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The History of the Dipodoidea (Rodentia, Mammalia) in the Miocene of Asia: 4. Dipodinae at the Miocene–Pliocene Transition

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Abstract—Late Miocene and Early Pliocene three-toed jerboas from Mongolia, Tuva, Kazakhstan, and the southern part of Western Siberia are investigated. The earliest members of the genera *Dipus*, *Stylodipus*, *Plioscirtopoda*, and *Jaculus* are indicated. The following twelve species are described: Late Miocene *Dipus conditor* sp. nov., *Plioscirtopoda antiqua* sp. nov., and *Jaculus sibiricus* sp. nov.; Early Pliocene *Dipus essedum* sp. nov., *D. singularis* sp. nov., *Stylodipus iderensis* sp. nov., *S. perfectus* sp. nov., *Plioscirtopoda rapida* sp. nov., *P. zykini* sp. nov., and *Jaculodipus yavorensis* gen. et sp. nov.; and Miopliocene *Scirtodipus kazakhstanicus* Savinov, 1970 and *Dipus fraudator* (Schlosser, 1924). The taxonomic composition of the extinct Dipodinae is revised.

INTRODUCTION

Jerboas of the subfamily Dipodinae are known from the Late Miocene (MN12–MN13) onwards. To date, three Late Miocene species have been described, i.e., *Sminthoides fraudator* from China (Schlosser, 1924); *Scirtodipus kazakhstanicus*, and *S. kalbicus* from Kazakhstan (Savinov, 1970). In addition, finds of *Sminthoides fraudator* in the Early Pliocene of China (Qiu and Qiu, 1995) and *Scirtodipus* sp. in the Pontian of the Crimea Peninsula (Mos'kina and Matsui, 1992) were indicated. The remains described from the Miopliocene of Mongolia as *Scirtodipus* sp. (Pevzner *et al.*, 1982) in actual fact belong to *Dipus*.

In the present study, material on Late Miocene and Early Pliocene three-toed jerboas from Mongolia, Tuva, Kazakhstan and the southern part of Western Siberia from the collection of the Geological Institute of the Russian Academy of Sciences (GIN) are described. The data on early adaptive radiation of the Dipodinae are substantially enlarged.

The material examined was found in the following 16 localities (the correlation with the mammalian zones was performed by Zazhigin).

Russia, Omsk Region: Cherlak 1A, Lower Pliocene, lower part of MN14, basal horizon of the Rytovo Formation in its stratotype in a river bluff of the right bank of the Irtysh River near the village of Cherlak; Rytovo Formation, dated Early Ruscinian (Zazhigin and Zykin, 1984; Zykin *et al.*, 1991).

Russia, southern Tuva: Kholu (right bank of the Kholu River, northern slope of the Ubsunur Depression at the foot of the Tannu Ola), Upper Miocene–Lower Pliocene, MN13/MN14, clayish silt unit in the lower part of the section, previously dated Middle Pliocene (Devyatkin *et al.*, 1968).

Kazakhstan: Pavlodar 1A, Upper Miocene, MN12 (Zazhigin and Lopatin, 2000), Pavlodar Formation; Pavlodar 1B and Pavlodar 2A, Lower Pliocene, lower part of MN14, Rytovo Formation; Pavlodar 2B, Lower Pliocene, MN15 (based on the composition of the Microtinae), Beteke (?) Formation, sand with the Unionidae in the mines of Pavlodar; Selety 1A (left bank of the Selety River, 4 km upstream the village of Il'inka), Upper Miocene, MN13 (Storch and Zazhigin, 1996), Kedei Formation; and Beteke (right bank of the Beteke River, Ishim Region), Lower Pliocene, MN15 (Zazhigin and Zykin, 1984), Beteke Formation.

Mongolia, Great Lakes Valley: Khirgis-Nur 2 (northern bank of Khirgis-Nur Lake), Upper Miocene, upper part of MN13, Lower Khirgis-Nur Subformation, interval 17–24 m; Lower Pliocene, lower part of MN14, basal part of the Upper Khirgis-Nur Subformation, intervals 37–40 and 57–60 m (Pevzner *et al.*, 1982); Yavor 1 and Yavor 2 (Yavor Tract at the mouth of the Dzabkhan River to the north of the village of Dzabkhan), Lower Pliocene, lower part of MN14, basal part of the Upper Khirgis-Nur Subformation; Dzagso-Khairkhan 1 and Dzagso-Khairkhan 4 (interfluve between the Dzabkhan and Khungui rivers, 3 and 13 km to the southeast of Dzagso-Khairkhan-Obo Mountain), Lower Pliocene (Middle Pliocene after Devyatkin *et al.*, 1984), upper part of MN14, Upper Khirgis-Nur Subformation; Ider (right bank of the Ider River, mine 30 km upstream the village of Toson-Tsengel), Lower Pliocene (Middle Pliocene after Zazhigin, 1989), upper part of MN14, reddish brown sandy clay, enclosing detrital rock; Chono-Khariakh 1 and Chono-Khariakh 2 (at the

Chono-Khariakh Stream), Lower Pliocene (based on the Microtinae), MN14/MN15, upper part of the Upper Khirgis-Nur Subformation.

The material was collected mainly by Zazhigin during the years 1963 to 1983, some specimens from the Selety 1A and Beteke localities were found by V.S. Zykin in 1983.

Abbreviations: (GIN) Geological Institute of the Russian Academy of Sciences, Moscow; (IZ) Institute of Zoology of the National Academy of Sciences of Kazakhstan, Alma-Ata; (PIN) Paleontological Institute of the Russian Academy of Sciences, Moscow; and (PIU) Lagrelius Collection of the Paleontological Institute of Uppsala University, Sweden.

SYSTEMATIC PALEONTOLOGY

Family Dipodidae Fischer, 1817

Subfamily Dipodinae Fischer, 1817

Tribe Dipodini Fischer, 1817

Genus *Dipus* Zimmermann, 1780

Dipus: Zimmermann, 1780, p. 355.

Sminthoides: Schlosser, 1924, p. 34.

Type species. *Mus sagitta* Pallas, 1773; Recent.

Diagnosis. Medium-sized. Upper incisors with distinct longitudinal groove. P^4 well developed. Molars relatively low-crowned and bunolophodont, with massive round cusps. On M^1 and M^2, main cusps of either pair oppose each other. Anteroloph of M^1 usually weak and low, resembles cingulum, anterocone weakly developed or undeveloped, posteroloph undeveloped. Paracone extended labially. Metacone relatively large and directed anterolabially. Endoloph low and formed by massive anterior projection of hypocone; on M^1 and M^2, it connected to lingual part of paracone; on M^3, it fused with protocone or reduced. M^1 and M^2 frequently possessing spur of paracone directed posteriorly or to labial edge of crown. Metaconid of M_1 weakly projecting anteriorly and equal to protoconid in size. Entoconid of M_1 and M_2 connected to hypoconid. Anterolophid of M_2 with long labial arm. Anterolophid of M_3 rudimentary or undeveloped.

Composition. *Dipus sagitta* (Pallas, 1773), Pleistocene and Recent, Eastern Europe, southwestern Siberia, Iran, Kazakhstan, Central and Middle Asia; *D. fraudator* (Schlosser, 1924), Upper Miocene and Lower Pliocene, northern China, Mongolia, and Tuva; *D. conditor* sp. nov., Upper Miocene, Mongolia; *D. essedum* sp. nov.; and *D. singularis* sp. nov., Lower Pliocene, Mongolia.

Comparison. *Dipus* is distinguished from the other genera of the Dipodini by well developed P^4, low crowns and bunolophodont structure of the molars, massive metacone of M^1; and by the structure of the endoloph on M^1–M^3.

Dipus fraudator (Schlosser, 1924)

Sminthoides fraudator: Schlosser, 1924, p. 34, pl. 3, figs. 2 and 3; Schaub, 1930, p. 626; 1934, p. 3, text-fig. 1, pl. 1, fig. 21; Jacobs *et al.*, 1985, p. 64, pl. 3, fig. 8.

Holotype. Holotype was not designated. The lectotype [Schaub, 1934] is a fragmentary left maxilla, containing M^1 and M^2 (PIU, no. M.3364.25); China, Inner Mongolia, Ertemte 1; Upper Miocene.

Description (Figs. 1a–1f). A relatively large member of the genus. The anterocone of M^1 is undeveloped, the anteroloph is low. The protocone is substantially displaced anteriorly in relation to the paracone. The spur of the paracone is weak and directed posterolabially. The metacone is moderately massive and possesses a flattened anterior wall. The endosinus is straight.

The anteroconid of M_1 is small or undeveloped. The metaconid extends anterolingually, a contact with the protoconid is weak. The other contacts (protoconid–entoconid, entoconid–hypoconid, and hypoconid–hypoconulid) are well-pronounced. The metastylid and the ectostylid are present. The anteroconid of M_2 is weakly detached and small, the labial arm of the anterolophid is long, low, and flat. The upper half of the hypoconid is isolated from the entoconid. The hypoconulid is very small and weakly detached. The anterolophid of M_3 is reduced and looks like a small ridge connected to the labial side of the metaconid and separated from the protoconid by a very narrow fold. The protoconid extends posterolingually and is connected to a small rounded entoconid that fused posteriorly with the hypoconid.

Measurements, length × width, mm. Kholu locality: M^1: (GIN, no. 953/1) 2.2 × 2.0; M_1: (GIN, no. 953/4) 2.25 × 2.0 and (GIN, no. 953/3) ? × 1.95; M_2: (GIN, no. 953/5) 1.9 × 1.8; M_3: (GIN, no. 953/2) 1.65 × 1.5; Khirgis-Nur 2: M_1: (GIN, no. 956/2021) 2.35 × 2.0; M_2 (GIN, no. 956/2012) 2.15 × 1.9. The crown height of M^1 is 1.75, the ratio between the height and length is 79.5%.

Comparison. *Dipus fraudator* is distinguished from *D. sagitta* by a weak contact between the entoconid and the hypoconid on M_2 and by a less reduced anterolophid on M_3.

Remarks. We assigned *Sminthoides fraudator* Schlosser, 1924 to the genus *Dipus* and regarded the name *Sminthoides* as a synonym of the latter. The main basis of this is the fact that *D. fraudator* possesses a massive metacone on M^1 and M^2 that is characteristic of the genus *Dipus* only. As the occlusal surface is worn, enamel is substantially thickened on the anterior side of the metacone. This clearly distinguishes *Dipus* from other members of the Dipodinae. The lectotype *D. fraudator* is characterized by such a structure (Schlosser, 1924; Schaub, 1934; Jacobs *et al.*, 1985). In addition, it can be referred to as *Dipus* based on the presence of a large P^4 (judging from the size of the alve-

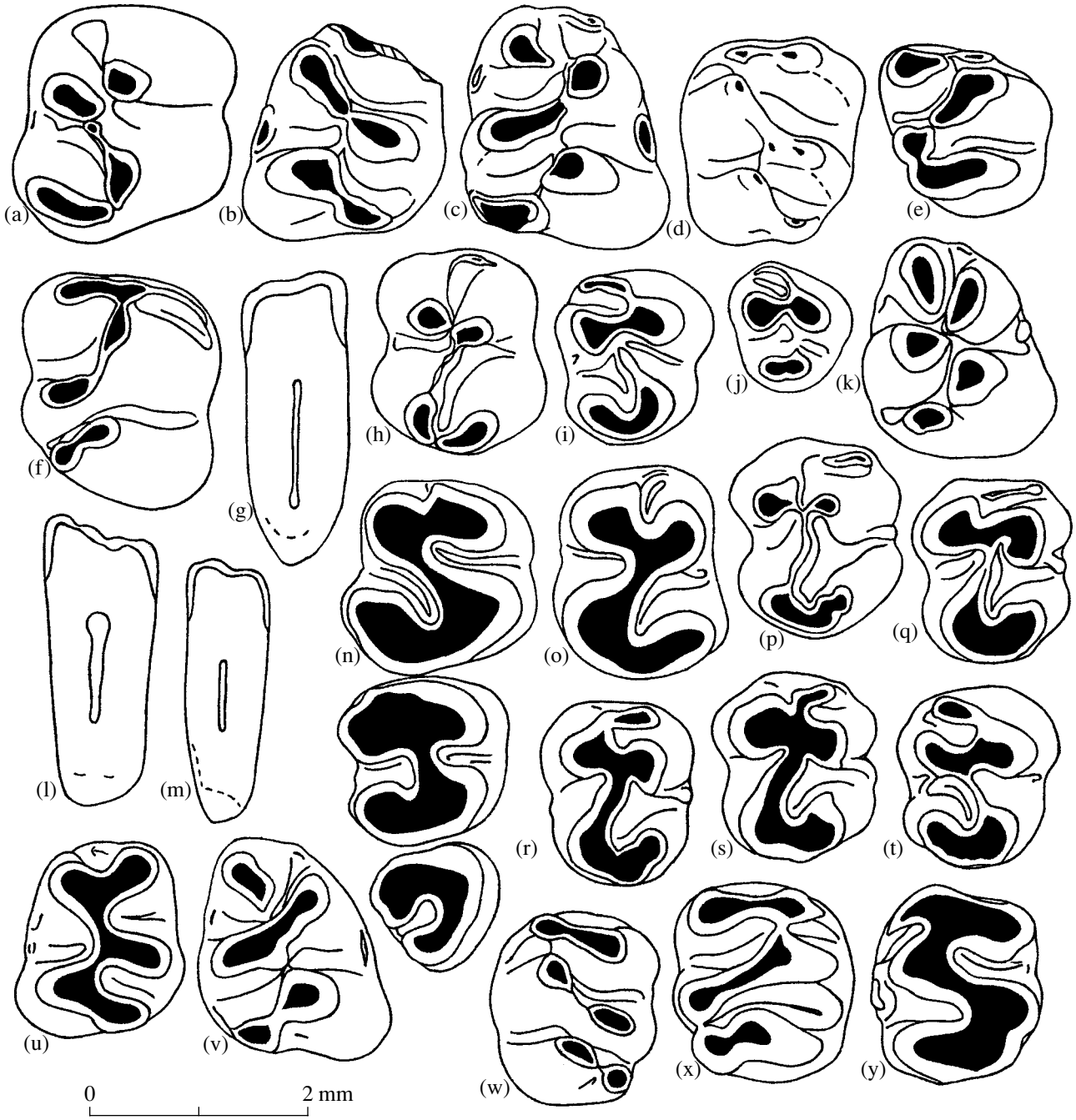

Fig. 1. *Dipus*: (a–f) *D. fraudator* (Schlosser, 1924): (a) GIN, no. 953/1, right M^1; (b) GIN, no. 953/3, left M_1; (c) GIN, no. 953/4, right M_1; (d) GIN, no. 953/5, left M_2; (e) GIN, no. 953/2, right M_3; and (f) GIN, no. 956/2012, right M_2; (g–k) *D. conditor* sp. nov.: (g) GIN, no. 956/2014, right upper incisor; (h) GIN, no. 956/2004, left M^1; (i) GIN, no. 956/2002, right M^2; (j) GIN, no. 956/2001, right M^3; and (k) holotype, GIN, no. 956/2005, right M_1; and (l–y) *D. essedum* sp. nov.: (l) GIN, no. 956/2015, left upper incisor; (m) no. 1100/4007, left upper incisor; (n) GIN, no. 956/2010, right M^1–M^3; (o) GIN, no. 1100/4004, left M^1; (p) GIN, no. 956/2006, left M^2; (q) GIN, no. 956/2008, left M^2; (r) GIN, no. 956/2007, left M^2; (s) GIN, no. 956/2009, left M^2; (t) GIN, no. 1100/4000, right M^2; (u) GIN, no. 1100/4003, left M_1; (v) holotype, GIN, no. 956/2011, right M_1; (w) GIN, no. 1100/4005, left M_2; (x) GIN, no. 1100/4006, right M_2; and (y) GIN, no. 1100/3, left M_2. (a–e) Kholu; (f, l, n, p–s, v) Khirgis-Nur 2, interval 37–40 m; (g–k) Khirgis-Nur 2, interval 17–24 m; (m, o, t, u, w, x) Dzagso-Khairkhan 4; and (y) Dzagso-Khairkhan 1.

olus) and the structure of the endoloph on M^1 and M^2 and anteroloph on M^1.

D. fraudator was described on the basis of M^1 and M^2. *Dipus* from the Kholu locality is assigned to this species based on large sizes and identical structure of M_1. Large M_1 and M_2 of *Dipus* from the Khirgis-Nur 2 locality correspond in structure to those of *D. fraudator* from Kholu. M_1, M_3, and two strongly worn M^1 from Pavlodar 2A are determined as *D.* aff. *D. fraudator.*

Material. M^1, two M_1, M_2, and M_3 from Kholu; M_1 and M_2 from Khirgis-Nur 2 (interval 37–40 m).

Dipus conditor Zazhigin et Lopatin, sp. nov.

Etymology. From Latin *conditor* (founder).

Holotype. GIN, no. 956/2005, right M_1; Mongolia, Khirgis-Nur 2; uppermost strata of the Miocene (MN13), lower Khirgis-Nur Subformation, interval 17–24 m.

Description (Figs. 1g–1k). A small-sized member of the genus. A groove on the upper incisors is weakly developed. On M^1 and M^2, the protocone is slightly displaced anteriorly in relation to the paracone. The transverse spur of the paracone is weak and poorly detached. The metacone is stout and its anterior wall convex. The anteroloph of M^1 is narrow and low and the anterocone is absent. The anteroloph of M^2 is complete and connected to the protocone. M^3 is short and wide, the anteroloph is well developed, and the endoloph is strongly reduced. The main cusps of M_1 are stout, strongly drawn to each other, and isolated by folds. The metaconid is oriented almost longitudinally. The hypoconulid is detached. A large ectostylid and a well-pronounced crest of the metastylid are present.

Measurements, length × width, mm. M^1: (GIN, no. 956/2004) 1.9 × 1.7, (GIN, no. 956/2022) 1.95 × 1.75, and (GIN, no. 956/2003) 2.1 × 1.9; M^2: (GIN, no. 956/2002) 1.6 × 1.5; M^3: (GIN, no. 956/2001) 1.05 × 1.2; and M_1 (holotype) 2.1 × 1.8. Crown height of M^1 is (GIN, no. 956/2003) 1.55, the ratio height/length is 74%.

Comparison. The new species is distinguished from *D. sagitta* and *D. fraudator* by smaller measurements and by the structure of M_1. In addition, it is distinguished from *D. sagitta* by a weak groove on the upper incisors and by relatively low crowns (in unworn M^1 of extant species, the ratio height/length of crown is approximately 100%).

Material. In addition to the holotype, two fragmentary upper incisors, three M^1, M^2, and M^3 from the type locality.

Dipus essedum Zazhigin et Lopatin, sp. nov.

Etymology. From Latin *essedum* (two-wheeled military chariot).

Holotype. GIN, no. 956/2011, fragmentary right mandible, containing M_1; Mongolia, Khirgis-Nur 2; Lower Pliocene (MN14), base of the Upper Khirgis-Nur Subformation, interval 37–40 m.

Description (Figs. 1l–1y). A small member of the genus. The groove on the upper incisors is well-pronounced. On M^1, the protocone is slightly displaced anteriorly in relation to the paracone; on M^2, the anterior cusps are positioned strictly opposite to each other. The anteroloph of M^1 is weak and the anterocone is undeveloped. The anteroloph of M^2 is complete and connected to the protocone, or it is incomplete. The transverse spur of the paracone is well developed, frames the posterior base of the cusp, and reaches the labial margin of the occlusal surface. The metacone of M^1 and M^2 is stout, the anterior wall is convex. M^3 bears a well-pronounced longitudinal endoloph. On M_1, the metaconid is oriented anterolingually, connected to the protoconid, and, occasionally, drawn close to the entoconid. The protoconid is fused with the entoconid, the entoconid is connected to the hypoconid, and the hypoconid is in contact with the hypoconulid. The crest of the metastylid is weak or absent, a small ectostylid or ectocingulid is developed. The anteroconid of M_2 is well-pronounced and large, the labial arm of the anterolophid is high. The hypoconid is isolated from the entoconid down to a strong degree of wear. The hypoconulid is relatively large and round. In some cases, a large ectostylid is developed.

Measurements, length × width, mm. Khirgis-Nur 2: (GIN, no. 956/2010): M^1, 1.85 × 1.7; M^2, 1.55 × 1.6; and M^3, 1.1 × 1.2; M^2: (GIN, no. 956/2007) 1.7 × 1.45, (GIN, no. 956/2008) 1.7 × 1.5, (GIN, no. 956/2009) 1.7 × 1.55, and (GIN, no. 956/2006) 1.8 × 1.55; M_1: (holotype) 2.05 × 1.85. Dzagso-Khairkhan: M^1: (GIN, no. 1100/4004) 1.95 × 1.6; M^2: (GIN, no. 1100/4000) 1.6 × 1.5 and (GIN, no. 1100/1) 1.75 × 1.6; M_1: (GIN, no. 1100/4003) 1.85 × 1.6 and (GIN, no. 1100/4) 1.95 × 1.65; and M_2: (GIN, no. 1100/4005) 1.8 × 1.6 (GIN, no. 1100/3) 1.85 × 1.6 (GIN, no. 1100/4006) 1.85 × 1.7 and (GIN, no. 1100/2) 1.9 × 1.8.

Comparison. The new species is distinguished from the other species of the genus *Dipus* by a well developed transverse spur of the paracone on M^2. In addition, it is distinguished from *D. sagitta* by small measurements and an isolated position of the hypoconid on M_2; from *D. conditor*, by the structure of M_1; and from *D. fraudator*, by smaller measurements, relatively more massive metacone on M^1, the absence of the anteroconid on M_1, and by the structure of M_2 (large anteroconid, high anterolophid, and clearly detached hypoconulid).

Material. In addition to the holotype, a fragmentary maxilla, containing M^1–M^3; two upper incisors; and four M^2 from the type locality; M^1 and M^2 from the Yavor 1 locality; two M^1 from the Yavor 2 locality; (GIN, no. 1100/1-4) M^2, M_1, and two M_2 from Unit 3 of the Dzagso-Khairkhan 1 locality; fragmentary mandible with M_1, and isolated (GIN, nos. 1100/4003 and 4002) M_1 from Unit 3 of the Dzagso-Khairkhan 4 local-

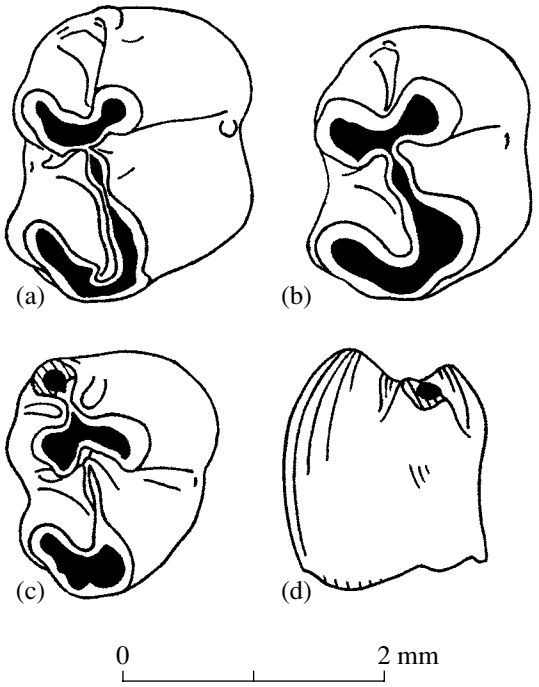

Fig. 2. *Dipus singularis* sp. nov.: (a) GIN, no. 956/2017, right M^1; (b) GIN, no. 956/2018, right M^1; and (c, d) holotype, GIN, no. 956/2019, right M^2: (c) occlusal surface and (d) front view.

ity; and isolated teeth: (GIN, nos. 1100/4007 and 4008) two upper incisors, (GIN, no. 1100/4004) M^1, (GIN, nos. 1100/4000 and 4001) two M^2; and (GIN, nos. 1100/4005 and 4006) two M_2 from Unit 2 of the Dzagso-Khairkhan 4 locality.

Dipus singularis Zazhigin et Lopatin, sp. nov.

Etymology. From Latin *singularis* (peculiar, singular).

Holotype. GIN, no. 956/2019, right M^2; Mongolia, Khirgis-Nur 2; Lower Pliocene (MN14), base of the Upper Khirgis-Nur Subformation, interval 57–60 m.

Description (Fig. 2). A relatively large member of the genus. M^1 and M^2 are lengthened. The protocone and the paracone are positioned opposite to each other. The spur of the paracone is well-pronounced but short and only approaches the edge of the occlusal surface. The metacone is moderately massive. The anteroloph of M^1 is well developed, the anterocone is present. The anteroloph of M^2 is complete and connected to the protoloph. The anterostyle is large and round. A small anterior fold is located between the anterostyle and the protocone.

Measurements, length × width, mm: M^1 (GIN, no. 956/2017) 2.25 × 1.95 and (GIN, no. 956/2018) 2.05 × 1.7 and M^2 (holotype) 1.85 × 1.65. Crown height of (GIN, no. 956/2017) unworn M^1 is 2.0, the ratio height/length is 89%; the same parameters of the holotype are 1.9 and 103%, respectively.

Comparison. The new species is distinguished from all known species of the genus by the structure of M^2: the anterostyle is extremely large, the anterior fold is present, and the anteroloph is connected to the protoloph, instead of to the protocone. In addition, it is distinguished from the most similar species, *D. conditor* and *D. essedum*, by lengthened upper molars and by the presence of the anterocone on M^1.

Material. In addition to the holotype, two M^1 and a strongly worn M_1 from the type locality.

Genus *Scirtodipus* Savinov, 1970

Scirtodipus: Savinov, 1970, p. 114.

Type species. *S. kazakhstanica* Savinov, 1970; Upper Miocene of Kazakhstan.

Diagnosis. Medium-sized. Groove on upper incisors weakly developed. P^4 reduced. Molars relatively low-crowned, but clearly lophodont in structure. Cusp bases round. On M^1 and M^2, paracone and protocone distinctly alternate in arrangement. Anteroloph and anterocone well developed, posteroloph reduced. Paracone extended labially. Metacone compressed longitudinally. Endoloph of M^1–M^3 high, strongly oblique, and connected to paracone; points of endoloph–paracone contact and paracone–protocone contact distinctly isolated from each other. Longitudinal posterior spur of paracone usually developed to greater or lesser extent. M^3 with well developed anteroloph. On M_1, metaconid and protoconid equal in size; metaconid connected to protoconid and substantially displaced anteriorly. Entoconid of M_1 and M_2 connected to hypoconid. Anterolophid of M_2 with long labial arm. M_3 with well developed labial anterolophid.

Composition. Type species.

Comparison. *Scirtodipus* is distinguished from *Plioscirtopoda* by rounded outlines of cusps, relatively weak anterior displacement of the metaconid on M_1, and by the presence of a well developed labial arm of the anterolophid on M_2. The main differences from *Stylodipus* consist in the structure of M_1 (equal sizes of the metaconid and the protoconid) and M^3 (oblique endoloph). In addition, *Scirtodipus* is distinguished from the latter by the alternation of anterior cusps of M^1 and M^2, possible presence of a spur of the paracone, a stronger developed anteroloph on M^1 and M^2, the presence of an anterocone on M^1, a well developed anteroloph on M^3 and anterolophid on M_3, and by a weak longitudinal groove on the upper incisors. It is distinguished from *Dipus* by a well-pronounced lophodont structure of molars, alternation of anterior cusps on M^1 and M^2, a more labial position of the contact between the endoloph and the paracone, by the structure of M^3, a more anterior position of the metaconid in relation to the protoconid on M_1, and by a well developed anterolophid

on M_3. The differences from *Jaculus* and *Eremodipus* consist primarily in a more complex structure of the occlusal surface and in lower crowns of molars.

R e m a r k s. The assignment of *S. kalbicus* Savinov, 1970 from the Upper Miocene of Kazakhstan to the genus *Scirtodipus* is doubtful. The figures and description in Savinov's paper (1970) do not allow one to distinguish this form from *Dipus fraudator.* Whether or not these names are synonyms is an open question. We regard *S. kalbicus* as a nomen dubium.

***Scirtodipus kazakhstanicus* Savinov, 1970**

Scirtodipus kazakhstanica: Savinov, 1970, p. 114, text fig. 8.

H o l o t y p e. IZ, no. M-648/60-P, fragmentary left mandible, containing M_1–M_3; Kazakhstan, Pavlodar 1A (Gusiny Perelet); Upper Miocene, Pavlodar Formation.

D e s c r i p t i o n (Fig. 3). The alveolus of P^4 is very small. M^1 is lengthened and usually bears a well developed anterocone and a reduced posteroloph. The anterocone is developed in 70% of specimens and appears as a clearly detached cusp between the anterior arm of the protocone and the anteroloph; in 20% of cases, the anterior arm of the protocone bears a thickening; and only three specimens (10%) lack anterocones. The posteroloph is present in 86% of weakly worn specimens (in 36%, it is developed as a small projection of the metacone on the occlusal surface and a well-pronounced ridge extending to the posterior side of the crown; and in 50%, this is a weak projection of the metacone and a poorly developed ridge). The spur of the paracone is developed to a greater or lesser extent in 14 specimens (52%). M^2 is relatively short. The anteroloph is well developed and usually has an expansion in place of the anterocone (one specimen has a large anterocone). The paracone lacks a spur. The posteroloph is absent, the lingual part of the metacone projects slightly posteriorly. M^3 is small and round, it bears a long anteroloph and is similar in structure to M^2, but its posterior cusps are fused.

M_1 bears the anteroconid with a frequency of 90%. The anteroconid is usually isolated; however, in some cases it is connected to the metaconid. The ectocingulid is present in 92% of specimens (in 59%, it is weakly developed; in 33%, it is stout and possesses an ectostylid). The hypoconulid is extended (63%) or round. M_2 bears a large anteroconid. In all cases, the connection between the hypoconid and the entoconid is well-pronounced. M_3 is short and wide and usually has a long labial arm of the anterolophid.

M e a s u r e m e n t s, mm: length of M_1–M_2 (GIN, no. 640/215) 4.7; length × width: M_1, 2.4 × 1.95, and M_2, 2.3 × 2.1. The measurements of isolated teeth from the Pavlodar Formation are given in Table 1.

The greatest values of the height/length ratio in unworn or weakly worn teeth are as follows, %: (M^1) 78, (M^2) 90, (M^3) 100, (M_1) 93, (M_2) 85, and (M_3) 84.

Table 1. The measurements of isolated teeth of *Scirtodipus kazakhstanicus* from the Pavlodar Formation

Tooth	Length			Width		
	n	limits	mean	*n*	limits	mean
M^1	26	2.15–2.70	2.37	26	1.90–2.25	2.03
M^2	14	1.90–2.15	2.03	14	1.75–2.10	1.88
M^3	3	1.45–1.50	1.48	3	1.40–1.60	1.48
M_1	26	2.05–2.50	2.29	26	1.65–2.10	1.87
M_2	20	1.95–2.45	2.24	21	1.70–2.15	2.01
M_3	18	1.40–1.85	1.65	18	1.30–1.75	1.57

The metatarsus (GIN, no. 640/344) is approximately 26.5 mm long, 3.25 mm wide in the proximal part, and 4.9 mm wide in the distal part.

The measurements of teeth from the Rytovo Formation (length × width, mm) are as follows: M^2 (GIN, no. 640/3006) 1.9 × 1.7, M_1: (GIN, no. 640/3008) 2.25 × 1.75 and (GIN, no. 640/3007) 2.35 × 2.0, M_2: (GIN, no. 1108/8) 2.0 × 1.75 and (GIN, no. 1108/9) 2.4 × 2.15. The crown height of a weakly worn M^2 is 1.55, the ratio height/length is 81.5%.

O c c u r r e n c e. Kazakhstan; Upper Miocene to Lower Pliocene (MN12–MN14).

M a t e r i a l. Fragmentary jaws (four with M^1, one with M^3, one with M_1 and incisor, one with M_1 and M_2, and two with M_1), nine upper incisors, 24 M^1, 15 M^2, 2 M^3, 26 M_1, 24 M_2, 18 M_3, and four incomplete metatarsals from the Pavlodar 1A locality; M^2 and two M_1 from the Pavlodar 1B locality; and two M_2 and a fragmentary metatarsus from the Pavlodar 2A locality.

Genus *Stylodipus* Allen, 1925

Stylodipus: Allen, 1925, p. 4.

T y p e s p e c i e s. *S. andrewsi* Allen, 1925; Recent.

D i a g n o s i s. Small and medium-sized. Upper incisors with deep longitudinal groove. P^4 reduced or undeveloped. Molars lophodont and ranging from low-crowned to high-crowned. Cusps round at base. On M^1–M^3, main cusps of each pair positioned opposite to each other. Anteroloph of M^1 reduced to state of low cingulum, anterocone undeveloped, and posteroloph rudimentary. Paracone of M^1 and M^2 extended anterolabially. Metacone transverse. Endoloph of M^1 and M^2 high, oblique, and formed by posterolingual projection of paracone and anterior projection of hypocone. Endoloph of M^3 relatively straight, located centrally, and connected to lingual part of paracone or protocone. Anteroloph of M^3 reduced. On M_1, metaconid substantially larger than protoconid and strongly displaced anteriorly. Entoconid of M_1 and M_2 connected to hypoconid. Anterolophid of M_2 possessing labial arm. Anterolophid of M_3 rudimentary or undeveloped.

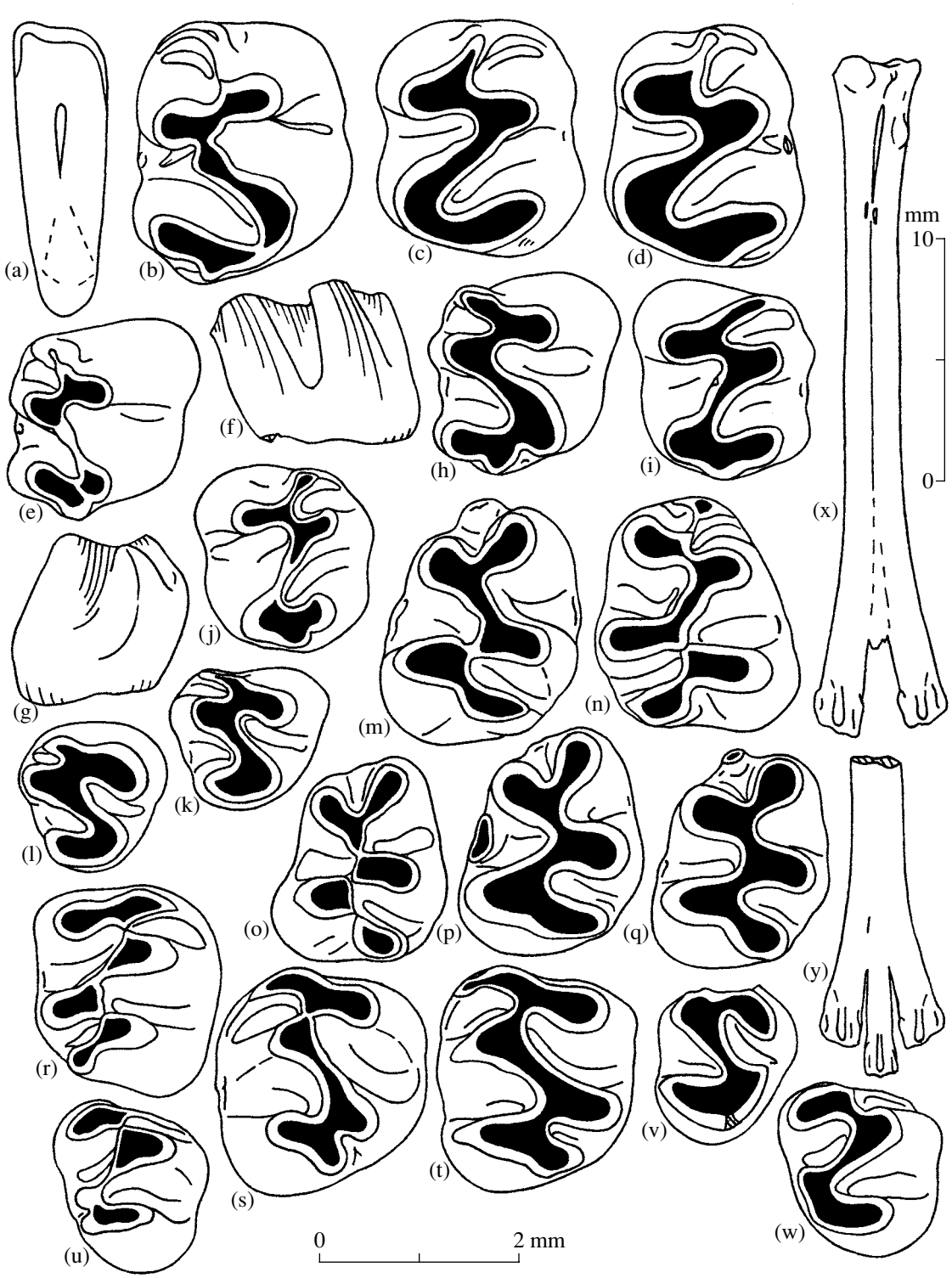

Fig. 3. *Scirtodipus kazakhstanicus* Savinov, 1970: (a) GIN, no. 640/296, left upper incisor; (b) GIN, no. 640/305, right M^1; (c) GIN, no. 640/306, left M^1; (d) GIN, no. 640/309, left M^1; (e–g) GIN, no. 640/330, right M^2: (e) occlusal surface, (f) lingual view, and (g) front view; (h) GIN, no. 640/328, right M^2; (i) GIN, no. 640/339, left M^2; (j) GIN, no. 640/3006, left M^2; (k) GIN, no. 640/342, right M^3; (l) GIN, no. 640/343, right M^3; (m) GIN, no. 640/221, left M_1; (n) GIN, no. 640/232, right M_1; (o) GIN, no. 640/225, left M_1; (p) GIN, no. 640/3007, left M_1; (q) GIN, no. 640/3008, left M_1; (r) GIN, no. 640/248, right M_2; (s) GIN, no. 640/263, left M_2; (t) GIN, no. 640/265, left M_2; (u) GIN, no. 640/272, right M_3; (v) GIN, no. 640/282, left M_3; (w) GIN, no. 640/273, right M_3; (x) GIN, no. 640/344, left metatarsus, and (y) GIN, no. 640/346, distal fragment of left metatarsus. (a–i, k–o, r–y) Pavlodar 1A and (j, r, q) Pavlodar 1B.

C o m p o s i t i o n. *S. telum* (Lichtenstein, 1823), Pleistocene to Recent, Eastern Europe, Siberia, Kazakhstan, and Central Asia; *S. andrewsi* Allen, 1925 and *S. sungorus* Sokolov et Shenbrot, 1987, Recent, Mongolia; and *S. iderensis* sp. nov., and *S. perfectus* sp. nov., Lower Pliocene, Mongolia.

C o m p a r i s o n. *Stylodipus* is distinguished from the genera *Plioscirtopoda, Dipus, Jaculus*, and *Eremodipus* by the same characters as *Scirtodipus*. The differences from the latter consist primarily in a reduced anteroloph and anterocone on M^1, the orientation of the paracone on M^1 and M^2, the position of the endoloph on M^3, the ratio between the metaconid and protoconid on M_1, and in a reduced anterolophid on M_3.

Stylodipus iderensis Zazhigin et Lopatin, sp. nov.

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

H o l o t y p e. GIN, no. 1102/1, left M_1; Mongolia, Ider River; Lower Pliocene (MN14).

D e s c r i p t i o n (Figs. 4a–4x). A relatively large member of the genus. The alveolus of P^4 is developed to a greater extent than those of Recent species. The molars are low-crowned. M^1 is rounded rectangular. The anteroloph looks like a narrow cingulum; in one specimen, it bears a small thickening (rudimentary anterocone). The protocone and the paracone are drawn close together. The posteroloph is rudimentary, looks like a small posterolabial projection of the metacone. M^2 is short and bears an anterolingually projecting protocone. The anteroloph is relatively well developed. The posteroloph is absent; however, in its place, the metacone projects slightly posteriorly. M^3 is small and rounded, the posterior lobe is narrowed. The anteroloph and the anterofossette are reduced and very small. The endoloph is located centrally. The labial fold usually possesses a narrow entrance, but in some cases, it is closed.

M_1 is rounded triangular and extends longitudinally. The anteroconid is commonly present; it is large and detached (50%) or small and drawn close to the metaconid. The metaconid is round in outline and substantially more massive than the protoconid. The protoconid is more compressed. The hypoconulid is relatively large and round down to late stages of wear. The ectocingulid ranges from weak to stout; occasionally, it bears an ectostylid. The metastylid is absent. On M_2, cusps are longitudinally compressed. The metaconid is fused with the anteroconid, the protoconid with the entoconid, and the hypoconid with the hypoconulid. The contacts between the anteroconid and the protoconid and between the entoconid and the hypoconid are weak. The posterior lobe is narrowed, the hypoconid is reduced, and the hypoconulid is weakly detached. In some cases, the entoconid closely adjoins the hypoconulid. M_3 is narrow. The anterolophid is absent (in two cases, it is present as a rudiment, an extremely narrow enamel ridge, on the anterior wall of the crown below the wear surface). Anteriorly and posteriorly, the protoconid is connected to the metaconid and to a round small entoconid fused with the hypoconid, respectively. Lingual folds are very small; as the crown is worn, they become enclosed and, subsequently, disappear.

Table 2. The measurements of isolated teeth of *Stylodipus iderensis*

Tooth	Length			Width		
	n	limits	mean	*n*	limits	mean
M^1	12	2.05–2.40	2.20	12	1.90–2.25	2.00
M^2	6	1.85–2.10	1.98	7	1.75–2.10	1.93
M^3	9	1.40–1.65	1.51	9	1.40–1.70	1.50
M_1	15	2.30–2.55	2.42	15	1.75–2.10	1.89
M_2	13	2.05–2.45	2.23	13	1.95–2.25	2.07
M_3	6	1.50–1.65	1.55	6	1.35–1.50	1.42

The metatarsus is large, relatively short, and massive; the distal part is expanded.

M e a s u r e m e n t s, mm: length × width (holotype) 2.45 × 2.0. The measurements of isolated teeth are given in Table 2.

The ratio between the mean length of M^1 and M^2 is 111%. The greatest values of the ratio height/length, %: (M^1) 89, (M^2) 95, (M^3) 84, (M_1) 85, (M_2) 86, and (M_3) 90.

In the metatarsals, length × width of the proximal part × width of the distal part: (GIN, no. 1102/82) $29.3 \times 3.7 \times 5.7$ and (GIN, no. 1102/83) $29.0 \times 3.8 \times 5.6$.

C o m p a r i s o n. The new species is distinguished from the Recent species by a smaller metaconid on M_1, and substantially lower crowns (in *S. telum*, the mean ratio between the height and length of crowns in unworn molars is 140–150%), and by a stout metatarsus (Figs. 4x and 4y).

M a t e r i a l. In addition to the holotype, two fragmentary upper jaws (one with M^1); a fragmentary lower jaw, containing M_1; isolated teeth: seven upper incisors, 15 M^1, eight M^2, nine M^3, 15 M_1, 17 M_2, and six M_3; and six metatarsi, including two complete, one almost complete, and three distal parts, from the Ider locality.

Stylodipus perfectus Zazhigin et Lopatin, sp. nov.

E t y m o l o g y. From Latin *perfectus* (perfect, accomplished).

H o l o t y p e. GIN, no. 957/2003, left M_1; Mongolia, Chono-Khariakh 2; Lower Pliocene (MN14/15), upper part of the Upper Khirgis-Nur Subformation.

D e s c r i p t i o n (Fig. 5). A small member of the genus. The molars are relatively low-crowned. M^1 is large and wide. The anteroloph is a weak cingulum; occasionally, it is clearly detached from the base of the protocone. The protocone and the paracone are drawn close together. The posteroloph is absent. M^2 is substantially smaller than M^1 and short, the protocone

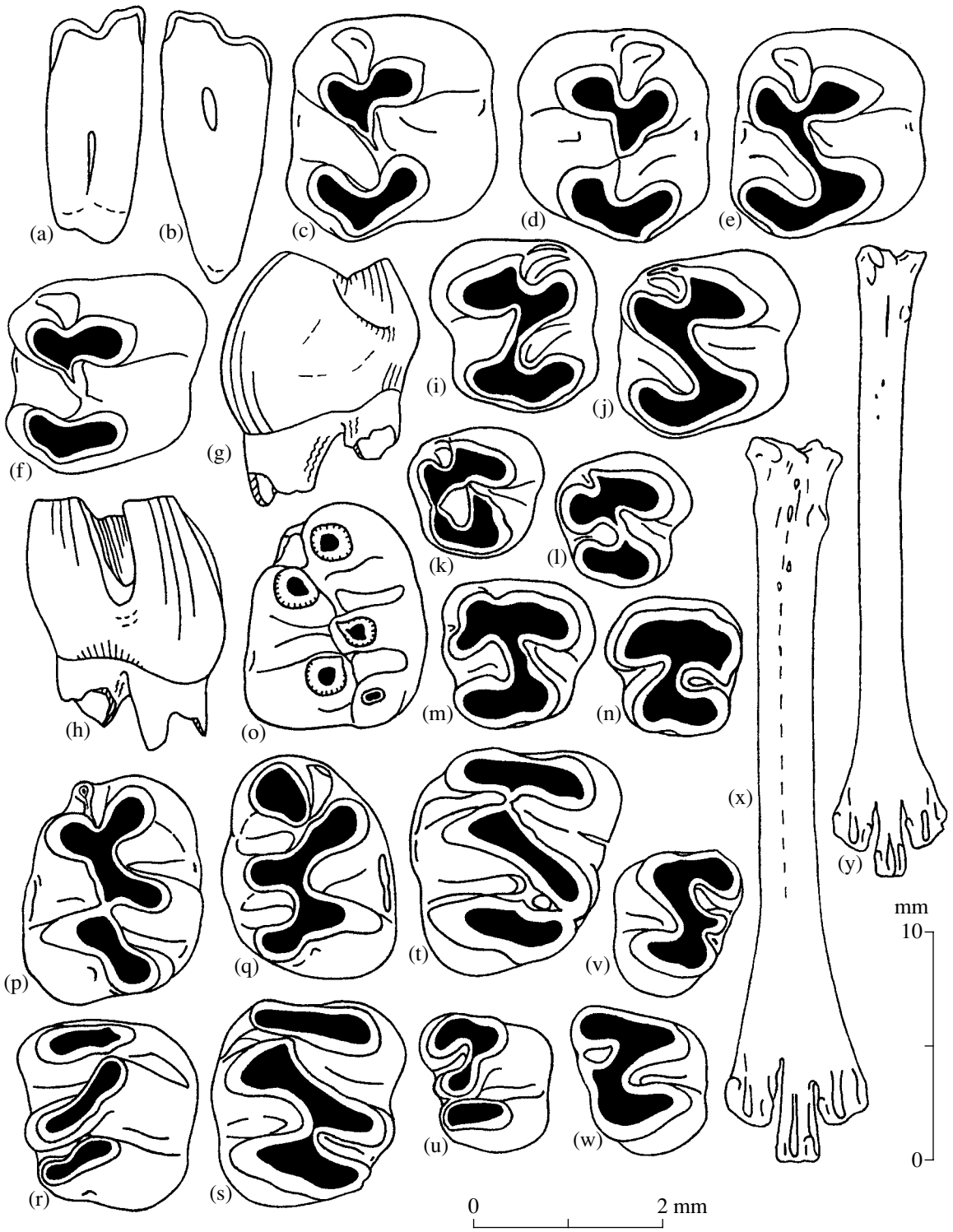

Fig. 4. *Stylodipus*: (a–x) *S. iderensis* sp. nov.: (a) GIN, no. 1102/43, right upper incisor; (b) GIN, no. 1102/44, left upper incisor; (c) GIN, no. 1102/52, right M^1; (d) GIN, no. 1102/54, left M^1; (e) GIN, no. 1102/56, right M^1; (f–h) GIN, no. 1102/70, right M^2: (f) occlusal surface, (g) front view, and (h) lingual view; (i) GIN, no. 1102/68, left M^2; (j) GIN, no. 1102/72, right M^2; (k) GIN, no. 1102/76, right M^3; (l) GIN, no. 1102/79, right M^3; (m) GIN, no. 1102/73, right M^3; (n) GIN, no. 1102/77, left M^3; (o) holotype, GIN, no. 1102/1, left M_1; (p) GIN, no. 1102/12, left M_1; (q) GIN, no. 1102/10, right M_1; (r) GIN, no. 1102/23, right M_2; (s) GIN, no. 1102/20, left M_2; (t) GIN, no. 1102/27, left M_2; (u) GIN, no. 1102/39, right M_3; (v) GIN, no. 1102/35, left M_3; (w) GIN, no. 1102/37, right M_3; and (x) GIN, no. 1102/83, left metatarsus; and (y) *S. telum* (Lichtenstein, 1823), GIN, no. 1120/4, left metatarsus, Recent, Kazakhstan.

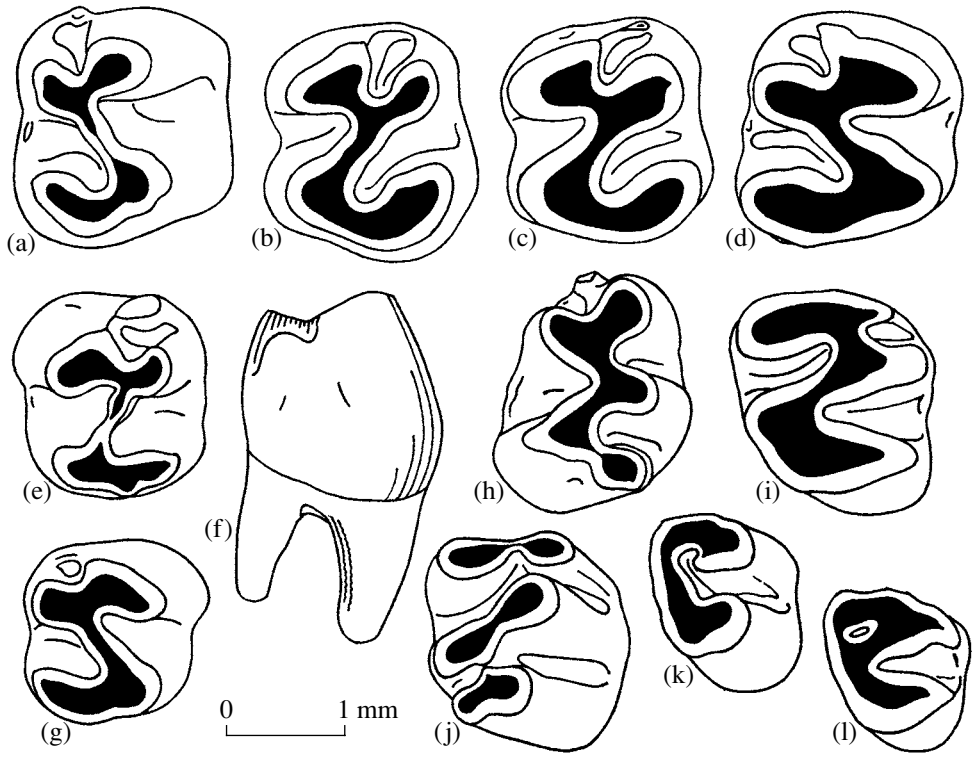

Fig. 5. *Stylodipus perfectus* sp. nov.: (a) GIN, no. 957/2000, right M^1; (b) GIN, no. 957/1001, left M^1; (c) GIN, no. 957/2005, left M^1; (d) GIN, no. 957/2001, right M^1; (e, f) GIN, no. 957/2006, left M^2: (e) occlusal surface and (f) front view; (g) GIN, no. 957/2002, right M^2; (h) holotype, GIN, no. 957/2003, left M_1; (i) GIN, no. 957/2008, right M_2; (j) GIN, no. 957/2007, right M_2; (k) GIN, no. 957/2004, right M_3; and (l) GIN, no. 957/1000, right M_3. (a, c–k) Chono-Khariakh 2 and (b, l) Chono-Khariakh 1.

projects externally. The anteroloph is either weak or massive; however, in all cases, it is isolated from the protocone by a well-pronounced constriction.

The anteroconid of M_1 is small and fused with the metaconid. The metaconid is wide and substantially more massive than the protoconid. The hypoconulid is relatively large and rounded. The ectocingulid is weak. On M_2, the main cusps are longitudinally compressed and united with each other to form transverse crests. The contacts between the anteroconid and the protoconid and between the entoconid and the hypoconid are weak at the early stages of wear. The hypoconulid is weakly detached from the hypoconid and drawn close to the entoconid. M_3 is narrow and short. The anterolophid is rudimentary or undeveloped. The protoconid is connected to the metaconid, the latter is connected to the entoconid that is merged with the hypoconid. At the early stages of wear, the posterior projection of the protoconid is isolated from the entoconid. The anterior lingual fold is closed and the posterior fold absent.

Measurements, length × width, mm: M^1: (GIN, no. 957/2009) 2.0 × 1.85, (GIN, no. 957/2005) 2.05 × 1.8 (GIN, no. 957/2001) 2.05 × 1.9 (GIN, no. 957/1001) 2.1 × 1.85, and (GIN, no. 957/2000) 2.1 × 1.9; M^2: (GIN, no. 957/2002) 1.6 × 1.5 and (GIN, no. 957/2006) 1.7 × 1.7; M_1 (holotype) 2.0 × 1.6; M_2: (GIN, no. 957/2007) 1.75 × 1.75 and (GIN, no. 957/2008) 1.9 × 1.75; and M_3: (GIN, no. 957/1000) 1.3 × 1.25 and (GIN, no. 957/2004) 1.4 × 1.3.

The mean ratio between the length of M^1 and M^2 is 126%. The ratio height/length of tooth crown, %: (GIN, no. 957/2000) M^1, 93; (GIN, no. 957/2006) M^2, 106; (GIN, no. 957/2007) M_2, 94; and (GIN, no. 957/2004) M_3, 93.

Comparison. The new species is distinguished from Recent species by a smaller metaconid of M_1 and relatively low crowns of the molars. It is distinguished from *S. iderensis* by small measurements, relatively higher crowns, a weakly developed anteroloph, the absence of posteroloph on M^1 and M^2, a greater reduction of M^2 in relation to M^1, and by the structure of M_3, i.e., the lingual folds and the ectolophid are reduced.

Material. In addition to the holotype, (GIN, nos. 957/2000–2002 and 2004–2009) four M^1, two M^2, two M_2, and one M_3 from the type locality; and (GIN, no. 957/1000) M^1 and (GIN, no. 957/1001) M_3 from the Chono-Khariakh 1 locality.

Genus *Plioscirtopoda* Gromov et Schevtchenko, 1961

Plioscirtopoda: Gromov and Shevchenko, 1961, p. 978.

Type species. *P. stepanovi* Gromov et Schevtchenko, 1961; Lower Pleistocene of the Ukraine.

D i a g n o s i s. Medium-sized. P^4 absent. Molars distinctly lophodont and ranging from low-crowned to relatively high-crowned, cusps strongly compressed longitudinally. On M^1 and M^2, paracone and protocone opposite to each other or weakly alternate; on M_1, cusps in pairs protoconid–entoconid and hypoconid–hypoconulid frequently opposed. Anteroloph and anterocone on M^1 and M^2 developed to varying degree, posteroloph reduced. Endoloph on M^1–M^3 strongly oblique and connected to paracone. M^3 with small anteroloph. On M_1 metaconid increased, projects anteriorly, and connected to anterior part of protoconid. Entoconid on M_1 and M_2 connected to hypoconid. Labial arm of anterolophid of M_2 and anterolophid of M_3 reduced or undeveloped.

C o m p o s i t i o n. *P. stepanovi* Gromov et Schevtchenko, 1961, Lower Pleistocene, Ukraine; *P. antiqua* sp. nov., Upper Miocene, Kazakhstan; *P. rapida* sp. nov., Lower Pliocene, Kazakhstan and the southern part of Western Siberia; and *P. zykini* sp. nov., Lower Pliocene, Kazakhstan.

C o m p a r i s o n. *Plioscirtopoda* is distinguished from the genera *Scirtodipus, Stylodipus*, and *Dipus* by a strong longitudinal compression of cusps and peculiar structure of M_1 and M_2. It is distinguished from *Jaculus* and *Eremodipus* by a complicated structure of the occlusal surface and by relatively low crowns of the molars.

R e m a r k s. *Plioscirtopoda* sp. is known from the Upper Pliocene to Lower Pleistocene of the southern part of Western Siberia (Zazhigin, 1980; Zazhigin and Zykin, 1984).

Plioscirtopoda antiqua Zazhigin et Lopatin, sp. nov.

E t y m o l o g y. From Latin *antiquus* (ancient).

H o l o t y p e. GIN, no. 951/1003, right M^1; Kazakhstan, Selety 1A; Upper Miocene (MN13), Kedei Formation.

D e s c r i p t i o n (Figs. 6a–6c). A large member of the genus. The molars are low-crowned. M^1 is lengthened. The anterocone is large, the anteroloph is well-pronounced, and the anterostyle is distinctly developed. The protocone and the paracone are in accumbent positions and united with each other, the protoloph is absent. The paracone is massive. The protocone is strongly compressed longitudinally and tapering lingually. The endoloph connects the hypocone to the lingual part of the paracone. The endosinus slants slightly anteriorly. M_1 bears a large hypoconulid possessing a stout posterolabial projection. M_3 is of a complicated structure, i.e., the protoconid is connected to the entoconid, the labial arm of the anterolophid is present (although it occupies a low position), and the metaconid is not connected to the entoconid.

M e a s u r e m e n t s, mm: the holotype is 2.6 mm long; width of M_1 (GIN, no. 951/1004) is 2.05 and length × width of M_3 (GIN, no. 951/1005) is 1.75 × 1.45.

C o m p a r i s o n. The new species is distinguished from *P. stepanovi* by large measurements, low crowns, merged anterior cusps, a stronger developed anteroloph, the presence of the anterostyle on M^1, and by a complicated structure of M_3.

M a t e r i a l. In addition to the holotype, fragmentary M_1 and complete M_3 from the Selety 1A locality.

Plioscirtopoda rapida Zazhigin et Lopatin, sp. nov.

E t y m o l o g y. From Latin *rapidus* (rapid, fast).

H o l o t y p e. GIN, no. 1110/1, left M^1; Russia, Omsk Region, Cherlak; Lower Pliocene (MN14), Rytovo Formation.

D e s c r i p t i o n (Figs. 6d and 6e). A large member of the genus. The molars are relatively low-crowned. M^1 is lengthened. The anterocone is large, the anteroloph is a cingulum closing the anterofossette. An extremely small anterostyle is present. The protocone is weakly displaced anteriorly in relation to the paracone; the lingual side is narrow and the posterior side is straight. The protoloph is short. The paracone extends transversely. A narrow endoloph connects the hypocone to the middle of the paracone. The posteroloph is weak. The endosinus is weakly slanting anteriorly. M^2 is similar to M^1; however, it is characterized by more rectangular outlines of the occlusal surface. The posterior lobe is narrower somewhat than the anterior lobe. The anteroloph is stout and long, it bears distinct expansions in place of the anterocone and the anterostyle. The lingual side of the protocone is rounded and the posteroloph is undeveloped. The endosinus is straight and transverse.

M e a s u r e m e n t s, length × width, mm: (holotype) 2.5 × 2.25 and (GIN, no. 640/3005) M^2, 2.35 × 2.05.

C o m p a r i s o n. The new species is distinguished from *P. stepanovi* by large dimensions, relatively low crowns, a stronger developed anteroloph, and by the presence of the anterostyle on M^1 and M^2. It is distinguished from *P. antiqua* by a more anterior position of the protocone and by the presence of the protoloph.

M a t e r i a l. In addition to the holotype, M^2 from the Pavlodar 1B locality.

Plioscirtopoda zykini Zazhigin et Lopatin, sp. nov.

Plioscirtopoda sp.: Zazhigin and Zykin, 1984, p. 42.

E t y m o l o g y. The species is named in honor of the geologist V.S. Zykin.

H o l o t y p e. GIN, no. 945/300, right M_2; Kazakhstan, Beteke; Lower Pliocene (MN15), Beteke Formation.

D e s c r i p t i o n (Figs. 6f–6l). A small member of the genus. The molars are relatively high-crowned. M^1 is characterized by an anteriorly projecting protocone.

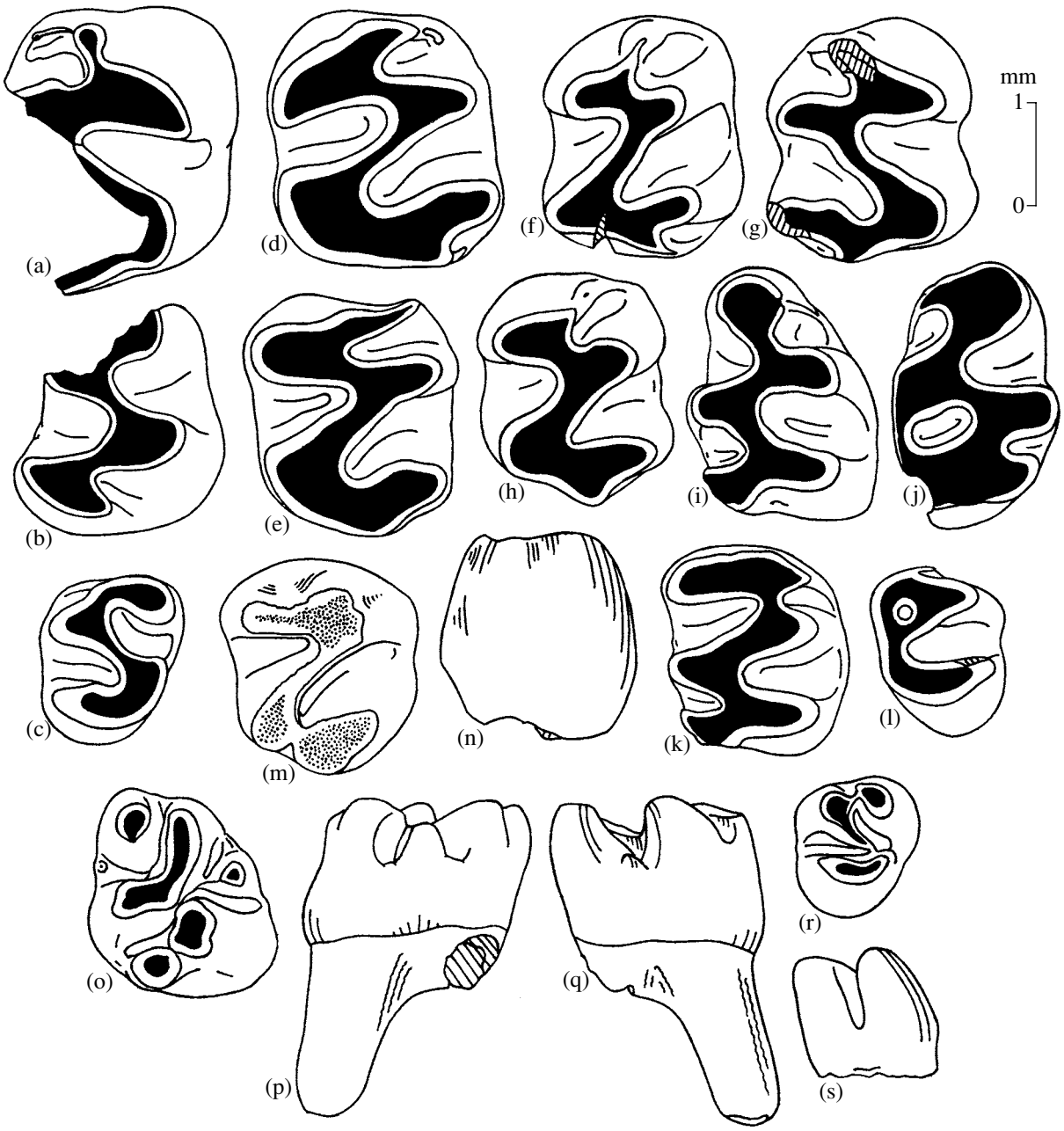

Fig. 6. *Plioscirtopoda*, *Jaculus*, and *Jaculodipus* gen. nov.: (a–c) *Plioscirtopoda antiqua* sp. nov.: (a) holotype, GIN, no. 951/1003, fragmentary right M^1; (b) GIN, no. 951/1004, fragmentary right M_1; and (c) GIN, no. 951/1005, left M_3; (d, e) *P. rapida* sp. nov.: (d) holotype, GIN, no. 1110/1, left M^1 and (e) GIN, no. 640/3005, left M^2; (f–l) *P. zykini* sp. nov.: (f) GIN, no. 1108/1001, left M^1; (g) GIN, no. 1108/1002, right M^1; (h) GIN, no. 1108/1003, left M^2; (i) GIN, no. 945/301, right M_1; (j) GIN, no. 1108/1004, left M_1; (k) holotype, GIN, no. 945/300, right M_2; and (l) GIN, no. 1108/1005, right M_3; (m, n) *Jaculus sibiricus* sp. nov., holotype, GIN, no. 951/1006, left M^2: (m) occlusal surface and (n) front view; and (o–s) *Jaculodipus yavorensis* gen. et sp. nov.: (o–q) holotype, GIN, no. 958/2, right M_1: (o) occlusal surface, (p) labial view, and (q) lingual view; (r, s) GIN, no. 958/1, left M_3: (r) occlusal surface and (s) labial view. (a–c, m, n) Selety 1A, (d) Cherlak, (e) Pavlodar 1B, (f–h, j, l) Pavlodar 2B, (i, k) Beteke, and (o–s) Yavor.

The anterocone is weakly detached, the anteroloph looks like a cingulum. The protocone and the paracone are positioned almost opposite to each other, the protoloph is short. The paracone extends transversely or is slightly turned anterolabially. The endoloph connects the hypocone to the lingual part of the paracone. The posteroloph is relatively well developed and forms a noticeable projection on the occlusal surface and a distinct crest on the posterior side of the crown. The endosinus is straight. M^2 is similar to M^1 in structure,

being distinguished by more rectangular outlines, the absence of anterocone, and by a rudimentary posteroloph.

M_1 is broad. The metaconid is massive and occupies an anterior position. A narrow anterocingulid frames the anterior valley and forms a distinct rib rising along the labial wall of the metaconid to the occlusal surface. The protoconid is weakly displaced anteriorly in relation to the entoconid. The hypoconid is strongly elongated transversely, the hypoconulid is large. As the tooth is strongly worn, the labial fold becomes enclosed, and the anterocingulid looks like an anterolabial projection of the metaconid. M_2 is characterized by the presence of reduced labial arm of the anterolophid. The structure of the posterior part is similar to that of M_1. M_3 bears a deep labial fold. The lingual fold is closed and becomes a small rounded lake, the anterolophid is rudimentary and looks like a weak ridge on the anterior side of the crown.

Measurements, length × width, mm: M_1 (GIN, no. 945/301) 2.45 × 1.9 and M_2 (holotype) 2.2 × 1.8 from the Beteke locality; M^1: (GIN, no. 1108/1001) 2.3 × 1.95 and (GIN, no. 1108/1002) 2.3 × 2.0, M^2: (GIN, no. 1108/1003) 2.2 × 1.85, M_1 (GIN, no. 1108/1004) 2.55 × 1.6, and M_3 (GIN, no. 1108/1005) 1.45 × 1.3 from the Pavlodar 2B locality.

Comparison. The new species is distinguished from *P. stepanovi* by lower crowns and by the presence of a weakly reduced labial arm of the anterolophid on M_2; it is distinguished from *P. rapida* by smaller dimensions, a less reduced posteroloph, and by weakly developed anterocone and anteroloph on M^1 and M^2. It is distinguished from *P. antiqua* by measurements and by the structure of M^1, M_1, and M_3.

Material. In addition to the holotype, M_1 from the Beteke locality; two M^1, M^2, M_1, and M_3 from the Pavlodar 2B locality.

Genus *Jaculus* Erxleben, 1777

Jaculus: Erxleben, 1777, p. 404.

Type species. *Mus jaculus* Linnaeus, 1758; Recent.

Diagnosis. Medium-sized and large. Longitudinal groove on upper incisors undeveloped or hardly distinguishable. P^4 absent. Molars mesodont and lophodont, with strongly compressed cusps. On M^1 and M^2, main cusps of either pair positioned opposite to each other. Anteroloph and posteroloph undeveloped. On M^1 and M^2, endoloph connected to paracone; on M^3, to protocone. On M^2, anterofossette absent. On M_1, main cusps of either pair positioned opposite to each other, protoconid compressed transversely. Entoconid of M_1 and M_2 connected to hypoconulid or to hypoconulid and hypoconid. On M_2, labial arm of anterolophid well developed. On M_3, posterior cusps completely merged and anterolophid absent.

Composition. Recent species: *J. jaculus* (L., 1758), North Africa and Near East; *J. orientalis* Erxleben, 1777, North Africa; *J. blanfordi* (Murray, 1884) Iran, Pakistan, Afghanistan, and Turkmenistan; and *J. sibiricus* sp. nov. Upper Miocene of Kazakhstan.

Comparison. *Jaculus* is distinguished from *Dipus*, *Scirtodipus*, *Stylodipus*, and *Plioscirtopoda* by mesodont molars, characterized by a simplified structure of the occlusal surface, i.e., M^1 lacks an anteroloph and M^2 lacks an anterofossette; on M_1 and M_2, the entoconid is connected to the hypoconulid. It is distinguished from *Eremodipus* by the absence of an anteroloph and a posteroloph, the position of the endoloph on M^1 and M^2, and by the structure of lower teeth.

Jaculus sibiricus Zazhigin et Lopatin, sp. nov.

Etymology. From Siberia.

Holotype. GIN, no. 951/1006, left M^2; Kazakhstan, Selety 1A; Upper Miocene (MN13), Kedei Formation.

Description (Figs. 6m and 6n). A medium-sized member of the genus. M^2 almost lacks wear marks. The crown is high and rounded rectangular in outline. The anterior lobe is substantially wider than the posterior lobe. The protocone is strongly compressed longitudinally and fused with a more massive paracone. Anteriorly, the boundary between them is marked by a weak depression. An extremely weak anterolabial groove on the paracone indicates that it includes a rudimentary anteroloph. The endoloph is high and narrow, it connects the paracone and the hypocone. The endosinus is transverse. A stout metacone forms the posterior part of the crown. A relatively small hypocone is isolated by a distinct posterolingual groove and fused with the metacone.

Measurements, mm. Holotype: length, 1.85; width, 1.5; and height, 2.0; the ratio height/length is 108%.

Comparison. *J. sibiricus* is characterized by a substantially lower M^2 than in Recent species, in which the ratio height/length of the crown is, at least, 120%. With reference to the size, the new species is similar to *J. blanfordi*, smaller than *J. orientalis*, and larger than *J. jaculus*.

Material. Holotype.

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

Etymology. From generic names *Jaculus* and *Dipus*.

Type species. *J. yavorensis* sp. nov.

Diagnosis. Medium-sized. Molars relatively low-crowned and bunolophodont. Main cusps of M_1 drawn close together and slanting externally, metaconid and protoconid equal in sizes, positioned opposite to each other, and oriented longitudinally; protoconid strongly compressed transversely. Posterior cusps alternate in arrangement. Entoconid connected to hypoconid and isolated from hypoconulid. Large ecto-

stylid present and connected to protoconid. On M_3, posterior cusps completely merged, anterolophid absent.

Composition. Type species.

Comparison. The new genus is distinguished from *Dipus*, *Scirtodipus*, *Stylodipus*, and *Plioscirtopoda* by a longitudinal orientation of anterior cusps, transversely compressed protoconid, very large ectostylid on M_1, and reduced entoconid on M_3. It is distinguished from *Eremodipus* by a complicated structure and low crowns of molars. The differences with *Jaculus* consist in the absence of contacts between the entoconid and the hypoconulid, strong medial slanting of the protoconid and entoconid, more posterior position of the hypoconid and hypoconulid in relation to the entoconid, the presence of a large ectostylid on M_1, and by a lesser degree of M_3 reduction.

Jaculodipus yavorensis Zazhigin et Lopatin, sp. nov.

Etymology. From Yavor Tract.

Holotype. GIN, no. 958/2, right M_1; Mongolia, Yavor 1; Lower Pliocene (MN14), base of the Upper Khirgis-Nur Subformation.

Description (Figs. 6o–6s). M_1 is broad and bears relatively small anterior cusps, a large entoconid, and a massive hypoconid. The metaconid and the protoconid extend longitudinally and are isolated from each other in the upper part. A small metastylid is located at the posterolingual base of the metaconid. The protoconid is fused with the entoconid. A narrow crest deviates from the point of fusion, extends labially, and adjoins a large and high ectostylid. The base of the posterolabial part of the entoconid adjoins the hypoconid. The hypoconulid is well-pronounced, large, rounded, and isolated from the entoconid by a deep closed posterofossettid. M_3 is small and bears a deep labial fold. Anteriorly, the protoconid is fused with the metaconid; posteriorly, it is connected to the lingual part of the posterior lobe by a long projection. The entoconid is undeveloped, the lingual fold is closed.

Measurements, length × width × height, mm. Holotype: $2.15 \times 1.85 \times 1.6$, M_3 (GIN, no. 958/1) $1.4 \times 1.2 \times 1.35$.

Remarks. The crown shape and the structure of the anterior cusps of M_1 of *Jaculodipus* resemble those of *Jaculus*, whereas the middle and posterior parts of tooth are more similar to the morphotype of *Dipus*. This complex of characters combined with a large ectostylid indicate that *Jaculodipus* occupies an original position among the Dipodini.

Material. In addition to the holotype, M_3 from the type locality.

DISCUSSION

At the end of the Late Miocene, at least, four genera of three-toed jerboas existed in Asia: *Scirtodipus* (since MN12) *Plioscirtopoda*, *Dipus*, and *Jaculus* (since MN13). This indicates that the onset of adaptive radiation in the Dipodinae occurred earlier. Judging from the tooth structure, the origin of the Dipodinae should be associated with the Cardiocraniinae.

Scirtodipus is similar in tooth morphology to *Stylodipus* and can be regarded as the ancestor of the latter. The findings of Early Pliocene *Stylodipus iderensis* and *S. perfectus* that are similar to both Recent members of the genus *Stylodipus* and *Scirtodipus* corroborates this hypothesis. Judging from the structure of the metatarsus, *S. iderensis* was a member of a specialized lineage within the genus; this deviated from the main trunk comprising Recent species and, probably, *S. perfectus.*

Scirtodipus is probably related to the genus *Plioscirtopoda*, previously known from the Upper Pliocene to the Lower Pleistocene of the Ukraine (Gromov and Shevchenko, 1961; Topachevsky *et al.*, 1998) and from the upper part of the Lower Pliocene (MN15) to the Lower Pleistocene of Western Siberia (Zazhigin, 1980; Zazhigin and Zykin, 1984). Our data indicate that this genus appeared in Kazakhstan, at least, at the end of the Miocene (*P. antiqua*).

Regarding the tooth structure, *Dipus* occupies a novel position among the Dipodinae. *D. conditor* represents an early evolutionary stage of the genus, being the ancestor of *D. singularis* and *D. essedum.* The latter is probably related to Recent *D. sagitta*. *D. fraudator* probably belonged to a lineage, deviating from the main developmental line of the genus.

To date, *Jaculus* has been known beginning from the Late Pliocene (Jaeger, 1970). The presence of *J. sibiricus* in the Selety locality indicates that, by the end of the Miocene, this genus had already emerged. The oldest remains of *Eremodipus* Vinogradov, 1930 (not yet described) were found in the lower part of the Pliocene (Rytovo Formation, Pavlodar).

Early Pliocene *Jaculodipus yavorensis* is intermediate in M_1 structure between the genera *Dipus* and *Jaculus*, whereas in the structure of M_3, it is more similar to the latter genus. *J. yavorensis* probably represented an endemic lineage which originated from *Dipus* at the initial stages of the formation of the group of desert jerboas.

The genus *Paradipus* Vinogradov, 1930 is distinguished as a tribe, Paradipodini (Pavlinov and Shenbrot, 1983; Pavlinov and Rossolimo, 1987), or a subfamily, Paradipodinae (Shenbrot, 1992; Shenbrot *et al.*, 1995). Extinct members of the genus *Paradipus* were found in the Kagazly-Suidzhi locality in Badkhyz, Turkmenistan (Shenbrot, 1986). This locality was dated the Late Pliocene; however, a find of *Microtus* cf. *afghanus* Thomas indicates that it should be aged the end of the Early Pleistocene or even later. With reference to the molar structure, *P. badhysus* Shenbrot, 1986 is identical to Recent *P. ctenodactylus* (Vinogradov, 1929). Thus, at present, data on the course of evolutionary development of teeth in *Paradipus* are not avail-

able; and the relationships between this genus and other genera of the Dipodinae are uncertain.

Thus, the generic composition of Recent members of the subfamily Dipodinae was accomplished predominantly at the boundary between the Miocene and the Pliocene. In addition to *Paradipus*, three phylogenetic groups of the Dipodinae are distinguished: the first includes only *Dipus*; the second consists of *Scirtodipus*, *Stylodipus*, and *Plioscirtopoda*; and the third comprises *Jaculus*, *Eremodipus*, and, probably, *Jaculodipus*.

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