

The History of the Dipodoidea (Rodentia, Mammalia) in the Miocene of Asia: 6. Lophodont Lophocricetinae

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Abstract—Two new lophocricetine genera from the Mio-Pliocene of the southern part of Western Siberia and Kazakhstan are established. *Sibirosminthus* gen. nov. includes four species, which are characterized by large sizes and clearly lophodont molars: *S. seletyensis* sp. nov. (MN13), *S. latidens* sp. nov., *S. irtyshensis* sp. nov. (MN13–MN14), and *S. betekensis* sp. nov. (MN15). *Sibirosminthus* probably originated from the genus *Lophocricetus*, namely, from the lineage *L. (L.) vinogradovi*–*L. (L.) grabau*. *Lophosminthus* gen. nov. includes two species, *L. savinovi* sp. nov. (MN12/MN13) and *L. fugax* sp. nov. (MN13). These forms are relatively small and display only weakly developed lophodonty. *Lophosminthus* originates from one of the most advanced Late Miocene forms of the genus *Heterosminthus*, which was similar to *H. saraicus*.

INTRODUCTION

In the previous studies (Zazhigin and Lopatin, 2000a; Lopatin, 2001; Zazhigin *et al.*, 2002), we considered the Miocene history of the previously known genera of the subfamily Lophocricetinae, *Heterosminthus* and *Lophocricetus*. Below, we describe two new lophocricetine genera, which appeared as a result of Late Miocene adaptive radiation of the subfamily.

The material comes from the following localities: **Novaya Stanitsa 1A**, Upper Miocene, upper part of MN13, Novaya Stanitsa Formation; **Cherlak 1A**, Lower Pliocene, lower part of MN14, basal horizon of Rytovo Formation (Russia, Omsk Region); **Kedei**, Upper Miocene, lower part of MN13, Kedei Formation (Kazakhstan, Kedei River, right tributary of the Selety River); **Zhelezinka**, Upper Miocene, upper part of MN13, Novaya Stanitsa Formation; **Pavlodar 1B**, Lower Pliocene, lower part of MN14, Rytovo Formation; **Pavlodar 1C**, Neopleistocene sands with cryoturbation, material redeposited, presumably belongs to the Beteke Formation (Kazakhstan, Pavlodar Region); and **Beteke 1B**, Lower Pliocene, MN15, Beteke Formation (Kazakhstan, Beteke River). The material was collected by V.S. Zazhigin from 1976 to 2000, by V.S. Zykina in 1979 and 1983, and by R.A. Zinova in 1968. We also reexamined specimens of the Lophocricetinae previously described by Savinov (1970) from the Semipalatinsk Region of Kazakhstan. In addition, we studied material from the boreholes drilled in the Priobskoe Steppe Plateau: borehole 101 of the Klyuchi Party of the West Siberian Geological Expedition (ZSGE), depth of 32.1–34.9 m (collected in 1966); borehole 18, Borodulikha Party of the West Siberian Geological Expedition (ZSGE), depth of 53.6–59.2 m (collected in

1966); and borehole 59 (depth of 187 m) and borehole 60 (depth of 136.5–137.2 m), Romanovo Party of the ZSGE (collected in 1970).

The age and geographical position of the localities were previously considered (Zazhigin and Lopatin, 2000b, 2001; Zazhigin *et al.*, 2002). The deposits from the boreholes in the Priobskoe Plateau in the above-mentioned intervals were dated to the Early Pliocene.

When describing the dental structure, we use terminology proposed earlier (Zazhigin and Lopatin, 2000a). The figures were produced by A.V. Lopatin.

The following abbreviations are used in this study: (GIN) Geological Institute of the Russian Academy of Sciences, Moscow; (IZ) Institute of Zoology and Animal Gene Pool of the Academy of Sciences of Kazakhstan, Almaty; and (ZSGE) West Siberian Geological Expedition.

SYSTEMATIC PALEONTOLOGY

Family Dipodidae Fischer, 1817

Subfamily Lophocricetinae Savinov, 1970

Genus *Sibirosminthus* Zazhigin et Lopatin, gen. nov.

Etymology. From Siberia and the Greek *smnthus* (mouse).

Type species. *S. latidens* sp. nov.

Diagnosis. Large lophocricetines with lophodont and relatively high-crowned molars. Main cusps, styles, and styliids strongly compressed and fused to form transverse crests. On M¹ and M², protocone connected to paracone and hypocone connected to metacone. Anteroloph well developed. Mesocone and mesoloph absent. Endoloph connected to paracone.

Posteroloph connected to metacone and lingually isolated from hypocone. Labial arm of posteroloph absent. M^3 with two main transverse crests, paracone and metacone labially displaced and located close to each other, endoloph absent, and anteroloph and posteroloph reduced. On M_1 , protoconid substantially or strongly reduced; metaconid and endolophid fused. Hypoconid connected to entoconid. Hypoconulid fused with hypoconid. On M_2 , protoconid connected to metaconid and strongly extended labially. M_3 of simplified structure, i.e., anterior and posterior lobes with only one transverse crest each. M_1 with posterior basal cingulid; M_2 and M_3 with anterior basal cingulid.

Species composition. *S. latidens* sp. nov., *S. irtyshensis* sp. nov., uppermost Miocene (MN13) to Lower Pliocene (MN14) of Western Siberia and Kazakhstan; *S. betekensis* sp. nov., Lower Pliocene (MN15) of Kazakhstan; and *S. seletyensis* sp. nov., Upper Miocene (MN13) of Kazakhstan.

Comparison. The new genus differs from *Heterosminthus* Schaub, 1930 and *Lophocricetus* Schlosser, 1924 by the well-pronounced lophodonty and simplified structure of the occlusal surface.

Sibirosminthus latidens Zazhigin et Lopatin, sp. nov.

Etymology. From the Latin *latidens* (broad-toothed).

Holotype. GIN, no. 948/23, fragmentary left dentary containing M_1 – M_3 ; Western Siberia, Omsk Region, Novaya Stanitsa 1A; uppermost Miocene (uppermost MN13), basal horizon of the Novaya Stanitsa Formation.

Description (Figs. 1 and 2). A large-sized member of the genus. The zygomatic processes of the upper jaw are stout and broad; their posterior base is on a level with the anterior edge of M^1 . The infraorbital canal is dorsally unclosed; i.e., the lateral wall of the canal does not adjoin the body of the maxilla. The posterior edge of the incisor foramina is located anterior to P^4 alveolus at approximately the same distance as the alveolar length. The masseteric tubercle is well developed and laterally extended. The palate is very narrow and has a stout palatine crest. The tooth rows only slightly posteriorly diverge.

P^4 is strongly longitudinally compressed; the occlusal surface has only one transverse crest in the center. The anterior and posterior lobes of M^1 are almost equal in width; at the base, they are partly isolated from each other by clear notches. The anteroloph is short, narrow, and opposed to the protocone. The protostyle and protocone are only partially fused; i.e., the lingual segment of the anterior transverse crest is partially isolated from the central segment by a weak constriction. All folds are open, very deep, and wide. Labially, the posteroloph adjoins the metacone, and the labial arms of the posteroloph and posterofossette are absent; at the crown base behind the metacone, there is

a clear basal cingulum. The posterior lobe of M^2 is substantially narrower than the anterior lobe; the anteroloph is located on a level with the protocone; the protocone, hypocone, and posteroloph are strongly labially extended. M^3 is short and round. The posteroloph looks like a short and posterolingually oriented ridge; occasionally, it is completely reduced (Fig. 1e). The endosinus is very deep and posterolabially extended; the posterosinus is rudimentary or absent.

The lower jaw has a large mental tubercle and a strongly projecting lower masseteric ridge. The mental foramen is located on the dorsolateral surface of the diastema of the dentary.

The lower molars are transversely expanded and clearly lophodont. The metaconid of M_1 is narrow, ridged, completely fused with the endolophid, and anterolingually extended. The protoconid is strongly reduced. The anteroconid looks like a cingulid. The ectostylid and posterostylid are undeveloped. The anterior labial fold behind the protoconid is limited to the ectocingulid. The ectomesolophid and entoconid are clearly opposite to each other and form an integral transverse crest at the midlength. The posterior labial fold (sinusid) is straight. The ectostylid on M_2 is undeveloped. The transverse crests on M_3 are completely isolated from each other. The posterior basal cingulid of M_1 and the anterior basal cingulid of M_2 and M_3 are well developed.

Measurements, mm. Novaya Stanitsa 1A: (holotype) length of M_1 – M_3 , 7.2; M_1 – M_2 , 5.65; and M_2 – M_3 , 4.3; length \times width: M_1 , 3.05×2.45 ; M_2 , $2.75 \times ?$; and M_3 , 1.7×1.75 ; labial depth of the jaw at the posterior edge of the diastema, 4.75; under M_1 , 5.5; and under M_2 , 4.5. Length \times width of M^1 : (GIN, no. 948/42) $? \times 2.65$, M^2 (GIN, no. 948/25), 2.3×2.2 , M^3 : (GIN, no. 948/27) 1.45×1.65 , (GIN, no. 948/28) 1.45×1.6 , and (GIN, no. 948/41) $? \times 1.5$; M_1 (GIN, no. 948/24), 2.85×2.3 ; M_2 (GIN, no. 948/29), $? \times 2.1$; and M_3 (GIN, no. 948/30), 1.5×1.5 .

Cherlak 1A: length \times width: M^2 (GIN, no. 1110/489), 2.3×2.25 ; M^3 (GIN, no. 1110/495), 1.25×1.45 ; M^3 (GIN, no. 1110/486), 1.45×1.55 ; and M_3 (GIN, no. 1110/491), 1.2×1.3 .

Borehole 101: (GIN, no. 955/8): length of left P^4 – M^1 is 3.7 and right P^4 – M^1 is 3.6; length \times width: P^4 , 0.7×1.2 (left) and 0.75×1.2 (right); M^1 , 3.0×2.45 (right) and 3.1×2.5 (left); and width of damaged right M^2 , 2.25. Width of the palate between the alveoli of the posterior lingual roots of M^1 , 1.5.

Ratio of length to width, %: P^4 , 58–62.5; M^1 , 122.5–124; M^2 , 102–104.5; M^3 86–93.5; M_1 , 124–124.5; and M_3 , 92–100.

Occurrence. Uppermost Miocene to basal Pliocene (MN13–MN14) of Western Siberia.

Material. In addition to the holotype, the collection of the GIN includes nine isolated teeth and tooth fragments from the type locality: two M^1 , M^2 , three M^3 , M_1 , M_2 , and M_3 ; in addition, fragmentary M^1 , M^2 , two

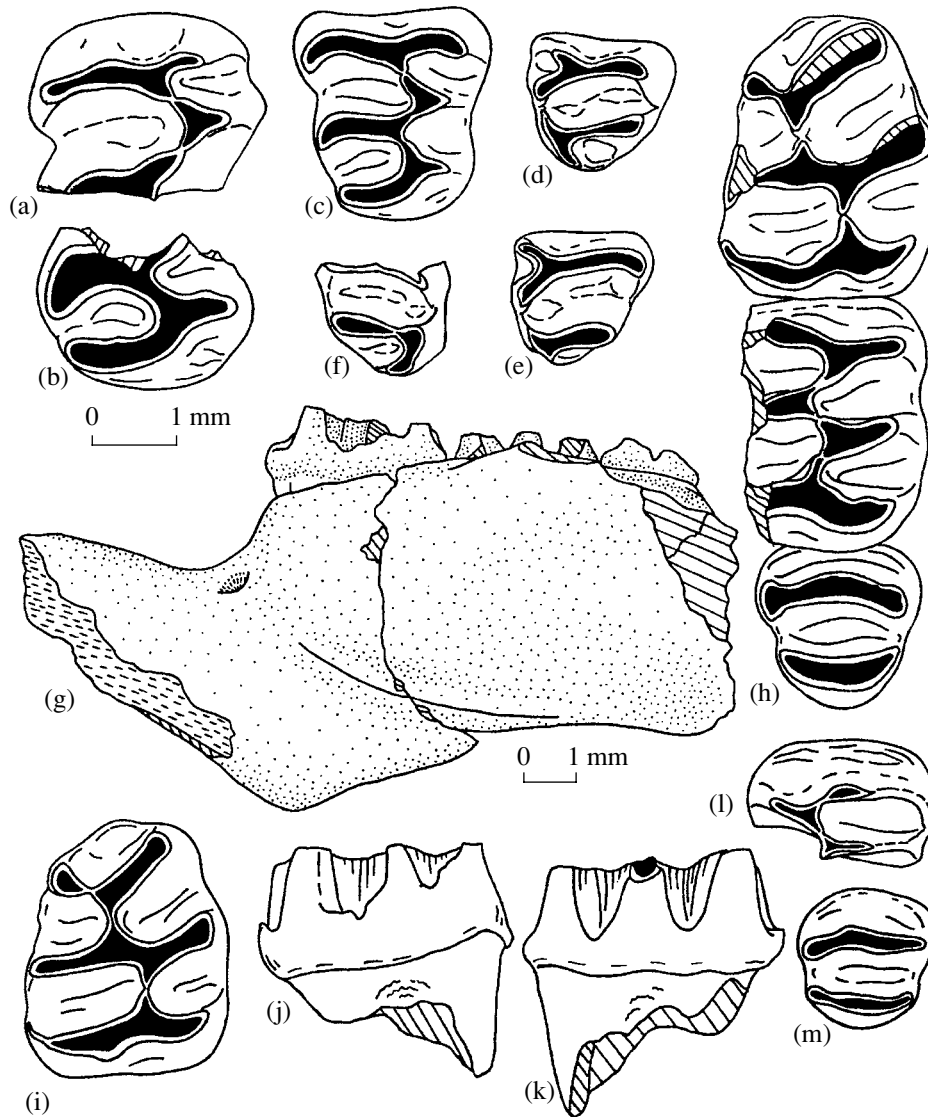


Fig. 1. *Sibirosminthus latidens* sp. nov. from the Upper Miocene of Western Siberia: (a) GIN, no. 948/42, fragmentary left M^1 ; (b) GIN, no. 948/26, fragmentary left M^1 ; (c) GIN, no. 948/25, left M^2 ; (d) GIN, no. 948/27, right M^3 ; (e) GIN, no. 948/28, right M^3 ; (f) GIN, no. 948/41, left M^3 ; (g and h) holotype GIN, no. 948/23, fragmentary left dentary with M^1 – M^3 : (g) general appearance, labially, and (h) occlusal surface of M^1 – M^3 ; (i–k) GIN, no. 948/24, left M^1 : (i) occlusal surface, (j) labially, and (k) lingually; (l) GIN, no. 948/29, fragmentary right M^2 ; and (m) GIN, no. 948/30, left M^3 ; Novaya Stanitsa 1A locality, MN13, Novaya Stanitsa Formation.

M^3 , three fragmentary M^1 , fragmentary M^2 , and M^3 from the Rytovo Formation of the Cherlak 1A locality; and upper jaw containing right P^4 – M^2 and left P^4 – M^1 from borehole 101.

Sibirosminthus irtyshensis Zashigin et Lopatin, sp. nov.

E t y m o l o g y. From the Irtysh River.

H o l o t y p e. GIN, no. 948/13, fragmentary right dentary containing M^1 – M^3 ; Kazakhstan, Pavlodar

Region, Zhelezinka locality; uppermost Miocene (uppermost MN13), Novaya Stanitsa Formation.

D e s c r i p t i o n (Fig. 3). A large member of the genus. M^1 is broad; at the base, the anterior and posterior lobes are partly isolated from each other by clear notches. The anteroloph is long, narrow, and substantially anteriorly displaced with reference to the protocone. Occasionally, a weak anterostyle is developed (Fig. 3g). The lingual segment of the anterior transverse crest has a well-pronounced constriction; a rudimentary protostyle is present (Figs. 3c and 3d). The posterior

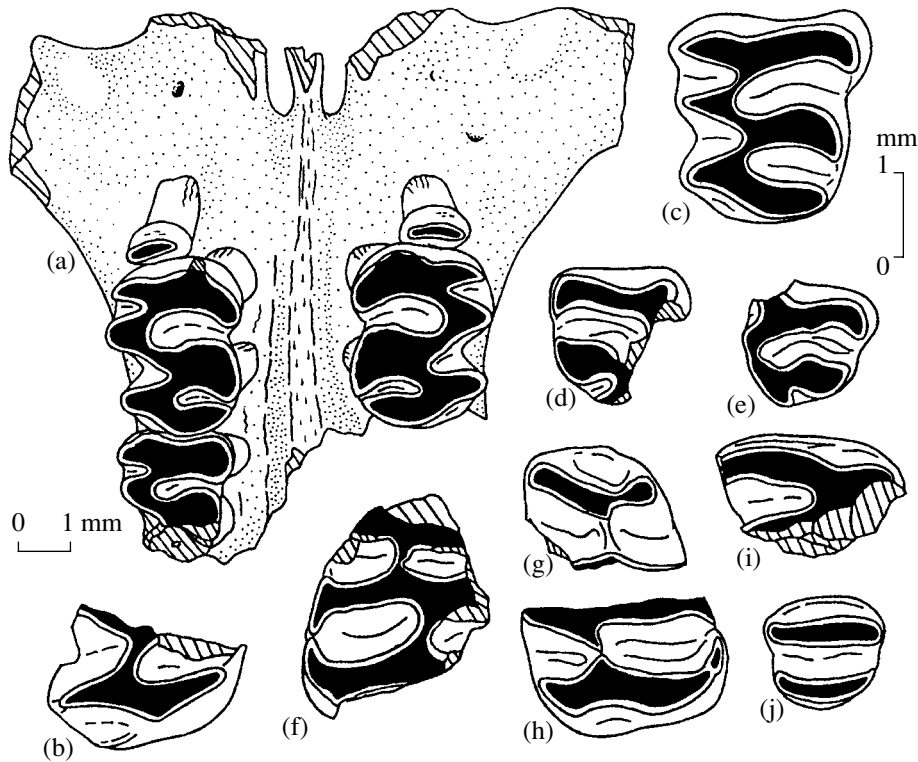


Fig. 2. *Sibirosminthus latidens* sp. nov. from the Lower Pliocene of Western Siberia: (a) GIN, no. 955/8, fragmentary upper jaw with right P^4 - M^2 and left P^4 - M^1 , borehole 101; (b) GIN, no. 1110/490, fragmentary right M^1 ; (c) GIN, no. 1110/489, right M^2 ; (d) GIN, no. 1110/496, left M^3 ; (e) GIN, no. 1110/495, right M^3 ; (f) GIN, no. 1110/493, left M^1 ; (g) GIN, no. 1110/492, fragmentary right M^1 ; (h) GIN, no. 1110/497, fragmentary right M^1 ; (i) GIN, no. 1110/494, fragmentary left M^2 ; and (j) GIN, no. 1110/491, right M^3 ; Cherkak 1A locality, MN14, Rytovo Formation.

basal cingulum is clearly differentiated. M^2 is relatively narrow; the protocone, hypocone, and posteroloph are stout and weakly transversely expanded. The hypocone has a posterior projection. The anteroloph is short and located at the same transverse line as the protocone.

The mental tubercle and the lower masseteric ridge of the lower jaw are well developed.

The lower molars are extended and quite lophodont. The metaconid of M^1 is massive. The endolophid is weakly differentiated. The protoconid is round and somewhat reduced relative to the metaconid. The anteroconid is small and conical or absent. The entoconid is only partially fused with the ectomesolophid; these structures weakly alternate. The posterior labial fold is straight or weakly oblique anteriorly. The ectocingulid is either present or absent. The ectostylid and the posterostylid of M^1 and M^2 are well pronounced; M^2 has a supplementary stylid behind the ectostylid. The posterior basal cingulid of M^1 and anterior basal cingulid of M^2 and M^3 are weakly developed. The transverse crests on M^3 are isolated in the central part but adjoin each other labially.

Measurements, mm. Holotype: length: M^1 - M^3 , 6.6; M^1 - M^2 , 5.2; and M^2 - M^3 , 3.85; length \times width: M^1 , 2.8×1.9 ; M^2 , 2.5×1.95 ; and M^3 , 1.5×1.4 ; labial depth

of the lower jaw at the posterior edge of the diastema, 4.4; under M^1 , 5.25; and under M^2 , 4.75.

Length \times width: (GIN, no. 955/1) M^1 from borehole 59, 2.9×1.9 . (GIN, no. 955/5) from borehole 60: length of M^1 - M^2 , 4.7; length \times width: M^1 , 2.6×1.75 ; M^2 , 2.25×1.75 . (GIN, no. 955/9) length \times width of M^2 from borehole 18, 2.2×1.7 .

Pavlodar 1B: M^1 : (GIN, no. 640/3010) 3.1×2.55 and (GIN, no. 640/3011) 3.0×2.25 ; M^2 : (GIN, no. 640/3013) 2.3×1.8 ; (GIN, no. 640/3014) length of M^1 - M^2 , 5.1; length \times width of M^1 , $2.8 \times$ ca. 2.0; M^2 , 2.6×2.07 ; and (GIN, no. 640/3015) width of M^3 , 1.6.

Ratio of length to width, %: M^1 , 121.5-133; M^2 , 128; M^1 , 147-152.5; M^2 , 126-129; and M^3 , 107.

Comparison. The new species differs from *S. latidens* by relatively longer and narrower lower molars, a more massive metaconid, stronger developed protoconid, only partially fused entoconid and ectomesolophid of M^1 , better developed stylids on M^1 and M^2 , the presence of labial contacts between transverse crests on M^3 , weaker basal cingulids of M^1 - M^3 , the presence of a rudimentary protostyle, a more anterior position of the anteroloph on M^1 , and by a narrower M^2 .

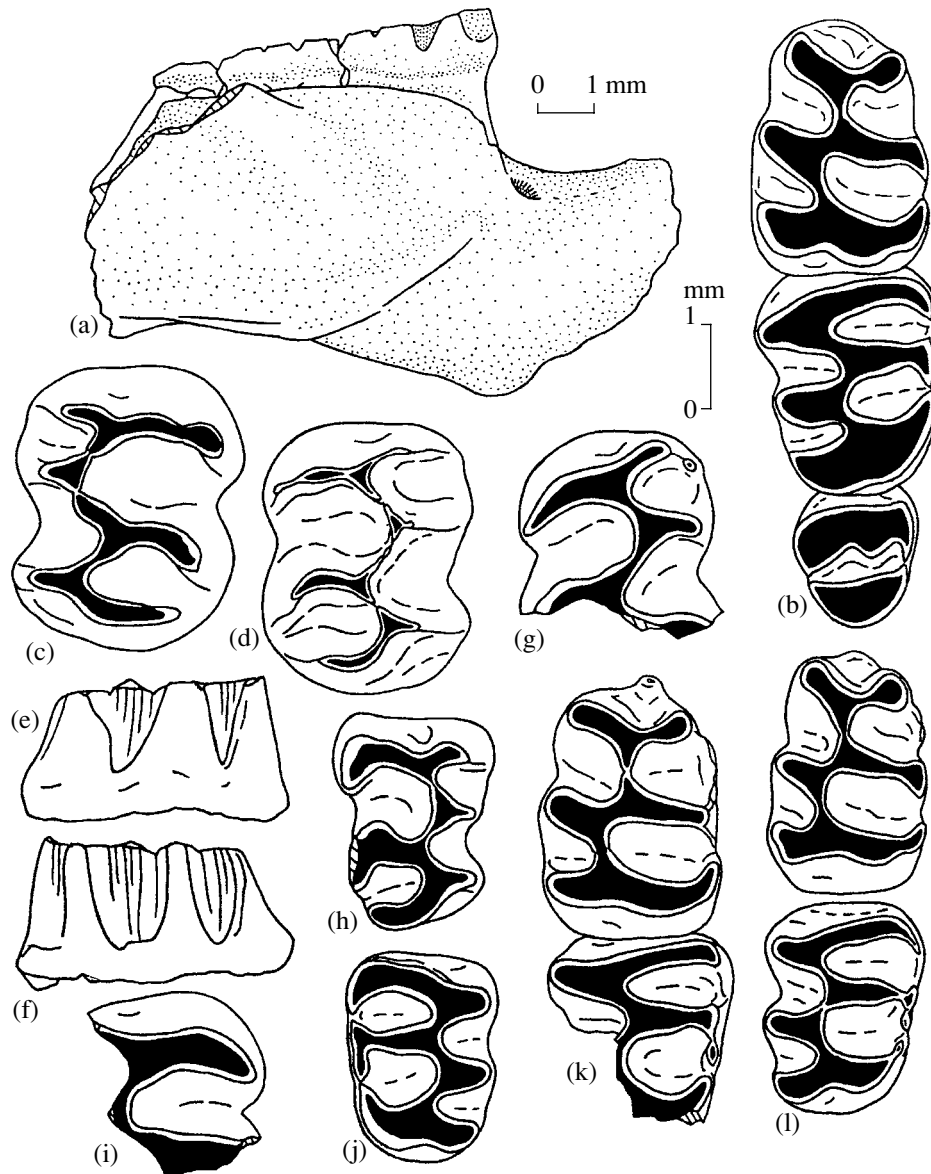


Fig. 3. *Sibirosminthus irtyshensis* sp. nov.: (a and b) holotype GIN, no. 948/13, fragmentary right dentary with M_1 – M_3 : (a) general appearance, labially, and (b) occlusal surface of M_1 – M_3 ; Zhelezinka locality, uppermost Miocene, MN13, Novaya Stanitsa Formation; (c) GIN, no. 640/3010, right M_1^1 ; (d–f) GIN, no. 640/3011, left M_1^1 : (d) occlusal surface, (e) lingually, and (f) labially; (g) GIN, no. 640/3012, left M_1^1 ; (h) GIN, no. 640/3013, left M_2^2 ; Pavlodar 1B locality, lowermost Pliocene, MN14, Rytovo Formation; (i) GIN, no. 955/6, fragmentary right M_1^1 ; (j) GIN, no. 955/9, left M_2^2 ; (k) GIN, no. 955/1, right M_1 and M_2 ; and (l) GIN, no. 955/5, right M_1 and M_2 ; boreholes in the Priobskoe Plateau, Lower Pliocene: (i and l) borehole 60, (j) borehole 18, and (k) borehole 59.

Occurrence. Uppermost Miocene to the basal Pliocene (MN13–MN14) of Western Siberia and Kazakhstan.

Material. In addition to the holotype, the collection of the GIN includes a fragmentary lower jaw containing M_1 and M_2 from borehole 59, fragmentary jaws containing M_1 – M_2 and damaged M^1 from borehole 60, M_2 from borehole 18, four M^1 , one M^2 , fragmentary lower jaw with M_1 and M_2 , strongly worn M_1 , and frag-

mentary M_3 from the Rytovo Formation of the Pavlodar 1B locality.

Sibirosminthus betekensis Zazhigin et Lopatin, sp. nov.

Etymology. From the Beteke River.

Holotype. GIN, no. 945/306, isolated right M^1 ; Kazakhstan, Beteke 1B locality; Lower Pliocene (MN15), Beteke Formation.

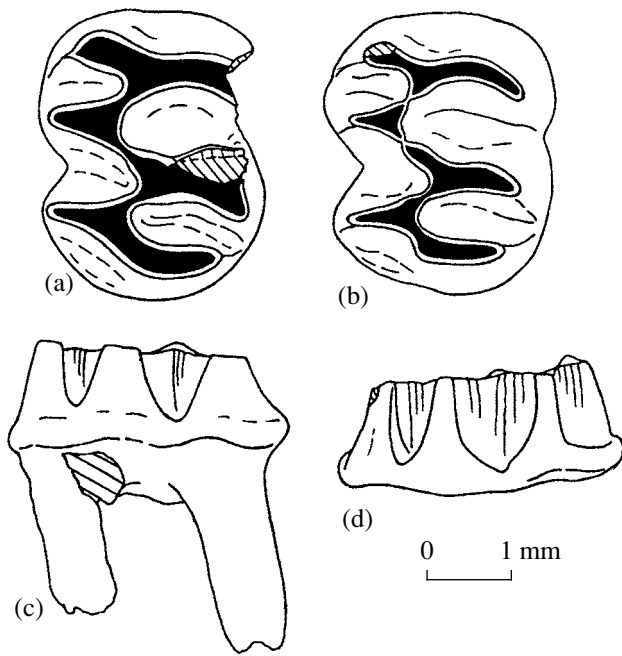


Fig. 4. *Sibirosmintus betekensis* sp. nov. from the Lower Pliocene of Kazakhstan: (a) holotype GIN, no. 945/306, right M^1 ; Beteke 1B locality, MN15, Beteke Formation; (b–d) GIN, no. 640/4000, right M^1 : (b) occlusal surface, (c) lingually, and (d) labially; Pavlodar 1C locality.

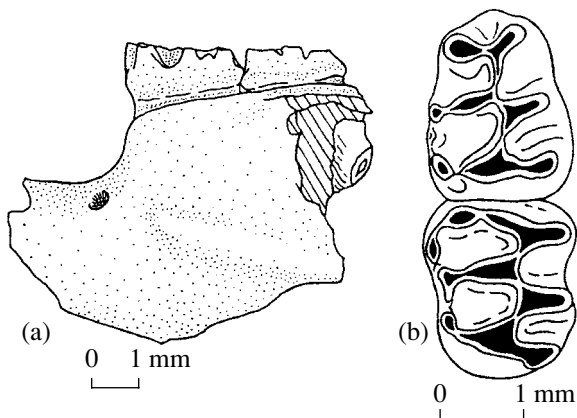


Fig. 5. *Sibirosmintus seletyensis* sp. nov., holotype GIN, no. 951/1032, fragmentary left dentary with M_1 and M_2 : (a) general appearance, labially, and (b) occlusal surface of M_1 and M_2 .

Description (Fig. 4). A large member of the genus. M^1 is massive. The anterior and posterior lobes of M^1 are equal in width, the lingual notch at the crown base is weak. The anteroloph is long, wide at the base, and substantially displaced anteriorly with reference to the protocone. The anterior transverse crest is integral; the protostyle is completely fused with the protocone. The posterior basal cingulum is well developed.

Measurements, mm. Length of M^1 (holotype), 3.2; (GIN, no. 640/4000) length \times width of M^1 , 3.15×2.55 ; the ratio of length to width of M^1 , 124%.

Comparison. The new species differs from *S. latidens* and *S. irtyschensis* by the shape of M^1 (weak lingual notch at the crown base), the presence of a stout anteroloph, and by the completely fused protostyle and protocone.

Occurrence. Lower Pliocene (MN15) of Kazakhstan.

Material. In addition to the holotype, (GIN, no. 640/4000) isolated M^1 from the Pavlodar 1C locality.

Sibirosmintus seletyensis Zazhigin et Lopatin, sp. nov.

Etymology. From the Selety River.

Holotype. GIN, no. 951/1032, fragmentary left dentary containing M_1 and M_2 ; Kazakhstan, Kedei River; Upper Miocene (lowermost MN13), Kedei Formation.

Description (Fig. 5). A small member of the genus. The lower masseteric ridge of the lower jaw is weakly developed. The lower molars are elongated and weakly lophodont. The protoconid of M_1 is somewhat smaller than the metaconid. The metaconid and the endolophid are only partially fused. The metaconid is round. The ectomesolophid is displaced anteriorly with reference to the entoconid. The posterior labial fold is anterolingually directed. The ectostylid and the posterostylid of M_1 and M_2 are clearly differentiated and have supplementary stylids. The supplementary stylid of M_1 is located in the ectocingulid between the ectostylid and the posterostylid. M_2 has two supplementary stylids in the labial segment of the anterolophid. The posterior basal cingulid of M_1 and the anterior basal cingulid of M_2 are hardly distinguishable.

Measurements, mm. Holotype: length of M_1 – M_2 , 4.0; length \times width: M_1 , 2.1×1.55 ; M_2 , 1.95×1.65 ; labial depth of the lower jaw at the posterior edge of the diastema, ca. 3.3; ratio of length to width: M_1 , 135.5%; M_2 , 118%.

Comparison. The new species differs from all other species of the genus by substantially smaller measurements. In addition, it differs from *S. latidens* and *S. irtyschensis* by a weaker lophodonty, better developed protoconid of M_1 , greater differentiation of stylids, and by weakly developed basal cingulids of M_1 and M_2 .

Material. Holotype.

Genus Lophosminthus Zazhigin et Lopatin, gen. nov.

Etymology. From the Greek *lophus* (crest) and the Greek *sminthus* (mouse).

Type species. *L. fugax* sp. nov.

Diagnosis. Medium-sized Lophocricetinae with weakly lophodont and low-crowned molars. Main cusps well differentiated. On M^1 , protoloph and endoloph independently connected to paracone. Anteroloph

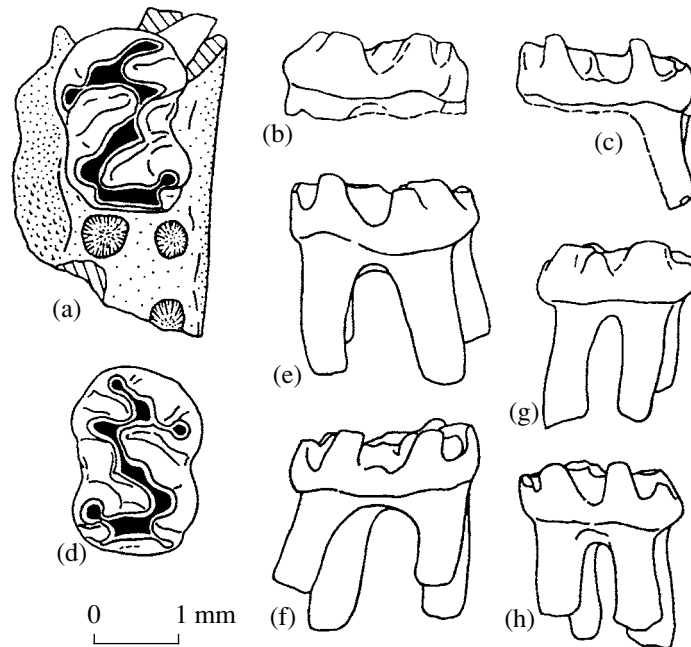


Fig. 6. Late Miocene species of the genus *Lophosminthus* gen. nov., (a–c) *L. fugax* sp. nov. and (d–f) *L. savinovi* sp. nov., compared with (g and h) *Heterosminthus saraicus* Zazhigin, Lopatin et Pokatilov, 2002; (a–c) holotype GIN, no. 948/31, fragmentary left maxilla with M^1 : (a) occlusal surface, (b) M^1 lingually, and (c) M^1 labially; Russia, Omsk Region, Novaya Stanitsa 1A locality, MN13, Novaya Stanitsa Formation; (d–f) holotype IZ, no. M-735/66-G, right M^1 : (d) occlusal surface, (e) lingually, and (f) labially; Kazakhstan, Semipalatinsk Region, Kalba Ridge, near the village of Makovka, MN12/MN13; (g and h) GIN, no. 1121/11, right M^1 : (g) lingually and (h) labially; Russia, Irkutsk Region, Lake Baikal, Olkhon Island, Olkhon 1 locality, MN12, Sasa Beds, Saraiskaya Member.

well developed. Protostyle well pronounced and postero-style absent. Mesocone large and massive and mesoloph short. Paracone, metacone, and hypocone small, substantially smaller than protocone and mesocone and comparable in size to protostyle. Hypocone only partially isolated from mesocone. Contacts of metacone and hypocone with metaconule not mediated by metaloph. Metaconule very large and broad. Arms of posteroloph reduced.

Species composition. *L. fugax* sp. nov., uppermost Miocene (MN13) of Western Siberia; and *L. savinovi* sp. nov., Upper Miocene (MN12/MN13) of Kazakhstan.

Comparison. The new genus differs from *Heterosminthus* and *Lophocricetus* by a distinct trend toward the lophodonty, reduced posterior cusps, strongly enlarged mesocone and metaconule, the absence of metaloph, and by a reduced posteroloph on M^1 . In addition, it differs from *Heterosminthus* by the presence of contacts between the endoloph and the paracone and between the protocone and the paracone. It differs from *Sibirosminthus* by the structure of M^1 and by a relatively weak lophodonty.

Lophosminthus fugax Zazhigin et Lopatin, sp. nov.

Etymology. From the Latin *fugax* (transient, galloping).

Holotype. GIN, no. 948/31, fragmentary left maxilla containing M^1 ; Russia, Omsk Region, Novaya Stanitsa 1A locality; Upper Miocene, uppermost MN13, Novaya Stanitsa Formation.

Description (Figs. 6a–6c). The anterior lobe of M^1 is substantially broader than the posterior lobe. The anteroloph is long and broad, and the anterostyle is undeveloped. The protocone is located at the same longitudinal line as the hypocone. The protostyle is large and only slightly differentiated from the protocone. The paracone and metacone are strongly reduced and longitudinally compressed; they are less massive than the protostyle. The metaconule is strongly expanded, i.e., twice as wide as the mesocone; the posteroloph lacks arms.

Measurements, mm. Holotype: length \times width, 2.0×1.55 .

Material. Holotype.

Lophosminthus savinovi Zazhigin et Lopatin, sp. nov.

Lophocricetus afanasievi (part.): Savinov, 1970, p. 106.

Etymology. The species is named in honor of the paleontologist P.F. Savinov.

Holotype. IZ, no. M-735/66-G, isolated right M^1 ; Kazakhstan, Semipalatinsk Region, Kalba Ridge, near the village of Makovka; Upper Miocene.

Description (Figs. 6d–6f). The anterior lobe of M^1 is somewhat wider than the posterior lobe. The lophs are weakly developed. The anteroloph is stout and short, and the anterostyle is large. The protocone is displaced to the center of the occlusal surface so that it is located at the same longitudinal line as the mesocone and metaconule. The protostyle is relatively small and clearly isolated from the protocone. The paracone and metacone are moderately reduced and only slightly inferior to the mesocone in stoutness. The metaconule is somewhat larger than the mesocone. The arms of the posteroloph are present and short.

Measurements, mm. Holotype: length \times width, 2.1×1.55 .

Comparison. *L. savinovi* differs from the type species by a weaker lophodonty, more central position of the protocone, better developed paracone and metacone, smaller metaconule, the presence of the arms of the posteroloph, and by a stronger developed anterostyle on M^1 .

Remarks. Savinov (1970) assigned the specimen described above to *Lophocricetus afanasievi*. However, the structure of M^1 (IZ, no. M-735/66-G) suggests that it belongs to the genus *Lophosminthus*, the differences from *Lophocricetus* were considered above. The precise age of the specimen is unknown. The material comes from a borehole (depth of 12–30 m); Savinov believed that it should be assigned to the Pavlodar Formation. However, Zazhigin *et al.* (2002) indicated that the specimens identified by Savinov (1970) as *Lophocricetus afanasievi* in actual fact belong to various lophocricetine species. They were probably found at different levels of nonstratified Mio-Pliocene deposits. Regarding the evolutionary morphological advantage, *Lophosminthus savinovi* is somewhat more primitive than *L. fugax* from Novaya Stanitsa 1A (terminal MN13), and, consequently, it could be somewhat older. We tentatively assign this specimen to the MN12–MN13 zones.

Material. Holotype.

DISCUSSION

Based on recent data, the Lophocricetinae emerged at the end of the Oligocene (Wang and Qiu, 2000). Up to the Late Miocene, they were represented by the only genus, *Heterosminthus*, characterized by bunodont and low-crowned molars. Different phylogenetic lineages of *Heterosminthus* showed certain common trends in the evolution of the dental system; i.e., the structure of the occlusal surface was simplified, and the main cusps and crests increased in height (Zazhigin and Lopatin, 2000a; Lopatin, 2001).

A Late Miocene lineage of *Heterosminthus* gave rise to the genus *Lophocricetus* (the earliest known records are dated as MN10) characterized by bunolophodont teeth (Zazhigin *et al.*, 2002). In *Lophocricetus*, the

development of lophodonty was accompanied by the modification of the dental structure directed to the rearrangement of relationships between cusps and providing an increase in the number of grinding surfaces. On the contrary, *Heterosminthus*, which existed almost to the end of the Late Miocene (MN12), retained an archaic dental structure and a primitive pattern of contacts between the main cusps. However, late members of the genus *Heterosminthus* substantially changed with reference to the shape of cusps and increase in the height of crests. Probably, the development of this tendency combined with the preservation of primitive dental structure resulted at the end of the Miocene in the emergence of more lophodont forms of the genus *Lophosminthus*, in which the relative sizes of cusps were substantially modified (Fig. 6 shows the structure of M^1 of *L. fugax* and *L. savinovi*, compared to those of the latest known species of the genus *Heterosminthus*, *H. saraicus* from MN12). In this lineage, the lophs were formed by the reduction of connecting crests and fusion between the cusps rather than by the growth of the crests.

On M^1 of *L. savinovi*, the main cusps are reduced; the anteroloph, protoloph, and posterior arms of the hypocone and metacone are strongly shortened; the increased mesocone is fused with the hypocone; the massive metaconule includes the metaloph and most of the posteroloph, although the narrow side arms of the posterior crest are retained. In the more advanced *L. fugax*, the main cusps are reduced to an even greater extent; the endoloph is shortened; the mesocone completely fused with the hypocone; and the posterior arms of the hypocone and metacone are lost. The latter cusps directly adjoin a strongly expanded metaconule, which is quite lophate in structure. The posteroloph lacks side arms.

The structure of M^1 and the degree of lophodonty in *Lophosminthus* are similar to those of the Recent five-toed dwarf jerboa *Cardiocranius paradoxus* Satunin, 1903. This primarily concerns the relative sizes and arrangement of the main cusps and the presence of a high and stout endoloph. Regarding the feeding specialization, *Lophosminthus* probably differed from the other small Lophocricetinae; *Heterosminthus* included forms feeding on seeds and insects and members of *Lophocricetus* were seed- and grass-eaters. By analogy with *Cardiocranius*, one can propose that the members of *Lophosminthus* were mainly seed-eaters consuming a large amount of herbaceous forage.

Savinov (1977, p. 32) distinguished the main stages of evolutionary changes of the molar occlusal surface of the genus *Lophocricetus*. In particular, *L. minuscilus* is characterized by the cusps structure and displays the initial stage of the formation of the third row of cusps (stylids) on M_1 , *L. vinogradovi* and *L. afanasievi* show somewhat lophate structure and well-developed cusps of the third row, and *L. pusillus* and *L. grabaui*

are characterized by the lophate structure and fusion between the stylids and respective external cusps.

In essence, we are dealing with an increase in lophodontology in two *Lophocricetus* lineages, which are considered to be of subgeneric rank, i.e., *Paralophocricetus* and *Lophocricetus* sensu stricto (Zazhigin *et al.*, 2002). It is worth noting that the development of folded bunolophodont structure followed different ways in the two subgenera. The characteristic feature of *Paralophocricetus* is the formation of three longitudinal rows composed of relatively well-differentiated cusps combined with an increase in their height and reduction of transverse connecting elements. This trend is especially well pronounced in the two latest members of the subgenus, *L. (P.) sibiricus* and *L. (P.) ultimus* (Zazhigin *et al.*, 2002). On the contrary, in the evolution of *Lophocricetus* sensu stricto, the cusps and crests gradually expanded and the styles and stylids became fused with the cusps. The progressive increase in lophodontology observed in the late forms of the subgenus *Lophocricetus* is probably associated with the transition from feeding on seeds and insects to feeding on seeds and green forage.

The increase in height, expansion of cusps and crests, and fusion of the latter is especially well pronounced in *Sibirosmintus*, the most lophodont member of the subfamily Lophocricetinae.

In *Sibirosmintus*, the grinding surface of the first two upper and lower molars is composed of three subtransverse lophi (lophids) connected to each other by short sublongitudinal crosspieces. M^3 and M_3 have two main transverse crests each.

The anterior loph of M^1 and M^2 consists of fused anteroloph, protocone, and protostyle. In the relatively primitive *S. irtyshensis*, the protocone and protostyle are differentiated within the lingual region of the anterior loph of M^1 , whereas, in the more advanced *S. latidens* and *S. betekensis*, these structures are completely fused.

The anterior lophid of M_1 is oblique and formed by fused metaconid and endolophid; the protoconid is reduced and connected to the posterolabial side of the metaconid. These characters are especially well pronounced in *S. latidens*. In the most primitive member of the genus, *S. seletyensis*, the metaconid and endolophid are well differentiated; the protoconid is only weakly reduced. *S. irtyshensis* displays intermediate condition of these characters. The middle lophid of *S. seletyensis* is formed by two transversely oriented and weakly alternating structures, i.e., (1) entoconid + anterior arm of the entoconid and (2) mesoconid + ectomesolophid + ectostylid. Each element is well differentiated. In *S. irtyshensis*, the alternation is developed to a lesser extent; the mesoconid, ectomesolophid, and ectostylid are completely fused. In *S. latidens*, the entoconid is opposed by the ectomesolophid and the central elements are arranged in an integrated transverse lophid. The posterior transverse lophid is formed by the

strongly expanded hypoconid and posterolophid and by the posterostylid. The latter element is clearly differentiated in *S. seletyensis*; in *S. irtyshensis*, it is distinguishable; in *S. latidens*, it is completely fused with the hypoconid.

On M_2 , gradual reduction of longitudinal contacts results in the formation of three pairs of posterolingually oriented structures: (1) anterolophid + metaconid, (2) (protoconid + ectostylid) + entoconid, and (3) hypoconid + posterolophid.

Regarding these structural characters and the degree of lophodontology of M_1 and M_2 , *S. seletyensis* is intermediate between the late members of *Lophocricetus* sensu stricto and advanced forms of *Sibirosmintus*. This allows us to associate the emergence of the genus *Sibirosmintus* with the lineage *Lophocricetus (L.) vinogradovi-L. (L.) grabau*. The stratigraphic position of *S. seletyensis* (lowermost MN13) indicates that *Sibirosmintus* deviated from the common stock earlier than *L. (L.) grabau* did.

At the end of the Miocene, *Sibirosmintus* was presented by two large-sized species of the same age, *S. irtyshensis* and *S. latidens*. Judging from the geographical position of the localities where the members of *Sibirosmintus* were found, the ranges of these species did not overlap. *S. irtyshensis*, which is more primitive in morphology, dwelt somewhat more south than the more advanced *S. latidens*. Each species probably descended from *S. seletyensis*.

The presence of *S. betekensis* in the Beteke Formation indicates that the genus *Sibirosmintus* existed to the later half of the Early Pliocene (MN15). The origin of *S. betekensis* remains uncertain, because the specimens of this species are extremely scarce.

The late species of the genus *Sibirosmintus* are characterized by well-developed lophodontology and relatively high-crowned molars; consequently, these rodents fed predominantly on green forage. This feeding adaptation probably promoted rapid and considerable growth of sizes in the *Sibirosmintus* lineage; as a result, in the MN13 Zone, the members of this genus became as large as the medium-sized species of the genus *Allactaga*.

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REFERENCES

- Lopatin, A.V., New Species of *Heterosminthus* (Dipodidae, Rodentia, Mammalia) from the Miocene of the Baikal Region, *Paleontol. Zh.*, 2001, no. 2, pp. 93–96.
- Savinov, P.F., Jerboas (Rodentia, Mammalia) from the Neogene of Kazakhstan, in *Materialy po evolyutsii nazemnykh*

pozvonochnykh (Materials on the Evolution of Terrestrial Vertebrates), Moscow: Nauka, 1970, pp. 91–134.

Savinov, P.F., A New Member of the Dipodoidea from Northern Kazakhstan, in *Materialy po istorii fauny i flory Kazakhstana* (Materials on the History of the Fauna and Flora of Kazakhstan), 1977, vol. 7, pp. 27–32.

Wang, B.-Y. and Qiu, Z.-X., Dipodidae (Rodentia, Mammalia) from the Lower Member of Xianshuihe Formation in Lanzhou Basin, Gansu, China, *Vertebr. Palasiat.*, 2000, vol. 38, no. 1, pp. 10–35.

Zazhigin, V.S. and Lopatin, A.V., The History of the Dipodoidea (Rodentia, Mammalia) in the Miocene of Asia:

1. *Heterosminthus* (Lophocricetinae), *Paleontol. Zh.*, 2000a, no. 3, pp. 90–102.

Zazhigin, V.S. and Lopatin, A.V., The History of the Dipodoidea (Rodentia, Mammalia) in the Miocene of Asia: 3. Allactaginae, *Paleontol. Zh.*, 2000b, no. 5, pp. 82–94.

Zazhigin, V.S. and Lopatin, A.V., The History of the Dipodoidea (Rodentia, Mammalia) in the Miocene of Asia: 4. Dipodinae on a boundary of the Miocene and Pliocene, *Paleontol. Zh.*, 2001, no. 1, pp. 61–75.

Zazhigin, V.S., Lopatin, A.V., and Pokatilov, A.G., The History of the Dipodoidea (Rodentia, Mammalia) in the Miocene of Asia: 5. *Lophocricetus* (Lophocricetinae), *Paleontol. Zh.*, 2002, no. 2, pp. 62–75.