New data on Plio-Pleistocene dipodine jerboas of the genus *Plioscirtopoda* from Eastern Europe (Mammalia: Dipodidae)

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Remains of dipodine jerboas, *Plioscirtopoda*, are described from the late Pliocene deposits of the Black Sea and Sea of Azov region. Dental morphology of the type species, *P. stepanovi*, is refined. A more primitive species, *P. novorossica* sp. n., is described from the Late Kujalnik deposits of Kryzhanovka 3. The new species differs from *P. stepanovi* in the simpler shape of anterior part of m1, larger dimensions and higher numbers of molar roots.

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Introduction

Plio-Pleistocene dipodine (tridactyl) jerboas were first recorded from Eastern Europe by Gromov & Schevtchenko (1961). The new genus and new species *Plioscirtopoda stepanovi* was described from the Early Pleistocene Allophaiomys fauna of the upper bed of Kryzhanovka site near Odessa, the Ukraine. Several molars were collected at that time. Gromov & Schevtchenko considered the new form as related to the recent *Stylodipus* (= *Scirtopoda*) *telum*. In late 60's and early 70's V.A. Topachevsky and his group collected and described more material from several localities of the same region. A few molars were added from the type locality and also from the geologically younger Early Pleistocene Allophaiomys faunas of Tarkhankut and Nogaisk. A particularly representative collection of *P. stepanovi* was described from Tarkhankut, Crimea. The detailed morphological analysis of *P. stepanovi* by Topachevsky (1973) showed that because of a unique combination of advanced and primitive characters this form cannot be a direct ancestor of recent *Stylodipus* species, but is rather a specialized independent branch of dipodine jerboas. Since that time, scanty remains of *Plioscirtopoda* were identified and listed from Early Pleistocene deposits of Don Basin (Kazantseva, 1990; Krasnenkov et al., 1992), Volga area (Sukhov, 1977), Western Siberia (Zazhigin, 1980) and Eastern Siberia (Pre-Baicalian region: Adamenko, 1975, 1977), and from even older, Late Pliocene Khapry faunas (MN17) of Eastern Europe (Topachevsky et al., 1979; Skorik, 1983; Topachevsky & Nesin, 1989), Southern Transurals (Ivakina et al., 1996), and Western Siberia (Zazhigin, 1980). In late 80's and early 90's a large amount of small mammal remains was collected from the stratified Kryzhanovka locality by an expedition of Geological Institute of the USSR Academy of Sciences (Tesakov, 1994; Pevzner et al., 1998). Remains of *Plioscirtopoda* were obtained from the two successive stratigraphic levels of Kryzhanovka section. Material from Late Pliocene level 3 underlying the type level 4 with *P. stepanovi* is of special interest. Morphological differences of *Plioscirtopoda* from level 3 warrant the description of a new species ancestral to *P. stepanovi*. The present paper deals with dental remains; some data on postrcranial morphology of this genus were published by Topachevsky (1973) and Topachevsky & Skorik (1977).

Methods. Dental remains of jerboas were drawn with the use of a camera lucida equiped binocular microscopes MBS-1 and MBS-10. Measurements were taken with the ocular measuring scale of the MBS-10 binocular microscope. The ocular scale was calibrated against standard object scale to remove distor-

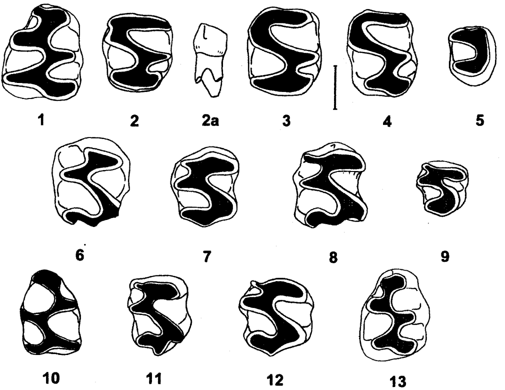

Fig. 1. Dental morphology. **1-12**, *Plioscirtopoda stepanovi* I. Gromov & Schevtchenko: **1**, **10**, **13**, m1; **2-4**, m2; **2a**, m2, anterior side view; **5**, m3; **6**, **11**, M1; **7-8**, **12**, M2; **9**, M3. 1-8, 13 – left; 9, 10-12 – right. **1-9**: Kryzhanovka 4, EMM-25/1-9; **10-12**: Tizdar (10 – EMM-29/20; 11-12 – EMM-10/65-66). **13**, *Plioscirtopoda novorossica* sp. n., Liventsovka 3.

tions introduced by human vision. All measurements are in millimetres. Scale bars in illustrations correspond to 1 mm. All remains of *Plioscirtopoda* are preserved in Geological Institute of the Russian Academy of Sciences (GIN): coll. EMM-25 (Kryzhanovka 4), EMM-31,32 (Kryzhanovka 3), coll. EMM-10,29 (Tizdar).

Dental cusps terminology. The basic terminilogy mainly follows that of Shenbrot (1984, 1986) with modifications after Martin (1994). For anterior cusplets in upper molars, anterocon is used instead of anteroconule. For anterior and posterior cusps of lower molars, anteroconid is used instead of anteroconulid, and hypoconulid instead of posterostylid. Upper case = upper dentition, lower case = lower dentition.

Genus **Plioscirtopoda** I. Gromov & Schevtchenko, 1961

Diagnosis (emend.). Pm4 absent. Molars mesodont with height in young specimens not exceeding occlusal length. Reentrants deep, not forming enamel islets. Anterior and posterior complications of upper molars present. Cusps alternation well-developed. Anteroconid of m1 half-fused with metaconid. Protoflexid of m2 reduced. Mental foramen shifted almost to middle part of lateral side of mandible.

Plioscirtopoda stepanovi I. Gromov & Schevtchenko, 1961
(Figs 1: 1-12)

Plioscirtopoda stepanovi Gromov & Schevtchenko, 1961: 976-979, fig. 2; Schevtchenko, 1965: 53-54, fig. 35d-e; Topachevsky, 1965: 70-74, fig. 16: 1-4, 17; Topachevsky, 1973: 52-74, fig. 10: 1, 11-14, 15: 1; Topachevsky & Skorik, 1977: 69-70; Sukhov, 1977: 88-89, fig. 1: 7-13.

Material examined. **Ukraine**, *Odessa Prov.*, Kryzhanovka 4: 1 m1, 3 m2, 1 m3, 1 M1, 2 M2, 1 M3; **Russia**, *Krasnodar Terr.*, Tizdar: 1 m1, 2 M2.

Geological age. Early Pleistocene, Early Biharian, small mammal associations dominated by *Allophaiomys* and lagurines.

Diagnosis (emend.). Molars relatively compressed antero-posteriorly. Anterior part of first lower molar flattened, with subequal metaconid and anteroconid.

Description. m1. Size: 2.34 × 1.85. Two round roots. Anterior part slightly biloph because of shallow anterior fold. The fold divides larger rounded metaconid and smaller cusplet, the anteroconid. Anterior tips of metaconid and anteroconid at the same level. Metaconid and protoconid broadly communicate. Posterior lobe (hypoconid + hypoconulid) broad.

m2. Size: 1.92 × 1.51, 2.12. × 1.85, 2.1 × 1.61. Three roots: two anterior and one posterior, flattened root. Posterior, hypoconid part narrower than anterior part. Metaconid and protoconid always widely fused. In one specimen (Fig. 1: 2), shallow second labial reentrant fold (protoflexid) separates protoconid and metaconid portions.

m3. Size: 1.12 × 0.98. Two rounded roots. Simple c-shaped form with a single deep labial reentrant. A very shallow anterior fold marks a relic of the second labial reentrant (Fig. 1: 5).

M1. Size: about 1.95 × 1.65. Four roots. A fragmentary molar shows meta-, hypo-, para-, proto-, and a weekly developed anterocon (Fig. 1: 6). Anterocon points anterolabially. Hypoflexus and metaflexus deep and slightly curving posteriorly (retrovergent). Paraflexus shallow, close to a right angle.

M2. Size: 1.85 × 1.66, about 2.05 × 1.71. Four roots; lingual roots thicker than labial ones. Occlusal structure similar to that of M1. First labial reentrant (paraflexus) shallow and forms an acute angle. Anterocon points labially. Protocon large. Incipient second lingual flexus present.

M3. Size: 1.27 × 1.12. Three roots: two anterior and one posterior. Posterior root with signs of fusion of anterior and posterior roots. Ocllusial structure resembles a smaller version of M2 with simplified posterior part.

Hypsodonty. Observed ratio of occlusal length to crown height varies in two anterior molars from 74 to 46 (n = 7).

Notes. The original publication (Gromov & Schevtchenko, 1961) listed *Plioscirtopoda* and other jerboas within Pliocene Mimomys-Dolomys association of the Kryzhanovka section. However, later Schevtchenko (1965) refined the biostratigraphy of Kryzhanovka samples. *Plioscirtopoda* remains turned out to be associated with Early Pleistocene, Allophaiomys small mammal association (Odessa complex). In the present terminology, it corresponds to upper bed of Kryzhanovka (Topachevsky et al., 1987; Recovets & Nadachowski, 1995) and Kryzhanovka 4 (Tesakov, 1994). *P. stepanovi* was based on two molars from Kryzhanovka; the holotype, first upper molar (Gromov & Schevtchenko, 1961: Fig. 2a), and a paratype, second upper molar with absent anteroexternal reentrant fold (ibid., Fig. 2b). However, contrary to recent *Stylodipus*, M1-2 of *Plioscirtopoda* never shows complete loss of this fold. Therefore, this specimen seems to be an inverted upper molar, likely M1. When inverted, the molar shows the obtuse anteroexternal fold typical to first upper molars of *Plioscirtopoda*. Two more molars from upper bed of Kryzhanovka (M1 and M2) were added by Topachevsky (1973). Another close stratigraphic match in Odessa, Zhevakhova Gora 5, yielded three molars: m1, M1, M3 (Topachevsky, 1965, 1973). The new material from the type locality, the upper bed of Kryzhanovka (Fig. 1: 1-9), described in the present paper, makes it possible to emphasize differences between the type form and the well defined Tatkhankut population. The main difference is in the size, the teeth from the Odessa samples (both from Kryzhanovka 4 and Zhevakhova Gora 5) are noticeably larger than those of the Crimean form. However, given the small sample size these differences are not considered statistically meaningful, possibly except for the lower m2, for which the difference is significant at 10% level. For now, it may be noted that the teeth from the two samples of *P. stepanovi* from the Upper Kujalnik Allophaiomys levels of the Odessa region seem to be larger and more robust as compared to those of other known Early Pleistocene representatives of the species (Nogaisk, Tizdar, Domashkinskie Vershiny). The early Allophaiomys small mammal association of Tizdar (Tesakov, 1998; Pevzner et al., 1998) yielded three molars of *P. stepanovi* (Fig. 1: 10-12). These molars are close in dimensions to other samples of this species. Dimensions of Tizdar specimens are: 1.95 × 1.42 (m1), 1.71 × 1.32 (M1), 1.78 × 1.50 (M2). The ratio of occlusal length to crown height is rather high: 76 (m1), 117 (M1), 85 (M2). The upper M2 has four roots. The anterior portion of the lower m1 from Tizdar is rounded and lacks a distinct anteroconid.

Plioscirtopoda novorossica sp. n.

(Figs 1: 13; 2: 1-19)

Plioscirtopoda sp.: Skorik, 1983: 50-51; Topachevsky & Nesin, 1989: 33-34, fig. 9.

Holotype. Isolated lower m1, GIN EMM-31/2 (Fig. 2: 2), **Ukraine**, *Odessa Prov.*, Kryzhanovka 3.

Paratypes. Kryzhanovka 3: 5 m1, 3 m2, 2 m3, 3 M1, 4 M2, 1 M3.

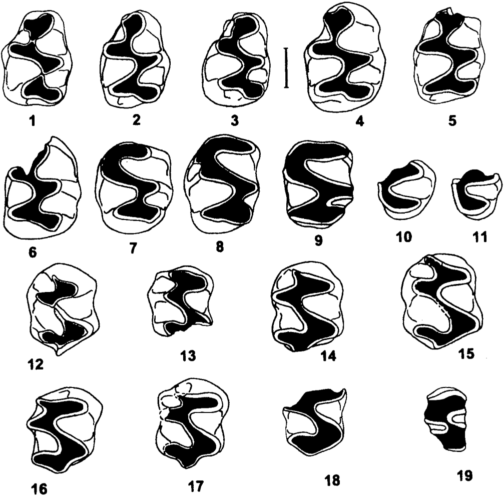

Fig. 2. Dental morphology of *Plioscirtopoda novorossica* sp. n., Kryzhanovka 3. **1-6**, m1; **7-9**, m2; **10-11**, m3; **12-15**, M1; **16-18**, M2; **19**, M3. 1-2, 4-7, 9, 13, 15, 17-19 – left; 3, 8, 10-12, 14 – right. **1-5**: EMM-31/1-5; **6-7**: EMM-32/10; **8-9**: EMM-31/6-7; **10-11**: EMM-32/17-18; **12-15**: EMM-32/12, 31/9, 31/8, 32/11; **16-19**: EMM-32/14, 32/13, 32/15-16. 3, 8, 13, 15, 17-19 inverted.

Additional material. Liventsovka 3: 1 m1.

Geological age. Late Pliocene, zone MN17a, association of *Mimomys praepliocaenicus* zone dominated by *Borsodia praehungarica.*

Diagnosis. Large *Plioscirtopoda* with relatively elongated molars. Compact anterior part of first lower molar with metaconid much larger than anteroconid and the anterior fold shifted to the labial side.

Description. Mandible. A fragmentary left mandible from the type locality preserves proximal part with m1-2 and an incomplete incisor (Fig. 3). Masseteric crests on the labial surface of the mandible meet each other below and slightly anterior to the anterior side of m1. They do not reach dorsal portion of the diastema. Mental foramen placed only slightly dorsal to the midpoint between ventral and dorsal sides of the labial face of lower jaw.

Molars. Occlusal surface flat, formed by distinctly alternating dentine cusps rimmed by narrow enamel bands. Cusps form rounded or triangular prisms with anterior and posterior enamel ridges almost perpendicular to the long axis of the dentition.

m1. Size: 2.39 × 1.56, 2.37 × 1.66, 2.2 × 1.37, 2.29 × 1.71, 2.32 × 1.61, 2.34 × 1.66. From two to four roots. Of the four specimens with preserved roots, two have two roots, one has three roots (anterior one is transversely divided into

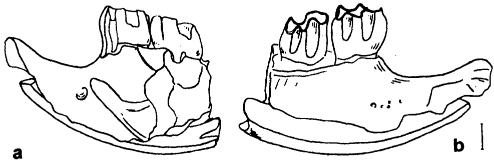

Fig. 3. Mandible of *Plioscirtopoda novorossica* sp. n., Kryzhanovka 3, GIN-EMM32/10. **a**, buccal side; **b**, lingual side.

two, the posterior root is transversely elongated), and one has four roots (two transversely placed anterior and posterior root pairs). Anterior part of m1 rounded, compact. Metaconid much larger than anteroconid. Anterior tip of metaconid more anterior in position than the anteroconid, the furrow between them shifted to the labial side of the metaconid complex. In one specimen (Fig. 2: 3), anteroconid isolated from the metaconid and represented by a low cingular cusplet. Another young specimen shows the metaconid, protoconid-entoconid, and hypoconid-hypoconulid parts still not connected by wear (Fig. 2: 1). Metaconid-protoconidandentoconid-hypoconid connections not wider than one enamel band width.

m2. Size: 2.29 × 1.76, 2.15 × 1.76, 2.15 × 1.56. Two specimens with roots preserved show four roots (one posterior transversely flattened and three anterior ones, two inner roots almost fused). Two lingual and one labial reentrants present. In one specimen, a small second labial reentrant (protoflexid) separates meta- and protoconids (Fig. 2: 8).

m3. Size: about 1.3 × 1.2. Two roots (anterior and posterior ones). Occlusal surface C-shaped, with one deep labial reentrant.

M1. Size: 2.2 × 1.85, 2.39 × 1.8, 1.95 × 1.07. Four (n = 1) to five (n = 1) roots (postero-labial root split in two). Two labial and one lingual reentrants; younger specimens have incipient third labial and second lingual reentrants. A small anterocon points anterolabially. Paraflexus (reentrant between proto- and paracone) close to obtuse angle. One young specimen has protocone-paracone and hypocon-metacon pairs still not connected by wear (Fig. 2: 12). Reentrants slightly curving posteriorly (retrovergent).

M2. Size: 1.8 × 1.32, 1.98 × 1.51, 1.93 × 1.66, ? × 1.76. Of the four specimens, three have four roots and one has five with the posterolingual root split into two. Two labial and one lingual reentrants. Posterior part in younger specimens with shallow incipient reentrants. Small anterocone points labially. Paraflexus shallow and close to an acute angle. Reentrants slightly retrovergent.

M3. Size: 1.51 × 1.22. Two anterior and one posterior roots. Molar bilobate. Anterior part formed by broadly fused protocone and paracone. Posterior part formed by fused hypo- and metacones. Anterior and posterior parts connected by very narrow dentine isthmus. Tips of para- and metaflexuses do not meet due to cusp alternation.

Hypsodonty. Ratio of occlusal length to crown height varies in two first molars of lower and upper dentitions from 84 to 55 (n = 14).

Comparison. The molars of *P. novorossica* sp. n. from Kryzhanovka 3 are larger than those of *P. stepanovi* from the type level of Kryzhanovka 4 and seems to be markedly larger than *P. stepanovi* from Tarkhankut. The difference is significant at 1% level in case of length of lower m1, and at 5% level in case of lower m2. The new species differs from *P. stepanovi* in the relatively more elongated first lower molars, more rounded and assymetric metaconid complex, and on the average higher number of molar roots.

Etymology: novorossica from the historical name of the northern coast of the Black Sea.

Notes. A form of *Plioscirtopoda* geologically older than the type (*P. stepanovi*) was known for many years on the basis of scanty material from Zhevakhova Gora, bed 11, and middle bed of Kotlovina (Skorik, 1983; Topachevsky & Nesin, 1989). Skorik was first to outline morphological differences of late Pliocene and Early Pleistocene forms. She noted larger dimensions and more elongated molars in the form from a Late Pliocene association of Zhevakhova Gora 11. But Skorik's suggestion that the Late Pliocene form has fewer roots in upper M1 than *P. stepanovi* turns out to be incorrect: both forms have specimens with bifurcated posterior external roots. The percentage of root number morphotypes cannot be assessed given the present limited material. But *P. novorossica* sp. n. seems to have a higher number of additional roots in both lower and upper molars. Broad variability of root numbers within samples and gradual decrease of root numbers between fossil and recent members of *Eremodipus* and *Paradipus* was described by Shenbrot (1986). According to personal observations, the recent *Stylodipus telum* also shows a marked variability of root numbers with almost all basic roots capable of splitting into two. A fragmentary first lower molar of *Plioscirtopoda* from the Late Pliocene fauna of Kotlovina 2 (Topachevsky & Nesin, 1989) matches *P. novorossica* in the relatively large size and assymetrical anterior complex with small labially shifted anterocon. A single lower m1 of *Plioscirtopoda* was recovered from level 3 of Liventsovka, a Late Pliocene assemblage geologically younger than Kryzhanovka 3 (coll. of V. Titov, Fig. 1: 13). The specimen shares the structure of anterior complex and molar proportions with *P. novorossica* and the small size with *P. stepanovi*. The molar is tentatively assigned to *P. novorossica*.

Discussion

Well developed alternation of cusps in lower and upper molars, differentiation of anterior and posterior parts of molars, enamel cutting edges almost perpendicular to the long axis of tooth rows, flattened occlusal surface and structure of proximal part of mandible possibly suggest "microtoid" dental specialization of propalinal jaw movement to increase efficiency of processing green vegetation. Thus, *Plioscirtopoda* seems to be a specialized steppe genus with predominantly a grass diet. Compared to the Late Pliocene *P. novorossica* sp. n., the Early Pleistocene *P. stepanovi* shows reduction in size and number of molar roots, higher differentiation of anterior part of m1, relatively wider occlusal surfaces, and somewhat higher hypsodonty.

Plioscirtopoda is known from Late Pliocene Mimomys faunas (*P. novorossica*) through diversified Allophaiomys faunas of the second part of Early Pleistocene (*P. stepanovi*) in steppe and forest-steppe faunas of Eastern Europe and Western Siberia. The known geological range of those forms extends from about 2.5 to 1.0 Ma. This time range may be even longer because *Plioscirtopoda* remains were reported from Early-Middle Pliocene Biteke fauna in Western Siberia (Zazhigin, 1980) and from latest Early Pleistocene (Tiraspol) Il'inka fauna in Eastern Europe (Krasnenkov et al., 1992).

The presently known distribution area of *Plioscirtopoda* (Fig. 4) is comparable to that of recent *Stylodipus* (though shifted to the north) and marks Late Pliocene and Early Pliocene steppe and forest steppe zone of western Palearctic. It is interesting that outside the Black Sea area all other finds are situated north of 50th parallel.

A Miocene ancestry of *Plioscirtopoda* is so far unknown. The Late Turolian *Scirtodipus* (Savinov, 1970) has plesiomorphic states for most charachters known in *Plioscirtopoda*. The two genera share the well developed cusps alternation, enamel cutting edges subnormal to long axis of dentition, flat occlusal surfaces, mesodont molars and may form an ancestor-descendant pair. The *Plioscirtopoda* lineage seems to end blindly at the end of Early Pleistocene and there are no direct descendants of this genus in the recent fauna. Among recent jerboas the closest dental match to *Plioscirtopoda* is *Stylodipus*. However, molar structure observed in *Plioscirtopoda* looks more derived in differentiation of elements of occlusal surface as compared to *Stylodipus*. Each of the three recent species of *Stylodipus* (Sokolov & Shenbrot, 1987) shares some characters with *Plioscirtopoda*: *S. andrewsi* shows reduction of the antero-labial reentrant (protoflexid) of lower m2; *S. sungorus* has a deep postero-lingual flexid and relics of anteroconid fused with metaconid of m1; all three species, including *S. telum*, have developed cusp alternation, etc. However, *Stylodipus* is more hypsodont, has more fused and less pointed cusps, more shallow reentrants, and less flattened occlusal surface than *Plioscirtopoda*. This suggests that the two genera do not represent a direct phyletic succession and might share a common ancestor (like *Scirtodipus*) not later than early Pliocene. Most other recent tridactyl jerboas have more or less opposite cusps in dentitions with cuspate occlusal surfaces likely as an adaptation to mixed grain and grass diets. One exception, a specialized desert grass-eating *Paradipus*, is the most hypsodont modern form with flattened occlusal surfaces. However, this form developed a very different sygmoid dental pattern (Shenbrot, 1986).

According to a cladistic analysis of dental characters in dipodines done by Shenbrot (1992), several genera of tridactyl dipodines form a natural group of closely related forms. According to Shenbrot, they sequentially ramify from the common ancestral stalk in the fol-

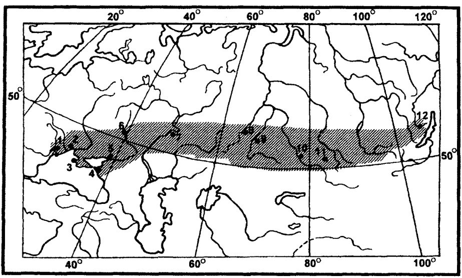

Fig. 4. Geographic distribution of known *Plioscirtopoda* localities. **1**, Kotlovina 2 (Topachevsky & Nesin, 1989); **2**, Odessa region localities: Kryzhanovka, Zhevakhova Gora, Tiligul, Luzanovka, etc. (Topachevsky, 1973; Topachevsky et al., 1979; Skorik, 1983; Recovets & Nadachowski, 1995); **3**, Tarkhankut (Topachevsky, 1973); **4**, Tizdar (Pevzner et al., 1998); **5**, Liventsovka 3; **6**, Middle Don localities: Korotoyak (Ostrogozhskaya Suite), Il'inka IV (Kazantseva, 1990; Krasnenkov et al., 1992); **7**, Domashkinskie Vershiny (Sukhov, 1977); **8**, Zverinogolovskoe (Ivakina et al., 1996); **9**, Biteke (Zazhigin, 1980); **10**, Podpusk (reported as 'Dipodinae gen.', Zazhigin, 1980); **11**, Ob' Steppe Plateau area: Kizikha, Razdolie, Makhanovo (Zazhigin, 1980); **12**, Malye Goly 3, Nikeley (Adamenko, 1975, 1977).

lowing order: *Dipus*, *Stylodipus*, *Eremodipus*, *Jaculus*. If valid, this scheme likely leaves a place for *Plioscirtopoda* to branch off between *Dipus* and *Stylodipus*.

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