

The History of the Dipodoidea (Rodentia, Mammalia) in the Miocene of Asia: 5. *Lophocricetus* (Lophocricetinae)

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Abstract—The Late Miocene and Early Pliocene Asiatic Lophocricetinae (Dipodidae) are studied. Ten species, including *Heterosminthus saraicus* sp. nov. (MN12) and *Lophocricetus* (*Paralophocricetus*) *progressus* subgen. et sp. nov. (MN14) from Eastern Siberia; *L. (L.) minuscilus* Savinov (MN10) and *L. (L.) vinogradovi* Savinov (MN12–MN13) from Kazakhstan; *L. (L.) reliquus* sp. nov., *L. (P.) intermedius* sp. nov. (MN13) and *L. (P.) pusillus* Schaub (MN14) from Mongolia; and *L. (P.) afanasievi* Savinov (MN13), *L. (P.) sibiricus* sp. nov. (MN14), and *L. (P.) ultimus* sp. nov. (MN14–MN15) from Western Siberia, are described. The genus *Lophocricetus* is revised.

INTRODUCTION

In the Early and Middle Miocene, the subfamily Lophocricetinae is represented by the genus *Heterosminthus*, known from Central Asia, Kazakhstan, and Eastern Siberia (Qiu, 1996; Qiu and Wang, 1999; Höck *et al.*, 1999; Zazhigin and Lopatin, 2000a; Lopatin, 2001). In the Late Miocene of Asia and southern part of Eastern Europe, late members of *Heterosminthus* persisted; however, new evolutionarily advanced forms of the genus *Lophocricetus* dominated. The latter remained in Asia up to the end of the Early Pliocene. The study of new material from the Upper Miocene and Lower Pliocene of Siberia, Kazakhstan, and Mongolia allows us to revise the composition of the genus *Lophocricetus* and reconstruct the relationships between the species.

Below is the description of the majority of Asiatic *Lophocricetus* species. It is preceded by a description of the latest *Heterosminthus*, which reached a great similarity to early forms of the genus *Lophocricetus*.

MATERIALS

We examined material on the Lophocricetinae from more than 20 Late Miocene and Early Pliocene localities of southwest Siberia, Tuva, Mongolia, and Olkhon Island (Lake Baikal). Most of localities are in the southern regions of the West Siberian Plain, and many are in Kazakhstan.

The material from the Late Miocene localities of southwest Siberia comes from the following formations: Ishim (Petropavlovsk 1A locality, Kazakhstan, Petropavlovsk; MN10), Pavlodar (Pavlodar 1A locality, Kazakhstan, stratotype of the formation is in Pavlodar;

MN12), Kedei (Selety 1A locality, Kazakhstan, Selety River, 4 km upstream the village of Il'inka; lower MN13), and Novaya Stanitsa (Novaya Stanitsa 1A locality, Russia, southern outskirts of Omsk; basal horizon of the stratotype of the formation, upper MN13). The Early Pliocene material was collected in the following formations: Rytovo (Cherlak 1A locality, Omsk Region; basal horizon of the stratotype of the formation, lower MN14; Pavlodar 1B locality, Kazakhstan, Irtysh River, outskirts of Pavlodar; lower MN14; and Pavlodar 2A locality, mines in the city of Pavlodar; MN14), Kuskol (Beteke 1A locality, Kazakhstan, Beteke River; MN14), Peshnevo (Peshnevo locality, southern part of the Tyumen Region, Ishim River at the village of Peshnevo; MN14; Petropavlovsk 1B locality, Kazakhstan, Petropavlovsk; MN14; and Andreevka 1A locality, Omsk Region, village of Andreevka at the Om' River; MN14), Beteke (Polovinnoe locality, Omsk Region, Lake Polovinnoe; MN15; Andreevka 2B locality, Omsk Region, village of Andreevka at the Om' River; MN15; Beteke 1B locality, Kazakhstan, Beteke River; MN15; and Pavlodar 1B locality, mines in the city of Pavlodar; MN15); and Livenka (Speranskoe locality, Omsk Region, Om' River; MN15). In addition, the Lophocricetinae were found in the Lower Pliocene beds of the Omsk Region (Cherlak 1B and Olkhovka localities, MN14–MN15), the exact position of which in the local stratigraphic scale has not been established. We also examined specimens from the boreholes drilled in the Priobskoe Steppe Plateau (Romanovo party of the West Siberian Geological Expedition), including those from borehole 59, depth of 187.0 m and borehole 61, depth of 194.5–195 m).

Mio-Pliocene material from northwestern Mongolia comes from various stratigraphic levels of the Khirgis-Nur Formation outcropping near Lake Khirgis-Nur. The following localities were studied: Khirgis-Nur 2 locality, Upper Miocene, upper MN13, Lower Khirgis-Nur Subformation, intervals 17 and 23–24 m; Lower Pliocene, bottom of MN14, base of the Upper Khirgis-Nur Subformation, interval 37–40 m; Lower Pliocene, MN14, Upper Khirgis-Nur Subformation, interval 50–60 m; and Khirgis-Nur 1, Yavor 1, and Yavor 2 localities, Lower Pliocene, MN14, Upper Khirgis-Nur Subformation. At the Kholu River (Tuva), the material was collected in nonstratified Upper Miocene and Lower Pliocene beds (Kholu locality, MN13–MN14).

The beds listed above were aged on the basis of paleontological and paleomagnetic data in previous studies (Zazhigin and Lopatin, 2000b, 2001). The correlation of the localities with the European Neogene Mammalian zones was performed by Zazhigin. The Ishim Formation from Petropavlovsk is aged as MN10 based on voles of the genus *Ischimomys*. The Novaya Stanitsa Formation is assigned to the terminal Miocene based on paleoclimatic and paleomagnetic data (Zykin *et al.*, 1995).

The material from the Mio-Pliocene of southwest Siberia, Tuva, and Mongolia was collected mainly by Zazhigin. V.S. Zykin participated in this work in Western Siberia in 1963 to 2000; E.V. Devyatkin, V.I. Zhegallo, and V.S. Zykin worked in Tuva and Mongolia in 1966 to 1984.

A.G. Pokatilov collected fossil lophocricetines on Olkhon Island (Irkutsk Region, Lake Baikal, Saraiskaya Bay, outcrop 520) in two members of the Sasa Beds, i.e., Saraiskaya (Member A) and Odonimskaya (Member B) members (Mats *et al.*, 1982). In the present study, these localities first receive individual names, Olkhon 1 (Saraiskaya Member) and Olkhon 2 (Odonimskaya Member). The Olkhon 1 locality is compared to Pavlodar 1A (MN12) based on large mammals, and the Olkhon 2 locality is correlated with Cherlak 1A (MN14) based on rodents.

The material from the listed localities is housed at the Geological Institute of the Russian Academy of Sciences. In addition, we examined the type series of fossil lophocricetines described from Kazakhstan (Savinov, 1970, 1977) and Ukraine (Topachevsky *et al.*, 1984).

When describing the teeth, 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; (PIU) Paleontological Institute, Uppsala University, Sweden; and (ZSGE) West Siberian Geological Expedition.

SYSTEMATIC PALEONTOLOGY

Family Dipodidae Fischer, 1817

Subfamily Lophocricetinae Savinov, 1970

Genus *Heterosminthus* Schaub, 1930

Heterosminthus saraicus Zazhigin, Lopatin et Pokatilov, sp. nov.

Lophocricetus sp. (1): Pokatilov in Mats *et al.*, 1982, p. 104, pl. IV, figs. 1–6.

E t y m o l o g y. From the Saraiskaya Bay.

H o l o t y p e. GIN, no. 1121/4, fragmentary left maxilla containing P^4 – M^2 ; Eastern Siberia, Irkutsk Region, Lake Baikal, Olkhon Island, Olkhon 1; Upper Miocene (MN12), Sasa Beds, Saraiskaya Member.

D e s c r i p t i o n (Fig. 1). A relatively large member of the genus. The posterior edge of the incisor foramina is on a level with the center of P^4 . The anterior surface of the upper incisor is weakly convex and lacks a longitudinal groove. The central cusp of P^4 is relatively high; the posterior basal cingulum is weak. Two small accessory cusps are usually developed anterior to the central cusp; the first is located somewhat labially, and the second is somewhat lingually or directly ahead of the central cusp. M^1 and M^2 are elongated. The anteroloph of M^1 is weakly developed or absent; the anterostyle is small. The protoloph and endoloph form independent contacts with the paracone. The protostyle is well developed. The mesoloph is short. The metaconule is large; the arms of the posteroloph are short. The endoloph of M^2 is weakly developed or absent. The protoloph is straight and extends parallel

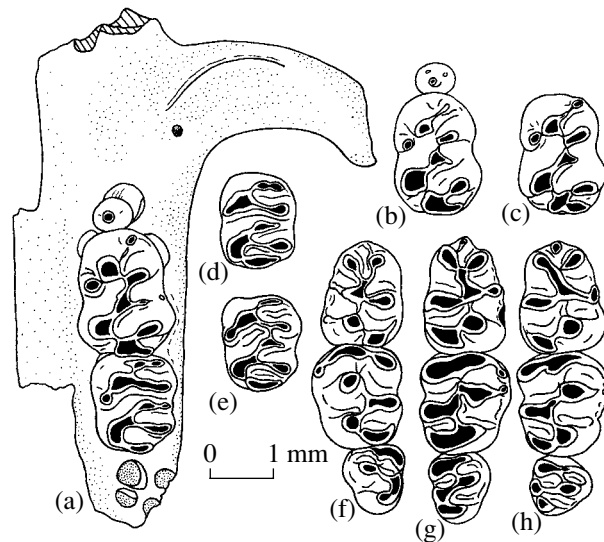


Fig. 1. *Heterosminthus saraicus* sp. nov.: (a) holotype GIN, no. 1121/4, fragmentary left maxilla containing P^4 – M^2 ; (b) GIN, no. 1121/1, left P^4 and M^1 ; (c) GIN, no. 1121/6, left M^1 ; (d) GIN, no. 1121/2, left M^2 ; (e) GIN, no. 1121/3, left M^2 ; (f) GIN, no. 1121/23, left M_1 – M_3 ; (g) GIN, no. 1121/26, right M_1 – M_3 ; and (h) GIN, no. 1121/27, right M_1 – M_3 .

to the metaloph. The mesoloph is long. The posteroloph is well developed; the posterofossette is open.

On M_1 , the anteroconid is connected to the metaconid or is isolated. The protoconid is connected to the metaconid at the point of contact with the endolophid, forms separate contacts with the metaconid and endolophid, is connected only to the endolophid, or is completely isolated. The mesoconid is triangular and frequently extended longitudinally and fused with the ectomesolophid. The hypoconid and entoconid adjoin the posterolingual corner of the latter at the same point. The hypoconulid is large; the posterolophid is short. The ectostylid is well developed; the ectocingulid is low but well pronounced. The M_2 is almost as large as the M_1 . The anterolophid is long and free or adjoins the protoconid labially. The anteroconid is well developed. The protoconid is connected to the anteroconid or isolated. Occasionally, a weak rudimentary mesolophid is present. Important structural features of M_3 are the absence of a lingual arm of the anterolophid and the presence of contacts between the anteroconid and the protoconid, between the protoconid and the entoconid, and between the entoconid and the hypoconid. Occasionally, the metaconid directly adjoins the entoconid on the lingual edge of the occlusal surface.

Measurements, mm. Holotype, length \times width of teeth: (P^4) 0.55×0.6 , (M^1) 1.95×1.5 , and (M^2) 1.55×1.3 ; length: (P^4 - M^2) 4.0, (P^4 - M^1) 2.5, and (M^1 - M^2) 3.45. The measurements of isolated teeth are as follows:

Tooth	Length			Width		
	<i>n</i>	limits	average	<i>n</i>	limits	average
P^4	3	0.5–0.575	0.54	3	0.6–0.675	0.625
M^1	6	1.85–2.0	1.91	6	1.35–1.525	1.43
M^2	6	1.45–1.65	1.56	6	1.2–1.325	1.275
M_1	11	1.525–1.75	1.65	11	1.15–1.325	1.26
M_2	10	1.4–1.625	1.55	10	1.2–1.4	1.33
M_3	4	0.925–1.025	0.98	4	0.825–0.95	0.91

Length of tooth row:

Tooth row	P^4 - M^2	P^4 - M^1	M^1 - M^2	M_1 - M_3	M_1 - M_2	M_2 - M_3
	<i>n</i>	1	2	2	3	7
Limits	4.0	2.35–2.5	3.45–3.6	4.15–4.3	3.0–3.275	2.55–2.6
Average	–	2.425	3.525	4.22	3.17	2.575

Comparison. The new species differs from Early and Middle Miocene species by a weak anteroloph and weak mesoloph on the M^1 , very large metaconule and short arms of the posteroloph on the M^1 , straight protoloph and reduced endoloph on the M^2 , the absence of a mesolophid and the presence of a ectocingulid on the M_1 , and the absence of a posterior arm of the protoconid on the M_2 . It differs from *H. gansus* Zheng, 1982 and *H. mugodzhariensis* Zazhigin et Lopatin, 2000 by a reduced anteroloph on the M^1 and from

H. gabuniai (Lungu, 1981) by a relatively shorter M^1 , the absence of a lingual arm of the anteroloph on the M^2 , and a relatively small ectostylid and weak ectocingulid on the M_1 .

Remarks. *H. saraicus* is the latest *Heterosminthus* species, which expands the upper limit of the stratigraphic distribution of the genus to the MN12 Zone. Previously, the Chinese *H. gansus* dated to MN11 was considered to be the latest species of the genus (Qiu, 1996; Qiu and Wang, 1999). *Lophocricetus* cf. *gansus* from Mongolia (which we refer to as *Heterosminthus* sp.) is dated to the middle of the Late Miocene (Höck *et al.*, 1999).

H. simplicidens Zheng, 1982 was described from Gansu simultaneously with the type series of *H. gansus*. We believe that the M_1 assigned to this species (Zheng, 1982, p. 142, text-fig. 3B) actually belongs to *H. gansus*. An extremely strongly reduced metaconid on the M_2 (Zheng, 1982, text-fig. 3A, holotype) clearly distinguishes *H. simplicidens* from all known Lophocriceinae (however, this is probably an aberrative specimen of *H. gansus*). On this basis, we regard *H. simplicidens* as nomen dubium.

Material. In addition to the holotype, six fragmentary upper jaws (one lacking teeth and five containing one of the following series: incisor, P^4 , and M^1 ; P^4 ; M^1 and M^2 ; M^1 ; and M^2), 11 fragmentary lower jaws (three with M_1 - M_3 , four with M_1 and M_2 , one with incisor and M_1 , one with M_1 , one with incisor, and one lacking teeth), and 12 isolated teeth (three M^1 , three M^2 , two M_1 , three M_2 , and one M_3) from the type locality.

Genus *Lophocricetus* Schlosser, 1924

Lophocricetus: Schlosser, 1924, p. 41; Savinov, 1970, p. 102; Qiu, 1985, p. 42.

Type species. *L. grabaui* Schlosser, 1924, uppermost Miocene of Central Asia.

Diagnosis. Medium-sized member of Lophocriceinae with relatively high-crowned bunolophodont teeth. Alternation of cusps well pronounced and crests well developed. On M^1 and M^2 , protocone and endoloph independently adjoining paracone; hypocone connected to metacone; mesoloph rudimentary or absent; and posterostyle present or absent. Mesocone usually developed on M^1 but absent on M^2 . On M^1 , posteroloph connected to metacone; on M^2 , posteroloph connected to hypocone or to hypocone and metacone. On M_1 hypoconid connected to mesoconid or entoconid. Hypoconulid large. M_2 , lacking posterior arm of protoconid. Protoconid of M_2 connected to anteroconid or metaconid. Stylids and ectocingulid of M_1 and M_2 well developed.

Composition. Two subgenera: *Lophocricetus* sensu stricto and *Paralophocricetus* subgen. nov.

Comparison. The genus is distinguished from *Heterosminthus* by the higher tooth crowns showing clear alternation of cusps and well-developed crests and

by different arrangement of the main cusps: the protocone of M^1 and M^2 is connected to the paracone rather than to the protoloph; the hypocone of M^1 is connected to the metacone rather than to the posteroloph; the hypoconid of M_1 is connected mainly to the entoconid rather than to the mesoconid; the protoconid of M_2 is connected mainly to the metaconid rather than to the anteroconid.

Subgenus *Lophocricetus* sensu stricto

Type species. *L. grabaui* Schlosser, 1924.

Diagnosis. Anteroloph on M^1 well developed; anteroloph on M^2 singular or double (anteroloph II predominantly developed). Hypocone on M^1 and M^2 integral, posterostyle absent. On M_1 , protoconid connected mainly to metaconid. Hypoconid connected to entoconid. Ectomesolophid usually well pronounced. Protoconid of M_2 connected to metaconid. External cusps of M_1 and M_2 extended transversely; stylids and ectocingulid developed to greater or lesser degree. On M_3 , entoconid completely fused with posterolophid.

Composition. *L. (L.) minusculus* Savinov, 1977, Upper Miocene (MN10–MN11) of Kazakhstan and Ukraine; *L. (L.) complicidens* Topachevsky et Scorik, 1984, Upper Miocene (MN10) of Ukraine; *L. (L.) vinogradovi* Savinov, 1970, Upper Miocene (MN12–MN13) of Kazakhstan; *L. (L.) grabaui* Schlosser, 1924, uppermost Miocene (MN13) of China; *L. (L.) reliquus* sp. nov., uppermost Miocene (MN13) of Mongolia.

Remarks. We consider *L. sarmaticus* Topachevsky et Scorik, 1984 from the Upper Sarmatian of Ukraine to be a synonym of *L. complicidens* and *L. maeoticus* Topachevsky et Scorik, 1984 from the Lower Meotian of Ukraine to be a synonym of *L. minusculus*.

Lophocricetus (Lophocricetus) minusculus Savinov, 1977

Lophocricetus minusculus: Savinov, 1977, p. 27, text-figs. 1–4; 1988, p. 22, text-figs. 1a–1d.

Lophocricetus maeoticus: Topachevsky et al., 1984, p. 37, text-fig. III.

Holotype. IZ, no. M-824/72-PP, isolated left M_1 ; Kazakhstan, right bank of the Ishim River, Petropavlovsk 1A locality; Upper Miocene (MN10), Ishim Formation.

Description (Figs. 2a–2d). A small member of the genus. The M^1 is longitudinally extended and has a well-developed mesocone and a small mesoloph. The anteroloph is short. The protostyle is strongly displaced posteriorly with reference to the protocone; the hypocone is large; the posteroloph is weak; the posterostyle is open. The posteroloph is connected to the lingual side of the metacone at the point of junction with the metaloph.

The anteroconid on the M_1 is small and connected to the metaconid or isolated. The protoconid is connected to the metaconid. The endolophid connects the mesoconid to the metaconid. The mesoconid is small and fused with a long ectomesolophid. The ectostylid is

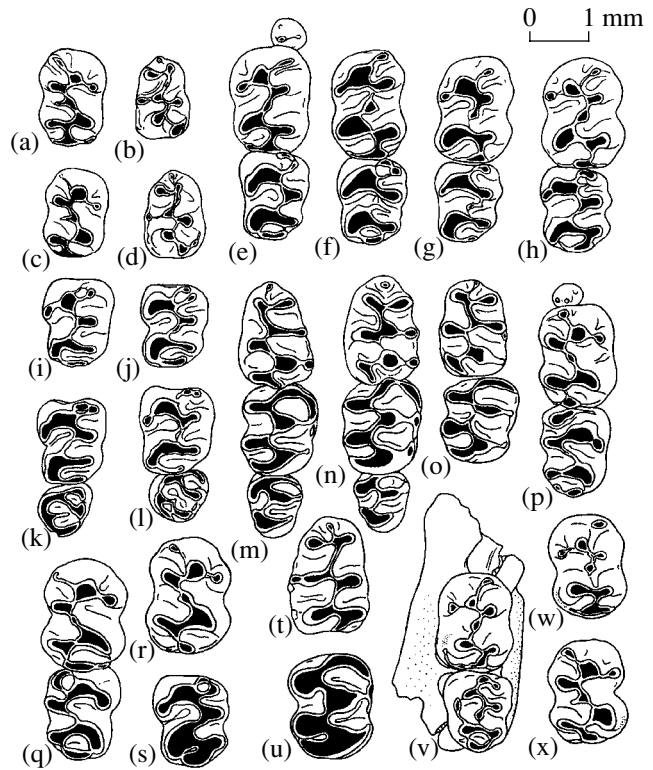


Fig. 2. Late Miocene species of *Lophocricetus* sensu stricto: (a–d) *L. (L.) minusculus* Savinov, (e–u) *L. (L.) vinogradovi* Savinov, and (v–x) *L. (L.) reliquus* sp. nov.: (a) GIN, no. 952/3, right M^1 ; (b) GIN, no. 952/4, left M_1 ; (c) IZ, no. M-830/72-PP, right M^1 ; (d) holotype IZ, no. M-824/72-PP, left M_1 , Kazakhstan, Petropavlovsk 1A locality; (e) GIN, no. 640/480, left P^4 – M^2 ; (f) GIN, no. 640/483, left M^1 and M^2 ; (g) GIN, no. 640/481, left M^1 and M^2 ; (h) GIN, no. 640/482, left M^1 and M^2 ; (i) GIN, no. 640/494, left M^2 ; (j) GIN, no. 640/495, left M^2 ; (k) GIN, no. 640/491, left M^2 and M^3 ; (l) GIN, no. 640/492, left M^2 and M^3 ; (m) GIN, no. 640/396, right M_1 – M_3 ; (n) GIN, no. 640/398, right M_1 – M_3 ; (o) GIN, no. 640/483, right M_1 and M_2 , Kazakhstan, Pavlodar 1A locality; (p) GIN, no. 951/1026, right P^4 – M^2 ; (q) GIN, no. 951/1008, right M^1 and M^2 ; (r) GIN, no. 951/1011, right M^1 ; (s) GIN, no. 951/1010, left M^2 ; (t) 951/1018, left M_1 ; (u) GIN, no. 951/1025, right M_2 , Kazakhstan, Selety 1A locality; (v) GIN, no. 956/2023, fragmentary left maxilla containing M^1 and M^2 ; (w) GIN, no. 956/2022, left M^1 ; and (x) GIN, no. 956/2024, right M^1 , Mongolia, Khirgis-Nur 2 locality.

well pronounced. The anterior arm of the entoconid is connected to the mesoconid; the posterior arm adjoins the anterior projection of the hypoconid. The hypoconid is very large; the posterolophid is weakly developed. The ectocingulid is narrow and observed only at the labial base of the hypoconid, and the posterostylid is absent.

Measurements (length × width), mm. (GIN, no. 952/3) M^1 , 1.65 × 1.125; (GIN, no. 952/4) M_1 , 1.4 × 0.925.

Comparison. *L. (L.) minusculus* differs from other species by extremely small measurements. In addition, it differs from *L. (L.) grabaui* and *L. (L.) vinogradovi* by certain primitive characters (a better developed mesoloph and a more lingual position of the protoloph–metacone contact on the M^1) and from *L. (L.) complicidens* by the relatively shorter M^1 .

Remarks. *L. maeoticus* was described by Topachevsky *et al.* (1984) based on single M^1 from the Meotian of Ukraine. However, this form does not differ from *L. minusculus* from Kazakhstan in either structure or measurements.

Occurrence. Upper Miocene of Kazakhstan (MN10) and Ukraine (MN10–MN11).

Material. In addition to the holotype, two M^1 and one M^1 from the type locality.

Lophocricetus (Lophocricetus) vinogradovi Savinov, 1970

Lophocricetus vinogradovi: Savinov, 1970, p. 102, text-fig. 4; 1988, p. 22, text-figs. 1e and 1f.

Holotype. IZ, no. M-136/60-P, fragmentary right maxilla containing P^4 – M^3 ; Kazakhstan, Pavlodar 1A locality (Gusinyi Perelet locality); Upper Miocene (MN12), Pavlodar Formation.

Description (Figs. 2e–2u). A medium-sized member of the genus. The posterior edge of the incisor foramina is located on a level with the center of P^4 . The P^4 is weakly longitudinally compressed. The posterior basal cingulum is weakly developed and isolated from the accessory cuspules. Almost without exception, the latter are well pronounced; the smaller cuspule is located just lingual to the central cusp, and the larger cuspule is located anterolabially. The M^1 is broad and has a well-developed mesocone and a short reduced mesoloph. The anteroloph is relatively long and complete. The protostyle is weakly displaced posteriorly with reference to the protocone. The posteroloph is usually double-armed and connected to the lingual part of the posterior side of the metacone close to the point of contact with the metaloph. The posterofossette and posterosinus are open. The M^2 lacks mesocone and has a complete endoloph and, usually, a closed posterofossette. The anteroloph is usually double. The anteroloph I is formed by the anterior arm of the protocone and a lingual projection of the anterostyle; it is frequently incomplete and looks like a short transverse ridge at the anterior edge of the occlusal surface. The anteroloph II is formed by a lingual projection of the protocone located close to the origin of the protoloph. Two anterostyles are usually present; however, they are drawn close to each other and frequently partially or completely merged. The endosinus of M^3 is closed; the anteroloph, endoloph, protoloph, and posteroloph are well developed.

On the lower molars, the protoconid and hypoconid are broadened; the stylids are small but distinctly differentiated. The ectocingulid is developed to a variable degree. On the M^1 , the anteroconid is usually connected

to the metaconid; in some cases, it is isolated. The protoconid is commonly connected to the metaconid, occasionally, to the endolophid, or to both. Almost without exception, the endolophid is connected to the metaconid. The presence of a long labial arm of the anterolophid is characteristic of M^2 . On the M^3 , the entoconid is merged with the posterolophid but isolated from the metaconid.

Variability. Among the specimens from the type locality, the morphotypic variation of M^1 is observed in the structure of the mesoloph and posteroloph. The mesoloph is frequently rudimentary (25 specimens, 54%); occasionally, it is complete (one specimen, 2%), incomplete and relatively long (six specimens, 13%), or absent (14 specimens, 31%). Double-armed posterolophs are most abundant (41 specimens, 91%); the lingual posteroloph (three specimens, 7%) and the posteroloph entirely formed by the metaconule (one specimen, 2%) are rare. In one specimen, the posterosinus is closed. The M^2 varies in the structure of anteroloph and posteroloph; the mesocone, incomplete endoloph, and a supplementary labial contact between the paracone and the metacone are observed in a small number of specimens. Double anterolophs (19 specimens, 76%) prevail, including the cases of complete development of anterolophs I and II (eight specimens, 32%), complete development of only anteroloph II (10 specimens, 40%), and incomplete development of both (one specimen, 4%). Singular anteroloph I or anteroloph II are relatively rare (three specimens, 12%, each). Labially, the posteroloph is merged with the metacone (16 specimens, 64%) or free (nine specimens, 36%); this determines whether the posterofossette is closed or open. On the M^1 the anteroconid is usually connected to the metaconid (43 specimens, 91.5%). The protoconid is connected mainly to the metaconid (41 specimens, 88%). The contact is usually at the point of connection between the metaconid and the endolophid (35 specimens, 74.5%). The protoconid is connected to the endolophid in four specimens (8%); in two specimens (4%), the protoconid has separate contacts with the metaconid and with the endolophid. The absence of contact between the endolophid and the metaconid is observed in only one specimens (2%).

Measurements, mm. Isolated teeth from the Pavlodar 1A locality:

Tooth	<i>n</i>	Length		<i>n</i>	Width	
		limits	average		limits	average
P^4	6	0.475–0.75	0.57	6	0.6–0.875	0.69
M^1	44	1.6–1.95	1.83	44	1.1–1.5	1.31
M^2	25	1.325–1.625	1.443	25	1.05–1.3	1.168
M^3	3	0.8–0.85	0.825	3	0.85–0.975	0.91
M^1	46	1.45–1.85	1.69	47	1.05–1.3	1.17
M^2	44	1.325–1.6	1.48	44	1.15–1.375	1.25
M^3	3	0.95–1.05	1.0	3	0.825–0.95	0.9

Length of tooth rows (Pavlodar 1A):

Tooth row	P ⁴ -M ²	P ⁴ -M ¹	M ¹ -M ²	M ² -M ³	M ₁ -M ₃	M ₁ -M ₂	M ₂ -M ₃
<i>n</i>	3	4	10	2	2	15	2
Limits	3.7– 3.75	2.1– 2.15	3.025– 3.425	2.125– 2.15	4.25	2.9– 3.3	2.55
Average	3.725	2.13	3.21	2.14	–	3.125	–

Measurements of isolated teeth from the Selety 1A locality:

Tooth	Length			Width		
	<i>n</i>	limits	average	<i>n</i>	limits	average
P ⁴	2	0.4–0.62	0.51	2	0.55–0.75	0.65
M ¹	10	1.65–2.125	1.875	8	1.2–1.55	1.34
M ²	3	1.5–1.575	1.54	3	1.2–1.28	1.25
M ₁	9	1.625–2.0	1.79	9	1.125–1.375	1.24
M ₂	1	1.75	–	1	1.4	–

Length of tooth rows (Selety 1A): P⁴-M² (GIN, no. 951/1026) 3.55; M¹-M²: (GIN, no. 951/1026) 3.2, (GIN, no. 951/1008) 3.325, and (GIN, no. 951/1010) 3.5; M₁-M₂ (GIN, no. 951/1009) 3.45.

Comparison. *L. (L.) vinogradovi* differs from *L. (L.) grabaui* by a less reduced mesocone of M¹ and the presence of two complete anterolophes on the M². It differs from *L. (L.) minusculus* and *L. (L.) complacidens* by larger measurements and relatively weak mesoloph of M¹. In addition, it differs from *L. (L.) complacidens* by the absence of mesoloph and mesostyle on the M².

Occurrence. Upper Miocene (MN12–MN13) of Kazakhstan.

Material. Sixty fragmentary jaws (three containing P⁴-M², one with P⁴ and M¹, nine with M¹ and M², two with M² and M³, one with P⁴, 13 with M¹, two with M², one with M³, one zygomatic arch, two with M₁-M₃, one with incisor and M₁ and M₂, 13 with M₁ and M₂, nine with M₁, one with M₂, and one lacking teeth) and 83 isolated teeth (P⁴, 20 M¹, nine M², lower incisor, 23 M₁, 28 M₂ and M₃) from the Pavlodar 1A locality; and nine fragmentary jaws (three with M¹ and M², three with M¹, one with M₁-M₂, one with M₁, and one lacking teeth) and 15 isolated teeth (P⁴, six M¹, seven M₁, and a M₂) from the Selety 1A locality.

Lophocricetus (Lophocricetus) reliquus Zazhigin,
Lopatín et Pokatílov, sp. nov.

Etymology. From the Latin *reliquus* (remaining).

Holotype. GIN, no. 956/2023, fragmentary left maxilla containing M¹ and M²; Mongolia, Khirgis-Nur 2; Upper Miocene (MN13), Lower Khirgis-Nur Subformation, interval of 17 m.

Description (Fig. 2v–2x). A medium-sized member of the genus. The M¹ has a large anterostyle, a narrow and weak anteroloph, and a well-pronounced mesocone. Occasionally, a reduced mesoloph is present. The posterolingual wall of the hypocone is separated from the wall of the crown base by a small projection formed by an extremely long lingual arm of the posteroloph. The M² has a well-developed anteroloph I, a large anterostyle, and a weak mesocone. The protostyle is longitudinally elongated and connected to the anterolingual edge of the hypocone. The posteroloph is connected to the hypocone and metacone.

Measurements (length × width), mm. M¹: (holotype) 1.675 × 1.3 (GIN, no. 956/2022) 1.7 × 1.25, and (GIN, no. 956/2024) 1.75 × 1.325; M²: (holotype) 1.3 × 1.15. Length of M¹-M² (holotype) 2.975.

Comparison. The new species differs from all other species of the subgenus by the structure of the posterolingual part of the hypocone. In addition, it differs from *L. (L.) grabaui* and *L. (L.) vinogradovi* by the presence of the mesocone on the M² and from *L. (L.) minusculus* and *L. (L.) complacidens* by the weaker mesoloph on the M¹.

Material. In addition to the holotype, two isolated M¹ from the type locality.

**Subgenus *Paralophocricetus* Zazhigin,
Lopatín et Pokatílov, subgen. nov.**

Etymology. From the Latin *para* (near) and the generic name *Lophocricetus*.

Type species. *Lophocricetus (Paralophocricetus) progressus* sp. nov.

Diagnosis. Anteroloph of M¹ reduced or absent. On M², anteroloph I (complete or incomplete) developed. Mesocone of M¹ and M² reduced; mesoloph absent; hypocone double, lingual part detached and form well-pronounced posterostyle. On M₁, protoconid connected to endolophid or metaconid. Endolophid in central position or inclined to metaconid. Hypoconid connected to mesoconid, labial part of entoconid, or to posterior arm of entoconid. Ectomesolophid reduced. Protoconid of M₂ connected to anteroconid or metaconid. Labial cusps of M₁ and M₂ rounded and distant from edge of occlusal surface, stylids and ectocingulid developed to varying degree. Entoconid of M₃ usually well developed.

Composition. *L. (P.) pusillus* Schaub, 1934, uppermost Miocene–lowermost Pliocene (MN13–MN14) of China and Mongolia; *L. (P.) intermedius* sp. nov., Upper Miocene (MN13) of Mongolia; *L. (P.) progressus* sp. nov., Lower Pliocene (MN14) of Eastern Siberia; *L. (P.) afanasievi* Savinov, 1970, Upper Miocene (MN13), *L. (P.) sibiricus* sp. nov., Lower Pliocene (MN14), and *L. (P.) ultimus* sp. nov., Lower Pliocene (MN14–MN15) of Western Siberia and Kazakhstan.

Comparison. The new subgenus differs from the subgenus *Lophocricetus* sensu stricto by the pres-

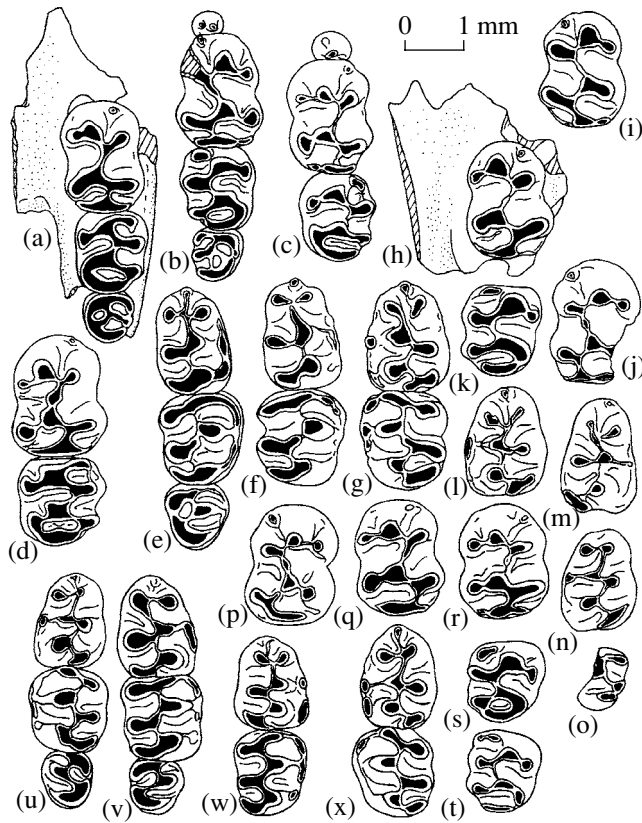


Fig. 3. Species of *Lophocricetus* (*Paralophocricetus*) from Eastern Siberia and Mongolia: (a–g) *L. (P.) progressus* sp. nov., (h–o) *L. (P.) intermedius* sp. nov., and (p–x) *L. (P.) pusillus* Schaub: (a) holotype GIN, no. 1121/32, fragmentary left maxilla containing M^1 – M^3 ; (b) GIN, no. 1121/33, right P^4 – M^3 ; (c) GIN, no. 1121/37, left P^4 – M^2 ; (d) GIN, no. 1121/39, left M^1 and M^2 ; (e) GIN, no. 1121/113, right M^1 – M^3 ; (f) GIN, no. 1121/107, right M^1 and M^2 ; (g) GIN, no. 1121/129, left M^1 and M^2 , Eastern Siberia, Olkhon 2 locality; Lower Pliocene, Sasa Beds, Odonimskaya Member; (h) holotype GIN, no. 956/2025, fragmentary left maxilla containing M^1 ; (i) GIN, no. 956/2027, right M^1 ; (j) GIN, no. 956/2028, right M^1 ; (k) GIN, no. 956/2026, right M^2 ; (l) GIN, no. 956/2030, left M^1 ; (m) GIN, no. 956/2031, right M^1 ; (n) GIN, no. 956/2033, left M^1 ; (o) GIN, no. 956/2034, left M^3 , Mongolia, Khirgis-Nur 2 locality; Upper Miocene, Lower Khirgis-Nur Subformation; (p) GIN, no. 956/2035, right M^1 ; (q) GIN, no. 956/2037, left M^1 ; (r) GIN, no. 956/2038, left M^1 ; (s) GIN, no. 956/2048, right M^2 ; (t) GIN, no. 956/2047, right M^2 ; (u) GIN, no. 956/2052, left M^1 – M^3 ; (v) GIN, no. 956/2051, right M^1 – M^3 ; (w) GIN, no. 956/76, right M^1 and M^2 ; and (x) GIN, no. 956/2055, left M^1 and M^2 , Mongolia, Khirgis-Nur 2 locality; Lower Pliocene, base of the Upper Khirgis-Nur Subformation.

ence of the posterostyle on the M^1 and M^2 , reduced anteroloph, the absence of the mesoloph on the M^1 , the structure of the anteroloph on the M^2 , the presence of contacts between the hypoconid and mesoconid of M^1 and between the protoconid and anteroconid of M^2 , the

shape of the labial cusps on the M^1 and M^2 , and by the better detached entoconid of M^3 .

Lophocricetus (*Paralophocricetus*) *progressus* Zazhigin, Lopatin et Pokatilov, sp. nov.

Lophocricetus sp. (2): Pokatilov in Mats *et al.*, 1982, p. 106, pl. IV, figs. 7–16.

Etymology. From the Latin *progressus* (advanced).

Holotype. GIN, no. 1112/32, fragmentary left maxilla containing M^1 – M^3 ; Eastern Siberia, Irkutsk Region, Lake Baikal, Olkhon Island, Olkhon 2 locality; Lower Pliocene (MN14), Sasa Beds, Odonimskaya Member.

Description (Figs. 3a–3g). A medium-sized member of the genus. The posterior edge of the incisor foramina is on a level with the anterior part of the P^4 alveolus. The P^4 is small and rounded. The posterior basal cingulum is short and weak; in addition to the central cusp, one or two accessory cusps are frequently developed; the first is located labially and the second occupies the anterior position. The M^1 is elongated; the posterior lobe is somewhat wider than the anterior lobe. The anteroloph is usually absent. The protocone weakly projects anteriorly with reference to the paracone. The mesoloph is usually absent. The metaconule is large and broad. The posterostyle is well developed; however, occasionally, it is only partially isolated from the hypocone. The posterostyle and the posterofossette are usually open. The M^2 has a well-developed and oblique endoloph, which connects the hypocone to the paracone. The anterostyle is large; the anteroloph is short. The anterofossette is occasionally partitioned by a narrow longitudinal crest connecting the anterostyle and the paracone. The hypocone is large and displaced to the center of the occlusal surface; the posterostyle is connected to a long posteroloph. The posterofossette is closed or open; occasionally, it is partitioned in the middle by a narrow additional crest connecting the posteroloph to the metaloph. The M^3 is small, round, and has a closed endosinus.

The anteroconid of M^1 is usually connected to the metaconid; occasionally, it is isolated or connected to either anterior cusp. The protoconid is usually connected to the metaconid at the origin of the endolophid; occasionally, it independently adjoins the metaconid and the endolophid, only one of these conids, or is isolated. The mesoconid is large. The ectomesolophid is narrow. The ectostylid, posterostylid, and ectocingulid are well developed. The hypoconid adjoins the posterolabial part of the entoconid or the posterolingual corner of the mesoconid (at the same point as the arm of the entoconid). The labial arm of the anterolophid of M^2 is long and free or fused with the base of the labial side of the protoconid, ectostylid, or ectocingulid. The anteroconid is poorly pronounced. The protoconid is usually connected to the anteroconid at the point of contact with the arm of the metaconid; less frequently, it is connected to the metaconid or its arm; in rare instances,

it is isolated. The stylids and ectocingulid are well developed. The M_3 is characterized by the presence of contact between the metaconid and the entoconid.

Measurements, mm. Holotype (length \times width): (M^1) 1.85×1.35 , (M^2) 1.3×1.25 , and (M^3) 0.825×0.85 ; length of M^1 – M^3 , 3.95; and M^1 – M^2 , 3.15; (specimen GIN, no. 1112/33) length of P^4 – M^3 is 4.45 and length of M^1 – M^3 is 4.075.

Measurements of isolated teeth, mm:

Tooth	Length			Width		
	<i>n</i>	limits	average	<i>n</i>	limits	average
P^4	6	0.325–0.575	0.492	6	0.4–0.65	0.554
M^1	52	1.75–2.125	1.932	52	1.325–1.65	1.487
M^2	38	1.3–1.6	1.46	38	1.225–1.45	1.34
M^3	3	0.825–0.9	0.867	3	0.85–1.025	0.917
M_1	67	1.575–2.0	1.76	72	1.15–1.475	1.3
M_2	47	1.4–1.8	1.575	48	1.15–1.55	1.39
M_3	1	1.1	–	1	1.05	–

Length of tooth row:

Tooth row	P^4 – M^2	P^4 – M^1	M^1 – M^2	M^2 – M^3	M_1 – M_3	M_1 – M_2	M_2 – M_3
<i>n</i>	5	6	18	2	1	12	1
Limits	3.625– 3.85	2.125– 2.4	3.15– 3.475	2.125– 2.275	4.375	3.15– 3.45	2.65
Average	3.745	2.3	3.343	2.2	–	3.3	–

Variability. See Table 1.

Comparison. The new species differs from *L. (P.) pusillus* and *L. (P.) afanasievi* by the opposite positions of the protocone and paracone on the M^1 , the presence of well-developed crests partitioning the anterofossette and posterofossette on the M^2 , and by the prevalence of contact between the protoconid and the anteroconid on the M_2 .

Material. In addition to the holotype, 28 fragmentary upper jaws (one containing P^4 – M^3 , four with P^4 – M^2 , one with P^4 – M^1 , one with P^4 , one with M^1 – M^3 , 12 with M^1 and M^2 , six with M^1 , one with M^2 , and one with M^3); 39 fragmentary lower jaws (one with M_1 – M_3 , 13 with M_1 and M_2 , one with the incisor and M_1 , 20 with M_1 , two with M_2 , and two lacking teeth); and 118 isolated teeth: 28 M^1 , 19 M^2 , 38 M_1 and 33 M_2 from the type locality.

Lophocricetus (Paralophocricetus) intermedius Zazhigin,
Lopatín et Pokatilov, sp. nov.

Etymology. From the Latin *intermedius* (intermediate).

Holotype. GIN, no. 956/2025, fragmentary left maxilla containing M^1 ; Mongolia, Khirgis-Nur 2 locality; Upper Miocene (MN13), Lower Khirgis-Nur Subformation, level of 24 m.

Description (Figs. 3h–3o). A small member of the genus. The posterior edge of the incisor foramina is

located on a level with the anterior edge of the P^4 alveolus. The posterior lobe of M^1 is substantially wider than the anterior lobe. The anteroloph on the M^1 is undeveloped; the anterostyle is small. The protostyle is moderately developed. The protoloph is short. The mesocone is weak or absent. The posterostyle is rudimentary, and the hypocone is weakly compressed in the middle; however, the anterior fold is absent, so that the lingual part of the hypocone is only slightly detached from the labial part. The posteroloph is connected to the posterolingual corner of the metacone. The posteroloph and posterofossette are open. The M^2 has a short anteroloph I and a narrow endoloph; the hypocone slightly bifurcates, the posterofossette is open, and the endosinus is straight.

The anteroconid of M_1 is isolated, the ectostylid is well developed, and the ectocingulid and the posterostylid are weak. The protoconid is connected to the endolophid or to the metaconid; occasionally, it is isolated. The hypoconid is connected to the entoconid or to the mesoconid. On the M_3 , the entoconid is clearly isolated from the posterolophid.

Measurements (length \times width), mm: M^1 : (GIN, no. 956/2027) 1.9×1.45 , (holotype) 1.9×1.425 , (GIN, no. 956/2028) $2.05 \times ?$, and (GIN, no. 956/2029) $1.825 \times ?$; M^2 : (GIN, no. 956/2026) 1.5×1.325 ; M_1 : (GIN, no. 956/2033) 1.65×1.25 , (GIN, no. 956/2030) 1.75×1.4 , and (GIN, no. 956/2031) 1.875×1.25 ; M_3 : (GIN, no. 956/2034) $1.0 \times ?$.

Comparison. The new species differs from the other species of the subgenus *Paralophocricetus* by the rudimentary posterostyle on the M^1 and M^2 and by the narrow anterior lobe of M^1 .

Material. In addition to the holotype, two fragmentary maxillae (one with M^1 and one with M^2) and seven isolated teeth: two M^1 , four M_1 , and one M_3 from the type locality (interval 23–24 m).

Lophocricetus (Paralophocricetus) pusillus Schaub, 1934

Lophocricetus grabaui (part.): Schlosser, 1924, p. 41, pl. 3, fig. 31.

Mus sp.: Schlosser, 1924, p. 44, pl. 3, fig. 30.

Lophocricetus pusillus: Schaub, 1934, p. 35; Qiu, 1985, p. 52, text-figs. 18–32, pl. 1, figs. 4–6, pl. 3, figs. 19–30; Qiu and Storch, 2000, p. 189, pl. 6, figs. 35–38.

Lectotype [Qiu, 1985]. PIU, no. M3373.67, fragmentary right dentary containing M_1 and M_2 ; China, Inner Mongolia, Ertemte 1 locality; Upper Miocene (MN13).

Description (Figs. 3p–3x). A small member of the genus. The anteroloph on the M^1 is undeveloped, the anterostyle is well pronounced, the protostyle is large, and the mesocone is weak or absent. The posterostyle is large, distinctly detached from the hypocone by deep folds. The posteroloph is connected to the posterolingual corner of the metacone. The posteroloph and posterofossette are open. The M^2 has a short anteroloph I and a narrow endoloph; the hypocone weakly bifurcates, and the posterofossette is closed.

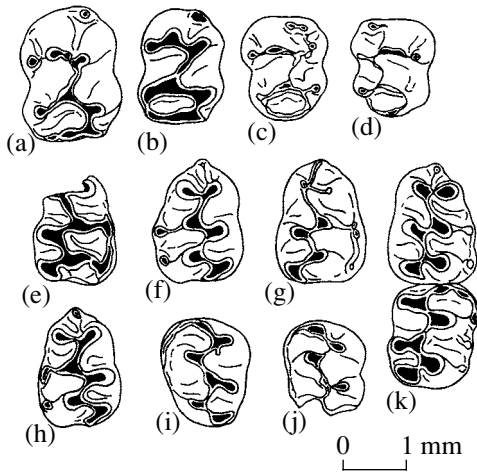


Fig. 4. Late Miocene *Lophocricetus* (*Paralophocricetus*) *afanasievi* Savinov: (a) GIN, no. 948/32, left M¹; (b) GIN, no. 948/21, left M¹; (c) GIN, no. 948/33, left M²; (d) GIN, no. 948/34, right M¹; (e) GIN, no. 948/36, right M¹; (f) GIN, no. 948/37, left M²; (g) GIN, no. 948/38, right M¹; (h) GIN, no. 948/39, left M¹; (i) GIN, no. 948/22, left M²; (j) GIN, no. 948/40, left M₂, Western Siberia Novaya Stanitsa 1A locality, Novaya Stanitsa Formation; and (k) holotype IZ, no. M-736/66-G, fragmentary right dentary containing M₁ and M₂, Kazakhstan, Makovka locality.

The M₁ is extremely diverse in structure. Characteristic features are the presence of the anteroconid, which is connected to the metaconid or isolated; a well-developed ectostylid; and a weak ectocingulid. The posterostylid is developed to a variable degree. The protoconid is usually connected to the endolophid or metaconid; occasionally, it is isolated. The hypoconid is connected to the entoconid or its arm; occasionally, it is connected to the mesoconid. The M₂ is characterized by the presence of a long labial arm of the anterolophid. The protoconid usually adjoins the anteroconid at the point of fusion with the arm of the metaconid; in rare cases, the protoconid is connected directly to the metaconid. On the M₃, the entoconid is usually fused with the posterolophid; occasionally, the anterolophid is strongly reduced.

Variability. The variation of the dental structure is shown in Table 1.

Measurements, mm. Isolated teeth from the Upper Khirgis-Nur Subformation, Khirgis-Nur 2 locality:

Tooth	Length			Width		
	<i>n</i>	limits	average	<i>n</i>	limits	average
M ¹	10	1.75–1.95	1.885	10	1.4–1.625	1.49
M ²	4	1.3–1.5	1.39	3	1.25–1.35	1.3
M ₁	23	1.55–1.95	1.72	25	1.1–1.4	1.27
M ₂	11	1.375–1.625	1.51	10	1.2–1.5	1.34
M ₃	3	0.85–0.925	0.88	3	0.85–0.9	0.88

Length of the lower tooth rows: M₁–M₃: (GIN, nos. 956/2051 and 2052) 3.85 and (GIN, no. 956/2053) 4.0; M₁–M₂: (GIN, no. 956/2052) 2.9, (GIN, no. 956/2051) 3.0, (GIN, nos. 956/2055 and 2057) 3.05, (GIN, nos. 956/2053 and 2056) 3.2, (GIN, nos. 956/2054 and 2058) 3.35, and (GIN, no. 956/2059) 3.45; and M₂–M₃: (GIN, no. 956/2051) 2.25, and (GIN, nos. 956/2052 and 2053) 2.3.

Comparison. *L. pusillus* differs from *L. (P.) progressus* by the structure of M¹ and M² and by the prevalence of the variant where the protoconid is connected to the arm of the metaconid on the M₂. It is distinguished from *L. (P.) afanasievi* by the smaller measurements and better developed posterostyle on the M¹ and M²; from *L. (P.) intermedius*, it is distinguished by the wider anterior lobe of M¹ and a well-developed posterostyle on the M¹ and M².

Occurrence. Upper Miocene to Lower Pliocene (MN13–MN14) of China, Mongolia, and Tuva.

Material. Fragmentary jaws (one with M¹, one with M², one with the incisor and M₁–M₃, three with the incisor and M₁ and M₂, two with M₁–M₃, three with M₁ and M₂, and two with M₁) and 29 isolated teeth (ten M¹, three M², 13 M₁, and three M₂) from the Upper Khirgis-Nur Subformation (intervals 37–40 and 50–60 m) of the Khirgis-Nur 2 locality; a fragmentary lower jaw containing M₁ and M₂ and isolated M₂ from the Khirgis-Nur 1 locality, six M¹, one M², fragmentary lower jaws (one with incisor, M₁, and M₂; one with M₂), seven M₁, and three M₂ from the Yavor 1 locality; fragmentary jaws (one with P⁴–M², one with M₁–M₃, and one with M₁ and M₂), and isolated teeth (two M² and one M₁) from the Yavor 2 locality; and two M¹ and one M₁ from the Kholu locality.

Lophocricetus (*Paralophocricetus*) *afanasievi* Savinov, 1970

Lophocricetus afanasievi (part.): Savinov, 1970, p. 106, text-fig. 5.

Holotype. IZ, no. M-736/66-G, fragmentary right dentary containing M₁ and M₂; Kazakhstan, Semipalatinsk Region, Kalbinskii Mountain Range, near the village of Makovka; Upper Miocene.

Description (Fig. 4). A relatively large member of the genus. The M¹ lacks anteroloph, and the anterostyle is large. The mesocone is weakly developed. The posterostyle is weakly detached, and the anterior fold is short and only approaches the base of the hypocone; the crest connecting the posterostyle to the hypocone is stout. The posterostylid is open or closed. The anteroloph of M² is short and isolated from the protocone. Occasionally, the anterofossette is partitioned by a low crest connecting the paracone to the anterostyle. The endoloph is complete, the posterostyle is weakly developed, and the posterofossette is closed. The M₃ has an incomplete endoloph and a closed anterofossette; the mesofossette and endosinus are closed.

The anteroconid on the M_1 is connected to the metaconid. The protoconid is connected to the metaconid or to the point of contact between the endolophid and the metaconid. The ectomesolophid is complete and low. The hypoconid is connected to the entoconid. On the M_2 , the protoconid is connected to the metaconid. The M_3 lacks ectocingulid.

Measurements, mm. M^1 : (GIN, no. 948/32) 2.1×1.55 , (GIN, no. 948/48) 1.9×1.45 , and (GIN, no. 948/21) 1.775×1.35 ; M^2 : (GIN, no. 948/33) 1.6×1.35 , (GIN, no. 948/34) 1.55×1.3 , (GIN, no. 948/47) 1.5×1.3 , (GIN, no. 948/35) $? \times 1.4$, and (GIN, no. 948/44) 1.35×1.15 ; M^3 : (GIN, no. 948/57) 0.85×0.9 ; M_1 : (GIN, nos. 948/37 and 38) 1.9×1.4 , (GIN, no. 948/43) 1.9×1.35 , (GIN, no. 949/39) 1.85×1.3 , and (GIN, no. 948/36) $? \times 1.3$; M_2 : (GIN, no. 948/22) 1.6×1.325 , (GIN, no. 948/50) 1.55×1.35 , (GIN, no. 948/49) 1.45×1.15 , and (GIN, no. 948/40) $? \times 1.3$; M_3 : (GIN, no. 948/45) 1.0×0.9 and (GIN, no. 948/46) 0.95×0.9 .

Comparison. *L. afanasievi* differs from *L. (P). progressus* by the absence of contact between the hypoconid and the mesoconid on the M_1 and between the protoconid and anteroconid on the M_2 . It differs from *L. (P). intermedius* by relatively large measurements, a wider anterior lobe of M^1 , and better developed postero-style on the M^1 and M^2 ; from *L. (P). pusillus*, it differs by larger measurements and weakly detached postero-style on the M^1 and M^2 .

Remarks. Savinov (1970) described *L. afanasievi* based on specimens from a borehole in the region of the village of Makovka. In addition to the holotype, he assigned three isolated teeth, i.e., one M^1 and two M_1 , to this species. We believe that M^1 does not belong to the genus *Lophocricetus*, and both M_1 should be assigned to *L. vinogradovi*. The depth at which these specimens were found had not been clearly identified. Savinov (1970) indicated 12–30 m of depth and assigned this interval to the Pavlodar Formation. Apparently, each form comes from different levels of nonstratified Mio-Pliocene beds; *L. vinogradovi* is known from MN12–MN13. Based on the specimens from the Novaya Stanitsa 1A locality, *L. afanasievi* is dated to the end of the Miocene (MN13).

Qiu (1985) believes that *L. afanasievi* is a synonym of *L. pusillus*. However, available material shows clear differences between these species.

Occurrence. Upper Miocene (MN13) of southwest Siberia and Kazakhstan.

Material. Eight M^1 , five M^2 , one M^3 , seven M_1 , four M_2 , and eight M_3 from the Novaya Stanitsa Formation of the Novaya Stanitsa 1A locality.

Lophocricetus (Paralophocricetus) sibiricus Zazhigin,
Lopatín et Pokatílov, sp. nov.

Etymology. From Siberia.

Holotype. GIN, no. 1110/347, fragmentary right dentary containing M_1 – M_3 ; Western Siberia, Omsk

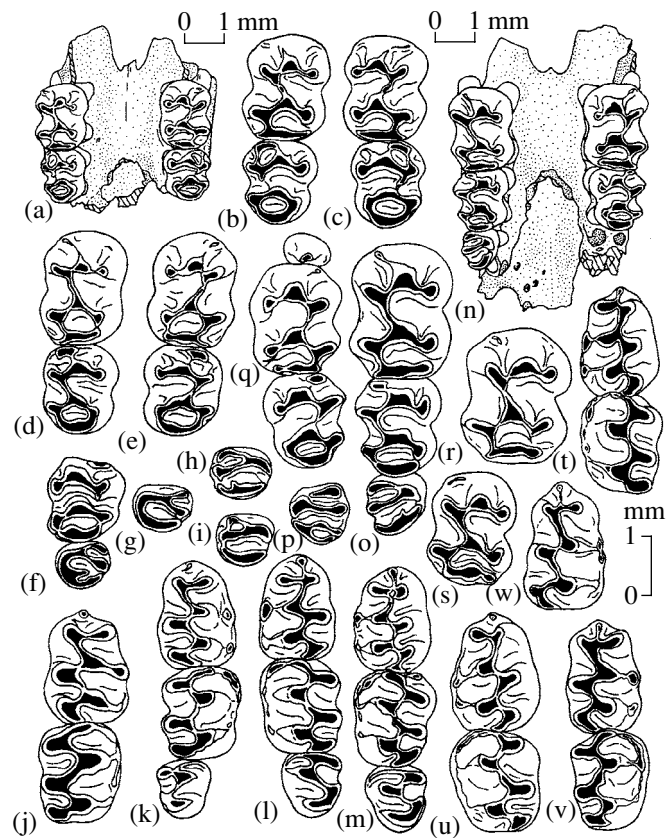


Fig. 5. Early Pliocene *Lophocricetus (Paralophocricetus)* species from Western Siberia, (a–m) *L. (P). sibiricus* sp. nov. and (n–w) *L. (P). ultimus* sp. nov.: (a–c) GIN, no. 1110/485, fragmentary upper jaw containing M^1 and M^2 : (a) palatal view, (b) right M^1 and M^2 , and (c) left M^1 and M^2 ; (d and e) GIN, no. 1110/484, fragmentary upper jaw containing M^1 and M^2 : (d) right M^1 and M^2 and (e) left M^1 and M^2 ; (f) GIN, no. 1110/194, left M^2 and M^3 ; (g) GIN, no. 1110/334, left M^3 ; (h) GIN, no. 1110/335, right M^3 ; (i) GIN, no. 1110/336, right M^3 ; (j) GIN, no. 1110/172, right M_1 and M_2 ; (k) holotype GIN, no. 1110/347, right M_1 – M_3 ; (l) GIN, no. 1110/345, left M_1 – M_3 ; (m) GIN, no. 1110/348, left M_1 – M_3 , Cherklak 1A locality; (n–p) GIN, no. 1111/10, fragmentary upper jaw containing M^1 – M^3 : (n) palatal view, (o) right M^1 – M^3 , and (p) left M^3 ; (q) GIN, no. 1111/25, left P^4 – M^2 ; (r) GIN, no. 1111/11, right M^1 ; (s) GIN 1111/15, right M^1 ; (t) holotype GIN, no. 1111/8, left M_1 and M_2 ; (u) GIN, no. 1111/7, left M_1 and M_2 ; (v) GIN, no. 1111/48, right M_1 and M_2 ; and (w) GIN, no. 1111/21, right M_1 , Olkhovka locality.

Region, Cherklak 1A locality; Lower Pliocene (MN14), Rytovo Formation.

Description (Figs. 5a–5m). A small member of the genus. The posterior edge of the incisor foramina is on a level with P^4 . The central cusp of P^4 is relatively high. The posterior and lateral sides of the occlusal surface are bordered by a well-developed cingulum, which forms anteriorly two small cingular cusps located on

a level with the anterior part of the central cusp. The labial cusp is markedly larger than the lingual cusp. Occasionally, the cingulum and cingular cuspules are reduced. The anteroloph on the M^1 is strongly reduced or absent. The anterostyle is small. The mesocone is weakly developed, and the mesoloph is undeveloped. The posterostyle is partially isolated from the hypocone by the anterior and posterior folds; occasionally, these cusps are completely isolated from each other. The posterostyle is usually open; in some cases, this fold is partially closed (i.e., the posteroloph adjoins the base of the posterostyle) or completely closed (i.e., the posterostyle is connected to the posteroloph by a supplementary lingual crest or fused with the latter at the base). The anteroloph on the M^2 is usually incomplete and isolated from the protocone. The anterofossette is usually integral; in individual cases, it is partitioned by a supplementary transverse crest connecting the anterostyle to the paracone. The morphotypes with the complete endoloph and closed posterofossette prevail. The M^3 lacks endoloph. Labially, the posteroloph adjoins the base of the paracone; lingually, it adjoins the base of the protocone; therefore, being partially worn, the mesofossette and endosinus become closed.

The anteroconid on the M_1 is isolated or connected to the metaconid or metalophid; occasionally, it is absent. The protoconid is usually connected to the metaconid or to the point of contact between the endolophid and the metaconid. The ectomesolophid is complete or incomplete; it is frequently absent. The hypoconid is always connected to the entoconid. The protoconid on the M_2 is usually connected to the metaconid; in individual cases, it is connected to the arm of the metaconid. The anterolophid has a low lingual arm. The M_3 usually has a well-developed ectocingulid extending from the labial arm of the anterolophid to the hypoconid. The hypoconid and entoconid are fused. Being strongly worn, the mesofossettid becomes closed.

Variability. The variation in dental structure is shown in Table 1.

Measurements, mm. Holotype: length: M_1 – M_3 , 4.2; M_1 – M_2 , 3.25; and M_2 – M_3 , 2.5. Length \times width: M_1 , 1.75 \times 1.25; M_2 , 1.5 \times 1.25; and M_3 , 0.95 \times 0.875.

Measurements of isolated teeth:

Tooth	Length			Width		
	<i>n</i>	limits	average	<i>n</i>	limits	average
P^4	5	0.5–0.6	0.545	5	0.55–0.725	0.655
M^1	150	1.55–1.975	1.79	143	1.15–1.55	1.39
M^2	79	1.225–1.55	1.38	79	1.15–1.45	1.27
M^3	7	0.775–0.875	0.83	7	0.9–1.025	0.954
M_1	140	1.475–1.925	1.7	148	1.0–1.35	1.22
M_2	99	1.25–1.675	1.5	99	1.1–1.5	1.26
M_3	6	0.95–1.05	1.0	6	0.85–0.975	0.92

Length of tooth row:

Tooth row	P^4 – M^2	P^4 – M^1	M^1 – M^2	M^2 – M^3	M_1 – M_3	M_1 – M_2	M_2 – M_3
<i>n</i>	1	1	5	3	5	15	5
Limits	3.6	2.2	3.1– 3.2	2.075– 2.25	3.925– 4.3	2.875– 3.5	2.45– 2.6
Average	–	–	3.17	2.13	4.17	3.175	2.525

Comparison. The new species differs from *L. (P.) progressus*, *L. (P.) intermedius* and *L. (P.) pusillus* by the stable display of such advanced characters as well-pronounced differentiation of the posterostyle on the M^1 and the presence of connection between the hypoconid and the entoconid on the M_1 and between the protoconid and the metaconid on the M_2 . In addition, it differs from *L. (P.) pusillus* by the presence of the lingual arm of the anterolophid. It differs from *L. (P.) afanasievi* by the smaller measurements, small anterostyle on the M^1 , and by the presence of a well-differentiated posterostyle on the M^1 and M^2 .

Occurrence. Lower Pliocene (MN14) of southwest Siberia and Kazakhstan.

Material. In addition to the holotype, a series of fragmentary upper jaws (two containing left and right M^1 and M^2 , two with P^4 – M^2 , one with P^4 and M^1 , four with M^1 and M^2 , three with M^2 and M^3 , one with P^4 , nine with M^1 , two with M^2 , three with M^3 , and one lacking teeth), lower jaws (four with M_1 – M_3 , 11 with M_1 and M_2 , seven with M_1 , two with M_2 , and one lacking teeth), six fragmentary zygomatic arches, and 421 isolated teeth (144 M^1 , 64 M^2 , M^3 , 128 M_1 , 83 M_2 , and M_3) from the type locality. In addition, M^1 and M_2 from the Peshnevo Formation of the Peshnevo locality, M_1 from the Kuskol Formation of the Beteke 1A locality, M_1 from the Peshnevo Formation of the Petropavlovsk 1B locality, M_1 from the Cherlak 1B locality, a fragmentary upper jaw containing M^1 and M^2 from borehole 61, and isolated M_1 and M_2 from borehole 59.

Lophocricetus (Paralophocricetus) ultimus Zazhigin,
Lopatin et Pokatillov, sp. nov.

Etymology. From the Latin *ultimus* (last, extreme).

Holotype. GIN, no. 1111/8, fragmentary left dentary containing M_1 and M_2 ; Western Siberia, Omsk Region, Olkhovka locality; Lower Pliocene (uppermost MN14–MN15).

Description (Figs. 5n–5v). A relatively large member of the genus. The posterior edge of the incisor foramina is on a level with the center of the P^4 crown. The palatine is long, extends far beyond the M^3 . The P^4 has a large central cusp and small accessory cuspules; the cingulum is undeveloped. The anteroloph on the M^1 is reduced or absent, the anterostyle is small, and the mesoloph and mesocone are undeveloped. The posterostyle is well pronounced. The posterostyle is usually open; occasionally, it is partially or completely closed.

The anteroloph of M^2 is usually incomplete and weakly differentiated from the protocone, the endoloph is complete, and the posterofossette is closed. The anteroloph and protoloph on the M^3 are well developed, and the metaloph is completely fused with the posteroloph or detached in the middle and separated from the latter by a closed posterofossette. The endoloph is absent, and the endosinus and mesofossette form an integral transverse valley, which is open labially and closed lingually.

The anteroconid on the M_1 is usually connected to the middle of the metalophid; in some cases, it is isolated or connected to the metaconid. The protoconid is connected to the point of contact between the endolophid and the metaconid or directly to the metaconid. The hypoconid is always connected to the entoconid. A characteristic feature of M_1 is the close positions of the main cusps of the labial and lingual rows; as a result, the anterolophid, endolophid, the arm of the entoconid, and the anterior and posterior arms of the hypoconid are positioned at a very small angle to the longitudinal axis and form an integral weakly waving line. The protoconid on the M_2 is connected to the metaconid; a rudimentary lingual arm of the anterolophid is frequently developed; occasionally, the latter appears as a weak cingulid located at the anterior base of the metaconid. The M_3 is not available.

Variability. The variation of the dental structure is shown in Table 1.

Measurements, mm. Holotype: length of M_1 – M_2 is 3.4; M_1 , 1.8×1.3 ; and M_2 , 1.55×1.325 .

Measurements of isolated teeth from the Olkhovka locality:

Tooth	Length			Width		
	<i>n</i>	limits	average	<i>n</i>	limits	average
P^4	1	0.6	–	1	0.75	–
M^1	14	1.7–2.25	2.01	14	1.4–1.75	1.56
M^2	12	1.45–1.675	1.53	10	1.25–1.5	1.4
M^3	2	1.0	–	2	1.0	–
M_1	18	1.575–2.15	1.85	22	1.15–1.425	1.31
M_2	9	1.525–1.775	1.67	9	1.2–1.55	1.38

Length of tooth rows: P^4 – M^2 : (GIN, no. 1111/25) 3.85; P^4 – M^1 : (GIN, no. 1111/25) 2.35; M^1 – M^3 : (GIN, no. 1111/10) 4.55; M^1 – M^2 : (GIN, no. 1111/25) 3.25, (GIN, no. 1111/10, dex.) 3.75, and (GIN, no. 1111/10, sin.) 3.825; M^2 – M^3 : (GIN, no. 1111/10) 2.55; and M_1 – M_2 : (GIN, no. 1111/48) 3.4 and (GIN, no. 1111/7) 3.6.

Measurements of teeth from other localities: M_1 : (GIN, nos. 945/305, 303, and 304, Beteke 1B locality) 1.75×1.325 , 1.95×1.35 , and 1.95×1.45 , respectively; (GIN, nos. 1116/1–3, Polovinnoe) 1.75×1.125 , 1.9×1.25 , and 2.1×1.4 , respectively; and (GIN, nos. 1112/3 and 2, Andreevka 2B) 1.75×1.25 and 2.05×1.375 ; M_2 : (GIN, no. 1112/6, Speranskoe) 1.65×1.425 ; (GIN,

no. 1108/1006, Pavlodar 2B) 1.7×1.3 ; and (GIN, no. 945/302, Beteke 1B) 1.75×1.5 .

Comparison. *L. (P). ultimus* differs from *L. (P). progressus*, *L. (P). intermedius*, and *L. (P). pusillus* by the larger measurements, stable display of a clearly differentiated posterostyle on the M^1 , and the presence of contacts between the hypoconid and the entoconid on the M_1 and between the protoconid and the metaconid on the M_2 . It differs from *L. (P). afanasievi* by the structure of M_1 and from *L. (P). sibiricus* by the higher frequency of the M^1 having the anteroloph, the absence of supplementary crest of the anterofossette on the M^2 , the prevalence of contacts between the anteroconid and the metalophid on the M_1 , close positions of cusps on the M_1 , and by the larger tooth measurements.

Occurrence. Lower Pliocene (MN14–MN15) of Western Siberia and Kazakhstan.

Material. In addition to the holotype, two fragmentary upper jaws containing teeth (one with both M^1 – M^3 rows and one with P^4 – M^2 and M^1 – M^2), fragmentary maxilla with M^1 , fragmentary zygomatic arch, five fragmentary lower jaws (three with M_1 and M_2 , one with M_1 , and one with M_2), and 41 isolated teeth (11 M^1 , seven M^2 , 12 M_1 , and 11 M_2) from the type locality. In addition, three M_1 from the Beteke Formation of the Polovinnoe locality; two M_1 and one fragmentary M^1 from the Beteke Formation of the Andreevka 2B locality; three M_1 and one M_2 from the Beteke Formation of the Beteke 1B locality; M_2 from the Livenka Formation of the Speranskoe locality; and M_2 from the Beteke Formation of the Pavlodar 2B locality.

DISCUSSION

Early in the Late Miocene (MN9), the genus *Heterosminthus* gave rise to the evolutionarily advanced species showing great similarity to *Lophocricetus*, i.e., *H. mugodzharcicus* in western Kazakhstan and *H. gabuniai* in Moldova. The earliest members of *Lophocricetus* were found in MN10; they include *L. minusculus* from the Petropavlovsk Fauna of Kazakhstan and *L. minusculus* and *L. complicidens* from the Upper Sarmatian of Ukraine. At the end of the Miocene, late *Heterosminthus*, including *H. gansus* from China (MN11) and *H. saraicus* sp. nov. from Eastern Siberia (MN12), coexisted with *Lophocricetus*, although none of studied localities contain both *Heterosminthus* and *Lophocricetus*.

The upper molar structure of Late Miocene *L. minusculus*, *L. complicidens*, and *L. vinogradovi* shows that the ancestor of the genus *Lophocricetus* belonged to *Heterosminthus* and had a complete anteroloph on the M^1 and double anteroloph on the M^2 . In *H. gabuniai* and *H. saraicus*, the anteroloph on the M^1 is strongly reduced and the M^2 is characterized by single anteroloph and reduced endoloph. Thus, these species should be excluded from probable ancestors of *Lophocricetus*. *H. mugodzharcicus* has a well-developed anteroloph on

Table 1. The frequencies of tooth morphotypes in Early Pliocene species of *Lophocricetus* (*Paralophocricetus*): *L. (P.) progressus* sp. nov., Baikal, Olkhon 2 locality, Odonimskaya Member; *L. (P.) pusillus*, Mongolia, Khirgis-Nur 2 locality; Upper Khirgis-Nur Subformation, interval 37–40 m; *L. (P.) sibiricus* sp. nov., Western Siberia, Cherlak 1A locality, Rytovo Formation; and *L. (P.) ultimus* sp. nov., Western Siberia, Olkhovka locality

Tooth	Element	Variant	<i>L. (P.) progressus</i>		<i>L. (P.) pusillus</i>		<i>L. (P.) sibiricus</i>		<i>L. (P.) ultimus</i>	
			<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
M ¹	anteroloph	– reduced	6	11.5	4	36	14	11	6	40
		– absent	46	88.5	7	64	114	89	9	60
	mesoloph	– rudimentary	2	4	0	0	1	0.8	0	0
		– absent	50	96	11	100	127	99.2	15	100
	posterosinus	– open	43	83	10	100	92	72	12	80.5
		– partially closed	7	13	0	0	19	15	1	6.5
– closed		2	4	0	0	17	13	2	13	
M ²	anterofossette	– partitioned by crest	9	24	0	0	15	19	0	0
		– integral	28	76	4	100	64	81	11	100
	endoloph	– present, complete	36	97	4	100	70	88.5	10	91
		– incomplete or absent	1	3	0	0	9	11.5	1	9
	posterofossette	– open	14	40	3	75	7	9	1	9
		– closed	21	60	1	25	72	91	10	91
– partitioned by crest		3	8	0	0	0	0	0	0	
– integral		33	92	4	100	79	100	11	100	
M ₁	anteroconid	– connected to metaconid	51	78.5	12	52	44	31	3	20
		– connected to metalophid	0	0	0	0	32	22	8	53
		– isolated	10	15.5	7	30	64	45	4	27
		– connected to two cusps	4	6	0	0	0	0	0	0
		– absent	0	0	4	18	3	2	0	0
	protoconid contacts	– with point of contact between endolophid and metaconid	37	55	5	21	64	45.6	10	62.5
		– double, with metaconid and endolophid	5	7.5	2	8	1	0.7	0	0
		– only with metaconid	6	9	11	46	74	53	6	37.5
		– only with endolophid	9	13.5	5	21	1	0.7	0	0
		– absent	10	15	1	4	0	0	0	0
	ectomesolophid	– long, complete	50	69.5	17	68	71	49.3	12	71
		– short or absent	22	30.5	8	32	73	50.7	5	29
hypoconid contacts	– with entoconid	44	64	16	67	14	100	17	100	
	– with mesoconid	25	36	8	33	6	0	0	0	
	– with anteroconid	25	51	6	50.5	0	0	0	0	
M ₂	anterior contact of protoconid	– with arm of metaconid	14	29	4	33	6	6	1	6
		– with metaconid	7	14	2	16.5	95	94	15	94
		– absent	3	6	0	0	0	0	0	0

the M¹; based on this character, it could be the ancestor of *Lophocricetus* (the M² of this species has not been found). The M₁ of *H. mugodzhariensis* has much in common with the M₁ of the most primitive *Lophocricetus*, i.e., the long ectomesolophid fused with the mesoconid, the arms of the hypoconid and entoconid are positioned

close to each other, and a weak posterostylid is present (Zazhigin and Lopatin, 2000a).

The patterns of connection between the metaconule and the metacone on the M¹ and between the hypoconid and the central part of the occlusal surface on the M₁ are important characters of the dental structure of *Lophocrice-*

tus. *L. (L.) minusculus* shows the most primitive structure of M_1^1 ; i.e., the metaconule is displaced toward the metacone to a substantially lesser extent than in the other species. Certain species of the subgenus *Paralophocricetus*, such as *L. (P.) progressus*, *L. (P.) intermedius*, and *L. (P.) pusillus*, show a primitive type of the M_1 structure characteristic of *Heterosminthus*, where the hypoconid is connected to the mesoconid (Table 1). An intermediate type, in which the hypoconid adjoins the arm of the entoconid, occurs in *L. (P.) progressus* and *L. (P.) pusillus*. An advanced type, i.e., the hypoconid connected to the entoconid, occurs in *L. (P.) intermedius*, prevails in *L. (P.) progressus* and *L. (P.) pusillus*, and is presents in all individuals of *L. (P.) afanasievi*, *L. (P.) sibiricus*, and *L. (P.) ultimus* and almost all species of the subgenus *Lophocricetus* sensu stricto. The sole exception is provided by one M_1 of *L. (L.) complicidens* described as the holotype *L. sarmaticus* (Topachevsky *et al.*, 1984, p. 34, text-fig. II, G₃). In this specimen, the hypoconid is connected to the arm of the entoconid near the mesoconid. The fact that *L. complicidens* has such a primitive morphotype agrees with the early geological age of this form. Similar changes occurred in the anterior contact of the protoconid on the M_2 , i.e., in *Heterosminthus* the protoconid is connected to the anteroconid; in *L. (P.) progressus*, it usually adjoins the anteroconid; in *L. (P.) pusillus*, the arm of the metaconid; in *L. (P.) afanasievi*, *L. (P.) sibiricus*, *L. (P.) ultimus*, and *Lophocricetus* sensu stricto, the metaconid. Thus, in the MN13 and MN14 zones, the lower teeth of *Paralophocricetus* followed the same evolutionary changes as those of *Lophocricetus* sensu stricto in MN10.

It is worth noting that the range of morphotypic variation of M_1 and M_2 in the earliest forms of *Lophocricetus* sensu stricto is uncertain because the findings of *L. minusculus* and *L. complicidens* are extremely scarce. However, the variation was probably comparable to that of early *Paralophocricetus*. *Paralophocricetus* most likely descends from a primitive species of *Lophocricetus* sensu stricto, the upper teeth of which were similar in structure to those of *L. (L.) minusculus* and *L. (L.) complicidens*, whereas the lower teeth showed the same variability as those of *L. (P.) progressus*, *L. (P.) intermedius*, and *L. (P.) pusillus* (i.e. included the *L. sarmaticus* morphotype). The posterostyle structure characteristic of M_1^1 of *Paralophocricetus* was probably formed relatively late. In *L. intermedius* and *L. afanasievi* (MN13), this element is incompletely isolated from the hypocone; in some cases, a weakly differentiated posterostyle occurs in *L. pusillus* (MN13–MN14) and *L. progressus* (MN14).

Each subgenus comprises groups of species distinguished by the dental morphology and probably belonging to separate evolutionary lineages. *Lophocricetus* sensu stricto is divided into two lineages, i.e., *L. (L.) minusculus* (including “*L. maeoticus*”) and the group *L. (L.) complicidens*–*L. (L.) vinogradovi*–*L. (L.) gra-*

baui. The latter lineage probably also includes *L. (L.) reliquus*, distinguished from other species by the structure of the hypocone and posteroloph of M_1^1 and by the mesocone of M_2^2 . Within the subgenus *Paralophocricetus*, East Siberian *L. (P.) progressus* is clearly distinguished by the opposite position of the paracone and the protocone on the M_1^1 and by the prevalence of primitive morphotypes of M_1 and M_2 . The other species of the subgenus belong to the other lineage. The groups *L. (P.) intermedius*–*L. (P.) pusillus* from Central Asia and *L. (P.) afanasievi*–*L. (P.) sibiricus*–*L. (P.) ultimus* from Western Siberia are probably characterized by the ancestor–descendant relationships.

The taxonomic diversity and abundance of fossils in a number of localities (Pavlodar 1A, Cherlak 1A, Khirgis-Nur 2, Olkhon 2, and Olkhovka) show that, late in the Miocene and early in the Pliocene, *Lophocricetus* was the dominant dipodoid genus. The extinction of this group was probably caused by global fall in temperature at the onset of the Villafranchian.

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REFERENCES

- Höck, V., Daxner-Höck, G., Schmid, H.P., *et al.*, Oligocene–Miocene Sediments, Fossils and Basalts from the Valley of Lakes (Central Mongolia)—An Integrated Study, *Mitt. österr. Geol. Ges.*, 1999, vol. 90, pp. 83–125.
- Lopatin, A.V., A New Species of *Heterosminthus* (Dipodidae, Rodentia, Mammalia) from the Miocene of the Baikal Region, *Paleontol. Zh.*, 2001, no. 2, pp. 94–97.
- Mats, V.D., Pokatilov, A.G., Popov, S.M., *et al.*, *Pliotsen i pleistotsen Srednego Baikala* (The Pliocene and Pleistocene of the Middle Baikal Region), Novosibirsk: Nauka, 1982.
- Qiu, Z.-D., The Neogene Mammalian Faunas of Ertemte and Harr Obo in Inner Mongolia (Nei Mongol), China: 3. Jumping Mice—Rodentia: Lophocricetinae, *Senckenb. Lethaea*, 1985, vol. 66, no. 1/2, pp. 39–67.
- Qiu, Z. and Storch, G., The Early Pliocene Micromammalian Fauna of Bilike, Inner Mongolia, China (Mammalia: Lipotyphla, Chiroptera, Rodentia, Lagomorpha), *Senckenb. Lethaea*, 2000, vol. 80, no. 1, pp. 173–229.
- Qiu, Z.-D. and Wang, X.-M., Small Mammal Faunas and Their Ages in Miocene of Central Nei Mongol (Inner Mongolia), *Vertebr. Palasiat.*, 1999, vol. 37, no. 2, pp. 120–139.
- 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 from Kazakhstan), 1977, vol. 7, pp. 27–32.
- Savinov, P.F., The Changes of the Small Mammal Faunal Assemblages from the Neogene of Kazakhstan, in *Materialy*

po istorii fauny i flory Kazakhstana (Materials on the History of the Fauna and Flora from Kazakhstan), 1988, vol. 10, pp. 20–37.

Schlosser, M., Tertiary Vertebrates from Mongolia, *Palaeontol. Sin., Ser. C*, 1924, vol. 1, no. 1, pp. 1–119.

Topachevsky, V.A., Skorik, A.F., and Rekovets, L.I., The Earliest Jerboas of the Subfamily Lophocricetinae (Rodentia, Dipodidae) from the Southwest of the European USSR, *Vestn. Zool.*, 1984, no. 4, pp. 32–39.

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. The Dipodinae at the Miocene–Pliocene Boundary, *Paleontol. Zh.*, 2001, no. 1, pp. 61–75.

Zheng, S., Middle Pliocene Micromammals from the Tianzhu Loc. 80007 (Gansu Province), *Vertebr. Palasiat.*, 1982, vol. 20, no. 2, pp. 138–147.

Zykin, V.S., Zazhigin, V.S., and Zykina, V.S., The Changes of Natural Environment and Climate in the Early Pliocene of the South of the West Siberian Plain, *Geol. Geofiz.*, 1995, vol. 36, no. 8, pp. 40–50.