 14139. 1, a fragmentary right mandible with p3 ~ m2 (Fig. 3); V 14139. 2, a fragmentary right mandible with broken p4 ~ m2; V 14139. 3, a fragmentary left mandible with m1 ~ m2; V 14139. 4, an isolated right m2; V 14140. 1, a fragmentary right maxilla with P3 ~ M2; V 14140. 2, a fragmentary right maxilla with P3 ~ M2; V 14141, a fragmentary right maxilla with P4 ~ M2; V 14142. 1, a fragmentary right maxilla with P3 ~ M2; V 14142. 2, a fragmentary right maxilla with P3 ~ M2; V 14142. 3, a fragmentary left maxilla with P3 ~ M2; V

14142.4, an right P4 (or M1) (Figs. 3, 4).

**Description** The incisor alveolus indicates that the incisor extends posteriorly to the trigonid of m2. The mandible is 6 mm deep and 3 mm thick at the position of m1. The p3 is single-rooted (Fig. 3; tooth measurements in Table 1 ~ 2). The anterior enamel of the tooth crown was worn in preservation, but it is still recognizable that the tooth is only lightly worn from mastication, suggesting that the specimen is not from an old individual. The low crown has a lateral fold that does not enter the alveolus. The p4 is molariform and the highest lower cheek tooth. The occlusal dimensions of teeth increase whereas the tooth height decreases posteriorly from p4 to m2. The morphology of p4 and m1 ~ 2 are similar. The trigonid is wide and has a thick layer of enamel on its posterior wall. A spike at the midpoint of the posterior wall, which is most distinct on p4, projects posteriorly. The talonid is narrow and positioned on the posterolingual side of the trigonid. The posterior portion of the talonid is worn at a greater degree than the anterior edge, so that a thin wall was left about the posterior base of the trigonid. The baseline of the wall is straight, indicating transverse movement of the lower jaw during mastication. The posterior border of the talonid is straight. The posterolabial corner of the talonid projects laterally and bears the thickest enamel of the talonid. The hypostrid is broad and does not enter the alveolus. The m3 is not preserved.

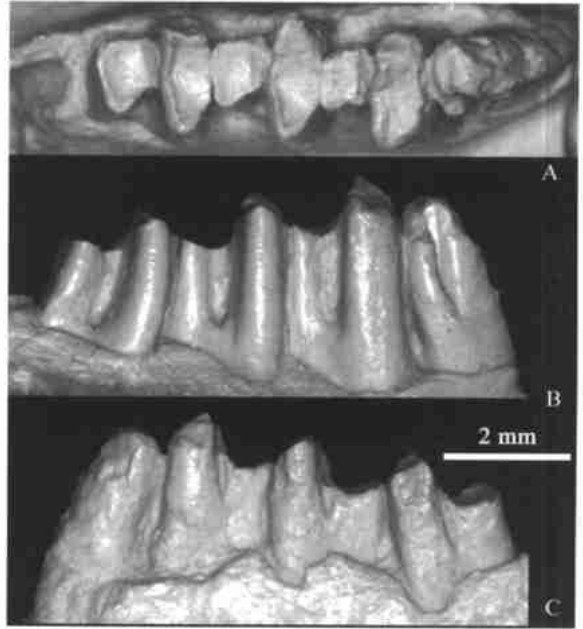


Fig. 3 A ~ C. occlusal, lateral and medial views of right p3 ~ m2 of *Desmatolagus* cf. *D. vetustus* (V 14139. 1) from late Eocene Yihesubu, Nei Mongol

The posterior portion of the talonid is worn at a greater degree than the anterior edge, so that a thin wall was left about the posterior base of the trigonid. The baseline of the wall is straight, indicating transverse movement of the lower jaw during mastication. The posterior border of the talonid is straight. The posterolabial corner of the talonid projects laterally and bears the thickest enamel of the talonid. The hypostrid is broad and does not enter the alveolus. The m3 is not preserved.

**Table 1** Measurements of upper dentitions

(mm)

	<i>Gobiorlagus major</i>	<i>Hypsimylus yihesubensis</i> sp. nov.	<i>Desmatolagus</i> sp.	<i>Desmatolagus</i> cf. <i>D. vetustus</i>							
				V 14140. 1	V 14140. 2	V 14141	V 14142. 1	V 14142. 2	V 14142. 3	V 14142. 4	
P2 L		2. 10									
P2 W		2. 40									
P3 L	2. 47	2. 78	2. 12	1. 61	1. 37			1. 61	1. 57		
P3 W	4. 52	5. 38	4. 56	3. 39	2. 69			3. 81	4. 62		
P4 L	2. 62	2. 85		1. 60	1. 37	1. 54	1. 62	1. 53	1. 58	1. 53	
P4 W	4. 92	8. 28		3. 48	3. 22	4. 50	4. 56	4. 58	5. 42	5. 45	
M1 L	2. 69			1. 53	1. 32	1. 36	1. 53	1. 45	1. 61		
M1 W	5. 65			3. 66	3. 26	4. 52	4. 10	4. 48	4. 82		
M2 L	2. 56			1. 37	1. 25	1. 38	1. 32	1. 33	1. 23		
M2 W	5. 41			3. 35	3. 05	4. 25	3. 47	3. 82	4. 03		

Note: L. length; W. width.

Table 2 Measurements of lower dentitions

(mm)

	<i>Gobiolagus major</i>	<i>Hypsimitylus yihesubuensis</i> sp. nov.		<i>Desmatorlagus</i> sp.	<i>Desmatolagus</i> cf. <i>D. vetustus</i>		
	V 14135	V 14136	V 14137	V 14144	V 14139.1	V 14139.3	V 14139.4
p3 L/ W (tri)					1.42/ ?		
p3 L/ W (tal)					1.34/ ?		
p4 L	2.80	3.33			1.45		
p4 L/ W (tri)	1.81/ 2.91	1.5/ 3.71			0.76/ 2.00		
p4 L/ W (tal)	1.00/ 2.10	1.86/ 2.34			0.75/ 1.10		
m1 L	2.89	3.87			1.68	1.85	
m1 L/ W (tri)	1.77/ 3.32	1.67/ 4.00			0.82/ 2.19	0.92/ 2.07	
m1 L/ W (tal)	1.23/ 2.10	2.22/ 2.91			0.89/ 1.21	0.97/ 1.17	
m2 L	3.12	3.60	3.70	2.95	1.62	1.80	2.46
m2 L/ W (tri)	1.64/ 3.52	1.46/ 3.96	2.05/ 3.96	1.36/ 3.48	0.82/ 2.10	0.89/ 2.14	1.12/ 2.41
m2 L/ W (tal)	1.50/ 2.45	2.15/ 2.60	1.68/ 2.61	1.62/ 2.18	0.85/ 1.35	0.93/ 1.35	1.36/ 1.36

Note: L., length; W., width; tri., triconid; tal., talonid.

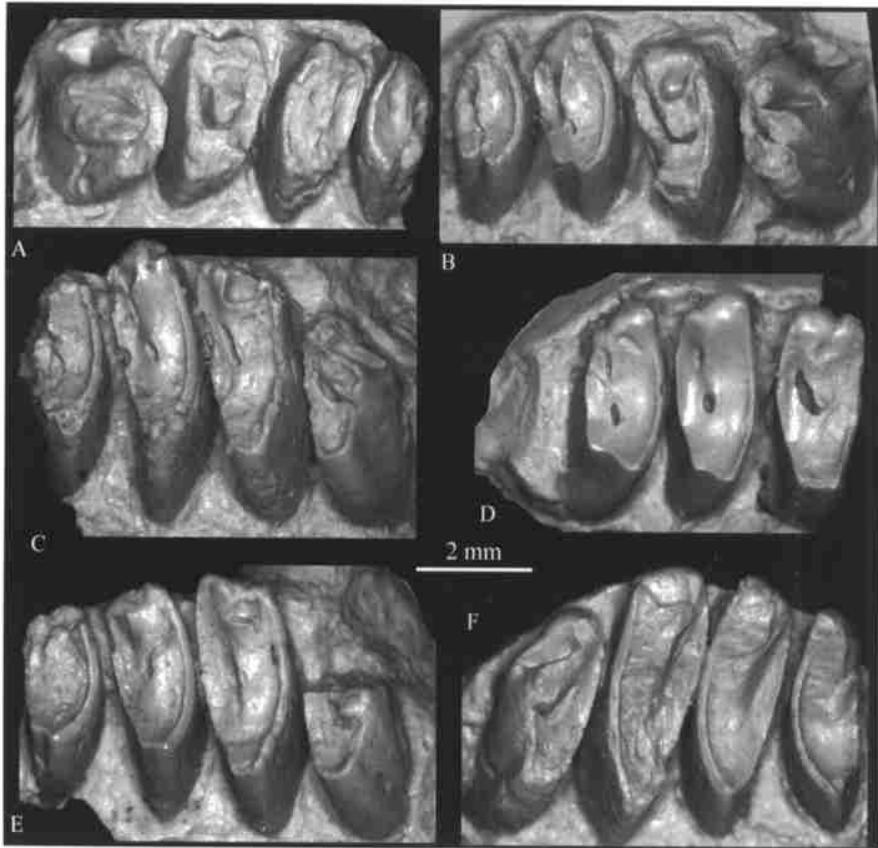


Fig. 4 A~F. occlusal views of upper cheek teeth of *Desmatolagus* cf. *D. vetustus* (V 14140.2, V 14140.1, V 14142.2, V 14141, V 14142.1, V 14142.3) from late Eocene Yihesubu locality, Nei Mongol, ranging roughly from the youngest to oldest



All the maxillas are fragmentary. But from what preserved it is clear that a premolar foramen is absent. Fig. 4A ~ F shows upper cheek teeth roughly ranging from the youngest to oldest. P2 is not preserved. Other cheek tooth has three roots. In unworn P3, the tooth tapers dorsally. The lingual cusp, presumably the protocone, is the largest. There is no hypostria. An anteroloph is absent. The crescentic valley opens anteriorly and extends posterolaterally as a curvature. In worn specimen (Fig. 4F) the valley becomes short and shallow. The central cusp has a vertical anterior surface and gradually becomes narrower posterolaterally. The fold that separates the central cusp and the labial cusp is open and shallow. P4 does not have the hypostria in all specimens. The anteroloph and posteroloph are complete. The central cusp is distinct. The crescentic valley between the cusp and the anteroloph is shallow than the posterior portion separating the posteroloph from the cusp, so that the anterior one is gone first with wear. The external valley is square-shaped, with its posterior side more lingually extended. The posterolabial corner of P4 is more labially extended than the anterolabial one. With wear P4 and molars will become transversely elongated. The elongation is primarily owing to constant growth of the lingual side of the tooth. Therefore the labial structures of the tooth, such as the external valley and the distance from the crescentic valley to the labial margin of the tooth, change very little proportionally.

M1 is similar to P4 in general morphology, but differs from the latter in having its anterolabial corner more labially positioned and in lacking the crescentic valley in any ontogenetic stage of the tooth. In relatively young specimens, a shallow hypostria is present, but in older specimens it is absent - so is the enamel fossette left from the labial portion of the hypostria. Compared to the M1 of *Gobiolagus major* described above, the trigon of M1 in *D. vetustus* is proportionally more shortened. The anterior wall of the tooth is the major shearing edge, equipped with the thickest enamel of the tooth. M2 is narrower than M1, with its posterior half being reduced. M3 is not preserved, but the alveolus indicates a small, single-rooted tooth.

#### Desmatolagus sp.

**Referred specimens** V 14143, a fragmentary left maxilla with damaged P3 ~ 4; V 14144, an isolated right m2 (Fig. 5).

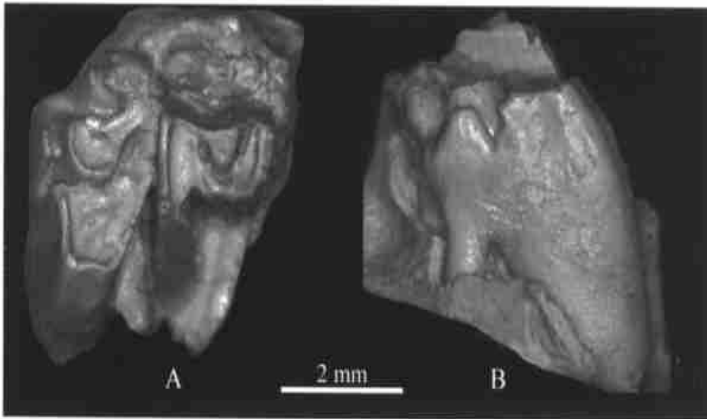


Fig. 5 A ~ B. P3 and broken P4 of *Desmatolagus* sp. (V 14143) from late Eocene Yihesubu, Nei Mongol

**Description** P3 has two labial roots. The lingual cusp has a squared lingual contour. A lower ridge is anterior to the central cusp and is separated from the lingual cusp by a gap (Fig. 5). Because of the existence of the partial loph the tooth is considerably wider labially than lingually. The central cusp is rounded, except at its posterolabial corner where it is connected to a strong poster-

labial cusp by enamel crest. P4 is broken, of which the central portion indicates a complete crescentic valley. The m2 matches the upper teeth in size. Its labial side is significantly higher than the lingual side.

These two specimens are larger than those referred to *Desmatolagus* cf. *D. vetustus* but smaller than those of *Gobiolagus major* and *Hypsimylus*. The size of these specimens is comparable to *D. robustus* and the morphology of P3 is similar to that of *D. robustus*; they differ from *D. robustus*, however, in having relatively lower crown. The fragmentary material does not permit more specific identification.

### 3 Discussion

#### 3.1 *Gobiolagus*

*Gobiolagus* is a leporid genus proposed by Burke (1941) based on specimens collected from Asia. A total of four species were named at the time the genus was established: *G. tolmachovi*, *G. andrewsi*, *G. (?) major*, and *G. (?) teilhardi*. All the type specimens are fragmentary lower jaws and those of *G. (?) major* and *G. (?) teilhardi* are particularly poor. Thus, these two species were named with uncertainty. One of the species, *G. (?) teilhardi*, was relocated to a different genus *Ordolagus* because of its high crown cheek teeth, in which the tooth crown extends into the alveolus (de Muizon, 1977; Huang, 1986). Compared to other early Tertiary lagomorphs, such as *Desmatolagus*, specimens of *Gobiolagus* are relatively rare. Since Burke (1941), possible *Gobiolagus* specimens have been reported from several localities of Asia (Li, 1965; Qi, 1988; Tong, 1997; Erbajeva, 1999; Meng et al., 1999; Zhang et al., 2001), all represented by poor specimens.

Possible upper teeth of *Gobiolagus* (V 3012) were first described from the Shara Murun beds at Ula Usu, Nei Mongol (Li, 1965), but these teeth were considered to belong to the North American *Mytonolagus* (Qi, 1988). Qi (1988) noted presence of the hypostria on the upper molars of Li's specimen, which does not seem consistent with the relatively low-crowned lower cheek teeth of *Gobiolagus*. However, the hypostria on V 3012 is only half of the crown height (Li, 1965) and may be lost with further wear. Qi (1988) considered an upper jaw from the Shara Murun beds, Ula Usu, to be from *G. tolmachovi*. Absence of the hypostria and transverse extension of the upper cheek teeth are the main features by which Qi assigned the specimen to *G. tolmachovi*. However, *Ordolagus teilhardi* has high-crown lower teeth but its upper teeth lack the hypostria (Huang, 1986). In addition, the width of the upper tooth of early lagomorphs is highly related to the degree of wear (Huang, 1986, 1987). The specimen described by Qi (1988) is heavily worn so that its width is at least partly age-related. The association of the upper and lower teeth we proposed here is not certain either, but the coexistence of these specimens in the same locality and their matching size and morphology favors their association. Based on similar maxillary features but smaller size and non-molariform P4 with the maxilla referred to *G. tolmachovi* by Qi (1988), Zhang et al. (2001) named a species, *G. lii*, from the Yuli member of the Heti Formation in Yuanqu, Shanxi Province. The type specimen of this species is a maxilla with P3 ~ M2.

*Gobiolagus major* has been the largest lagomorph of early Tertiary in Asia and is now only smaller than the specimen assigned to *Hypsimylus* (see below). The Yihesubu lower jaw (V 14135) described here is comparable to the type of *Gobiolagus major* (AMNH 26098). The cheek teeth are slightly smaller than those of AMNH 26098, but the difference is probably exaggerated by the wear of the lingual surfaces of the Yihesubu teeth. The lingual enamel ridge between the trigonid and talonid and the relatively wide talonid on m2 are shared features of the AMNH 26098 and the Yihesubu lower jaw.

#### 3.2 *Hypsimylus*

*Hypsimylus beijingensis* is known from the Changxindian Formation of Beijing (Zhai, 1977),

which is estimated as late Middle Eocene (Tong et al. , 1995). The taxon was placed in Eurymylidae based on high crown cheek teeth that are somewhat similar to those of *Rhombomylus*. Zhai (1977) also noted dental similarity of *Hypsimylus* to that of lagomorphs, but pointed out that the cheek teeth of *Hypsimylus* are larger and more hypsodont than those of lagomorphs of the same age, and uniquely have the third lobe. Zhai linked *Hypsimylus* with *Rhombomylus* based on the similarity of the deciduous p4 between the two taxa. Li and Ting (1985) placed *Hypsimylus* in Mimotonidae. However, Dashzeveg and Russell (1988) consider the tooth referred to a deciduous p4 by Zhai (1977) a permanent tooth, which is supported by the evidence of the Yihesubu specimen. We also agree with Dashzeveg and Russell (1988) that there are no significant characters indicating a relationship of *Hypsimylus* to mimotonids. Although placing the subfamily Hypsimylinae within Eurymylidae, Dashzeveg and Russell (1988) believed that the relationships are obscure. McKenna and Bell (1997) have placed *Hypsimylus* within Leporidae (in the electronic note they considered it a palaeolagine).

Based on the new specimens described here we think the lower teeth of *Hypsimylus* are different from those of *Rhombomylus* (Meng et al. , 2003). In *Rhombomylus*, the lower incisor extends to the end of m3 and is ventral to the roots of cheek teeth. The incisor condition of *Hypsimylus* is similar to that of lagomorph, in which the incisor extends medial to the roots of cheek teeth and ends variously between p3 and m1 (Bohlin, 1942). The lower cheek teeth of *Rhombomylus* are low-crowned and are significantly different from those of *Hypsimylus yihesubuensis*.

According to Zhai (1977), the unique feature of the *Hypsimylus* is the presence of the third lobe, formed by the hypoconulid, on the lower cheek teeth, which results in a trilobate crown pattern that differs from the common bilobate cheek teeth of lagomorphs. However, the trilobate tooth pattern does exist in lagomorphs, but usually on immature specimens, such as the North American *Megalagus turgidus* (Wood, 1940) and *Palaeolagus philoi* (Dawson, 1958). In both species, adult cheek teeth are bilobate whereas immature teeth show the trilobate condition. We provided the photographs of *Megalagus* to illustrate these conditions. A lower jaw of a young individual *Megalagus turgidus* (AMNH 5630; Fig. 6) clearly displays this morphology. That specimen has been the type of *Palaeolagus triplex* Cope, 1884, that differs from other lagomorph species primarily in having a third column posterior to the second, as the specific name apparently implies (Wood, 1940). Although Cope (1884) believed that the type specimen of *Palaeolagus triplex* represented a fully-grown animal and that the trilobate pattern remains fundamentally unchanged as far as the alveoli, Wood (1940) regarded that the type specimen of *Palaeolagus triplex* is a juvenile specimen of *Megalagus turgidus*. Wood argued that there is a distinct decrease in the depths of the accessory folds that mark the second and third lobes. In view of the extremely rapid wear in leporid cheek teeth, the "triplex" pattern will be eventually destroyed with aging. The tooth near the alveolus is distinctly nearer the pattern of *Megalagus turgidus*.

Carefully comparing adult specimens with AMNH 5630 and specimens presumably intermediate, such as AMNH 5641 (Fig. 6), we believe Wood's (1940) conclusion is correct. In AMNH 5641, the cheek teeth are more deeply worn than AMNH 5630, but less so than the holotype of *Megalagus turgidus*. The third lobe disappears on m1 but still persists on the less worn p4. Further wear will unquestionably delete the third lobe on p4. Although IVPP V 5242 and the Yihesubu specimen have lower tooth crown than *Megalagus turgidus*, which suggests that they are more primitive than the latter, the similar tooth pattern convinces us that V 5242 represents a young individual of a lagomorph, not an eurymylid.

Compared to the new specimen, *Hypsimylus beijingensis* (V 5242) is from a relatively older individual with the p4 being more fully erupted and the p4 and m1 being more worn. Still, the crowns of V 5242 are relatively higher than those of the Yihesubu specimen and the hypostrid and the grooves that define the third lobe are deeper than the Yihesubu specimen. In crown view the third lobe on p4 or m1 is larger than the same structure on the corresponding tooth of the Yihesubu speci-

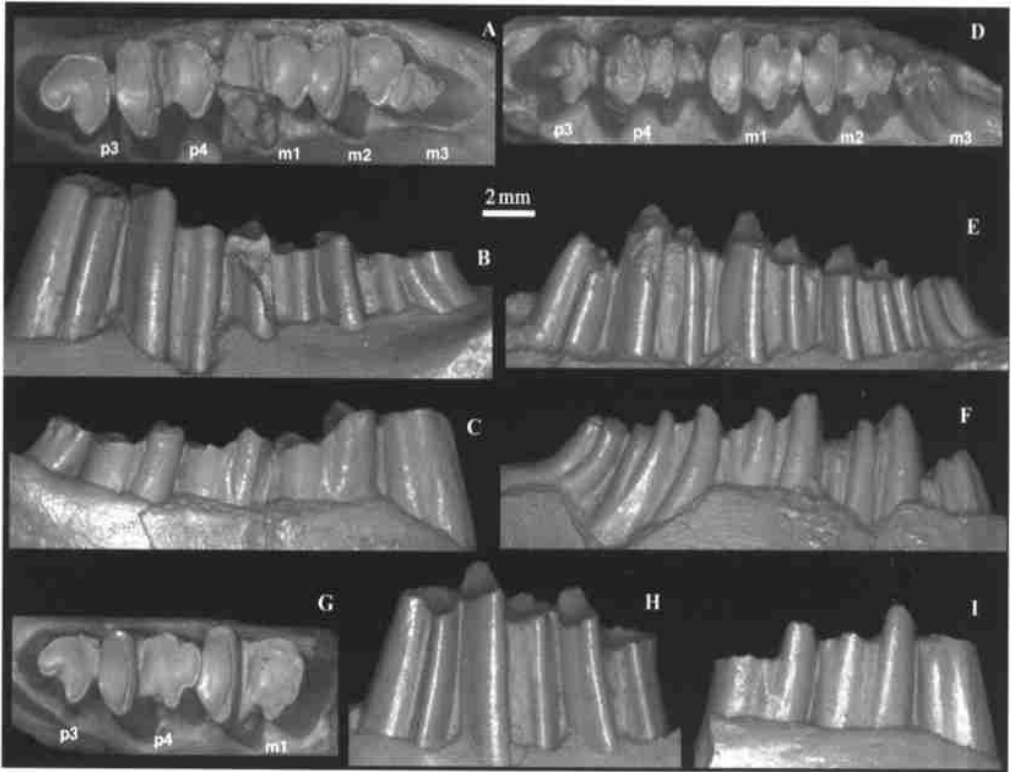


Fig. 6 Occlusal , lateral and medial views of *Megalagus turgidus*

A ~ C. AMNH 5635 (holotype) ; D ~ F. AMNH 5630 (young individual) ; G ~ I. AMNH 5641. See text and Wood (1940) for discussion

men - with wear the third lobe of the latter will become even smaller. Measurements of V 5242 were made by neither Zhai (1977) nor Dashzeveg and Russell (1988). However, based on figures and scales provided in the two studies the size of V 5242 is estimated as 3.18 mm long and 3.1 mm wide for p4 and 2.8 × 2.1 mm for m1. These teeth are significantly smaller than those of the Yihesubu specimen. Therefore, it is justified that the Yihesubu specimen represents a different species of the Beijing specimen.

Because lagomorph species are usually based on adult specimens and the diagnostic features of *Hypsimylus beijingensis* are now known all juvenile or subadult, whether *Hypsimylus* (Zhai, 1977) remains a valid genus becomes questionable. It is difficult to discuss the affinity of *Hypsimylus beijingensis* based only on the available material. If our reference of the specimens to *Hypsimylus yihesubuensis* is correct, the adult m2 and upper teeth from Yihesubu help to illuminate this issue.

The new species differs from other Asian Paleogene lagomorphs in its large size. *Gobiolagus major* and *Desmatolagus robustus* are the two species that are smaller but closer to the new species in size. Compared to *Gobiolagus major*, *Hypsimylus yihesubuensis* has a shorter incisor and the m2 assigned to the species lacks an enamel ridge connecting the lingual side of the trigonid and talonid. The general shape of the m2 is more comparable to that of *Desmatolagus robustus*, but they differ in several aspects. The new m2 is larger than that of *D. robustus* and is relatively low-crowned. Its talonid is rectangular, with the thickest enamel at the posterolateral corner of the tooth. In *D. robustus* (Matthew and Granger, 1923), the talonid is more rounded, with its midpoint of the lateral border projecting laterally and bearing the thickest enamel of the talonid. The bilobate P2 of *Hypsimy-*

*lus yihesubuensis* differs from the trilobate P2 of *D. robustus* (Sych, 1975; P2 unknown for *G. major*). The P3 central cusp of *H. yihesubuensis* is more labially positioned and the protocone is more lingually extended than in both *G. major* and *D. robustus*. It is clear that the Yihesubu specimens represent a species that differs from previously known early Tertiary lagomorphs.

### 3.3 Desmatolagus

Since the proposal of *Desmatolagus* (Matthew and Granger, 1923), about 10 species have been named from Asia and North America in various studies (Matthew and Granger, 1923; Teilhard, 1926; Burke, 1936, 1941; Bohlin, 1942). Huang (1987) considered the taxonomic position of the North American *Desmatolagus* is uncertain and concluded that there were five valid species of *Desmatolagus* in Asia, including *D. ardynese*, *D. vetustus*, *D. gobiensis*, *D. robustus*, and *D. pusillus*. One of the major issues related to *Desmatolagus* is the status of *Procaprolagus* (Gureev, 1960; Sych, 1975; de Muizon, 1977; Huang, 1987; Erbajeva and Sen, 1998; Erbajeva, 1999). According to Gureev (1960) and De Muizon (1977) *Procaprolagus* is characterized by low-crowned teeth in which the lingual and labial grooves do not enter the alveolus, lack of the foramen premolare on the palate medial to the premolar (see Bohlin, 1942: fig 17), lack of the third lophid on p4 and lower molars, transverse extension of the trigonids of lower p4 and molars, and presence of an enamel spike projecting posteriorly from the posterior wall of the trigonid. Gureev (1960) proposed *Procaprolagus* and pointed *Desmatolagus vetustus* as the type species of the new genus. This placement was followed by de Muizon (1977). Sych (1975: 184) regarded *Procaprolagus vetustus* as junior synonym of *Desmatolagus gobiensis*, but in other place of the same paper Sych (1975: 195) appears to consider *D. vetustus* a valid species of *Desmatolagus*. Huang (1987) agreed with Sych (1975) on synonymizing *D. radiciens* with *D. gobiensis*, but retained *D. vetustus* as a valid and primitive species of *Desmatolagus*. Erbajeva and Sen (1998) again considered *Procaprolagus* a junior synonym of *Desmatolagus* and pointed out that the third lophid on the lower cheek teeth is a juvenile feature, thus not adequate to distinguish *Procaprolagus*. The discussion concerning *Hypsimylus* endorses the conclusion of Erbajeva and Sen (1998).

Carefully reexamining the type of *D. vetustus* we think the differences of *D. vetustus* from other species of *Desmatolagus* is obvious. In *D. vetustus* the lower teeth are relatively low-crowned, with the hypostrid and the lingual groove shallow and above the alveolus. The height of cheek teeth decreases posteriorly at a lower degree. There is no posterior talonid fold in lower cheek teeth of known specimens. The talonid is relatively narrow compared to the trigonid, or the trigonid is more transversely extended. The foramen premolare is absent. In all these features the new specimens from the Yihesubu are similar to *D. vetustus*. In other species, including *D. gobiensis*, *D. robustus*, *D. pusillus*, and *D. ardynese*, the cheek teeth have much higher crown, the hypostrid goes into the alveolus, the anterior cheek teeth are much higher than m2 and m3, the posterior talonid fold is usually present in relatively young individuals, and the talonid is relatively wider. The low-crowned teeth of *D. vetustus* cannot be attributed to age or extensive wear of old individual, because the new specimen (Fig. 4) shows that when p3 is lightly worn, all the cheek teeth in that specimen are much lower than those of the holotype of *D. gobiensis*, which is more worn. It seems there is no significant difference in the upper dentition. Absence of the foramen premolare is not a stable feature, and can vary within a species such as *D. pusillus* (Huang, 1987).

Although the differences are truly present, most of those listed for *D. vetustus* are primitive, except the relatively narrower talonid. Whether this feature distinguishes a genus is subjective. In this study, we follow Huang (1987) to recognize *D. vetustus*. The specimens from Yihesubu are generally similar to the holotype of *D. vetustus*. They differ in two aspects: the Yihesubu specimens are slightly smaller and the posterior border of the talonid is straight. In the holotype of *D. vetustus*, the posterior border of talonid is rounded. Given these minor differences and the small sample size, we tentatively regard the Yihesubu specimens as *D. cf. D. vetustus*.

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## 消息

### 云南元谋发现大型恐龙化石

1998年6月,云南省楚雄州元谋县姜驿乡文化站的余良忠将半箐村发现的一些大型动物化石交到元谋人陈列馆,经鉴定为恐龙化石。至今年6月,共进行了两次抢救性发掘,出土巨型恐龙不全个体9具,其中一个(野外编号 Y2001)是典型的蜥脚类恐龙。1999~2004年,云南省考古所、楚雄州文管所和州博物馆、元谋县文体局和元谋人陈列馆共同对姜驿乡恐龙化石点进行多次调查,摸清分布情况及地层埋藏年代。发现恐龙化石点以半箐村为中心,东到贡茶、新海村,南至石坪子、阿谷租村,西邻乡政府所在地及羊腊昔村,北止于四川会理县黎洪乡和江竹乡,有20余处,总面积近40 km<sup>2</sup>。这些恐龙颈椎椎体长,神经棘发育,四肢粗壮,前后肢对称,骨壁厚,骨骼较直,身体长度比原蜥脚类大,均属蜥臀类。中科院古脊椎动物与古人类研究所董枝明研究员曾多次到元谋考察,他认为姜驿恐龙化石产地面积大,种类齐全,层位清楚,属中侏罗世地层,是云南发现的新属新种,与云南禄丰发现的早侏罗世恐龙化石不同,为恐龙研究提供了互补资料。

姜驿地处元谋盆地北面,位于金沙江北岸。它的北、东、西三面地势陡峻,高度都在海拔1800 m以上,属大雪山脉。元谋盆地的西部、东南部以及中部在古脊椎动物与古人类方面都有过重要的发现。例如在元谋东山发现过鱼化石,在元谋县城东南的大那乌发现过著名的“元谋人”化石,在物茂乡的小河和富老出土过丰富的蝴蝶古猿和晚中新世的哺乳动物和植物化石。至于新石器时代以后的考古遗存更是不胜枚举。就是在姜驿,除恐龙化石外,还发现过贝壳、鱼化石,也发现过晚中新世的象、马和鹿类化石以及新石器时代的人骨及磨制石斧、石箭头等遗物。

姜驿大型恐龙化石的发现为恐龙研究提供了新的资料,为进一步研究元谋盆地的生物史、地质史提供了新的证据。