Evolution and Taxonomy of the Pleistocene North Asian Zokors, Genus *Siphneus* (Myospalacidae, Rodentia, Mammalia)

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Abstract—According to the concept proposed by the authors of dividing modern rootless zokors and their ancestral Pleistocene rootless forms into the genera *Myospalax*, *Siphneus*, and *Eospalax*, Manchurian and Daurian zokors were assigned to the genus *Siphneus*. In this paper details of the morphological differences of the genus *Siphneus* and analysis of the evolutionary lineages among the genus are presented. A new phylogenetic scheme is proposed, in which a new species *S. tolaensis* sp. nov. ancestral to the Daurian zokors is described on the basis of remains from the Nalaikha locality (Mongolia, late Early−early Middle Pleistocene).

INTRODUCTION

During the last century, zokors have become the center of various discussions, and views on their evolution and taxonomy have been constantly changed and revised (Wilson and Reeder, 2005). The problematics of this group of Asian subterranean rodents began with the determination of their place in the order Rodentia Bowdich, 1821. The four most common hypotheses can be distinguished in this question: (1) determination of zokors within the independent family Myospalacidae Lilljeborg, 1866 (Reig, 1980) or Siphneidae (Zheng, 1994); (2) zokors as a subfamily Myospalacinae within the family Cricetidae Fischer, 1817 (Gromov and Erbajeva, 1995; Liu et al., 2014); (3) zokors as a subfamily Myospalacinae within the family Muridae Illiger, 1811 (Wilson and Reeder, 2005); and (4) zokors as a subfamily Myospalacinae within the family Spalacidae Gray, 1821 (Ognev, 1947; Norris et al., 2004). The identification of zokors as a subfamily within the Spalacidae family relies on the results of modern molecular studies (Norris et al., 2004; Liu et al., 2022). However, paleontological and morphofunctional data have been interpreted as evidence of a significant divergence between blind mole-rats and zokors (Wilson and Reeder, 2005; Tarasov et al., 2011; de Bruijn et al., 2023). Notably, molecular data also show a rather ancient divergence between these two groups (Liu et al., 2022). Therefore, we considered zokors within the independent family Myospalacidae.

The problematics of zokors are not limited to their taxonomic relationships with other groups of rodents.

The division of genera and species within Myospalacidae is also debatable. The first classifications divided zokors into two genera: the ancestral rooted *Prosiphneus* Teilhard de Chardin, 1926, and the descendant rootless *Siphneus* Brants, 1827—synonym *Myospalax* Laxmann, 1769 (Teilhard de Chardin and Young, 1931; Young, 1934; Pei, 1936; Teilhard de Chardin, 1940). Over time, this classification has become more complex with the distinguishing of genera such as *Mesosiphneus* Kretzoi, 1961, *Episiphneus* Kretzoi, 1961, *Allosiphneus* Kretzoi, 1961, *Yangia* Zheng, 1997, and *Eospalax* Allen, 1938 (Kretzoi, 1961; Zheng, 1994). To date, there is no consensus among researchers on the validity and species composition of particular genera. In a recent study, the authors proposed a scheme according to which modern zokors and their rootless ancestral forms can be divided into three genera: *Myospalax*, *Siphneus*, and *Eospalax* (Golovanov and Zazhigin, 2023). The basis for this division was the differences in the ontogenetic development of molars between the West Siberian lineage and all other species. However, the differences between North Asian zokors of the genus *Siphneus* and Chinese zokors of the genus *Eospalax* remain unclear.

The North Asian zokors include Manchurian and Daurian zokors, whose modern populations are distributed in the territories of Transbaikalia, Northeast Mongolia, the Far East, and Northern China (Fig. 1). These groups were originally defined as two species: *Siphneus aspalax* Pallas, 1776 (Daurian zokors) and *S. psilurus* Milne-Edwards, 1874 (Manchurian zokors)
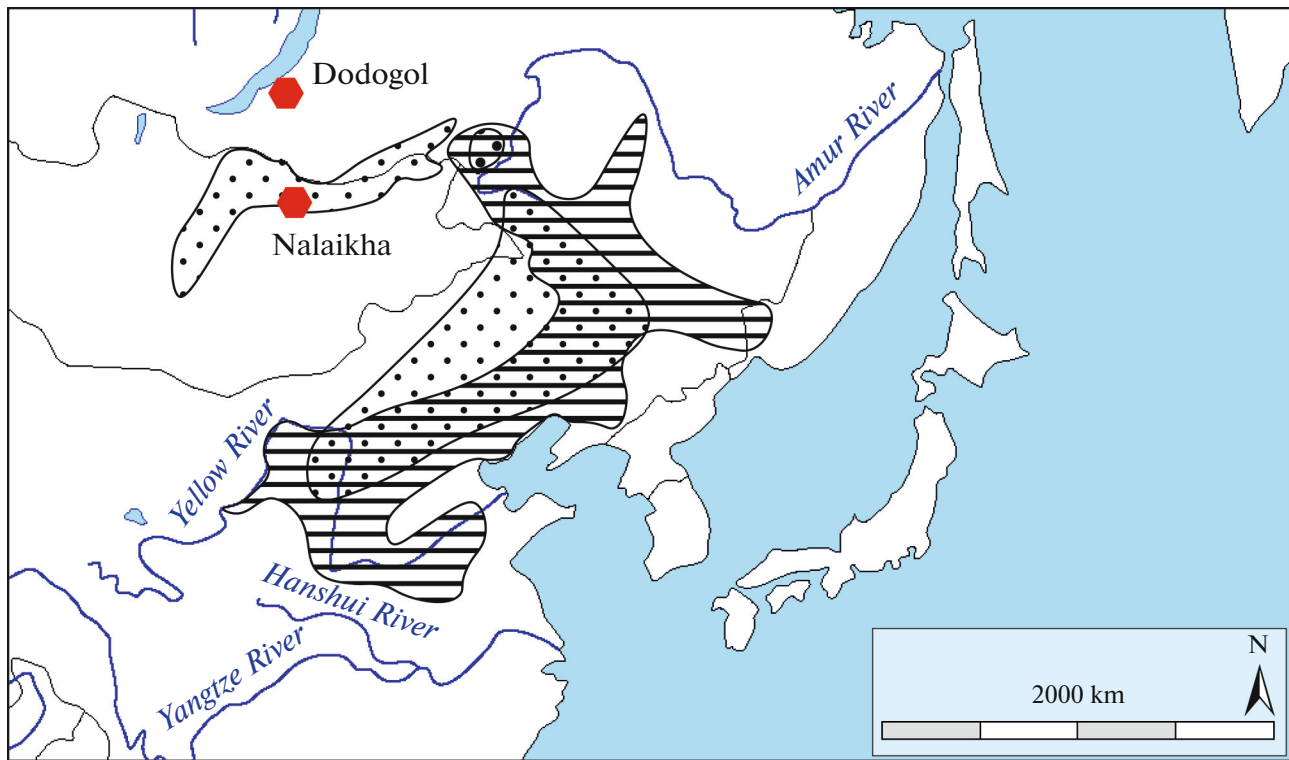
Fig. 1. Modern ranges of Manchurian (horizontal lines) and Daurian (dots) zokors (from Sokolov and Orlov, 1980; Puzachenko et al., 2013; Bazhenov and Pavlenko, 2020). Red hexagons indicate the Nalaikha and Dodogol localities.

(Ognev, 1947; Gromov and Erbajeva, 1995). In recent decades, molecular studies have shown the separation of Daurian zokors into the species *S. aspalax* and *S. armandii* Milne-Edwards, 1867, and Manchurian zokors into *S. psilurus* and *S. epsilanus* Thomas, 1912 (Puzachenko et al., 2009, 2013; Pavlenko et al., 2014). This view, however, has not been entirely accepted (Liu et al., 2022; Zhang et al., 2022). The determination of ancestral species for Daurian zokors is also problematic. The phylogenetic schemes of different authors may vary depending on whether they recognize *Prosiphneus pseudarmandi* Teilhard de Chardin, 1940 and *Siphneus wongi* Young, 1934 as intermediate forms between *P. youngi* and Daurian zokors (Teilhard de Chardin, 1940; Kretzoi, 1961; Vangengeim et al., 1966; Alexeeva and Erbajeva, 2008; Pokatilov, 2012; Erbajeva et al., 2021; Qin et al., 2021).

In the current paper, we tried to address two of the abovementioned problems: (1) detailed morphological characterization of the genus *Siphneus* and (2) revision of the evolution of Daurian zokors. In this study, we included zoological and paleontological collections collected from the territories of Russia, Mongolia, and China. The objects of our study were molars, as these teeth reflect evolutionary changes in zokor lineages (Teilhard de Chardin, 1940; Zheng, 1994). Additionally, molars are the most frequently found

remains in localities, while finds of whole skulls are rather rare.

MATERIALS AND METHODS

The studied fossil specimens (isolated molars and one skull) were stored at the Geological Institute (GIN) of the Russian Academy of Sciences under the numbers 1104/100−115 and 624/25−31. Specimens nos. 1104/100−115 were collected from the Nalaikha locality (Northern Mongolia). The locality belongs to the middle of the second unit of the Nalaikha section located on the left bank of the Tola River near the Nalaikha settlement upstream from Ulaanbaatar and was proposed as a key section for the Lower Pleistocene of Mongolia (Zhegallo et al., 1982; Devyatkin et al., 1989). The Nalaikha locality has been dated within a wide stratigraphic range from the late Early Pleistocene to the second half of the Middle Pleistocene (Zhegallo et al., 1982; Devyatkin et al., 1989). At the same time, it has been suggested that this locality can be dated within the late Early Pleistocene (Eisenmann and Kuznetsova, 2004). Samples nos. 624/25−31 originate from the Dodogol locality, which in some publications appears as Dodogol-3 or Dodogol-4 (Vangengeim et al., 1966; Alexeeva, 2006; Alexeeva and Erbajeva, 2008). The Dodogol locality is located in the Republic of Buryatia on the right bank of the

Uda River 0.7−1 km below the Dodogol ulus (in some variants Dodo-Gol) and is dated within the first half of the Middle Pleistocene (Vangengeim et al., 1966).

The studied collections of the extant zokor populations are stored in the Zoological Museum of the Lomonosov Moscow State University (ZMMU) and the Zoological Institute of the Russian Academy of Sciences (ZIN RAS, St. Petersburg). For comparison, we used photographs of collections from the former Institute of Biology and Soil Sciences of the Far Eastern Branch of the Russian Academy of Sciences (reorganized into the Federal Scientific Center of Terrestrial Biodiversity of East Asia, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok) and the Institute of Zoology of the Chinese Academy of Sciences (IOZ CAS, Beijing), which were provided to the authors by A.Yu. Puzachenko (Institute of Geography, Russian Academy of Sciences). In total, the samples of extant zokors from the genus *Siphneus* included 130 skulls with upper and lower jaw rows. Samples of the genera *Myospalax* and *Eospalax* were used for comparison.

In the description of zokor molars, we used the terminology (Fig. 2) presented in modern papers (Liu et al., 2014; Qin et al., 2021). Photographs of the paleontological material were obtained with a Leica DMC6200 microscope. Measurements of the material were made using the programs tpsUtil ver.1.82 and tpsDig2 ver.2.32 (Rohlf, 2015). The skull from the Dodogol locality was studied by computed tomography at the Paleontological Institute of the Russian Academy of Sciences (PIN RAS, Moscow) using a Neoscan N80 X-ray micro-CT scanner with the following parameters: 84 kV, filter—Cu 0.1 mm. The scanning data were processed in the NeoScan program version 3.0.2. The resulting image resolution was 20.5 μm per pixel, with a total resolution of 2704 × 1520 pixels per slice. Images of the tomography results were prepared in the CTvox program version 3.3.

TAXONOMY

Order Rodentia

Family Myospalacidae Lilljeborg, 1866

Genus Siphneus Brants, 1827

Mus: Pallas, 1778, p. 165 (part.).
Siphneus: Brants, 1827 p. 19.
Myospalax: Ognev, 1947, p. 664; Zheng, 1994, p. 57; Gromov and Erbajeva, 1995, p. 378.

T y p e   s p e c i e s. *Mus aspalax* Pallas, 1778, was described from specimens of extant populations from Dauria between the Ingoda and Argun Rivers.

D i a g n o s i s. During the ontogenetic development of molars, there is no stage at which roots are formed. The first upper molars have one to two reentrant angles on the lingual side (Fig. 3). In the case of two reentrant angles, there is no dentin tract on the lingual-anterior side of M1. The upper third molars
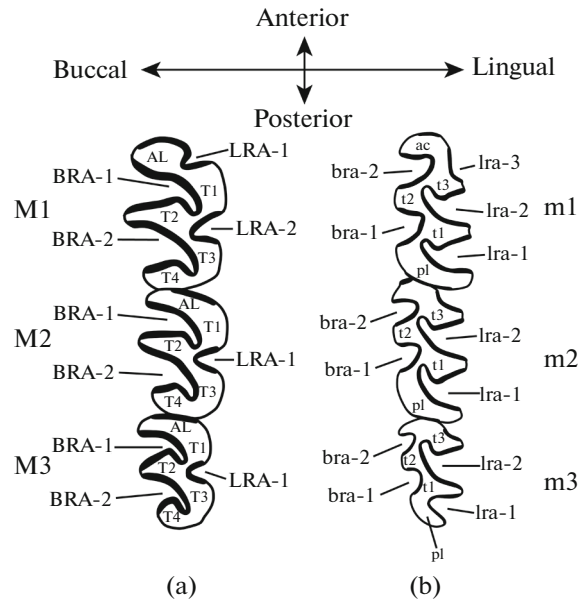

Fig. 2. Terminology of the dental structures of the upper (a) and lower (b) zokor molars. Designations: BRA/bra—buccal reentrant angles; LRA/lra—lingual reentrant angles; T/t—triangles; AL—anterior triangle of the upper molarsa; ac—anterior part of the first lower molar; pl—posterior triangle of the lower molars.

have only one reentrant angle on the lingual side. In M3, the posterior triangle (T4) is either less developed than the anterior triangle and the T2 triangle, or it is completely reduced and fused with T3. In those cases where T4 is not reduced, the triangle has an oval shape. The posterior triangle of the lower third molars was partially or completely reduced. Reentrant angles on the lingual side of m3 are poorly developed or completely absent (Fig. 3).

S p e c i e s   c o m p o s i t i o n. Genus includes four to six species relative to the molecular data interpretation: *S. aspalax* (modern species), *S. psilurus* (modern species), *S. armandii* (modern species, distinguished by molecular data), *S. epsilanus* (modern species, distinguished by molecular data), *S. prosilurus* (late Early Pleistocene), and *S. tolaensis* sp. nov. (late Early Pleistocene—early Middle Pleistocene).

C o m p a r i s o n. The genus *Siphneus* is distinguished from the genus *Prosiphneus* by the absence of the developmental stage of root formation in molar ontogeny. It differs from the genus *Myospalax* by the simplified ontogenesis of upper and two lower (m2—m3) molars, which is expressed in the absence of full formation and wear of enamel tubes at early stages of ontogenesis. *Siphneus* differs from the genera *Eospalax* and *Yangia* by the absence of a dentin tract on the lingual-anterior side of M1. Some species of the genus *Siphneus* also differ from other genera by the absence or underdevelopment of protoflexus (LRA-1) at M1 and by the form and degree of reduction of posterior triangles of the lower and upper third molars.
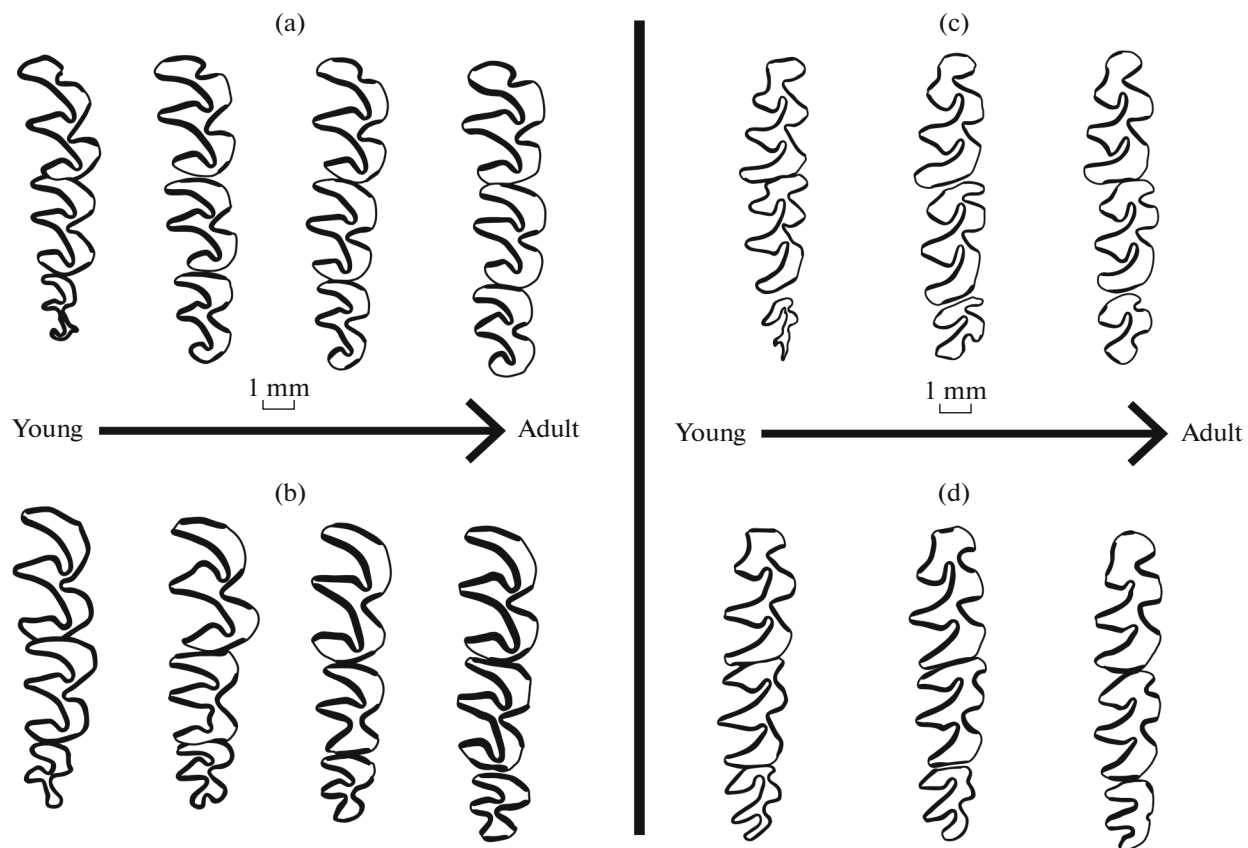
Fig. 3. Ontogenetic development of the molars of Daurian and Manchurian zokors: (a) development of upper molars of Manchurian zokors, (b) Daurian; (c) development of lower molars of Manchurian zokors, (d) Daurian.

Remarks. There are several concepts about the division of rooted zokors into different genera (Kretzoi, 1961; Zheng, 1994; Pokatilov, 2012; Liu et al., 2014; Li and Wang, 2015). Because the molars of rooted zokors significantly change during ontogeny, detailed ontogenetic schemes are needed to determine species and genus differences. A comparison of such schemes will reveal the main evolutionary trends in different lineages, which, in our opinion, should be the basis for the designation of taxa of genus rank. Currently, ontogenetic schemes are available only for a small number of species within the family Myospalacidae, so we refer all rooted zokors to one genus, *Prosiphneus*.

Siphneus tolaensis **Golovanov et Zazhigin, sp. nov.**

E t y m o l o g y. The name is derived from the Tola River, on the banks of which the Nalaikha locality is located.

H o l o t y p e. GIN, no. 1104/107; left lower m2 (Figs. 4a–4d); Mongolia, Nalaikha locality, left bank of the Tola River near the Nalaikha settlement upstream from Ulaanbaatar; late Early Pleistocene-early Middle Pleistocene, middle of the second unit of the Nalaikha section.

D e s c r i p t i o n (Figs. 4, 5). Zokors with continually growing molars (euhypsodont type), whose ontogeny includes a stage of closure of the buccal (mandibular row) or lingual (maxillary row) reentrant angles. This stage is only observed in adult specimens and is characterized by the beginning of the formation of enamel tubes in the basal part of the molars. In juvenile specimens, all reentrant angles of the molars are completely open, and a single enamel contour is present on the chewing surface (Fig. 5). The enamel contour is divided by dentin tracts at later stages of ontogenesis (together with the beginning of the formation of enamel tubes). The molar sizes are given in Table 1. The enamel thickness ranged from 0.04 to 0.12 mm.

In the structure of the lingual side of the second upper molar, there is one developed reentrant angle (LRA1) that is inclined toward the buccal side with a slight curvature toward the posterior part of the tooth. This angle closes at the basal part of the molar and forms an enamel tube. On the buccal side, there are two developed reentrant angles (BRA-1, BRA-2) oriented toward the opposite (lingual) side of the tooth with a slight curvature toward the posterior part of the molar. The dentin fields of triangles T1, T2, T3, and T4 are partially isolated from each other. The dentin
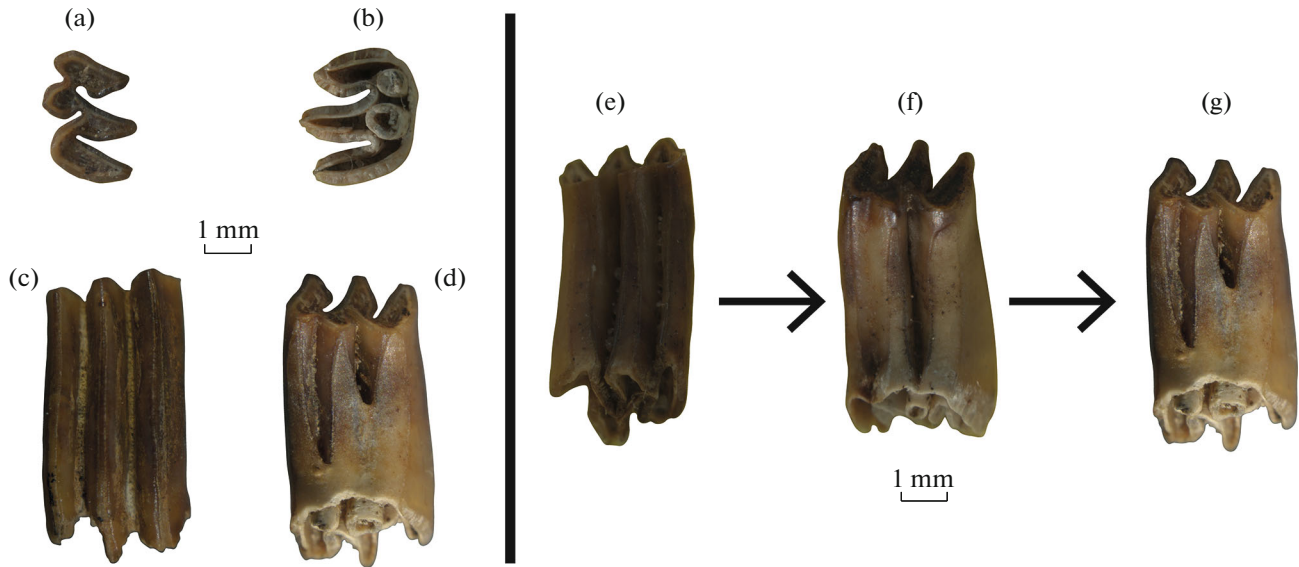
Fig. 4. *Siphneus tolaensis* sp. nov.: (a–d) holotype GIN, no. 1104/107, left m2: (a) chewing surface; (b) alveolar side of the molar; (c) lingual side of the molar; (d) buccal side of the molar; (e–g) series of ontogenetic stages on the buccal side of m2 GIN, no. 1104/105, 107, 109.
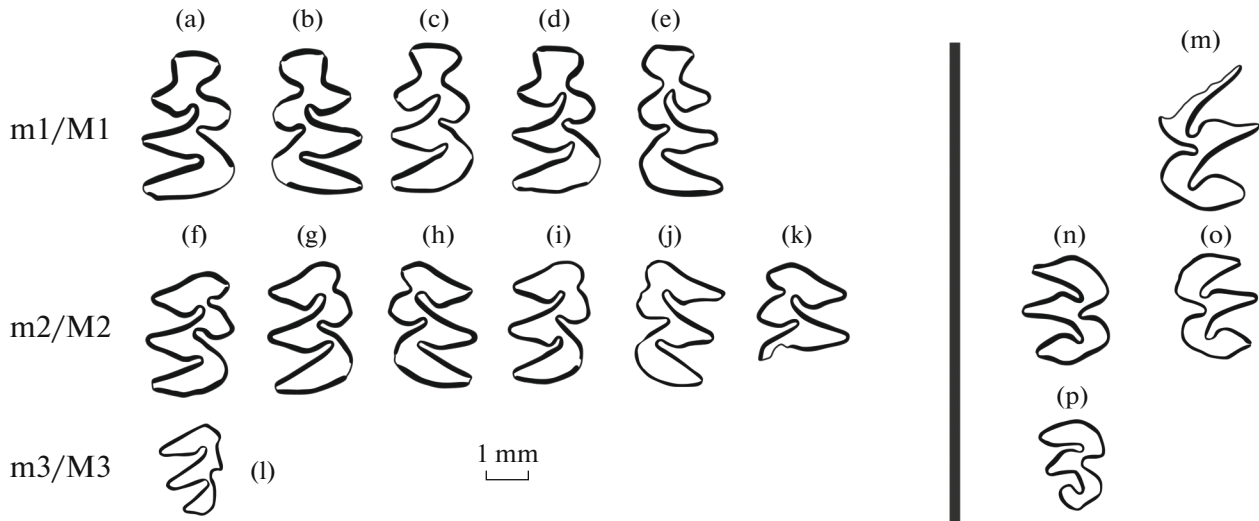

Fig. 5. *Siphneus tolaensis* sp. nov., GIN, nos. 1104/100–115, chewing surface. Lower molars (m1, m2 and m3) are shown on the left, and upper molars (M1, M2 and M3) are shown on the right. The sequence of numbering of the specimens is the same as the sequence of their designations in the figure: (a) no. 1104/100, (b) no. 1104/101... (p) no. 1104/115.

fields of the anterior triangle and T1 are fused together. T4 is rhomboidal in shape, with the anterior and posterior sides being convex. The anterior triangle and T2 had a concave posterior side and a convex anterior side.

On the lingual side of M3, there is one developed reentrant angle (LRA1). LRA1 is inclined toward the buccal side with a slight curvature toward the anterior part of the tooth. On the buccal side, there are two developed reentrant angles (BRA-1, BRA-2) oriented toward the opposite (lingual) side of the tooth. BRA-2

has a strong inclination toward the posterior side of the molar. The dentin fields of triangles T4 and T3 are partially fused, in contrast to the dentin fields of triangles T1, T2, and T3, which are isolated from each other to a greater degree. The dentin fields of the anterior triangle and T1 are completely fused together. Triangle T4 is well formed and rhomboidal in shape.

The first lower molar has three reentrant angles (lra-1, lra-2, lra-3) on the lingual side; lra-1 and lra-2 are well developed and oriented toward the opposite (buccal) side of the tooth with a slight curvature

Table 1. Molar size of *S. tolaensis* sp. nov.: N—number of specimens, min—minimum size, mean—average size, max—maximum size, s.d.—standard deviation

	Length, mm				Width, mm			
	N	min	mean	max	s.d.	min	mean	max	s.d.
M2	2	2.51	2.51	2.51		1.88	1.94	2.00	
M3	1	2.11	2.11	2.11		1.47	1.47	1.47	
m1	5	3.3	3.374	3.52	0.085	1.84	1.998	2.17	0.127
m2	5	2.85	2.944	3.03	0.066	1.75	1.846	1.91	0.059
m3	1	2.11	2.11	2.11		1.44	1.44	1.44	

toward the anteroconid side. At the same time, lra-2 is more bent toward the anteroconid than is lra-1; lra-3 is poorly developed and has the form of an open angle with orientation to the buccal-posterior side of the molar. On the buccal side are two reentrant angles (bra-1 and bra-2), which are less developed than those of the opposing lra-1 and lra-2. In turn, bra-1 is more developed than bra-2 and is oriented on the lingual side of the tooth with a slight curvature toward the anteroconid; bra-2 is oriented on the lingual side of the tooth without a significant curvature to one side or the other. At the adult stage, the buccal reentrant angles tend to close; as a consequence, an enamel tube is formed in the basal part of the molar. Because of this shape and orientation of the reentrant angles, the triangles pl and t1 are convex on the posterior side and concave (t1) or sublinear (pl) on the anterior side. The anterior side of the m1 anteroconid has a sublinear, slightly curved shape, and the anteroconid itself has a triangular shape. The dentin field of the anteroconid is widely fused with the dentin field of t3. There are high dentin tracts along the edges of the reentrant angles, forming gaps in the enamel contour on the chuwing surface.

In the structure of m2, two reentrant angles (lra-1, lra-2, bra-1, and bra-2) are present on the lingual and buccal sides of the molar. These reentrant angles have similar morphological characteristics to those on the lower m1. In adult specimens, bra-1 and bra-2 close at the basal part, forming two enamel tubes. Triangles pl, t1, and t3 are convex posteriorly and concave (t1 and t3) or sublinear (pl) anteriorly. The dentin fields of triangles pl, t1, t2 and t3 are partially isolated from each other. The dentin fields of the anterior triangle and t3 are fused together.

On m3, on the lingual side, there are two developed reentrant angles (lra-1, lra-2), which are oriented toward the lingual anterior part of the molar; lra-2 is more developed than lra-1. On the buccal side, there are two reduced reentrant angles (bra-1, bra-2); bra-1 is poorly expressed on the chewing surface and is almost absent in the basal part of the molar. bra-2 is expressed only in the form of a slight curvature of the contour. The posterior triangle is reduced in size compared to triangles t1 and t3. However, it is still well formed and has a triangular shape. The dentin field of the posterior triangle is isolated from the dentin field of t1.

M e a s u r e m e n t s. Table 1.

C o m p a r i s o n. The key diagnostic feature of *S. tolaensis* sp. nov. is the presence of completely open reentrant angles at early ontogenetic stages, which may partially close in the basal part of molars and form enamel tubes in older specimens. At the same time, the lingual angles on the mandibular row and the buccal angles on the maxillary row remain open. In all extant species of the genus *Siphneus,* the reentrant angles remain open throughout the whole ontogeny. Additionally, *S. tolaensis* sp. nov. differs from the zokors of the morphological group *aspalax—armandii*, *S. prosilurus* and *S. psilurus* in terms of the shape of the buccal reentrant angles on m2. In *S. tolaensis* sp. nov. bra-1 of m2 is more developed than bra-2, has an elongated form and is similar in shape to the reentrant angles on the lingual side. In other species of the genus *Siphneus,* bra-1 is almost identical in shape to bra-2; both reentrant angles are wide open and not elongated. Similar differences between *S. tolaensis* sp. nov. and other species of the genus *Siphneus* are characteristic for buccal reentrant angles on m1, although in this case, it is expressed less than on m2.

R e m a r k s. The only studied first upper molar of *S. tolaensis* sp. nov. is poorly preserved, which makes it impossible to characterize structure of the M1 for this species.

M a t e r i a l. Specimens from the type locality: GIN, no. 1104/100−115; upper molars: 1 M1 (anterior part of tooth is missing), 2 M2 and 1 M3; lower molars: 5 m1, 6 m2 and 1 m3.

MOLARS SHAPE VARIABILITY OF MANCHURIAN AND DAURIAN ZOKORS

The first division of the genus *Siphneus* into morphological groups can be made by the presence of one (Daurian zokors) or two (Manchurian zokors) reentrant angles on the lingual side of the upper M1 (Fig. 3). Several M1 morphotypes can be recognized in the Daurian zokors (Fig. 6): M1 with complete reduction of the protoflexus (morphotype I), with

partially reduced protoflexus without enamel (morphotype II) and with partially reduced protoflexus with enamel (morphotype III). The last morphotype is represented in single specimens and can be considered an anomaly. In addition to the upper M1 morphology, Manchurian and Daurian zokors are also separated by M3 and m3 morphology.

In the Daurian zokor group, the posterior triangle (T4) of M3 was reduced and completely fused with T3. The buccal and lingual reentrant angles are either poorly developed or are oriented perpendicular to the molar length axis without a strong bend toward the posterior side of the tooth. In the Manchurian zokor group, the posterior triangle was reduced compared to the anterior triangle and T2, but it was highly expressed, and the dentin field was only partially fused with the T3 field. The buccal reentrant angles are well developed and are oriented perpendicular to the molar length axis with a strong bend toward the posterior side of the tooth. In single cases, the second reentrant angle is poorly developed, causing the posterior triangle to fuse with T3.

The lower third molars in both groups had high shape variability. In the Daurian zokor group, there are morphotypes with developed or reduced posterior triangles. The number and depth of reentrant angles also vary due to the reduction in the first reentrant angle in some morphotypes. The buccal angles are almost not visible and are marked only by the enamel or are completely absent. In contrast, in the Manchurian zokor group, the buccal angles always developed to some degree. The posterior triangle, as in the Daurian group, can be distinct in some morphotypes and completely reduced in others. Due to the configuration of reentrant angles and triangles, dentin fields in the Daurian group were fused to a greater extent than those in the Manchurian group.

Among the extinct species considered ancestral to Daurian and Manchurian zokors, *Siphneus wongi* and *S. prosilurus* should be noted (Young, 1934; Pei, 1936; Vangengeim et al., 1966; Alexeeva, 2006; Alexeeva and Erbajeva, 2008; Qin et al., 2021). *S. prosilurus* has been described as an ancestral species of Manchurian zokors and is characterized by a smaller size than *S. psilurus* (Qin et al., 2021). A more disputable species is *S. wongi*, presumably the ancestral species for Daurian zokors. Some doubts have been raised about the validity of this species (Vangengeim et al., 1966). A smaller reduction in the posterior triangles on the lower and upper third molars was defined as a diagnostic trait for this species (Young, 1934; Pei, 1936). Our study indicated that morphotypes falling under these criteria are also found in modern populations of Daurian zokors.

The morphology of the new species *S. tolaensis* sp. nov. from the Nalaikha locality is highly different from that of all other species of the genus *Siphneus*. The closest species to *S. tolaensis* in terms of molar shape is
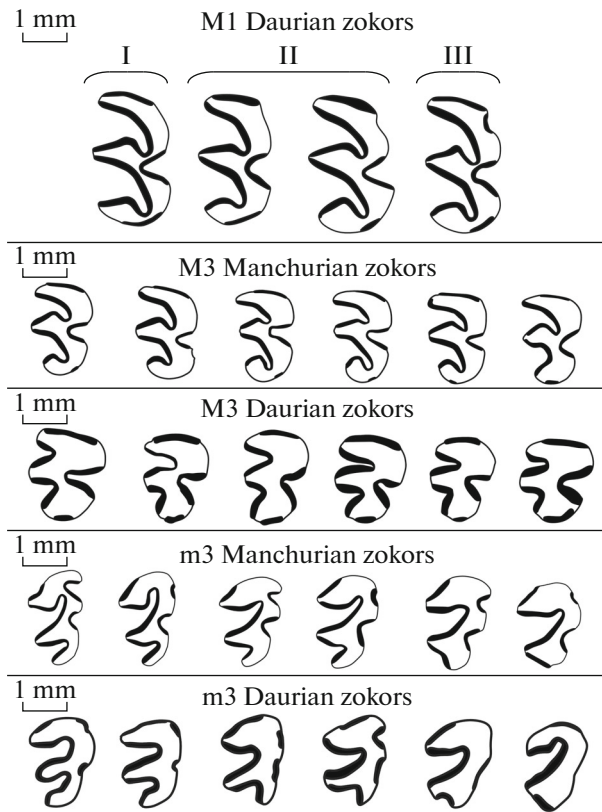

Fig. 6. Morphotypic variability of molars in the Daurian and Manchurian zokor groups. The M1 morphotypes of Daurian zokors are designated as follows: I—M1—with complete reduction of protoflexus, II—M1—with partially reduced protoflexus without enamel, and II—M1—with partially reduced protoflexus with enamel.

the rooted species *Prosiphneus pseudarmandi*. This Early Pleistocene species with root formation at late ontogenetic stages was described as ancestral to Daurian zokors (Teilhard de Chardin, 1940). From the species of *P. pseudarmandi* zokors from Nalaikha maintain the shape of the chewing surface and tendency to form enamel tubes (in the adult stage). In *P. pseudarmandi* molars, enamel tubes are formed early in ontogeny. CT scans of the skull from the Dodogol locality revealed no evidence of enamel tube formation or closure of the reentrant lingual angles on the maxillary row (Fig. 7). The morphology of molars from the Dodogol locality generally corresponds to certain morphotypes of modern Daurian zokors.

DISCUSSION

The molars of Daurian and Manchurian zokors have a number of traits that distinguish them from West Siberian (*Myospalax* genus) and Central Chinese (*Eospalax* genus) zokors. Daurian and Manchurian zokors differ from the West Siberian group in terms of the morphology of all molar teeth (Golovanov and
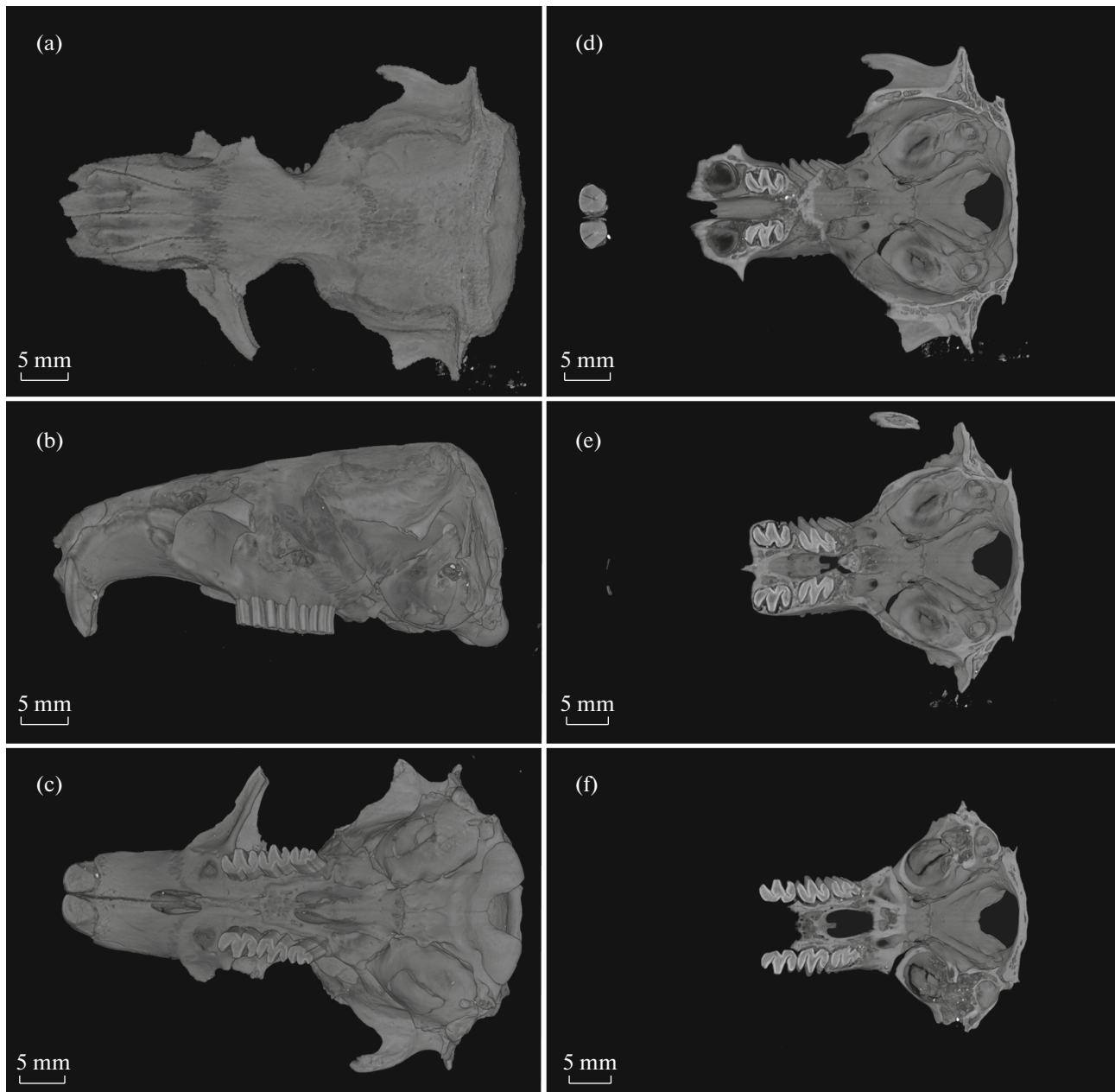
Fig. 7. *Siphneus aspalax* Pallas, 1776, GIN, no. 624/31, skull with right and left M1-3, computed tomography: (a) dorsal side, (b) left lateral side, (c) ventral side, (d–f) series of sections in axial projection showing basal part of upper molars; Russia, Buryatia, Dodogol locality; first half of the Middle Pleistocene.

Zazhigin, 2023). They also differ from species of the genus *Eospalax* in terms of M1 (absence of the dentin tract on the anterior side) and M3/m3 (reduction of posterior triangles) molars. We believe that such differences allow us to separate the Daurian and Manchurian groups into a separate genus, *Siphneus*, which we previously proposed (Golovanov and Zazhigin, 2023).

The number of species within the genus *Siphneus* may vary depending on different interpretations of molecular data (Puzachenko et al., 2009; Puzachenko et al., 2013; Pavlenko et al., 2014; Liu et al., 2022).

Based on the molar morphology, we can confidently distinguish Daurian and Manchurian zokors from each other by M1 and M3/m3. At the same time, these morphological groups have high morphotypic variability. It is necessary to note a certain geographical pattern in the distribution of morphotypes. In western populations of Daurian zokors, morphotype II of M1 was less frequent than in eastern populations. Manchurian zokors are characterized by a predominance of lower m3 morphotypes with a developed posterior triangle in the northwestern populations and a pre-

dominance of morphotypes with a reduced posterior triangle in the southeastern populations. However, it is still difficult to determine to what extent this variability corresponds to the difference between commonly distinguished species (*S. aspalax* and *S. psilurus*) and species recently separated from them (*S. armandii* and *S. epsilanus*).

The described morphological variability of the Daurian group includes traits on the basis of which the Middle Pleistocene species *S. wongi* was distinguished. Thus, it seems misleading to assign a species rank to this taxon. Rather, we should refer here to a chronological subspecies that can be identified in large samples using various morphometric methods. Until such studies appear, it is reasonable to exclude this taxon from phylogenetic schemes. In addition, computed tomography of the skull from the Dodogol locality revealed that all the traits characteristic of Daurian zokors already developed in the Middle Pleistocene.

The possible ancestral species for the Daurian group is *Siphneus tolaensis* sp. nov., the appearance of which must have occurred at the boundary of the Early and Middle Pleistocene. This species, described on the basis of remains from the Nalaikha locality, is an intermediate form between *Prosiphneus pseudarmandi* and Daurian zokors. The molars of *S. tolaensis* sp. nov. are missing roots but still tend to have enamel tubes. It can be suggested that zokors from the Nalaikha locality represent the final transition from hypsodont to euhypsodont molars in the corresponding lineage. The stratigraphic distribution of *S. tolaensis* sp. nov. was relatively short since Daurian zokors with modern molar structures appeared in the first half of the Middle Pleistocene.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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