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GOBIOLAGUS (LAGOMORPHA, MAMMALIA) FROM EOCENE ULA USU, INNER MONGOLIA, AND COMMENTS ON EOCENE LAGOMORPHS OF ASIA

Jin Meng, Yaoming Hu, and Chuankui Li

ABSTRACT

Lagomorph specimens collected in 1925 by the Central Asiatic Expedition from the late middle Eocene Shara Murun Formation at Ula Usu, Shara Murun Region of Inner Mongolia, are described. These specimens belong to *Gobiolagus tolmachovi* and a new species, *G. burkei*. *Gobiolagus burkei* sp. nov. is similar to other species of the genus in having the pear-shaped p4 trigonid, short talonid on p4 and m1, talonid transverse and shorter than trigonid except for m2, enamel ridge connecting the trigonid and talonid at the lingual side, p4 significantly smaller than m1, and m2 the largest cheek teeth. It differs from other species in being smaller and having lower crowned cheek teeth, incisor ventral to cheek teeth so that a lingual protuberance is absent, and incisor extending posteriorly below the talonid of m2. It further differs from *G. tolmachovi* and *G. andrewsi* in having a less reduced p4 talonid. Eocene lagomorph genera and species are briefly reviewed. Diagnoses are emended or provided for *G. tolmachovi, G. andrewsi, G. lii, Lushilagus, Shamolagus, Hypsimylus, Strenulagus,* and *Dituberolagus.* Two Eocene species of *Desmatolagus, D. vetustus* and *D. ardynense,* are also discussed. Photographs of holotype specimens housed in the American Museum of Natural History are presented.

Jin Meng. Division of Paleontology, American Museum of Natural History, Central Park West at 79th St., New York, NY 10024, USA. jmeng@amnh.org
Yaoming Hu. Division of Paleontology, American Museum of Natural History, Central Park West at 79th St., New York, NY 10024, USA.
Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, PO Box 643, Beijing 100044, China.
Biology Program, Graduate School and City College of New York, City University of New York, New York, NY 10016, USA. yhu@amnh.org
Chuankui Li. Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, PO Box 643, Beijing 100044, China. lichuankui@ivpp.ac.cn

KEY WORDS: lagomorphs, Eocene, taxonomy, holotype, Asia

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INTRODUCTION

Asian Eocene lagomorphs are mainly known from the Irdinmanhan, Sharamurunian, Ulangochuan, and Ergilian faunas that range from the middle Eocene to late Eocene. Nine genera of lagomorphs are known from these Eocene faunas, including *Lushilagus, Shamolagus*, *Gobiolagus*, *Hypsimylus*, *Strenulagus, Dituberolagus, Valerilagus, Annalagus* and *Desmatolagus*. Since the report on Paleogene lagomorphs of Matthew and Granger (1923), many studies have documented the rich fossil records from Asia (Teilhard de Chardin 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; Meng and Hu 2004). These forms represent the earliest radiation of the lagomorphs and are the stem taxa of the crown clade Lagomorpha (McKenna 1982). These species are also useful for biostratigraphic division and correlation of early Tertiary beds of the region because of their distinctive morphologies, restricted geological distributions, and numerical abundance (Huang 1987; Tong et al. 1995; Wang 1997a, b; Erbajeva and Tyutkova 1997).

Among the collections of fossil mammals made by the Central Asiatic Expedition by the American Museum of Natural History in 1925, there are 21 fragmentary specimens of lagomorphs from the Shara Murun Formation at the Ula Usu locality, Shara Murun region, Inner Mongolia. These specimens bear the field number 507, noted as miscellaneous from the “main Ula Usu pocket” in the field notebook (Granger 1925) and have been lumped in one catalog number, AMNH 21750. Several species belonging to *Gobiolagus, Desmatolagus,* and *Shamolagus* were discovered from localities, Ula Usu included, in the Shara Murun region of Inner Mongolia (Burke 1941; Li 1965; Qi 1988). The AMNH lagomorph specimens collected from Ula Usu belong to two species of *Gobiolagus*: *G. tolmachovi* and a new species. These specimens provide additional knowledge of the morphology of *Gobiolagus* and add to the diversity of Eocene lagomorphs of the region. In this study, we describe these specimens that have been in the collections for 80 years.

In addition to description of the new specimens from Ula Usu, we provide a brief review of the Eocene lagomorphs from Asia with focus on diagnoses of the genera and comments on the localities where the specimens came from. With discoveries of Eocene lagomorph species during the last few decades, a comparative study of these taxa appears needed. We also include photographs of the holotypes housed in the AMNH and believe these photographs will provide more detailed morphologies of the species than previously illustrated. Most of the previous studies provided only line drawings of the specimens, which do not display the detailed morphologies critical in identifying the species. For instance, the line drawing of the holotype of *G. andrewsi* was somewhat idealized and did not display detailed structures on the p3 and worn condition of other cheek teeth that are critical for the establishment of the species.

In the description, 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). Measurements of teeth were made using an Ultra-Call Mark III digital caliper. Abbreviations: AMNH, American Museum of Natural History; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing.

SYSTEMATIC PALEONTOLOGY

Order LAGOMORPHA Brandt, 1855
Family LEPORIDAE Fischer de Waldheim, 1817

Genus *GOBIOLAGUS* Burke, 1941

Type Species: *Gobiolagus tolmachovi* Burke, 1941.

Emended Diagnosis: Cheek tooth crown higher than that of *Shamolagus* but lower than that of *Desmatolagus* except for *D. vetustus*; p3 and m3 are proportionally smaller than those of *Shamolagus* but larger than those of *Desmatolagus*; incisor extending to m1 or m2; lower cheek tooth trigonid transversely extended; talonid shorter than trigonid except for m2; enamel ridge connecting the trigonid and talonid at the lingual side; p4 significantly smaller than m1; p4 talonid reduced and trigonid anteroposteriorly elongated; m2 the largest cheek teeth; m2 talonid much lower than the trigonid in contrast to the condition in p4 or m1; P4 nonmolariform and significantly smaller than M1; P3-4 not lingually extended; M3 reduction moderate.

Included Species: *Gobiolagus andrewsi, G. major, G. lii,* and *G. burkei* sp. nov.

Comments: *Gobiolagus* is a leporid genus proposed by Burke (1941) based on specimens collected from central Asia, although the genus was recently placed under Leporidae with a query (Zhang et al. 2001). 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 fragmentary specimens. 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 partial 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 later assigned 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). *Ordolagus teilhardi* is an early Oligocene species from the Hsanda Gol Formation of Mongolia. Specimens that are identified with certainty to *Gobiolagus* are mostly from the late Eocene Shara Murun Formation and Ulan Gauche Formation of the Shara Murun region, Inner Mongolia, except a few isolated teeth assigned to *G.* cf. *major* from the Oligocene of Kazakhstan (Erbajeva 1999). Isolated teeth assigned to *Gobiolagus* are reported from the Sharamurunian beds of Henna, south China (Tong 1997) and of Inner Mongolia (Li 1965; Meng et al. 1999), and from the upper Oligocene of Zaisan Depression, Kazakhstan (Erbajeva 1999), and the lower Oligocene Valley of Lakes, Mongolia (Erbajeva and Daxner-Hoeck 2001). *Gobiolagus lii* was reported recently from the middle Eocene Yuli member of the Heti Formation, Yuanqu, Shanxi Province, China (Zhang et al. 2001).

Gobiolagus tolmachovi Burke, 1941

Emended Diagnosis: Smaller than *G. major* but larger than *G. lii* and *G. burkei* sp. nov.; p3 internal reentrant at the anterolingual side of the tooth; p4 trigonid pear-shaped.

Locality and Age: The holotype (AMNH 26142, Figure 1.1, Figure 2) and a referred specimen (AMNH 26143) are from the late middle Eocene Shara Murun Formation near Baron Sog, Inner Mongolia (Burke 1941). Additional specimens described here are from the Shara Murun Formation, Ula Usu, Inner Mongolia.

Referred specimens: AMNH 141277, right maxilla with P4-M2, alveoli of P2-3 and partial alveolus of M3; AMNH 141278, right maxilla with P4-M2 of a relatively young individual; AMNH 141279, left maxilla with broken P4-M2; AMNH 141280, left maxilla with broken P4-M2; AMNH 141281, right maxilla with P3-4 of a relatively young individual; AMNH 141282, right maxilla with P4 and broken M1-2; AMNH 141283, left maxilla with P3-M1, alveolus of p2 and partial alveolus of M2; AMNH 141284, left maxilla with broken P4-M2; AMNH 141285, left maxilla with broken P3-M2; AMNH 141286, left maxilla with broken P4 and broken M1-2; AMNH 141287, left maxilla with M1-2; AMNH 141288, left mandible with p3-m1; AMNH 141289, right mandible with broken p4-m1; AMNH 141290, right mandible with broken p4-m2; AMNH 141291, left mandible with m1-3; AMNH 141292, right mandible with p4-m1; AMNH 141293, right mandible with broken m2; AMNH 141294, left mandible with m1; AMNH 141295, left mandible with p4-m2. The referred specimens were collected in 1925 and were associated with the field number 507 and catalog number AMNH 21750.

Description: Measurements of the teeth are given in Table 1. The p3 is preserved in AMNH 141288 (Figure 3.1-2). The tooth is less worn than in the holotype of *G. tolmachovi* (Figure 2) so that the lingual and labial reentrants in the new specimen are deeper. However, because of relatively smaller size of AMNH 141288 (Table 1), the absolute height of the tooth is lower than that of the holotype. In occlusal view, the tooth is narrower anteriorly than posteriorly. The lingual reentrant is at the anterolingual side of the tooth crown and is about one third of the tooth height. The hypostriid (labial reentrant) is much more distinct and over half of the tooth height.

In labial or lingual view, the cheek teeth appear to have two separate roots, but broken specimens (AMNH 141295; Figure 4.2) show that the roots in all cheek teeth are fused. The part of the root supporting the trigonid is wider and is formed by fusion of two smaller roots. The part of the root supporting the talonid is narrower but longer and is in a circular contour in cross sectional view. The hypostriid and the lingual reentrant extend continuously to the end of the fused root on the labial and lingual sides of the tooth.

The p4 is molariform but much smaller than m1 (Figure 3.1-4). The p4 trigonid is pear-shaped, with its lateral side being wider and rounded. The

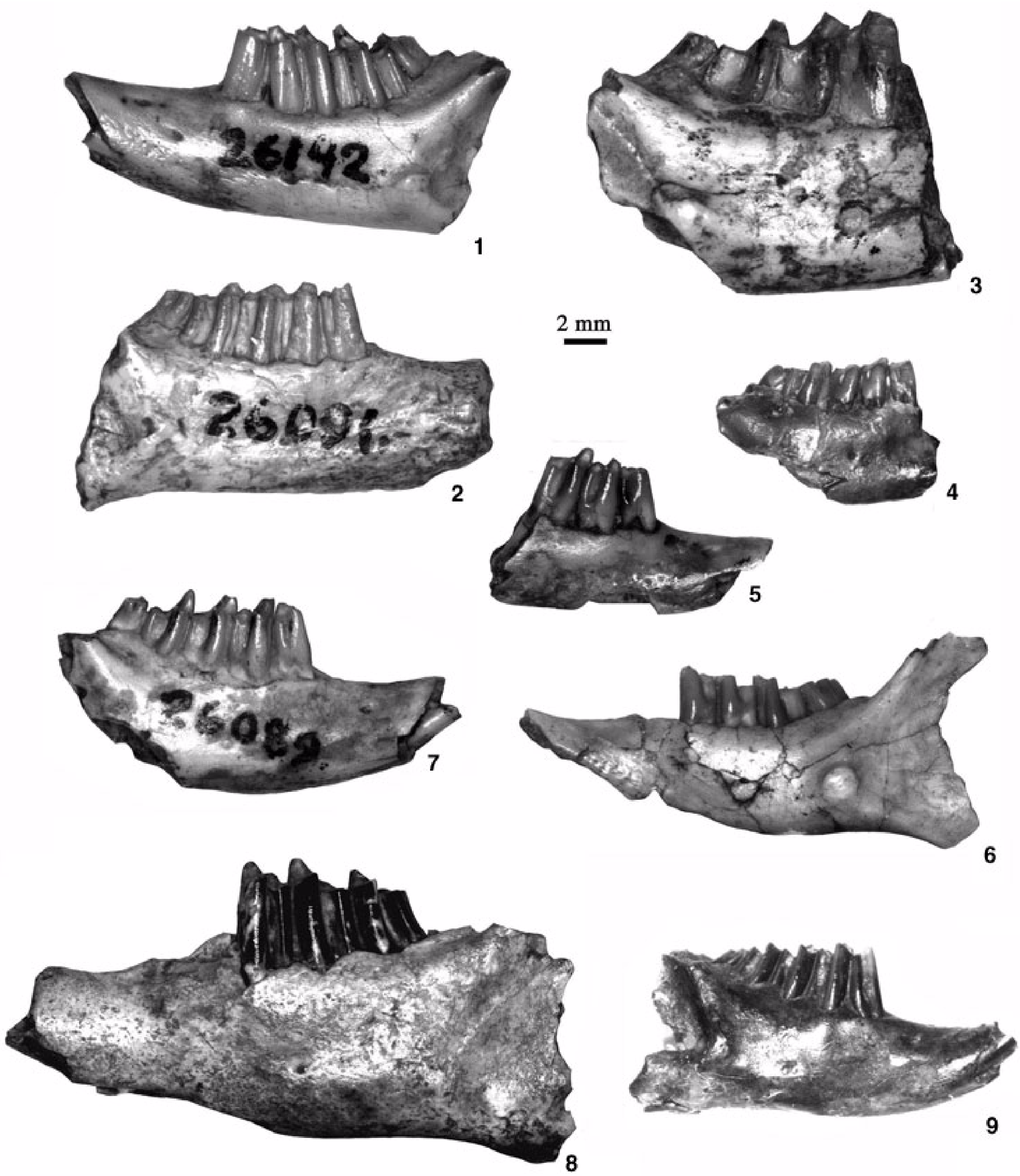

Figure 1. Lateral views of holotype specimens of species of *Shamolagus, Gobiolagus* and *Desmatolagus* that are housed in the AMNH collection. **1,** *Gobiolagus tolmachovi* (AMNH 26142, left mandible with p3-m3); **2,** *G. andrewsi* (AMNH 26091, right mandible with p3-m3); **3,** *G. major* (AMNH 26098, right mandible with p4-m3); **4,** *G. burkei* sp. nov. (AMNH 141275, right mandible with p3-m3); **5,** *Shamolagus medius* (AMNH 26144, right mandible with p3-m1); **6,** *S. grangeri* (AMNH 26289, left mandible with p4-m3); **7,** *Desmatolagus vetustus* (AMNH 26089, right mandible with p3-m3); **8,** *D. ardynense* (AMNH 20373, left mandible with p4-m2); **9,** *D. gobiensis* (AMNH 19102, right mandible with p3-m3).

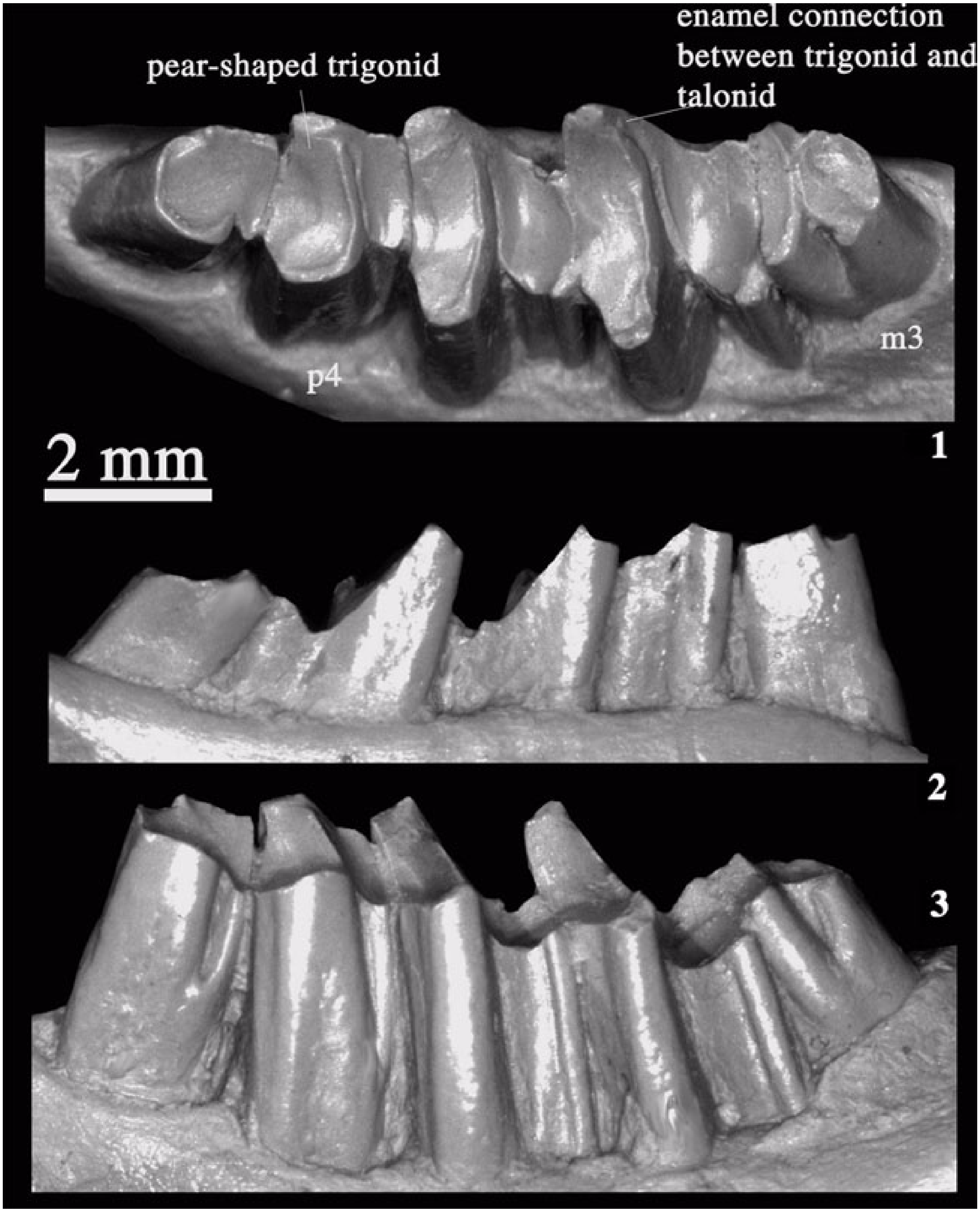

Figure 2. 1-3, Occlusal, medial and lateral views of the left p3-m3 of *Gobiolagus tolmachovi* (holotype, AMNH 26142). Images taken from gray-toned casts.

Table 1. Measurements of teeth (in mm) of lagomorphs from Ula Usu, Inner Mongolia; asterisk indicates estimated measurement; tri, trigonid; tal, talonid.

Lower teeth		**Length**	**Width (tri/tal)**
Gobiolagus burkei			
AMNH 141275	p3-m3	7.75	
(holotype)	p3	1.35	1.12
	p4	1.40	1.66/1.20
	m1	1.42	1.93/1.29
	m2	1.87	2.06/1.66
	m3	1.43	1.12/0.89
AMNH 141276	m1	1.59	2.05/1.39
	m2	1.79	2.20/1.61
G. tolmachovi			
AMNH 141288	p3	1.69	1.35
	p4	1.75	1.94/1.45
	m1	2.22	2.54/1.71
AMNH 141289	m1	2.37	2.83/1.77
AMNH 141290	p4	2.08	2.83/1.77
	m1	2.04	3.01/2.15
	m2	2.85	3.23/2.44
AMNH 141291	m1	2.06	2.98//2.02
	m2	2.93	3.02/2.28
	m3	1.88	1.65/1.31
AMNH 141292	p4	1.64	1.93/1.36
	m1	2.17	2.65/1.60
AMNH 141294	m1	1.99	2.33/1.64
AMNH 141295	p4	1.54	1.61/1.24
	m1	2.01	2.41/1.53
	m2	2.32	2.54/1.78
Upper teeth of *G. tolmachovi*			
		Length	Width
AMNH 141277	P4	1.82	4.61
	M1	2.08	5.64
	M2	1.94	4.84
AMNH 141278	P4	1.84	4.42
	M1	2.31	4.35*
	M2	2.16	4.30
AMNH 141279	P4	1.82	4.14
	M1	1.98	4.72
	M2	1.98	4.12*
AMNH 141281	P3	1.60	3.68
	P4	1.70	4.21
AMNH 141282	P4	1.84	4.43
AMNH 141283	P3	1.50	3.14
	P4	1.60	3.77
	M1	1.82	5.22
AMNH 141284	P4	1.59	4.08
	M1	1.81	4.63
	M2	1.93	4.52*
AMNH 141286	P4	1.63	5.02
AMNH 141287	M1	1.90	5.13
	M2	1.70	4.78

talonid is short and, in contrast to the trigonid, the lingual side is wider than the labial. The trigonid and talonid are not connected at the lingual side, which differs from the condition of the molars.

The m1 is significantly larger than p4 (Figure 3.1-6). The m1 trigonid is transversely wide. The talonid is shorter than the trigonid but is much larger than that of p4. The two lobes are connected at the lingual side by a narrow band of enamel. The m2 is the largest lower cheek tooth. Its talonid is longer than the trigonid and is proportionally more expanded than in p4 and m1. The hypostriid reaches the edge of the alveolus and is much wider than that of m1. The posterolateral corner of the talonid is squared and the posterolingual corner is rounded. The m3 trigonid is short and is also wider labially than lingually. The talonid is oval-shaped and much longer than the trigonid. As in m1 and m2, the two lobes are connected by the enamel ridge at the lingual side.

The maxilla (Figure 4.1) and upper teeth (Figure 5.1-3) are associated with the mandible and lower teeth because of their similar sizes and due to the distinctive size increment between P4 and M1, which is consistent with that of the lower dentition. A palatine foramen is completely within the palatine. There is no premolar foramen. The posterior border of the incisive foramen levels with the anterior edge of the alveolus for P2. The posterior edge of the palate is at the level of M1. The anterior root of the zygomatic arch bears a ventral process. An antorbital fossa is present anteromedial to the process or lateral to P3-4. The posterior edge of the anterior zygomatic root is lateral to the anterior half of M1. The external outline of the maxilla is not so convex as in the maxilla assigned to *G. tolmachovi* by Qi (1988) and in *G. lii* (Zhang et al. 2001).

P2 is not preserved, but a single rooted, triangular tooth can be estimated from the alveolus (Figures 4.1, 5.3). P3 is trilobate and oval-shaped in occlusal view (Figure 5.1-2). It has two roots, located lingually and labially. Its lingual side is higher than the labial, but the difference is not so much as in P4. The two valleys (reentrants) are simple. The labial valley is shallow and wide and opens anterolabially. The lingual valley is narrow and extends posterolabially around the central cusp; this condition is better seen in a worn specimen (Figure 5.2). The lingual cusp, presumably the protocone, has a squared lingual outline and bears no hypostria. As shown in AMNH 141283 (Figure 5.1), this cusp is worn earlier than the central cusp in ontogeny. The central cusp is circular in outline except at its posterolabial side where it connects to the rest of the tooth. The posteroloph

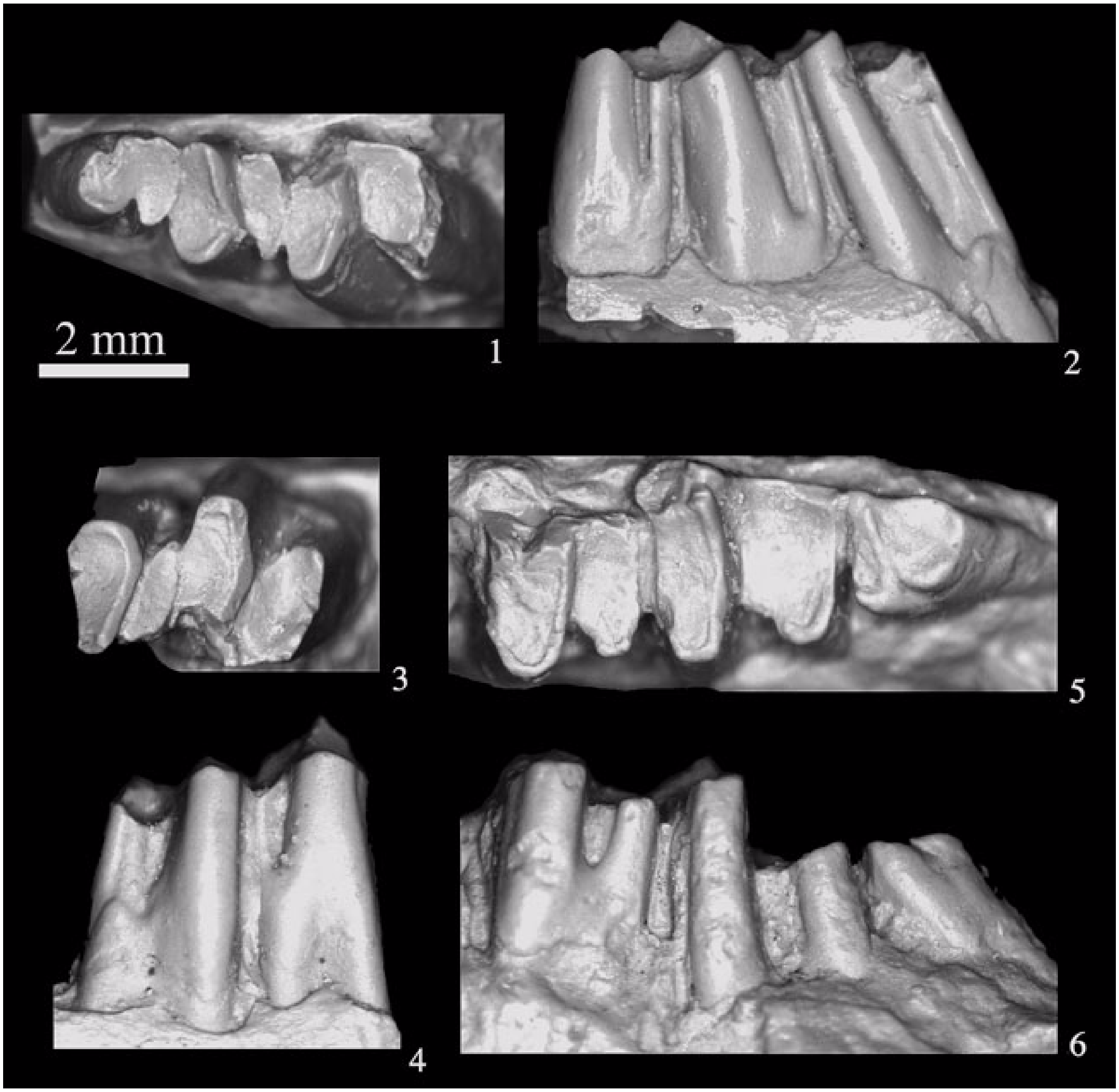

Figure 3. Lower dentitions of *Gobiolagus tolmachovi* from the late middle Eocene Shara Murun Formation, Ula Usu, Shara Murun Region of Inner Mongolia. **1-2,** Occlusal and lateral views of left p3-m1 (AMNH 141288); **3-4,** Occlusal and lateral views of right p4-m1 (AMNH 141292); **5-6,** Occlusal and lateral views of left m1-3 (AMNH 141291). Images taken from gray-toned casts.

extends from the lingual cusp to the labial one. The lingual arch of the tooth is not great; therefore, with increasing wear, the transverse extension of the occlusal surface of the tooth is limited.

P4 is also two-rooted, nonmolariform and with an oval-shaped occlusal view (Figure 5.1-2). P4 is wider than P3, and its lingual side is much more hypsodont than P3. In a worn specimen, such as AMNH 141286, P4 can be as wide as, or wider than the molars. The anteroloph is complete so that the valleys on P4 become two enamel fossettes that bound the central cusp lingually and labially, respectively. The labial fossette is much shallower than the lingual one and bears very thin enamel. The lingual fossette, or the crescentic valley, is curved and is framed with a thick enamel wall labially and a thin wall lingually. The labial cusp is small and does not show any sign of division.

M1 is significantly larger than P4 (Figure 5). It has two small roots on the labial side. The hypostria and crescentic valley are absent in all specimens. The crown surface is characterized by an oval enamel contour on the occlusal surface. The

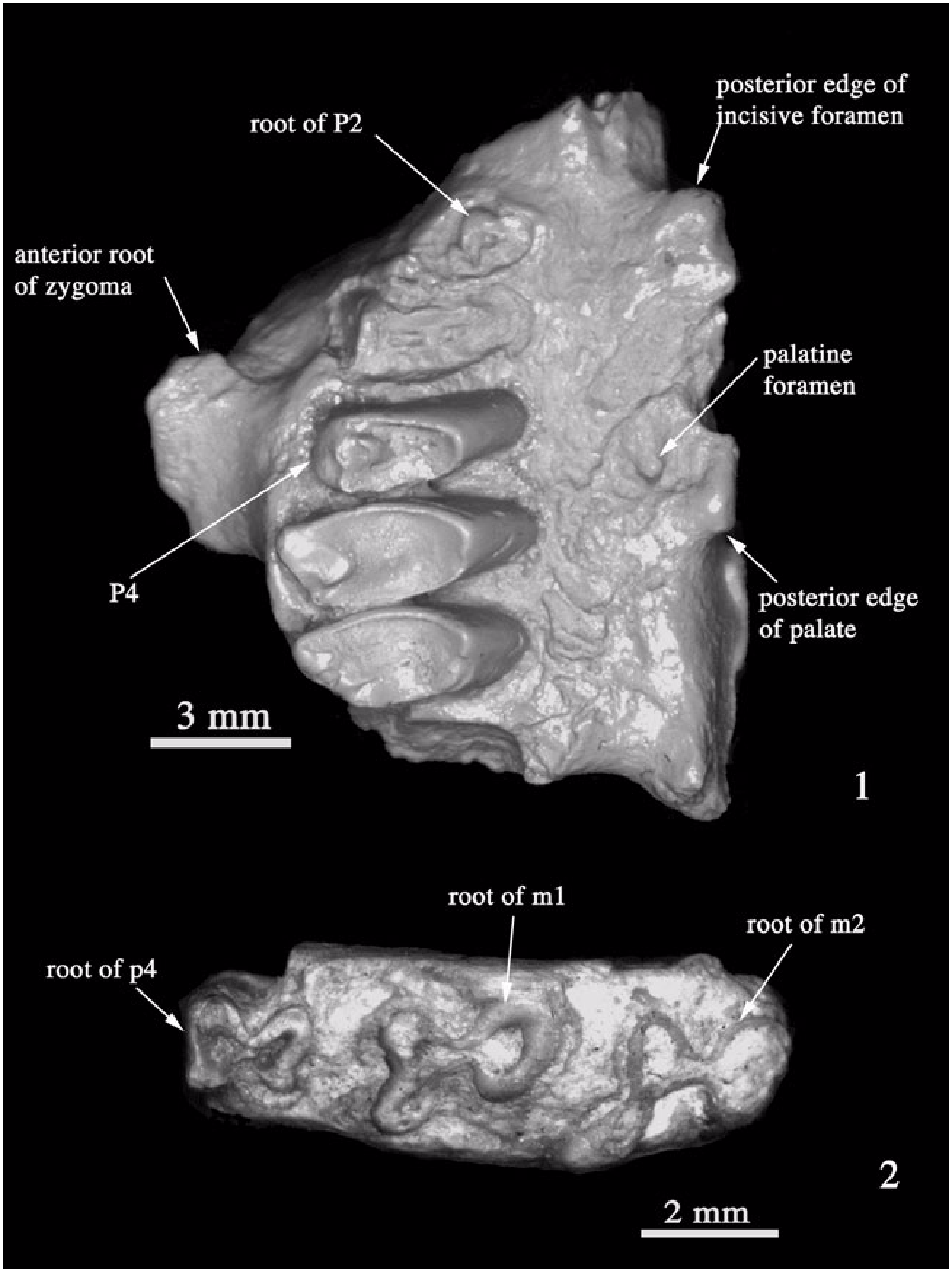

Figure 4. 1, Ventral view of the maxilla of *Gobiolagus tolmachovi* (AMNH 141277) from the late middle Eocene Shara Murun Formation, Ula Usu, Shara Murun Region of Inner Mongolia; **2,** Ventral view of AMNH 141295 showing the root condition of p4-m2 of *G. tolmachovi.* Images taken from gray-toned casts.

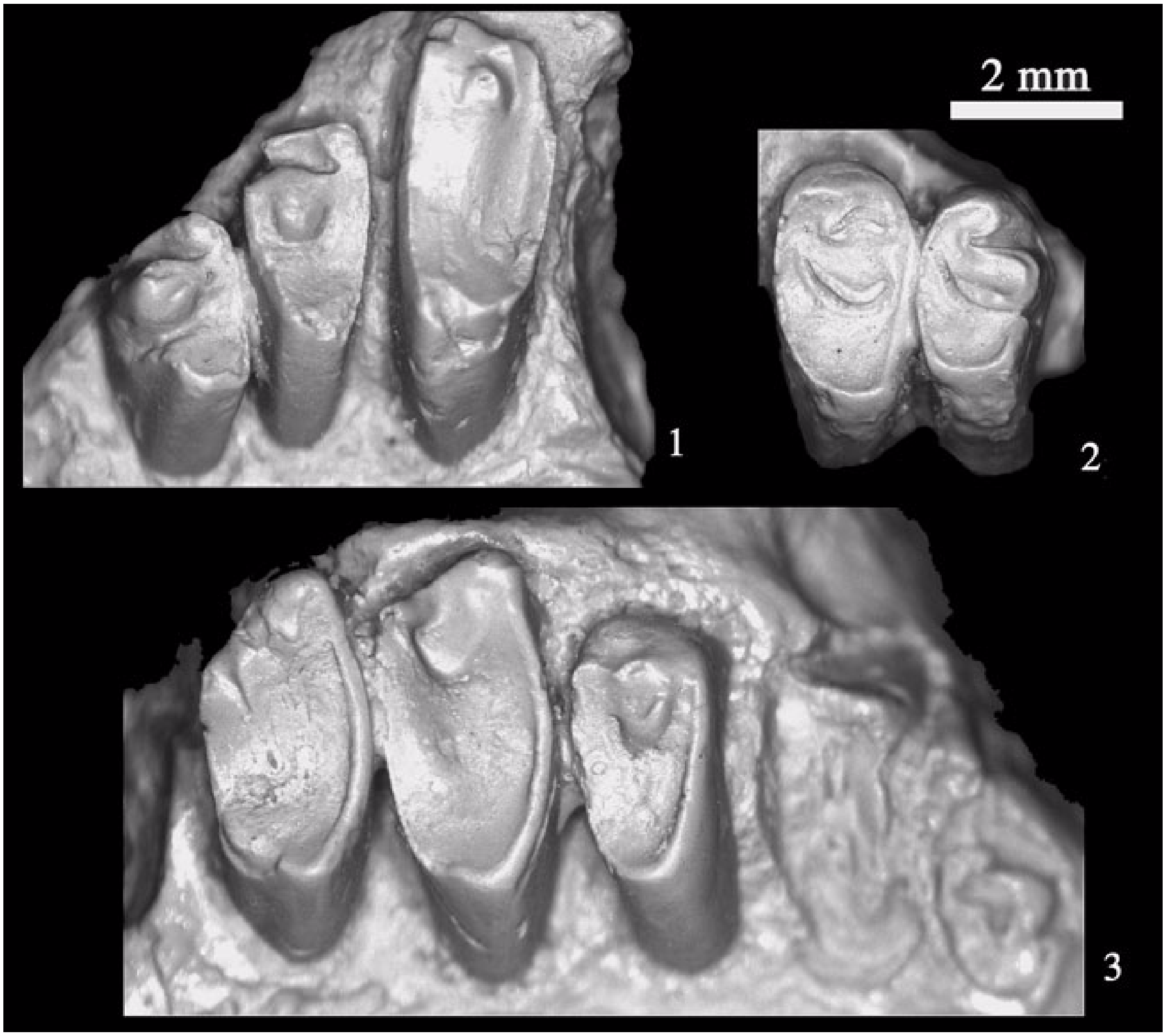

Figure 5. Occlusal views of upper dentitions of *Gobiolagus tolmachovi* from the late middle Eocene Shara Murun Formation, Ula Usu, Shara Murun Region of Inner Mongolia. **1-3,** Left P3-M1 (AMNH 141283), right P3-4 (AMNH 141281), and right P3-M2 (AMNH 141277). Images taken from gray-toned casts.

enamel along the anterior edge of the tooth is much thicker than that along the posterior edge. The labial side of the tooth is an enamel loop indicating the shape of the external valley. The round anterolabial corner suggests only one labial cusp.

M2 is similar to M1 (Figure 5.3). Its posterior half is narrower. A weak curvature at the lingual edge of the tooth indicates presence of a shallow hypostria that marks the boundary of the protocone and hypocone. A shallow, transverse groove separates the trigon and the posteroloph of the tooth. M3 is not preserved in any of the specimens, but the partial alveolus of 141277 indicates a sizeable tooth (Figure 4.1).

Comments: The Shara Murun fauna is from the Shara Murun Formation that overlies the "Tukhum" Fm. at the locality Ula Usu. When proposed, the Shara Murun Fm. was not described and was believed to lie underneath the Irdin Manha Fm. (Berkey and Granger 1923). Later these two formations were considered to be roughly equivalent (Berkey and Morris 1924). The Shara Murun Fm. was formally described by Berkey and Morris (1927), with a faunal list presented. Its younger age than Irdin Manha was based on faunal composition, not on superposition of sediments (Radinsky 1964). Russell and Zhai (1987, p. 210) stated that: "nowhere in Inner Mongolia can the Shara Murun Formation be seen overlying the Irdin Manha." The superpositional relationship of Shara Murun and Irdin Manha formations is probably present at the Bayan Ulan section (Meng et al. 1999). The Sharamurunian is now recognized as the late mid-

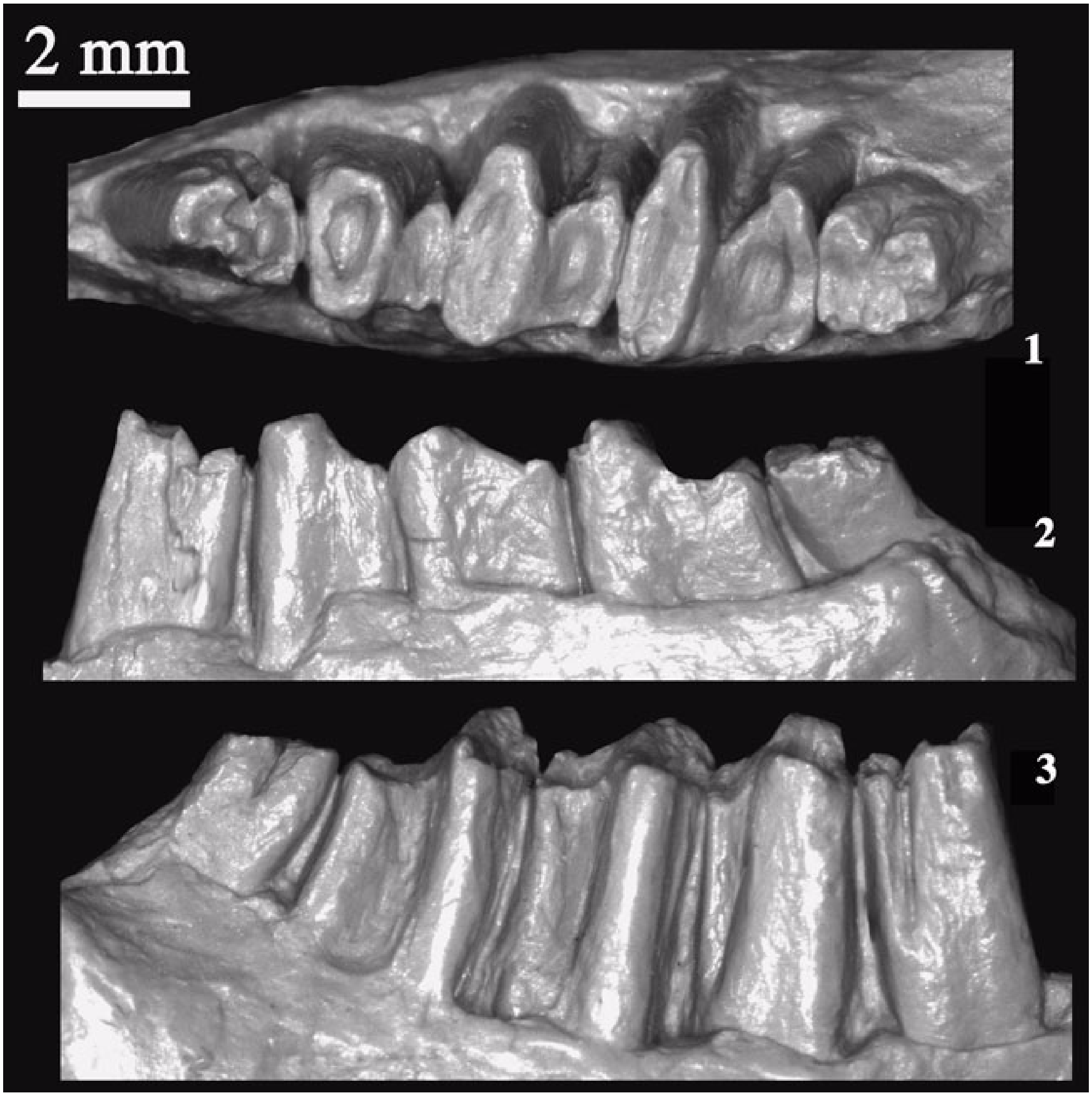

Figure 6. 1-3, Occlusal, medial and lateral views of the right p3-m3 of *Gobiolagus andrewsi* (holotype, AMNH 26091). Images taken from gray-toned casts.

dle Eocene land mammal age of Asia (Tong et al. 1995; Meng and McKenna 1998).

The dentitions reported here are generally similar to those of the holotype of *G. tolmachovi* (AMNH 26142). Compared to AMNH 26142, they have relatively lower crowns, in which the hypostriid on the lateral surface of the cheek teeth usually ends above the alveolus for specimens at different wear stages.

The p3 is critical to distinguish *G. tolmachovi* from *G. andrewsi* (Burke 1941; Figures 2, 6). The new specimen (AMNH 141288; Figure 3.1-2) is somewhat intermediate between those of the holotypes of the two species. The lingual reentrant seems more posteriorly positioned than that of *G. tolmachovi* but more anteriorly than in *G. andrewsi*. In crown view, the tooth is narrower than that of *G. tolmachovi* but wider than that of *G. andrewsi*. With further wear, the tooth would become wider. These detailed features suggest that the holotypes of the two species may actually represent individual variation within the same species (see below).

All species of *Gobiolagus* were based on lower teeth except for *G. lii* (Zhang et al. 2001). Possible upper teeth of *Gobiolagus* (IVPP V3012) were first described from the Shara Murun beds at Ula Usu, Inner Mongolia (Li 1965), but these teeth were considered to be more similar to the North

American *Mytonolagus* (Qi 1988). Qi (1988), erroneously citing specimen number V3011, noted presence of the hypostria on the upper molars of Li's specimen, which does not seem comparable to the relatively low crown lower cheek teeth of *Gobiolagus*. However, the partial hypostria on V3012 may be lost with further wear. Moreover, absence of the hypostria on the upper molars does not necessarily correspond to low crowned lower molars. For instance, *Ordolagus teilhardi* has high crown lower teeth but its upper teeth lack the hypostria (Huang 1986).

Qi (1988) instead assigned a maxilla with P4-M3 (V8430) from the Shara Murun beds, Ula Usu, to *G. tolmachovi* and recognized absence of the hypostria on cheek teeth and the transverse extension of the upper cheek teeth as features by which V8430 was assigned to *G. tolmachovi*. It has been demonstrated that tooth width and condition of the hypostria in the upper teeth of early lagomorphs are highly related to age and wear (Huang 1986, 1987). The specimen described by Qi (1988) is heavily worn so that its width and absence of the hypostria are at least partly age related.

P4 of V8430 is similar to the upper teeth, described above (Figures 4, 5) but is distinctively smaller than M1. Qi (1988) considered the P4 of V8430 to be molariform. However, because the cheek teeth of V8430 were extensively worn so that the tooth pattern was not well preserved, it is uncertain whether the P4 is molariform. The only structure that can be recognized from the P4 of V8430 is the anteroloph, which is complete as in the specimens described in this study. A complete anteroloph differentiates V8430 from *Lushilagus,* in which P4 is still trilobate, but it alone does not necessarily make a molariform P4. The P4 in the specimens assigned to *G. tolmachovi* in this study is similar to P3 in general morphology except for being larger and having a complete anteroloph. It has neither the division of the trigon and talon, nor division of cusps on the labial side of the tooth. We consider such a P4 nonmolariform.

V8430 described by Qi (1988) has the premolar foramen medial to the junction of P4 and M1 on the palate, which differs from the maxilla described here. The premolar foramen is usually within the maxilla and medial to the premolars in some lagomorphs (Matthew and Granger 1923; Bohlin 1942, figure 17; Huang 1987). The premolar foramen is not a stable feature and can vary within a species, such as in *Desmatolagus pusillus* (Huang 1987). Huang (1987, table 18) has surveyed several species of *Desmatolagus*, *Bellatona* and *Ochotona* and concluded that the premolar foramen shifts posteriorly in geologically younger species. For instance, the foramen is medial to P3 in *D. gobiensis,* but medial to P4 in *Ochotona nihewanica*. Compared to those species listed by Huang, the position of the premolar foramen in V8430 seems to be quite posteriorly positioned, at the junction of P4 and M1 (Qi 1988, figure 1).

Gobiolagus andrewsi Burke, 1941

Emended Diagnosis: Similar to *Gobiolagus tolmachovi* in morphology and size but differing from the latter in having the p3 more compressed transversely with main lingual reentrant more posterior (on worn teeth opposite buccal reentrant; Figures 1.2, 6).

Locality and Age: The holotype (AMNH 26091) and a referred specimen (AMNH 26092) were from Jhama Obo, East Mesa, Shara Murun Region, Inner Mongolia. Another referred specimen (AMNH 26097) was from Twin Obo, East Mesa of the same region. All of the specimens were from the Ulan Gochu horizon, which is now considered to be late Eocene (Wang 1997a, 1997b; Meng and McKenna 1998).

Comments: The holotype of *G. andrewsi* (AMNH 26091; Figure 6) is generally similar to that of *G. tolmachovi*, as realized by Burke (1941), and is from a relatively younger individual, judging from the degree of tooth wear, than the holotype of *G. tolmachovi.* The major difference between the two species is that in *G. andrewsi* the p3 is more compressed transversely with the lingual reentrant opposite the labial reentrant. Other differences listed by Burke (1941, p. 8) are relatively trivial, some of which are probably caused by preservation or artifact. For instance, the lingual side of the anterior half of the p3 in *G. andrewsi* was apparently damaged, and the enamel was peeled off, which makes the tooth appear narrower. As shown in Figure 6, the trigonid and talonid of cheek teeth in AMNH 26091 are pitted, an unusual condition for any known lagomorph. The shearing wear of the lagomorph teeth does not seem able to create such a pitted wear surface on a cheek tooth. The position of the lingual reentrant varies with wear and probably does so from individual to individual. As shown above, the new specimen of *G. tolmachovi* from Ula Usu has a p3 in which the lingual reentrant is more posterior than that in holotype of the species. It is highly possible that *G. andrewsi* is but a junior synonym of *G. tolmachovi.*

Gobiolagus major Burke, 1941

Emended Diagnosis: Larger than other species of the genus; p4 talonid less reduced; lower incisor

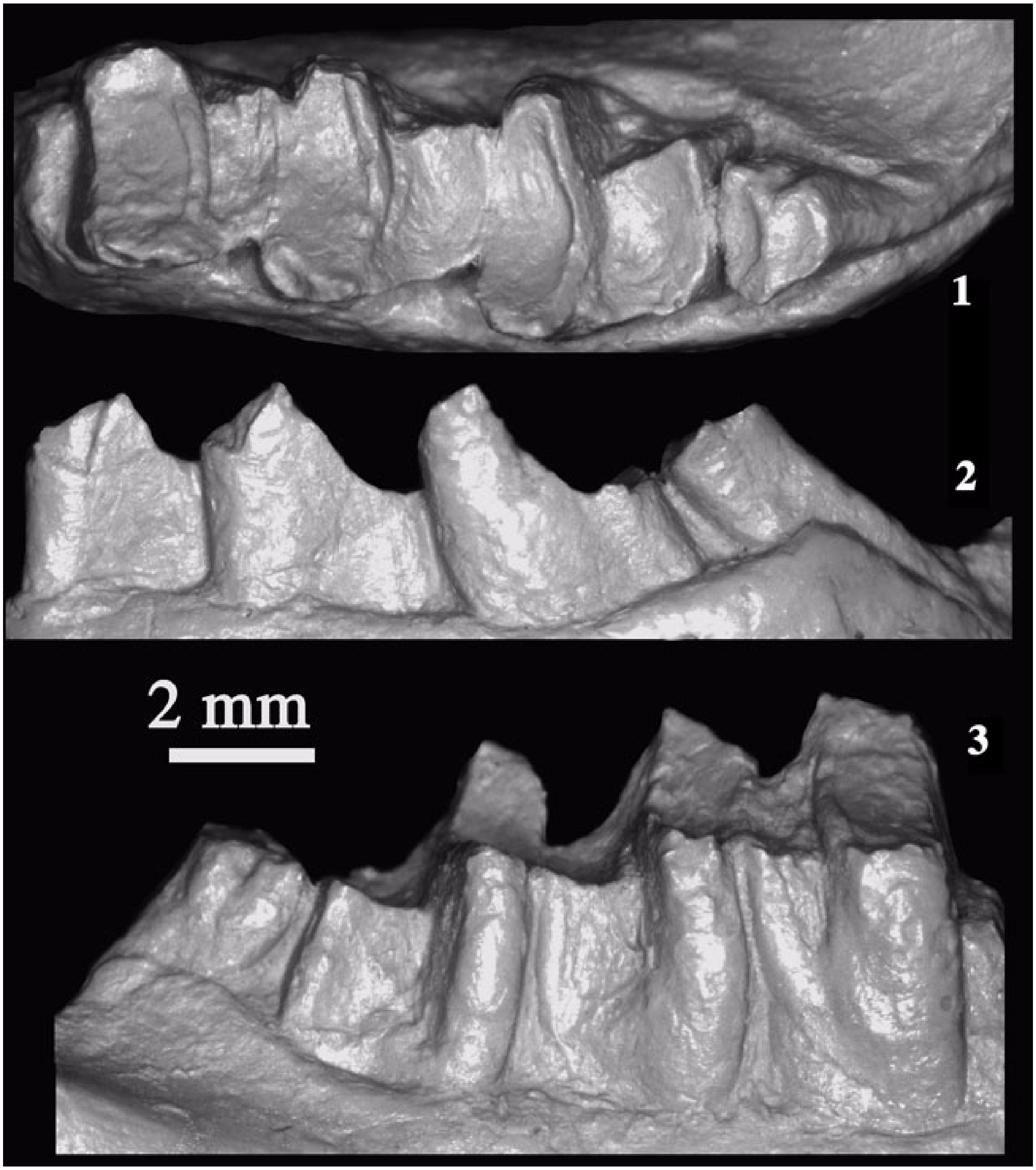

Figure 7. 1-3, Occlusal, medial and lateral views of the right p4-m3 of *Gobiolagus major* (holotype, AMNH 26098). Images taken from gray-toned casts.

ending at the level of m2 talonid and forming a distinct protuberance on the lingual surface of the mandible. Differs from *G. tolmachovi* and *G. lii* in having P3-4 triple-rooted; the P4 crescentic valley V-shaped and central cusp triangular; M1 oval in occlusal view (Figures 1.3, 7).

Locality and Age: The holotype of *Gobiolagus major* (AMNH 26098) was collected from the late Eocene Ulan Gochu beds at Urtyn Obo, East Mesa, Shara Murun Region, Inner Mongolia (Burke 1941). Additional specimens assigned to the species were from Yihesubu, about 18 km southeast of Nomogen village, at the north rim of the Ulan Shireh platform, Inner Mongolia, of possible Upper Eocene age (Meng and Hu 2004).

Comments: Burke (1941) named *G. major* with uncertainty. He noted that the cheek teeth of *G. major* were similar to those of *Desmatolagus* but the p4 was of the *Gobiolagus* type. After re-examining the holotype and additional specimens assigned to *Gobiolagus major* (Meng and Hu 2004), we consider *G. major* a valid species that shares several dental features with other species of the genus, including trigonids of lower cheek teeth transversely extended, talonids transverse and shorter than trigonids except for m2, enamel ridge connecting the trigonid and talonid at the lingual side, m2 the largest cheek tooth, m2 talonid much lower than the trigonid, nonmolariform P4 significantly smaller than M1, P3-4 not lingually extended and M3 reduction moderate.

Gobiolagus lii Zhang, Dawson, and Huang, 2001

Diagnosis: "Differs from *G. tolmachovi* in being smaller, having much less well-developed buccal cuspules on P4 and M1, and nonmolariform P4" (Zhang et al. 2001, p. 70).

Locality and Age: Yuli member of the Heti Formation at Houshipo, Guojia village, Yuanqu County, Shanxi; middle Eocene (Irdinmanhan).

Comments: *G. lii* is the earliest species of the genus (Zhang et al. 2001). The holotype, the only specimen, of this species is a fragmentary maxilla with P3-M2 (IVPP V12755). According to Zhang et al. (2001, p. 259), taxonomic identification of *G. lii* was based primarily on comparison with the maxilla assigned to *G. tolmachovi* (Qi 1988). Both species are similar "in the shape of the maxilla, zygoma, and infraorbital foramen, and in possessing a premolar foramen" (Zhang et al. 2001, p. 259). As we discussed above, the identification of the maxilla as *G. tolmachovi* by Qi (1988) is itself uncertain, which provides a weak basis for the taxonomic identification of *G. lii.* However, the specimens we here assign to *G. tolmachovi* resemble that of *G. lii* in some aspects of dental morphology, e.g., P3-4 morphology. These specimens differ from the holotype of *G. lii* in being larger, lacking the premolar foramen, and having a less convex external outline of the maxilla.

Gobiolagus burkei sp. nov.

Holotype - AMNH 141275, a fragmentary right mandible with p3-m3 (Figures 1.4, 8).

Referred Specimens: AMNH 141276, a fragmentary mandible with m1-2. AMNH 141275-6 were collected in 1925 under the same field and catalog numbers (507 and AMNH 92307) as those referred to *G. tolmachovi* (see above) from the same locality.

Etymology: The specific name is in honor of Dr. J.J. Burke, who made the first systematic study of early Tertiary lagomorphs from the Mongolian Plateau.

Diagnosis: Resembles *Lushilagus* in relatively lower tooth crown and trilobate lingual shape of p3; similar to *Gobiolagus* in having the pear-shaped p4 trigonid, short talonid on p4 and m1, lower cheek tooth trigonid transversely extended, talonid shorter than trigonid except for m2, enamel ridge connecting the trigonid and talonid at the lingual side, p4 significantly smaller than m1, and m2 the largest cheek tooth; differing from other species of *Gobiolagus* in being smaller and having lower crown cheek teeth, incisor ventral to cheek teeth and lingual protuberance absent, and incisor extending posteriorly below the talonid of m2; and further differing from *G. tolmachovi* and *G. andrewsi* in having less reduced p4 talonid.

Locality and Age: Shara Murun Formation at Ula Usu, Inner Mongolia; late middle Eocene.

Description: The smallest species of *Gobiolagus* (Figure 1.4, Table 1). The posterior portion of the incisor is preserved and ends posteriorly below the talonid of m2. The incisor is ventral to the roots of cheek teeth; therefore, there is no protuberance on the lingual surface of the mandible. On the lateral surface, two small posterior mental foramina are under p4 and m1 with the anterior one being larger than the posterior. The cast of matrix left at the breakage below the diastema indicates an anterior mental foramen. The mandible measures 4.95 mm deep and 2.67 thick at m1.

The cheek teeth are low-crowned, rooted, and the height difference is not distinct for all cheek teeth (Figures 1.4, 8). The p3 is longer than wide in occlusal view and its width increases posteriorly. On the lateral surface a hypostriid extends a third of the crown height from the occlusal surface and the tooth is divided into a long, narrow anterior lobe and a short, wide posterior lobe. On the lingual side, there are two weak grooves (internal reentrants) that are shallower and shorter than the hypostriid. In occlusal view the tooth is trilobate.

The p4 is molariform, but is notably smaller than m1. As in molars, the occlusal surface is uneven, with the lingual side higher than the labial one in both the trigonid and talonid. The trigonid and talonid are separated by a narrow groove filled with cement except at the lingual side of the tooth where a narrow enamel band connects the posterolingual corner of the trigonid with the anterolingual corner of the talonid. The talonid is short but wide, with the labial side being narrower than the lingual side. The hypostriid is similar to that of p3.

The m1 is similar to p4 in general morphology, but is larger than the latter. The m2 is significantly larger than m1. The trigonid and talonid of m2 are also proportionally larger than those of m1. In lat-

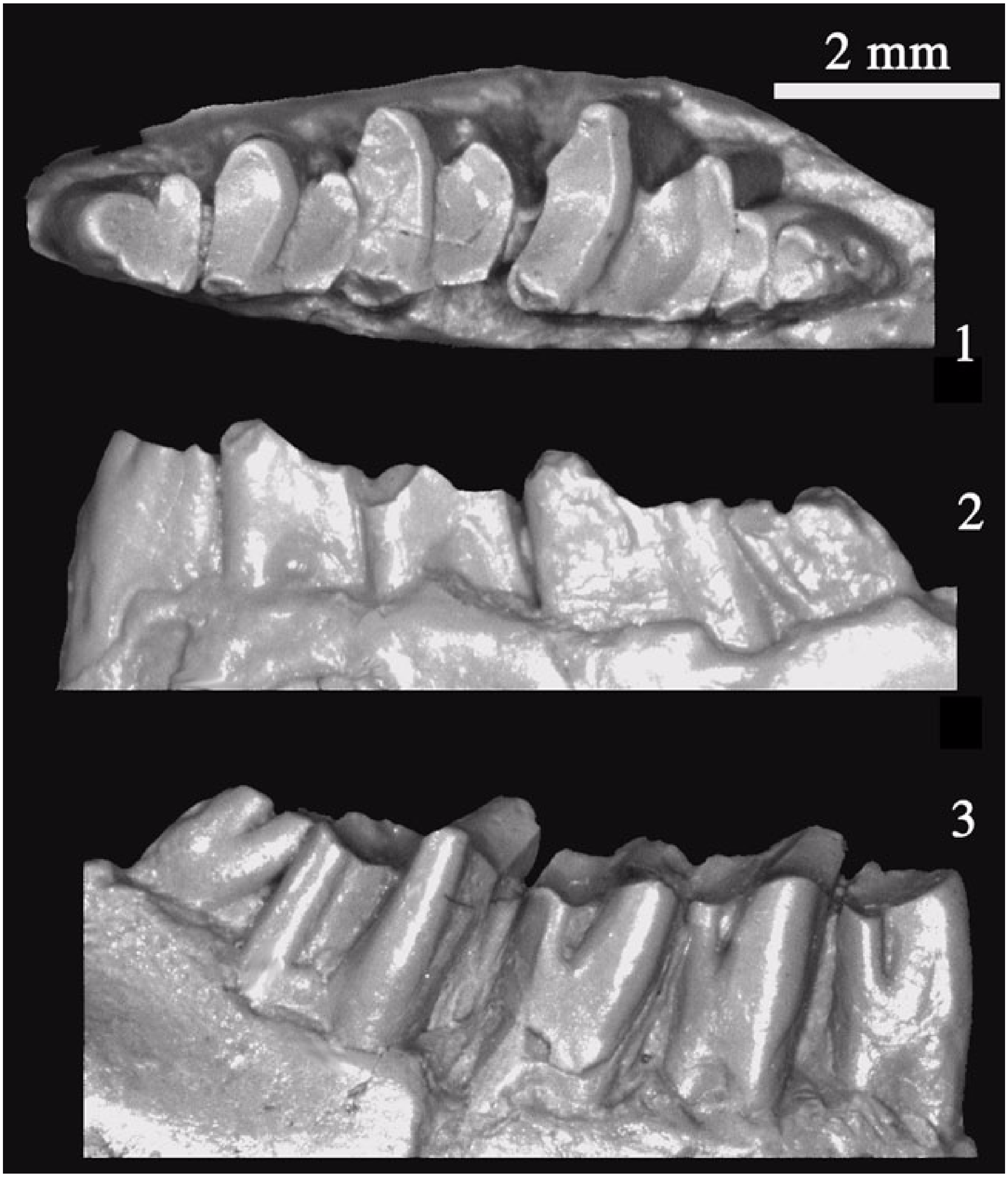

Figure 8. 1-3, Occlusal, medial and lateral views of the right p3-m3 of *Gobiolagus burkei* sp. nov. (holotype, AMNH 141275) from the late middle Eocene Shara Murun Formation, Ula Usu, Shara Murun Region of Inner Mongolia. Images taken from gray-toned casts.

eral view the hypostriid of m2 is much wider and deeper than that of m1. Unlike p4 and m1 where the trigonid is slightly longer than the talonid, the talonid of m2 is longer than the trigonid, although the difference is minor. The enamel on the lingual surface of m3 was broken so that the tooth appears smaller than it is. The m3 is greatly reduced but still has both the trigonid and talonid lobes. The trigonid of m3 is wider, but shorter, than the talonid. The hypostriid of m3 is the narrowest and shortest of the cheek teeth.

Comments: AMNH 141275 is considered a species of *Gobiolagus* because it has the basic features of the genus, including p3 and m3 proportionally smaller than those of *Shamolagus* but larger than those of *Desmatolagus*, incisor extending to m2, lower cheek tooth trigonid transversely extended, talonid transverse and shorter than trigonid except for m2, enamel ridge connecting the trigonid and talonid at the lingual side, p4 significantly smaller than m1, m2 the largest cheek tooth, and talonid of m2 much lower than the trigonid in contrast to the condition in p4 or m1.

Gobiolagus burkei differs from other species of the genus in being smaller and having relatively low-crowned cheek teeth. *Gobiolagus lii* is probably similar to the new species in size. However, because *G. lii* is represented only by upper teeth and *G. burkei* by lower ones, the comparison between the two species is difficult. In species of early lagomorphs where upper and lower dentitions from the same individual are known, such as *Shamolagus medius* (Li 1965), a lower cheek tooth is usually shorter than its upper counterpart. Given that relationship, it may be estimated that *G. burkei* is slightly smaller than *G. lii* (Zhang et al. 2001, table 1). Taking the different age and geographic distributions into account, we recognize both *G. lii* and *G. burkei*.

Gobiolagus burkei further differs from *G. tolmachovi* and *G. andrewsi*, but is similar to *G. major*, in having a less reduced p4 talonid. Its incisor extends to the level of the talonid of m2 and is less lingually offset than in other species. The p3 of *G. burkei* is similar to that of *Shamolagus*. One of the features originally diagnosing *Gobiolagus* was p3 "with modified *Shamolagus* pattern" (Burke 1941, p. 5). However, the p3 is unknown in *G. major.* In *G. tolmachovi* the anterior lobe of p3 is large and has a rounded occlusal outline. In *G. andrewsi* p3 is considered more compressed transversely (Burke 1941).

Genus *LUSHILAGUS* Li, 1965

Type Species: *Lushilagus lohoensis* Li, 1965.

Emended Diagnosis: Small lagomorphs with relatively low-crowned cheek teeth; P3 with large lingual lobe; P4 trilobate with an incomplete anteroloph; upper cheek teeth not transversely extended; labial tooth enamel folds absent when worn; M3 not significantly reduced; p3 anterior lobe conical and posterior lobe triangular, lingual side with one or two reentrants; m3 with the third lobe.

Included Species: *Lushilagus danjiangensis* Tong and Lei, 1987.

Locality and Age: Lushih (=Lushi) Formation, Menchiapu (=Mengjiapu), Lushih District, Honan (=Henan) (Li 1965); Hetaoyuan Formation, Shipigou, Xichun County, Henan (Tong and Lei 1987; Tong 1997); Liyang, Jiangsu, China (Qi et al. 1991); middle Eocene.

Comments: *Lushilagus lohoensis* was based on upper dentition (Li 1965; Qi et al. 1991) and some isolated lower teeth were later assigned to the species (Tong 1997). All specimens of *L. danjiangensis* are isolated teeth. This genus is primarily diagnosed by primitive characters and represents one of the earliest lagomorphs known.

Erbajeva (1999) transferred *L. danjiangensis* to *Zaissanolagus*. The type species of *Zaissanolagus*, *Z. gromovi*, was based on a P3 discovered from the late Oligocene Buran Formation in the Zaisan Depression (Erbajeva 1999). One of the features that distinguish *Zaissanolagus* from other Paleogene genera of the family Leporidae is the proportion of P3 dimensions. According to Erbajeva (1999), the P3 ratio of length to width is 49.3% in *Zaissanolagus*, 98% in *Shamolagus*, 83% in *Lushilagus,* and 43.5% in *Gobiolagus*. However, the length and width of P3 are 1.2 and 1.8 mm in *Lushilagus lohoensis*, and 1.3 and 2.1 mm in *Shamolagus* (Li 1965, p. 28), which give ratios of 67% and 62%, respectively. The P3 ratio is 46% (1.9 by 4.1 mm) in *Gobiolagus* based on the measurements of Qi (1988, table 1) and 45% (1.0 by 2.2 mm) in *L. danjiangensis* (Tong and Lei 1987, table 2). Moreover, the P3 ratio of *Zaissanolagus gromovi* is 81% based on the measurements given by Erbajeva (1999, 1.5 by 1.85 mm in table 1). These numbers are drastically inconsistent. Because the sources of data and methods of calculation used in Erbajeva (1999) are unclear to us, we are unable to verify the significant differences among these numbers. Nonetheless, it is clear that the P3 ratio is distinctive between *Z. gromovi* and *L. danjiangensis*; thus we recognize *L. danjiangensis* until additional evidence proves contrary.

Genus *STRENULAGUS* Tong and Lei, 1987

Type Species: *Strenulagus shipigouensis* Tong and Lei, 1987, the only known species of the genus.

Diagnosis: "Unilateral hypsodonty distinct. Anterior lobe of p3 conical, and narrower than posterior lobe; trigonid of p4-m2 compressed anteroposteriorly; talonid of p4 smaller relative to its trigonid, with distinctly compressed labial side and even lingual wall; on m1-2 talonid large, with a third lobe on little worn teeth; m3 less reduced, with a clear hypoconulid; p3 and p4 double-rooted, with trilobate occlusal surface; P3 labial lobe relatively developed; P4 metastyle enlarged, usually connected with parastyle; preprotocrista of P4 frequently unconnected with parastyle; metacone of M1 isolated, surrounded by U-shaped enamel valley; M2 and M3 consisting of V-shaped trigon and obliquely elongated hypocone; M3 less reduced" (Tong 1997, p. 202).

Locality and Age: Hetaoyuan Formation, Shipigou, Xichun County, Henan, China; Irdinmanhan, middle Eocene.

Comments: *Strenulagus shipigouensis* was named by Tong and Lei (1987) and additional specimens led to a thorough revision of the species diagnosis (Tong 1997).

Genus *DITUBEROLAGUS* Tong, 1997

Type Species: *Dituberolagus venustus* Tong, 1997, the only known species of the genus.

Diagnosis: "A small primitive lagomorph. Trigonid of midcheek teeth made up of conical protoconid and metaconid; valley between the two cusps deep, extending down along anterior wall of tooth; talonid of m2? longer and wider than trigonid; posterior lobe of p3 cingulum-like" (Tong 1997, p. 204).

Locality and Age: Hetaoyuan Formation at Shipigou, Xichun County of Henan, China; Irdinmanhan, middle Eocene.

Comments: Averianov (1998) noted that the lower teeth of *Dituberolagus venustus* are similar to those of *Bulatia aksyirica* (Gabunia and Shevyreva 1994). *Bulatia aksyirica* is based on an isolated m1 or m2 from the middle Eocene Sargamyss Formation in Zaisan depression and was originally referred to Mixodontia incertae familiae. Averianov (1998) considered *Bulatia aksyirica* a nomen dubium and referred it to as Mammalia incertae ordinis. Averianov (1998, p. 207) suggested that the M2 referred to *Lushilagus? danjiangensis* by Tong (1997) may belong to *Dituberolagus venustus* and that the tooth is "noticeably similar to upper molars of mimotonid *Aktashmys montealbus* from the early Eocene of Kirghizia."

Genus *SHAMOLAGUS* Burke, 1941

Type Species: *Shamolagus grangeri* Burke, 1941.

Emended Diagnosis: Teeth relatively low crowned; p3 trilobate; talonid of cheek teeth large; m3 not reduced and with a distinct hypoconulid; P4 not significantly smaller than M1; P4 crescentic valley with posterolabial extension; worn upper molar with circular central enamel lake.

Included Species: *Shamolagus medius* Burke, 1941 (see below for *S. ninae* Gabunia, 1984).

Locality and Age: Middle Eocene Ulan Shireh beds at the Chimney Butte locality, North Mesa, Shara Murun Region, Inner Mongolia; late middle Eocene Shara Murun Formation near Baron Sog, Inner Mongolia; middle Eocene of Heti Formation, Yuanqu, Shanxi Province.

Comments: *Shamolagus* represents one of the earliest lagomorph genus in Asia. The type species, *Shamolagus grangeri*, is based on a mandible with p4-m3 (holotype, AMNH 26289; Figures 1.6, 9.1-3) that came from "Ulan Shireh, Upper Eocene. Irdin Manha Beds" at the locality "Chimney Butte, North Mesa, Shara Murun Region, Inner Mongolia" (Burke 1941, p. 1). The Ulan Shireh beds at North Mesa of Shara Murun area were originally equated to the "Tukhum" Fm. (Berkey et al. 1929; Szalay and Gould 1966), but were also considered to be above the "Tukhum" Fm., underlying an unnamed sandy formation (Russell and Zhai 1987). In his faunal analysis, Ye (1983) used the term "Ulan Shireh beds" and thought that the Ulan Shireh fauna was a taphocoenosis of the Irdin Manha fauna. He did not explain why "beds" rather than "formation" was employed, but from the context it seems implied that the "Ulan Shireh beds" is part of the Irdin Manha Fm.

The holotype of *S. medius* (AMNH 26144; Figures 1.5, 9.4-6) is a fragmentary right mandible with p3-m1from Shara Murun Formation near Baron Sog, Inner Mongolia, and additional material was reported from the Ula Usu (Li 1965). *Shamolagus grangeri* and *S. medius* are similar in size and general tooth structures (Figure 9). Both are primitive in having relatively low-crowned teeth. An important character of *S. medius* is its trilobate p3 (Burke 1941; Li 1965; Figure 9.4). Other diagnostic features seem to be minor. Because p3 is not preserved in the holotype of *S. grangeri*, the difference between the two species is not fully revealed. The specimen from Ula Usu (Li 1965) and those from the Heti Formation (Tong 1997) assigned to *S. medius* and *S.* cf. *medius*, respectively, have a smaller m3 than that of *S. grangeri*. A reduced m3 with an indistinct hypoconulid lobe is by far the most convincing feature distinguishing *S. medius* from *S. grangeri*.

Isolated teeth assigned to *Shamolagus* sp. and *Shamolagus* cf. *medius* were also reported from the middle Eocene of Henan and Shanxi (Tong 1997).

Genus *HYPSIMYLUS* Zhai, 1977

Type Species: *Hypsimylus beijingensis* Zhai, 1977.

Emended Diagnosis: Large lagomorphs with hypsodont cheek teeth; the third lobe of p4-m3 distinct in relatively young individuals.

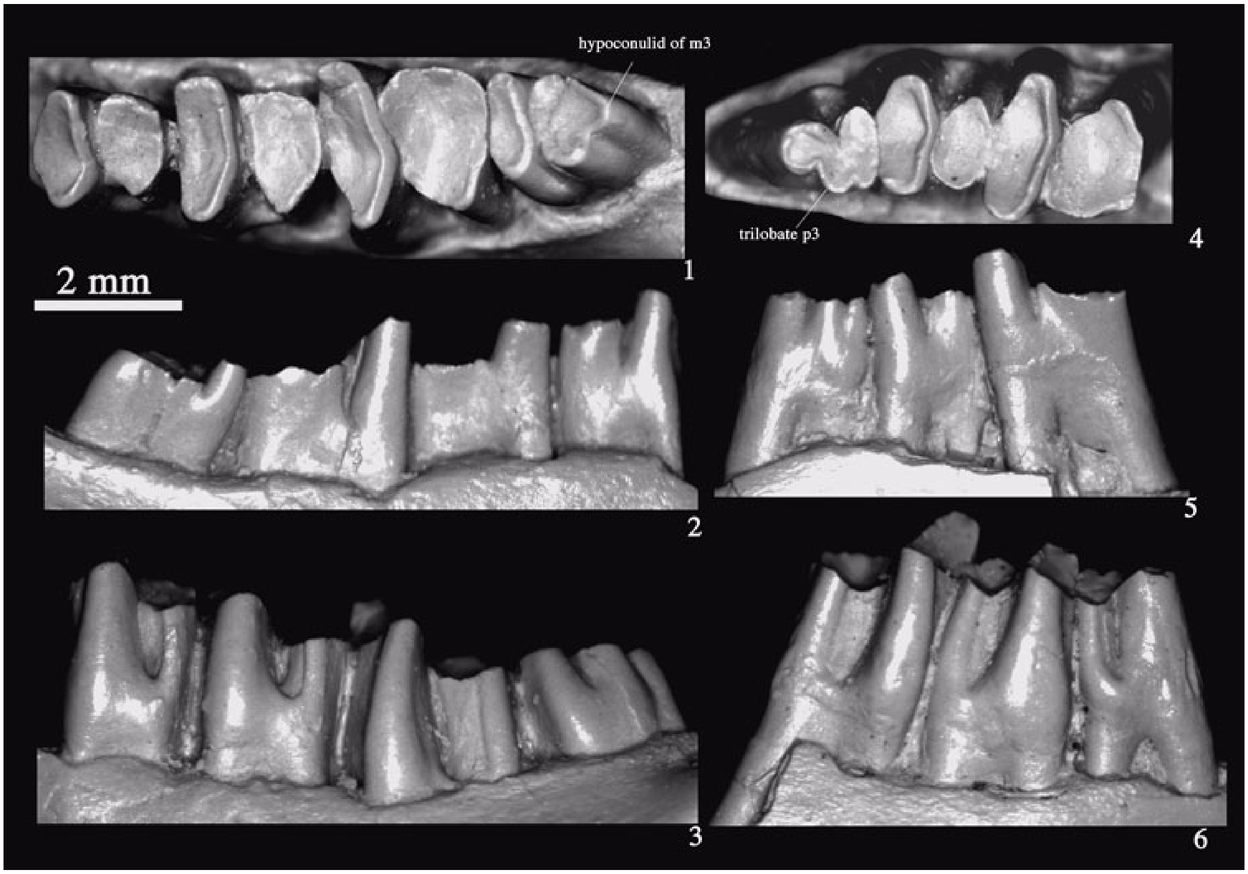

Figure 9. 1-3, Occlusal, medial and lateral views of the left p4-m3 of *Shamolagus grangeri* (holotype, AMNH 26289); **4-6,** Occlusal, medial and lateral views of the right p3-m1 of *Shamolagus medius* (holotype, AMNH 26144). Images taken from gray-toned casts.

Included Species: *Hypsimylus yihesubuensis* Meng and Hu, 2004. *Hypsimylus yihesubuensis* differs from *H. beijingensis* in being larger and having relatively lower crown height and wider m1 (Meng and Hu 2004).

Locality and Age: Late middle Eocene Changxindian Formation, Beijing; Yihesubu locality, Inner Mongolia; late Eocene.

Comments: The type species of the genus, *Hypsimylus beijingensis*, is based on lower teeth and was originally assigned to Eurymylidae because of the high-crowned cheek teeth that are somewhat similar to those of *Rhombomylus* (Zhai 1977). Although recognizing dental similarities between *Hypsimylus* and lagomorphs, Zhai (1977) noted that the cheek teeth of *Hypsimylus* are larger and more hyposodont than those of Eocene lagomorphs, and uniquely have a third lobe on lower cheek teeth. Li and Ting (1985) placed *Hypsimylus* in Mimotonidae. Dashzeveg and Russell (1988) found no significant character to indicate a relationship of *Hypsimylus* to mimotonids and established the subfamily Hypsimylinae under Eurymylidae. McKenna and Bell (1997) regarded *Hypsimylus* as a paleolagine lagomorph and placed it within Leporidae. Averianov (1998) considered that *Hypsimylus* is similar to *Valerilagus reshetovi* Shevyreva (1995; see below) and considered *Hypsimylus* as Lagomorpha incertae familiae. Meng and Hu (2004) described *Hypsimylus yihesubuensis* from the late Eocene Yihesubu locality and confirmed that *Hypsimylus* is not a eurymylid, but a lagomorph. The trilobate tooth pattern seen in *Hypsimylus* is not uncommon in lagomorphs; it is usually present on immature specimens, as noted in the North American *Megalagus turgidus* (Wood 1940) and *Palaeolagus philoi* (Dawson 1958).

Genus *DESMATOLAGUS*
Matthew and Granger, 1923

Type Species: *Desmatolagus gobiensis* Matthew and Granger, 1923.

Included Species: There are two Eocene species of the genus: *Desmatolagus vetustus* and *D. ardynense*.

Locality and Age: Eocene species are from Ulan Gochu beds, Jhama Obo, East Mesa, Shara Murun Region, Inner Mongolia; Ardyn Obo (Ergilin-Dzo), Mongolia; late Eocene.

Comments: Because the type species of the genus, *D. gobiensis*, is from the early Oligocene Hsanda Gol Formation, which is beyond the scope of this study, we do not provide a diagnosis for the genus except for the photographs of the type specimens of *D. gobiensis* (Figures 1.9, 10). About 10 species of *Desmatolagus* have been named from Asia and North America in various studies (Matthew and Granger 1923; Teilhard de Chardin 1926; Burke 1936, 1941; Bohlin 1937). Huang (1987) considered the taxonomic position of the North American *Desmatolagus* uncertain and concluded that there were five valid species of *Desmatolagus* in Asia, including *D. ardynense, D. vetustus, D. gobiensis, D. robustus,* and *D. pusillus*. The genus is mainly characterized by reduction of P2/p3 and M3/m3 (Huang 1987). Among these species, *D. vetustus* and *D. ardynense* (Burke 1941) are from late Eocene Ulan Gochu beds, Inner Mongolia and Ardyn Obo beds, Mongolia.

The holotype of *D. vetustus* (AMNH 26089; Figures 1.7, 10.1-3) from the Ulan Gochu beds, Jhama Obo, Inner Mongolia, is the earliest and most primitive species of *Desmatolagus* (Huang 1987). Because of its primitive low-crowned cheek teeth, this species has been removed from *Desmatolagus* and placed in *Procaprolagus* (Gureev 1960; Sych 1975; De Muizon 1977). 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 premolar foramen on the palate medial to the premolar, lack of the third loph 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. De Muizon (1977) synonymized *P. vetustus* with *Desmatolagus vetustus* and *P. radicidens* with *D. radicidens*, but Sych (1975) regarded these two species of *Dasmatolagus* as junior synonyms of *Desmatolagus gobiensis*. Huang (1987), following Sych (1975), synonymized *D. radicidens* with *D. gobiensis* but retained *D. vetustus* as a valid and primitive species of *Desmatolagus*; he considered the basic tooth pattern and reduction of terminal teeth in *D. vetustus* as typical of *Desmatolagus*. He also recognized that the premolar foramen is variably present within individuals of the same species, such as *D. pusillus*. Erbajeva and Sen (1998) again synonymized *Procaprolagus* with *Desmatolagus* and pointed out that the third lophid on the lower cheek teeth of some *Desmatolagus* is a juvenile feature, which is therefore not adequate to distinguish *Procaprolagus* as a different genus from *Desmatolagus*. In addition, we note that the enamel spike on the posterior wall of the trigonid is also present in the holotype of *D. vetustus* (Figure 11.1).

In a recent study on lagomorphs from the late Eocene of Inner Mongolia, Meng and Hu (2004) noted that differences of *D. vetustus* from other species of *Desmatolagus* are significant. In *D. vetustus* the lower teeth are relatively low crowned, with the hypostriid and the lingual groove shallow and above the alveolus. The height of cheek teeth decreases posteriorly to a lesser 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 premolar foramen is absent. In other species, including *D. gobiensis, D. robustus, D. pusillus,* and *D. ardynense*, the cheek teeth have much higher crowns and the hypostriid extends 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. The talonid is relatively wider. Although the differences are truly present, most of those listed for *D. vetustus* are primitive, except the relative narrower talonid. In addition, the posterior border of the palate is shifted more anteriorly than that in *D. gobioensis*. We follow Huang (1987) to recognize *D. vetustus*.

The holotype of *D. ardynense* (AMNH 20373; Figure 1.8, 10.4-6) is from Ardyn Obo, Mongolia. It was originally identified as *D. robustus* (Matthew and Granger 1925) and was later named as *D. ardynense* by Burke (1941). Matthew and Granger (1925) noted the “minute vestigial stump of a tooth” anterior to the alveolus of the p3, which was correctly indentified as the root of the dp3 (Burke 1941). The species is generally similar to *D. robustus* in morphology and size, but differs from the latter in having smaller p4, cheek teeth less compressed anteroposteriorly, and m1 the largest lower cheek tooth. Because the p3 and m3 are not preserved in the holotype, whether these teeth are reduced in size is unknown. In addition, because the specimen is from a relatively young individual, judging from retention of the dp3 root and presence of the posterior internal reentrant on m2, the features that distinguish the species from *D. robustus*, such as the relatively smaller p4 and longer talonid, may be age-related. Therefore, it is still possible

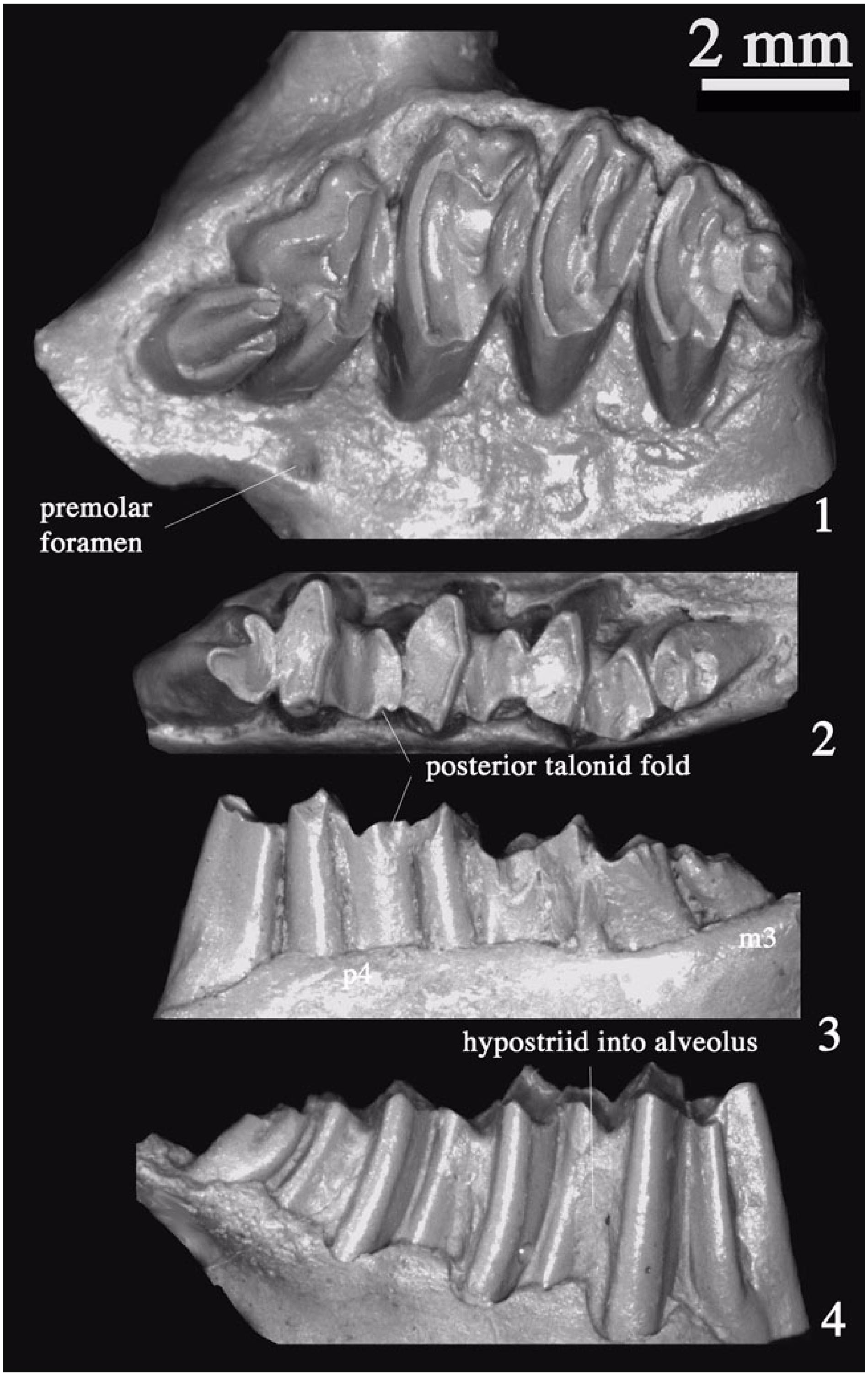

Figure 10. 1, Occlusal view of the left P2-M3 of *Desmatolagus gobiensis* (holotype, AMNH 19102); **2-4,** Occlusal, medial and lateral views of the right p3-m3 (holotype, AMNH 19102). Images taken from gray-toned casts.

that AMNH 20373 belongs to *D. robustus.* Nonetheless, this specimen represents a hypsodont species of lagomorph from the Eocene. Other species with similar hypsodonty are assigned to the genus *Hypsimylus*.

The age of Ardyn Obo beds is worth of a note. The "Ardyn Obo Formation" was proposed by Berkey and Granger (1923) and accepted thereafter (Berkey and Morris 1924, 1927). The locality, marked by the Ardyn Obo, was found at mile 487

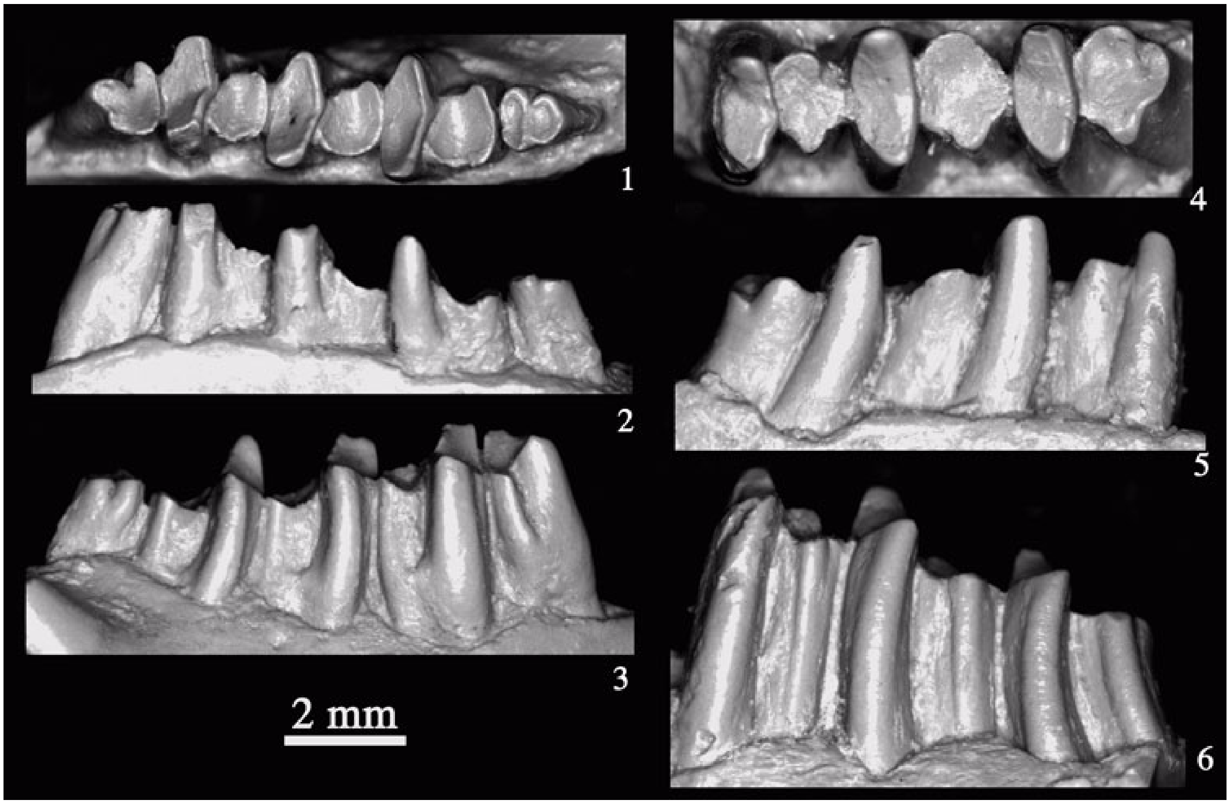

Figure 11. 1-3, Occlusal, medial and lateral views of the left p3-m3 of *Desmatolagus vetustus* (holotype, AMNH 26089); **4-6,** Occlusal, medial and lateral views of the right p4-m2 of *D. ardynense* (holotype, AMNH 20373). Images taken from gray-toned casts.

along the Kalgan-Uliasutai Trail (Berkey and Morris 1927, fig 84). Berkey and Morris (1927, p. 176) wrote: "The word 'ardyn,' meaning 'jewels,' proved to be the same word which we had spelled 'irdin' farther east. It refers to the glittering, highly polished pebbles of quartz and chalcedony which are found in the upper sandstones of the formation." The escarpment was afterwards explored more extensively by several expeditions during a 30 year period from 1946 to 1974 (Russell and Zhai 1987). The entire escarpment was then called the Ergilin Dzo, whereas the Ardyn Obo was equated to Ergil Obo. Russell and Zhai (1987) used "Ergilin-Dzo Svita" to include all the beds from the escarpment and cited *Desmatolagus robustus*, actually *D. ardynense,* as a member of the Ergilin-Dzo fauna. The Ergilin-Dzo fauna is now the basis for Ergilian, the late Eocene Asiatic land mammal age that has been widely recognized (Emry et al. 1998; Meng and McKenna 1998).

LAGOMORPHA incertae sedis

Several fragmentary specimens collected from the Eocene of Kazakhstan and Kyrgyzstan were assigned to various lagomorph species. The taxonomy of these species remains controversial, and the published data are insufficient to review them meaningfully. We only provide brief comments on their documentation.

Shamolagus ninae Gabunia (1984) is based on one m1 and one m2 from the late early or early middle Eocene Obaila Formation, at the Aksyir locality, Zaisan Basin, Kazakhstan. The teeth are small (m1 length / width, 1.8 x 2mm; m2, 1.8 x 1.9), brachydont, and are characterized by high and narrow trigonids, which are distinctive from other species of *Shamolagus*. Shevyreva (1996) regarded *S. ninae* a eurymylid, but Averianov (1998) considered it a lagomorph and treated the species as Lagomorpha incertae familiae because the poor specimens lack any diagnostic feature at the generic level.

Romanolagus hekkeri and *Valerylagus reshetovi*, purported lagomorphs, were mentioned by Shevyreva (1994) but were described in Shevyreva (1995), in which the latter species was spelled as *Valerilagus reshetovi.* The specimens of the two taxa are from the middle Eocene or possibly latest early Eocene Andarak 2 locality, Kyrgyzstan (Shevyreva 1995; Averianov 1998; Averianov and Godinot 1998). *Romanolagus hekkeri* is based on a maxillary fragment with M1. Averianov (1998, p.

207) noted that "the holotype of *R. hekkeri* could not be distinguished by the size or morphology from the known upper molars of the mimotonid *Anatolimys rozhdestvenskii* described from the same locality." Thus, Averianov (ibid.) regarded *R. hekkeri* a junior subjective synonym of *A. rozhdestvenskii*, a mimotonid. *Valerilagus reshetovi* is based on a fragmentary maxilla with labial portions of P3-4. Additional specimens are available from the Andarak 2 locality (Averianov 1996) but have not been described to our knowledge. *Valerilagus reshetovi* was placed in Mytonolagidae (Averianov 1996; Averianov and Godinot 1998), but the family is treated as a synonym of Leporidae (McKenna and Bell 1997). The line drawing of the holotype of *V. reshetovi* (Shevyreva 1995, figure 1) convincingly shows lagomorph morphology, as endorsed by Averianov and Godinot (1998).

Annalagus margarita is based on several isolated teeth from the late Eocene Aksyir Formation, Baldys, Zaisan depression, Kazakhstan (Shevyreva 1996). The holotype of the species is a dp3. The species was assigned to Amphilaginae, Palaeolagidae, Lagomorpha. Averianov (1998, p. 207) argued that dp3 is insufficient to diagnose the species and thus regarded *Annalagus margarita* Shevyreva, 1996 as a *nomen dubium* and suggested that the species "could be provisionally referred to the family 'Mytonolagidae' (paraphyletic group)."

CONCLUSIONS

The 21 lagomorph specimens collected in 1925 by the Central Asiatic Expedition from the late middle Eocene Shara Murun Formation at Ula Usu, Shara Murun Region of Inner Mongolia, are described. Among these specimens, two (AMNH 141275-6) are assigned to a new species, *Gobiolagus burkei* and the rest to *G. tolmachovi.* These specimens add to the Asian Eocene lagomorph diversity and to the morphology of known species.

Nine genera of lagomorphs are known from Asian Eocene beds, including *Lushilagus, Shamolagus, Gobiolagus, Hypsimylus, Strenulagus, Dituberolagus, Valerilagus, Annalagus,* and *Desmatolagus*. Most of the species are based on fragmentary specimens, and many original descriptions of these taxa are brief and poorly illustrated, which has caused difficulties and uncertainties in identification and taxonomy of the early lagomorphs in Asia. Thus, in addition to description of the new specimens from Ula Usu, we provide a brief review of the Eocene lagomorphs from Asia and comment on age issues for some of the localities. For some genera and species for which we have access to the type specimens, we provide emended diagnoses so that these species can be better characterized. Along with the diagnoses, we present photographs of the holotypes that are housed in the AMNH, in the hope that these images will help to identify and distinguish species of early lagomorphs in the future.

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