

Eocene Lagomorpha (Mammalia) of Asia: 2. *Strenulagus* and *Gobiolagus* (Strenulagidae)

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Abstract—Two species of early lagomorph, *Strenulagus solaris* sp. nov. (Mongolia, Khaychin-Ula 2 and 3 localities, Middle Eocene) and *Gobiolagus hekkeri* (Kyrgyzstan, Andarak 2 locality, terminal Lower Eocene), are described. A revision of *Romanolagus hekkeri* Shevyreva from the Andarak 2 locality has shown that it belongs to the genus *Gobiolagus*; consequently, the monotypic genus *Romanolagus* Shevyreva, 1995 is a junior synonym of *Gobiolagus* Burke, 1941. The diagnoses and species compositions of the genera *Strenulagus* and *Gobiolagus* are revised. *Zaissanolagus gromovi* Erbajeva from the Lower Oligocene of eastern Kazakhstan is shown to be the latest representative of the genus *Gobiolagus* and the family Strenulagidae.

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Key words: Lagomorpha, Strenulagidae, *Strenulagus*, *Gobiolagus*, Eocene, Asia.

INTRODUCTION

The present study continues a series of publications devoted to Eocene Asian Lagomorpha (see Averianov and Lopatin, 2005) and describes new material of the genera *Strenulagus* and *Gobiolagus*.

The specimens examined are housed in the Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN); Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIN); and Chernyshev' Central Museum of Geological Exploration, St. Petersburg (TsNIGR Museum) in St. Petersburg. The nomenclature of elements of the occlusal surface of early lagomorphs and the set of dental measurements taken by us were described in the previous paper (Averianov and Lopatin, 2005). All measurements are given in mm. Dentin is indicated in the figures in gray.

SYSTEMATIC PALEONTOLOGY

Order Lagomorpha

Family Strenulagidae Averianov et Lopatin, 2005

Genus *Strenulagus* Tong et Lei, 1987

Strenulagus: Tong and Lei, 1987, p. 208.

Type species. *Strenulagus shipigouensis* Tong et Lei, 1987; Middle Eocene of China.

Diagnosis. The genus is characterized by the following combination of (–) primitive and (+) derived characters and (?) characters of uncertain polarity. Anterior edge of zygomatic process of maxilla located in line with point between P³ and P⁴ (+), posterior edge of this process located in line with M¹ (+). Premolar

foramen undeveloped (+). P² relatively large (–). P³ and P⁴ similar in structure (–), with one labial root and well-pronounced centrocone, which is larger in P⁴ (–). M³ with one labial root, relatively small, two-thirds of the size of M² (+). Anterior mental foramen located under P₃ (–), posterior mental foramen under M₁ (–). Coronoid process gently sloping (–). Lower incisor originating under middle of M₂ (+). Lower cheek teeth with relatively high crowns (+) and distinct unilateral hypsodonty (+). P₃ with one external and two internal folds; in worn tooth, external and anterointernal folds retained (?). Hypoconulid of P₄–M₂ disappearing at early stages of wear (+); in M₃, it retained at later wear stages (–). In M₁, trigonid and talonid connected by lingual bridge formed at relatively early ontogenetic stage (+). M₂ somewhat larger than M₁ (+), M₃ slightly smaller than other lower molars (+).

Species composition. *S. shipigouensis* Tong et Lei, 1987, Middle Eocene (Irdinmanhan) of China; *S. solaris* sp. nov., Middle Eocene (Irdinmanhan) of Mongolia.

Comparison. *Strenulagus* differs from *Lushilagus* Li, 1965 in the more developed unilateral hypsodonty of teeth (+) and the more anterior position of the posterior edge of the zygomatic process of maxilla (+) (in *Lushilagus*, it is in line with M¹/M²). It differs from *Aktashmys* Averianov, 1994 (= *Valerilagus* Shevyreva, 1995) in the more anterior position of the posterior edge of the zygomatic process (+), the absence of large pre-molar foramen (+), symmetrical cross section of I² (?), more reduced M³ (+), and the absence of a lingual fold between the trigonid and talonid of P₄–M₃ at late wear

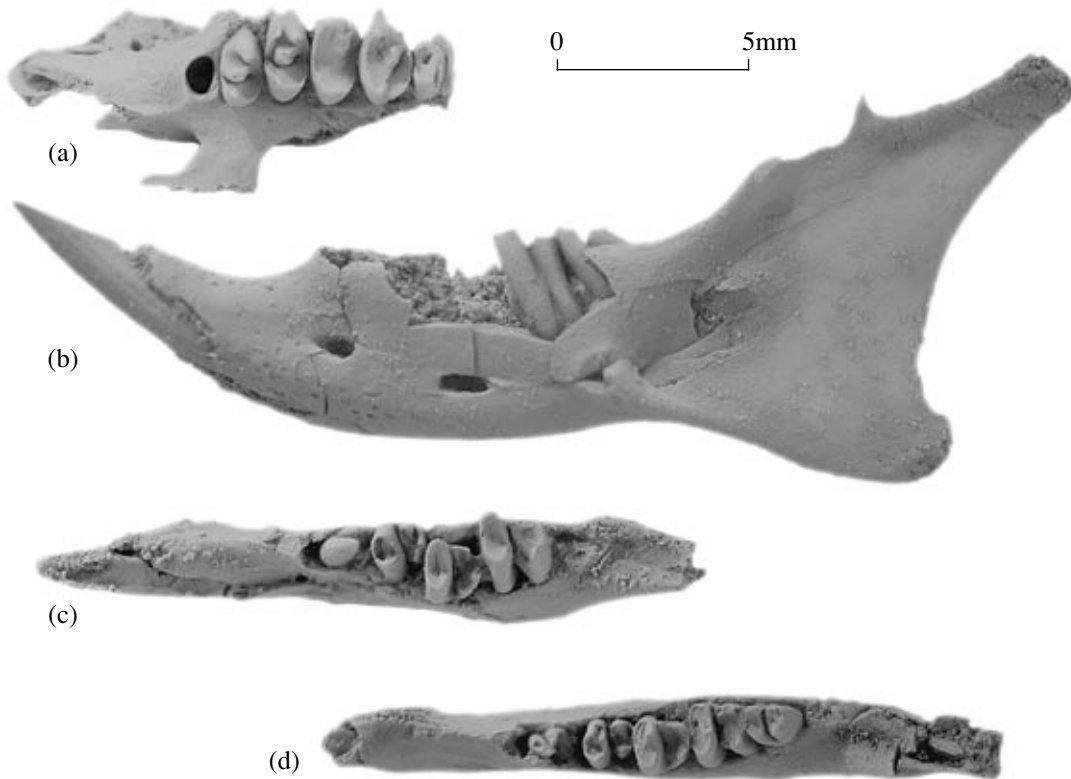


Fig. 1. *Strenulagus solaris* sp. nov.: (a) holotype PIN, no. 3403/304, left maxilla with P^3 – M^3 and alveolus of P^2 ; (b) specimen PIN, no. 3403/301, left dentary with incisor, M_2 – M_3 , and completely preserved articular and angular processes; (c) specimen PIN, no. 3403/303, left dentary fragment with incisor and P_3 – M_2 ; and (d) specimen PIN, no. 3403/302, left dentary fragment with P_3 – M_3 ; Mongolia, Khaychin-Ula 3 locality; Middle Eocene.

stages (+). It differs from *Gobiolagus* Burke, 1941 in the more anterior position of the posterior edge of the zygomatic process (+), in the positions of the mental foramina (–) and the base of the incisor (+), and in the nonreduced talonid of P_4 (–). The coronoid process of the dentary is more gently sloping (–), the hypoconulids more rapidly disappear as a result of wear (+), M_1 and M_2 are more similar in size (–), and M^3 is reduced to a lesser extent (–), than in *Shamolagus* Burke, 1941.

Remarks. The original description of *Strenulagus* lacks precision in certain respects. The tooth that was determined as left P^3 (Tong and Lei, 1987, text-fig. 3A) is in fact right M^2 . P^4 that was referred to *Lushilagus danjiangensis* (Tong and Lei, 1987, text-fig. 4B) in fact belongs to *Strenulagus shipigouensis*. A fragment of the presumed upper deciduous tooth referred to *L. danjiangensis* (Tong and Lei, 1987, text-fig. 6) is most likely an unworn crown of right P^4 of *S. shipigouensis*.

Strenulagus solaris Lopatin et Averianov, sp. nov.

Lagomorpha indet.: Reshetov, 1974, p. 159; Badamgarav and Reshetov, 1976, p. 265; Russell and Zhai, 1987, p. 143.

Lagomorpha gen. et sp. nov.: Badamgarav and Reshetov, 1985, pp. 43, 44, and 49.

Etymology. From the Latin *solaris* (solar).

Holotype. PIN, no. 3403/304, left maxilla with P^3 – M^3 and alveolus of P^2 ; Mongolia, Khaychin-Ula 3 locality; Middle Eocene, Khaychin Formation.

Description (Figs. 1–4). The bony palate is long; at the level of P^3 , its maxillary part is more than twice as long as the tooth. The posterior edge of the incisive foramen is in line with the middle of the alveolus of P^2 . Anteriorly, the suture between the palatine and the maxilla reaches the level of the anterior edge of P^4 .

Judging from the alveolus, P^2 was approximately half as wide as P^3 . P^3 and P^4 have one large labial root. The centrocone of P^3 is large, transversely compressed. The mesoflexia is much shorter than the paraflexia. The anteroloph is very short. The anterolabial cusp is absent. P^4 is distinguished by the greater width, the more massive, rounded, centrally positioned centrocone, the longer anteroloph, and the presence of a well-developed anterolabial cusp.

M^1 and M^2 have two labial roots each and a rudimentary hypostria. The occlusal surface of M^1 is symmetrical. Only a small site, the external sides of the labial cusps and the fold between them, are not worn. In the center of the occlusal surface, there is a sign of an enamel lake that probably corresponds to the deepest

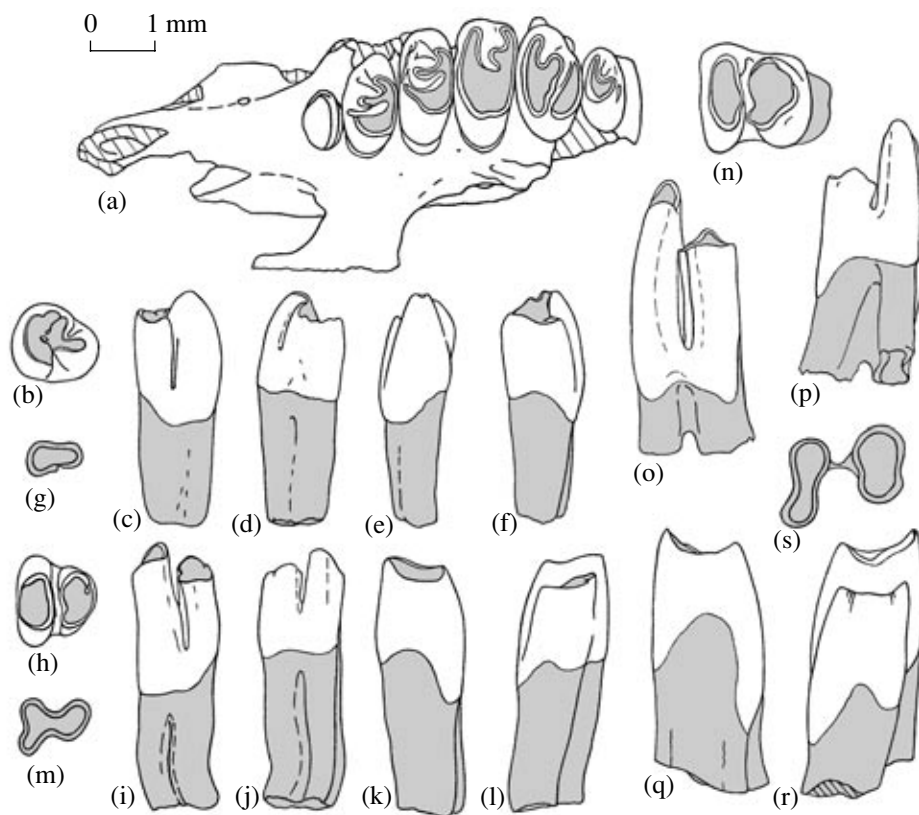


Fig. 2. *Strenulagus solaris* sp. nov.: (a) holotype PIN, no. 3403/304, left maxilla with P^3 - M^3 and alveolus of P^2 ; Mongolia, Khaychin-Ula 3 locality; Middle Eocene; (b-g) specimen PIN, no. 3107/450, right P_3 : (b) occlusal, (c) labial, (d) lingual, (e) anterior, (f) posterior, and (g) root views; (h-m) specimen PIN, no. 3107/451, left P_4 : (h) occlusal, (i) labial, (j) lingual, (k) anterior, (l) posterior, and (m) root views; (n-s) specimen PIN, no. 3107/453, left M_2 : (n) occlusal, (o) labial, (p) lingual, (q) anterior, (r) posterior, and (s) root views; Mongolia, Khaychin-Ula 2 locality; Middle Eocene.

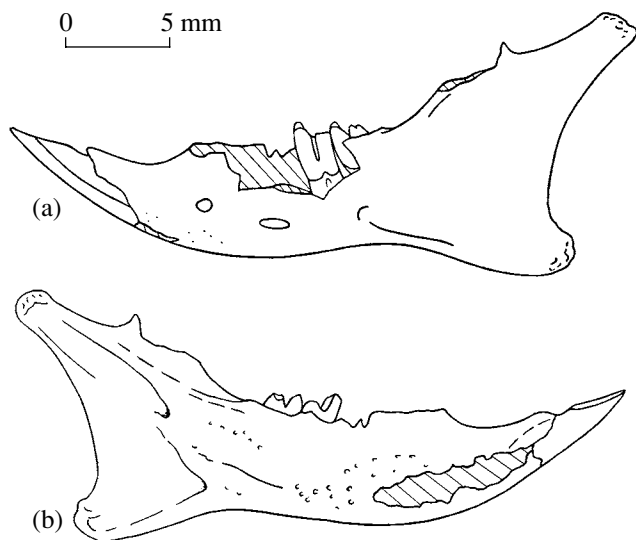


Fig. 3. *Strenulagus solaris* sp. nov., specimen PIN, no. 3403/301, left dentary with incisor, M_2 , M_3 , and completely preserved articular and angular processes: (a) labial and (b) lingual views; Mongolia, Khaychin-Ula 3; Middle Eocene.

part of the fold between the trigon and the postcingulum, which is obliterated by wear. M^2 is asymmetrical, has a large postcingulum separated from the trigon by a deep labial fold. The paracone is separated from the metacone by a small, deep fold.

M^3 is reduced, approximately two-thirds as long and two-thirds as wide as M^2 . The occlusal surface is oval in shape, the postcingulum is rudimentary, in the shape of a small projection separated from the trigon by a small fold. The paracone and metacone are widely separated by a deep labial fold, the metacone is displaced to the center of the occlusal surface. Only one labial root is present.

The lower jaw is relatively low. The diastema is short, a little more than half the length of the tooth row. The symphysis is weak, less than half as long as the diastema. The anterior mental foramen is large, circular, located close to the midheight of the horizontal ramus, in line with the anterior region of P_3 . The posterior mental foramen is larger, oval in shape, located under M_1 or the space between P_4 and M_1 , and approaches the ventral edge of the horizontal ramus. The middle region of the lingual surface of the horizon-

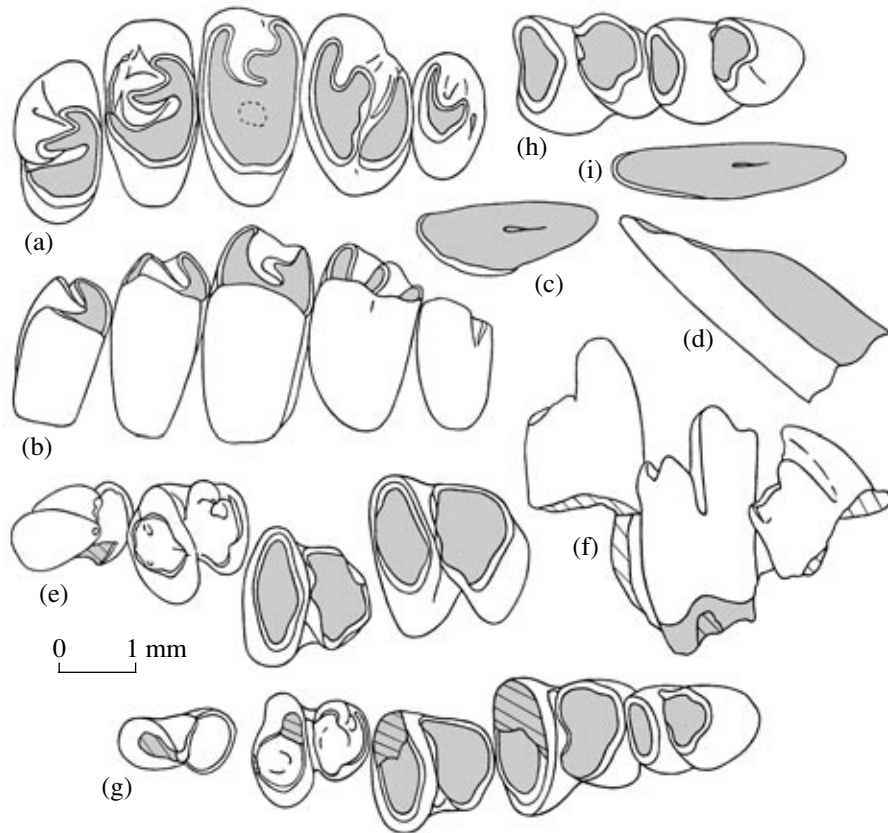


Fig. 4. *Strenulagus solaris* sp. nov.: (a, b) holotype PIN, no. 3403/304, left P^3 – M^3 : (a) occlusal and (b) lingual views; (c–f) specimen PIN, 3403/303, left dentary fragment with incisor and P_3 – M_2 : (c, d) lower incisor: (c) grinding surface and (d) labial view; (e) P_3 – M_2 , occlusal surface; and (f) P_3 – M_1 lingual view; (g) specimen PIN, no. 3403/302, left P_3 – M_3 ; (h, i) specimen PIN, no. 3403/301, left dentary with incisor, M_2 , and M_3 ; Mongolia, Khaychin-Ula 3 locality; Middle Eocene.

tal ramus is covered with numerous small nutrient foramina.

The ascending ramus is relatively low and short, the angular department is only slightly enlarged (Fig. 3). At the base of the coronoid process, the angle between the horizontal and ascending rami is approximately 130° . On the ventral side, the transition from the ascending ramus to the horizontal ramus is in the shape of a gentle bend. The masseteric fossa is generally superficial; however, it is more prominent in the anterior part because of a well-pronounced depression, a distinct lower masseteric crest, and the masseteric tubercle located in line with M_3 . The apex of the coronoid process is broken off, but its posterior base and the incisure between the coronoid and articular processes are preserved, suggesting the presence of a long dorsal projection, which was completely lost in advanced Lagomorpha (earlier, the presence of this structure in primitive Eocene lagomorphs has not been recorded). On the ventral side, the base of the coronoid process is bordered by a sharp crest descending to the horizontal ramus. The articular process ascends at an angle of approximately 30° . The condyle is relatively small, with a slightly elongated head. On the medial side, the

articular process has a narrow depression for the external pterygoid muscle, which terminates anteroventrally in the mandibular foramen located somewhat lower than the alveolar edge of the jaw. The posterior incisure between the articular and angular processes is superficial. The angular process is small, extended ventrally (its distal end is lower than the ventral edge of the horizontal ramus), and slightly curved, reaching caudally the level of the middle of the condylar neck. The medial surface of the angular process has an extensive triangular depression for the internal pterygoid muscle.

The lower incisor reaches caudally the middle of M_2 ; it is strongly transversely flattened, with an almost flat lingual side and a slightly convex labial side. Enamel is only observed on the anterolabial surface.

An unworn P_3 (in specimens PIN, nos. 3403/302 and 303, P_3 is incompletely erupted) has a prismatic talonid and a considerably higher dipetalous trigonid composed of a conical anterior cusp and a bladelike posterior cusp, which projects lingually (Figs. 4e–4g). Thus, the tooth initially has three deep folds: the labial and lingual folds are between the talonid and trigonid and the anterolingual fold is between the conids of the trigonid (traditionally, they are named the posteroexter-

Table 1. Measurements of the upper cheek teeth of *Strenulagus solaris* sp. nov.; Khaychin-Ula 3, Mongolia; Khaychin Formation, Middle Eocene

Specimen	P ³		P ⁴		M ¹		M ²		M ³	
	L	W	L	W	L	W	L	W	L	W
Holotype PIN, no. 3403/304	1.1	2.0	1.2	2.2	1.3	2.5	1.45	2.3	0.9	1.65

nal, posterointernal, and anterointernal folds, respectively). In addition, the posterolingual surface of the talonid of an unworn tooth has a short groove that marks the anterior boundary of the hypoconulid (Fig. 4f). In a slightly worn tooth, the labial and anterolingual folds are retained, whereas the lingual fold becomes closed (Fig. 2b); as a result, the talonid becomes fused with the posterior conid of the trigonid, forming an integral posterior lobe. Judging from the length of the respective grooves on the lateral sides of the crown (Figs. 2c, 2d), the labial and anterolingual folds are also retained in heavily worn teeth, separating the anterior lobe from the posterior lobe. The roots of P₃ are fused and have a common pulp canal (Fig. 2g).

P₄–M₃ are positioned at an angle to the jaw, so that the anterior inclination increases posteriorly. In P₄–M₃, the trigonid is substantially higher and wider than the talonid, while the metaconid is higher than the protoconid. The trigonid and talonid are connected in the central part, the lingual bridge is formed in considerably worn teeth.

In P₄, the trigonid and talonid differ in width to a greater extent than in molars. An unworn P₄ (specimens PIN, nos. 3403/302 and 303) retains rudimentary cusps on the occlusal surface (Figs. 4e–4g), demonstrating a small trigonid basin bordered by crests of the paracristid and protocristid and the cusps of the protoconid and metaconid. The talonid has a prominent conical entoconid, a flat angular hypoconid, and a wide hypoconulid, which is outlined by a small labial groove and a well-developed, though shallow, lingual fold. As the tooth is worn, the occlusal surface becomes flat; the posterolingual fold on the talonid is retained for a

longer time than the other elements described. The roots of P₄ and their pulp canals are fused (Fig. 2m).

M₁–M₃ are massive, M₂ is substantially larger than the other molars (Figs. 4e, 4g). Occasionally, M₃ is considerably reduced or, despite the reduction of its talonid, is almost equal in length to M₂ (Figs. 4g, 4h). The talonid of M₁ and M₂ is slightly longer and substantially narrower than the trigonid. In M₃, the talonid is substantially longer and slightly narrower than the trigonid. The pulp canals of all molars are isolated, although the roots are connected by bony bridges (Figs. 2o, 2p, 2s).

Measurements. Length of P³–M³, 6.0; alveolar length of P²–M³, 7.0 (holotype). Length of P₃–M₃, 7.8 (specimen PIN, no. 3403/302). Dentary length (from the anterior edge of the incisor to the condyle), approximately 23.5; the greatest distance between the apices of the articular and angular processes, 12.3 (specimen PIN, no. 3403/301). Length × width of the wear facet of the lower incisor, 3.0 × 0.75 (specimen PIN, no. 3403/301) and 2.25 × 1.0 (specimen PIN, no. 3403/303). Dentary depth at P₃, 4.7 (specimen PIN, no. 3403/302) and 4.8 (specimen PIN, no. 3403/301). For the measurements of the cheek teeth, see Tables 1 and 2.

Comparison. The new species differs from the type species in the size of P₃ (in *S. shipigouensis*, it is 30% shorter) and in the absence of anterolabial cusp on P³. The two species are almost identical in the structure of the cheek teeth (see Tong and Lei, 1987, text-figs. 1, 2, pl. 1; Tong, 1997, text-fig. 27, pl. 4, figs. 1–4).

Remarks. The extremely primitive structure of the dentary, in particular, the gently sloping ascending ramus (in *Shamolagus*, it ascends abruptly, see Li, 1965, pl. I, fig. 4), and the dorsal projection of the coronoid process, is evidence that *Strenulagus* represents a very early stage of the formation of a masticatory apparatus that is characteristic of lagomorphs.

Material. In addition to the holotype, the type locality yielded a left dentary with incisor, M₂, M₃, and complete articular and angular processes (specimen PIN, no. 3403/301); left dentary with P₃–M₃ (specimen PIN, no. 3403/302); and left dentary with incisor and P₃–M₂ (specimen PIN, no. 3403/303). The Khaychin-Ula 2 locality (Khaychin Formation) of the same age

Table 2. Measurements of the lower cheek teeth of *Strenulagus solaris* sp. nov.; Khaychin-Ula 2 (collection PIN, no. 3107) and Khaychin-Ula 3 (collection PIN, no. 3403), Mongolia; Khaychin Formation, Middle Eocene

Specimen	P ₃		P ₄		M ₁		M ₂		M ₃	
	L	W	L	W	L	W	L	W	L	W
PIN, no. 3107/450	1.8	1.6								
PIN, no. 3107/451			1.8	1.9						
PIN, no. 3403/302	>1.4	>0.9	1.55	1.4	1.5	1.55	1.65	1.8	1.2	1.2
PIN, no. 3403/303	>1.5	>1.0	1.55	1.6	1.6	1.65	1.85	1.9		
PIN, no. 3107/452							2.25	2.4		
PIN, no. 3403/301							1.75	1.45	1.75	1.35

yielded three isolated teeth: right P_3 (specimen PIN, no. 3107/450); left P_4 (specimen PIN, no. 3107/451); and left M_2 (specimen PIN, no. 3107/452). The specimens were collected by V.Yu. Reshetov (PIN, Joint Soviet–Mongolian Paleontological Expedition) in 1973.

Genus *Gobiolagus* Burke, 1941

Gobiolagus: Burke, 1941, p. 5; Gureev, 1964, p. 94; McKenna and Bell, 1997, p. 111.

Romanolagus: Shevyreva, 1995, p. 377.

Zaissanolagus [nomen nudum]: Erbajeva and Tyutkova, 1997, p. 211.

Zaissanolagus: Erbajeva, 1999, p. 84.

Zaysanolagus: Tyutkova *et al.*, 2003, p. 361.

Type species. *Gobiolagus tolmachovi* Burke, 1941, Middle Eocene of China.

Diagnosis. The genus is characterized by the following combination of (–) primitive and (+) derived characters and (?) characters of uncertain polarity. Anterior edge of zygomatic process of maxilla located in line with anterior edge of P^4 (+), posterior edge located between M^1 and M^2 (–) or slightly anterior to this point (+). In region of molars, labial edges of maxilla and tooth row oriented posterolingually (?). P^2 relatively small (–). P^3 and P^4 similar in structure (–). M^3 relatively large (–); in unworn condition, probably with distinct postcingulum (–). Anterior mental foramen in line with diastema of dentary, closer to alveolus of incisor (+), posterior mental foramen in line with P_4 or M_1 (–). Lower incisor originating under M_1 – M_2 (–). Lower cheek teeth with well-developed unilateral hypsodonty (+) and relatively high crowns (+). In worn P_3 , only posteroexternal fold preserved (?). Talonid of P_4 strongly reduced (+). Trigonid and talonid of P_4 – M_2 connected by lingual bridge at early stages of wear (+). Hypoconulid of P_4 – M_3 disappearing early in ontogeny (+). Trigonid of lower molars substantially wider than talonid (–). M_1 and M_2 almost equal in size (+), while M_3 somewhat smaller (+).

Species composition. *G. tolmachovi* Burke, 1941, Middle Eocene (Sharamurunian) of China; *G. hekkeri* (Shevyreva, 1995), terminal Lower Eocene (Irdinmanhan) of Kyrgyzstan; *G. lii* Zhang *et al.*, 2001, Middle Eocene (Irdinmanhan) of China; *G. andrewsi* Burke, 1941, Upper Eocene (Ulangochuian) of China; *G. major* Burke, 1941, Upper Eocene (Ulangochuian) of China; and *G. gromovi* (Erbajeva, 1999), Lower Oligocene (Shandgolian) of Kazakhstan. In addition, the small-sized *Gobiolagus* sp. recorded by Erbajeva and Tyutkova (1997) in the Middle Oligocene and Lower Miocene of Kazakhstan.

Comparison. *Gobiolagus* differs from all Strenulagidae in the position of the labial edge of the maxilla and the tooth row which are directed posterolingually in the region of the molars (?). In addition, it differs from *Lushilagus* in the better developed unilateral hypsodonty (+); from *Aktashmys* in the absence of lingual fold between the trigonid and talonid of P_4 – M_3 at late ontogenetic stages (+) and in the symmetrical

cross section of I^2 (?); from *Strenulagus*, in the more posterior position of the posterior margin of the zygomatic process (–), the positions of the mental foramina (+) and the base of the incisor (–), and in the unreduced talonid of P_4 (+); from *Shamolagus*, in the rapid wear of the hypoconulids (+), more similar sizes of M_1 and M_2 (–), and better developed M^3 (–).

Remarks. P^4 of specimen IVPP, no. V8430 of *G. tolmachovi* from the Shara Murun locality (Qi, 1988, text-fig. 1) is usually considered to be molariform (Qi, 1988, p. 224; Zhang *et al.*, 2001, p. 258). However, this tooth is extremely heavily worn and may have been nonmolariform. Nonmolariform P^4 is characteristic of all species of this genus in which this tooth has been examined (*G. hekkeri*, *G. lii*, and *G. gromovi*), as in the other Strenulagidae; therefore, this character is considered typical for the genus. P^3 and P^4 of *Gobiolagus* have one or two labial roots (see Meng and Hu, 2004).

The holotype of *G. andrewsi* is very similar in size and structure to the holotype of *G. tolmachovi* and differs primarily in the deeper dentary, which is possibly accounted for by age variation. Other characters distinguishing the two species are subject to individual variation. Thus, *G. andrewsi* Burke, 1941 is possibly a junior synonym of *G. tolmachovi* Burke, 1941.

Zaissanolagus gromovi Erbajeva, 1999 was originally described based on isolated upper teeth from the Lower Oligocene Buran Formation of the Zaisan Depression, Kazakhstan. The lower teeth of leporids from the type locality Podorozhnik were determined by Erbajeva as *Gobiolagus* sp. and *Gobiolagus* cf. *major*. In the original description, the holotype of *Z. gromovi* was determined as P^3 . However, judging from the absence of metastria, the presence of the anterolabial cusp, and the relatively large width of the tooth crown, this is P^4 . A tooth with “three conids” and two roots that was determined in the original description as P^2 (IZK [Institute of Zoology and Animal Gene Pool, Ministry of Sciences–Academy of Sciences of Republic of Kazakhstan], no. 35(15)816; Erbajeva, 1999, text-figs. 1d, 1e) is probably P^3 . In addition, Erbajeva assigned another right P^4 to this species (Erbajeva, 1999, text-figs. 1c, 1f). This heavily worn tooth most likely belongs to the genus *Desmatolagus* Matthew et Granger, 1923. P^3 and P^4 of “*Zaissanolagus*” *gromovi* and lower molars, including M_3 , that were assigned by Erbajeva to *Gobiolagus* are structurally identical to the respective teeth of *Gobiolagus* and differ only in the presence of cement, which is possibly a derived character of the Oligocene species. We believe that *Zaissanolagus* Erbajeva, 1999 is possibly a junior synonym of *Gobiolagus* Burke, 1941.

Gobiolagus hekkeri (Shevyreva, 1995)

Romanolagus hekkeri: Shevyreva, 1995, p. 377, text-figs. 1a–1c; Averianov, 1998, p. 206.

Strenulagus hekkeri: Lopatin, 2004, p. 92.

Holotype. PIN, no. 3486/200, right maxilla fragment with M^2 ; Kyrgyzstan, Batken Region, 3 km north-

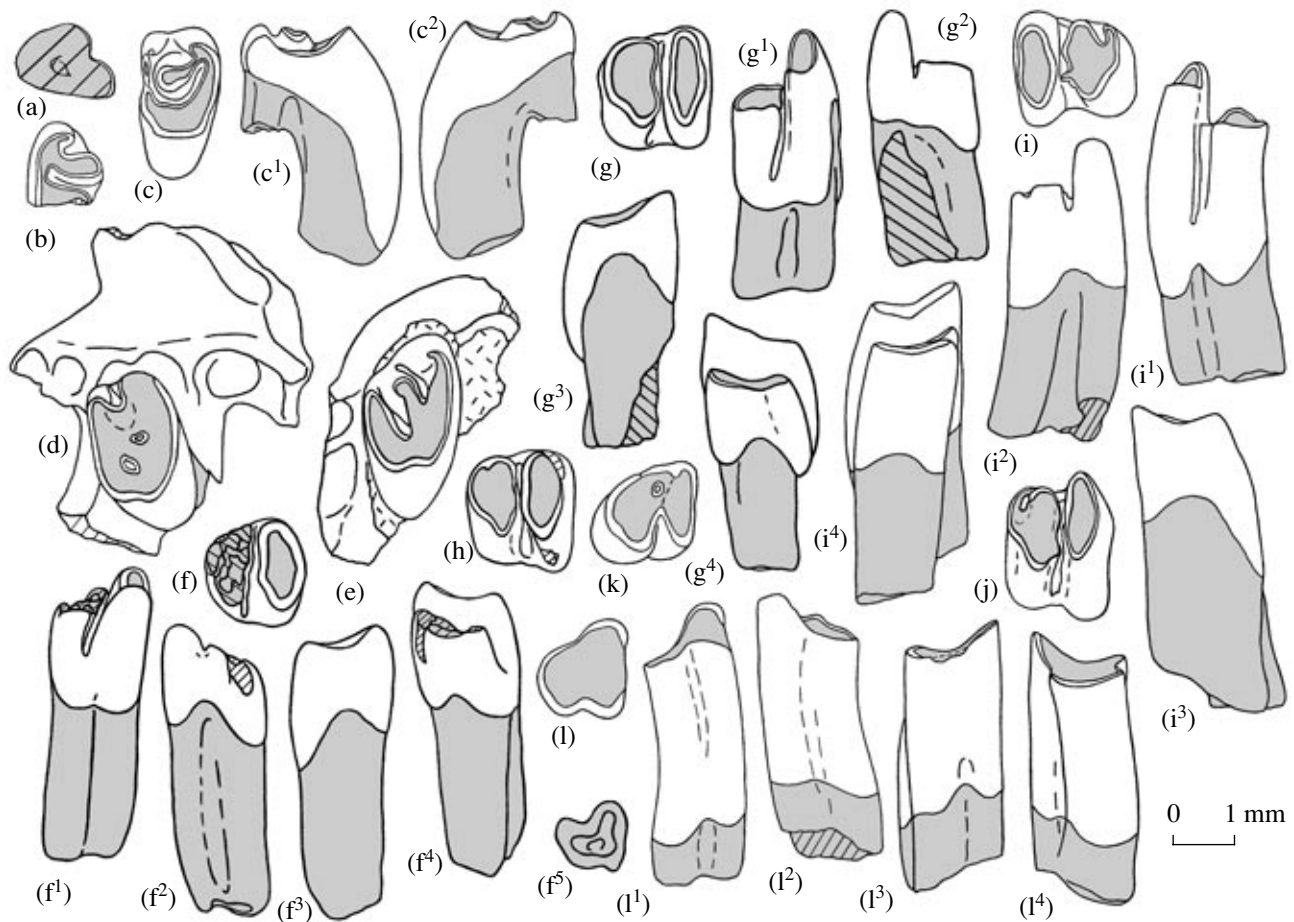


Fig. 5. *Gobiolagus hekkeri* (Shevyreva, 1995): (a) specimen PIN, no. 3486/31, right I²; (b) specimen ZIN, no. 88806, right P³; (c–c²) specimen ZIN, no. 79205, left P⁴: (c) occlusal, (c¹) anterior, and (c²) posterior views; (d) specimen ZIN, no. 79182, right maxilla fragment with M¹; (e) holotype PIN, no. 3486/200, right maxilla fragment with M²; (f–f⁵) specimen PIN, no. 3486/169, right P⁴: (f) occlusal, (f¹) labial, (f²) lingual, (f³) anterior, (f⁴) posterior, and (f⁵) root views; (g–g⁴) specimen PIN, no. 3486/146, right M¹: (g) occlusal, (g¹) labial, (g²) lingual, (g³) anterior, and (g⁴) posterior views; (h) specimen PIN, no. 3486/170, right M¹; (i–i⁴) specimen ZIN, no. 79184, left M²: (i) occlusal, (i¹) labial, (i²) lingual, (i³) anterior, and (i⁴) posterior views; (j) specimen PIN, no. 3486/193, right M²; (k) specimen ZIN, no. 79193, right M³; (l–l⁴) specimen ZIN, no. 79175, right M³: (l) occlusal, (l¹) labial, (l²) lingual, (l³) anterior, and (l⁴) posterior views; Kyrgyzstan, Andarak 2 locality; uppermost Lower Eocene.

east of the village of Andarak, Andarak 2 locality; Lower Eocene, Upper Ypresian, basal part of the Alai Beds.

Description (Fig. 5). The base of the zygomatic process of the maxilla is relatively narrow. The anterior margin of the zygomatic process is abrupt and originates in line with the anterior edge of P⁴. The crest for fibers of the profound portion of the masseter is stout and positioned obliquely to the tooth row. The posterior margin of the zygomatic process is in line with the point between M¹ and M² (specimen ZIN, no. 79182) or slightly anterior to this position (holotype). In the region of molars, the labial edge of the tooth row is positioned posterolingually, which is characteristic of the genus (Figs. 5d, 5e).

I² is slightly mesiodistally flattened, triangular in cross section (Fig. 5a). The groove on the anterior side lacks cement, positioned at the middle of the tooth; therefore, the mesial and distal lobes are almost equal in size. The enamel covers only the anterior side of the incisor.

In a worn D³, the centrocone is almost completely bordered by the closed crescent (“middle syncline” after Tobien, 1986). The hypostria is rudimentary.

P³ and P⁴ are nonmolariform, with a large single labial root. In P³, the centrocone is large, longitudinally extended. The mesoflexia is shorter than the paraflexia. The anterolabial cusp is absent (Fig. 5b). In P⁴, the centrocone is massive, circular; the anteroloph is long, closely approaching the level of the center of the centrocone. The anterolabial cusp is well developed. In

Table 3. Measurements of the upper cheek teeth of *Gobiolagus hekkeri* (Shevyreva, 1995); Andarak 2, Kyrgyzstan; Alai Beds, Lower Eocene, (*) holotype

Specimen	P ³		P ⁴		M ¹		M ²	
	L	W	L	W	L	W	L	W
ZIN, no. 79205			1.4	2.35				
ZIN, no. 79178					1.4	2.2		
ZIN, no. 79182					1.6	2.3		
ZIN, no. 3486/200*							1.75	2.5

Table 4. Measurements of the lower cheek teeth of *Gobiolagus hekkeri* (Shevyreva, 1995); Andarak 2, Kyrgyzstan; Alai Beds, Lower Eocene

Specimen	P ₄		M ₁		M ₂		M ₃	
	L	W	L	W	L	W	L	W
ZIN, no. 79175	1.5	1.7						
PIN, no. 3486/169	1.8	1.9						
PIN, no. 3486/170	2.0	2.2						
ZIN, no. 79184			2.1	2.0				
ZIN, no. 79197					1.8	1.9		
ZIN, no. 79198					1.8	2.0		
ZIN, no. 79199					1.9	2.0		
PIN, no. 3486/146					1.9	2.2		
PIN, no. 3486/193					2.0	2.0		
ZIN, no. 79193							1.6	1.5
PIN, no. 3486/183							1.8	1.5

specimen ZIN, no. 79205, the lingual side of the crown has a small concavity, which probably corresponds to a rudimentary hypostria (Fig. 5c).

M¹ and M² have two labial roots each. The hypostria is rudimentary. M¹ is only represented by heavily worn specimens. In specimen ZIN, no. 79182, there are two enamel lakes. The lingual enamel lake is somewhat larger and probably corresponds to a worn fold between the trigon and the postcingulum, while the labial lake corresponds to a fold between the paracone and metacone. In M², the postcingulum is large, separated from the trigon by a deep labial fold. The paracone and metacone are well developed, separated by a deep fold.

The lower incisor reached M₃. The masseteric tubercle on the anterior end of the masseteric crest is located under the talonid of M₂. The lower incisor is labiolingually flattened, with an almost flat lingual side and a convex labial side. Enamel is only present on the anterolabial side.

P₃ has not been recorded. The trigonid and talonid of P₄–M₃ substantially differ in height; this difference decreases in worn teeth. In unworn P₄–M₃, the metaconid is higher than the protoconid; as the teeth are worn, the difference in height between these cusps increases. The trigonid and talonid are connected by a

lingual bridge at relatively early stages of wear. In P₄, the talonid is narrower and substantially shorter than the trigonid. In M₁ and M₂, the talonid is almost as wide as and somewhat longer than the trigonid. The hypococonid is located at the center of the posterior side of the talonid and approximately half as wide. In M₃, the talonid is wider and longer than the trigonid. The anterior and posterior roots of all cheek teeth are fused or connected by a longitudinal bone bridge.

Measurements, mm. D³ (TsNIGR Museum, no. 5/12676): L = 2.0, W = 3.2. Tables 3 and 4 show measurements of permanent teeth.

Comparison. *G. hekkeri* is assigned to the genus *Gobiolagus* based on the characteristic oblique orientation of the maxilla and the posterior region of the tooth row (at M¹–M³), relatively small size of the talonid of P₄, and the formation of the lingual bridge between the trigonid and talonid of lower cheek teeth at the early stage of wear. *G. hekkeri* differs from the type species *G. tolmachovi* and *G. andrewsi*, *G. major*, and *G. gromovi* in the smaller dimensions; in addition, it differs from the last species in the absence of cement. It is similar in size to *G. lii* and differs in its narrower P³–M² and in the absence of anterolabial cusp on P³.

Remarks. The original description of *Romanolagus hekkeri* (Shevyreva, 1995) was only accompanied by a figure of a tooth of the holotype (PIN, no. 3486/200), which was regarded by Shevyreva as M¹. Averianov (1998) proposed that it was M³ of a mixodontian, probably, *Anatolimys rozhdvestvenskii* Shevyreva, 1994. The study of the holotype of *R. hekkeri*, which is completely figured in the present study for the first time (Fig. 5e), has shown that it is M², because it occupies a much more posterior position relative to the posterior margin of the zygomatic process, its postcingulum is well development, and the alveolus of the posteriorly adjoining tooth (M³) is relatively small.

Material. In addition to the holotype, the type locality has yielded 20 specimens: fragmentary I² (PIN, no. 3486/31); left D³ (TsNIGR Museum, no. 5/12676); fragmentary right P³ (ZIN, no. 88806); left P⁴ (ZIN, no. 79205); lingual part of left P⁴ (PIN, no. 3486/203); right maxilla fragment with M¹ and alveoli of P³, P⁴, and M² (ZIN, no. 79182); heavily worn right M¹ (ZIN, no. 79178); left dentary fragment with broken off I₂, M₁–M₂, and root of P₄ (PIN, no. 3486/302); right P₄ (ZIN, no. 79175; PIN, no. 3486/169); right M₁ (PIN, nos. 3486/146, 170); left M₁ (ZIN, no. 79192); right M₂ (ZIN, nos. 79197, 79198, 79199; PIN, no. 3486/193); left M₂ (ZIN, no. 79184); right M₃ (ZIN, no. 79193); left M₃ (PIN, no. 3486/183). The material was collected by A.K. Rozhdvestvensky in 1967 (specimen PIN, no. 3486/302); V.Yu. Reshetov and N.S. Shevyreva in 1975 (specimens PIN, nos. 3486/31, 146, 169, 170, 183, 193, 203); and by A.O. Averianov in 1988–1990, 1991, and 1995 (collections of ZIN and TsNIGR Museum).

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