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Morphotypic Variability in the Dentition of *Stenocranius gregalis* Pallas (Rodentia, Mammalia) from the Pleistocene of Denisova Cave

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Abstract—The morphological variability of *Stenocranius gregalis* Pallas from the Paleolithic site Denisova Cave (Altai) is examined. The variability of the unpaired anterior loop of M_1 is discussed. Seven morphological types are distinguished. Based on the morphometric analysis, the beds of the Denisova Cave are dated as the Upper Pleistocene.

INTRODUCTION

The material under study was collected in the Solonshenskii District of the Altai Region in the valley of the Anui River at the Paleolithic site of Denisova Cave in 1995 and 1996. The first data from Denisova Cave were obtained in the 19th century (Derevyanko and Molodin, 1994). In 1977, the cave was shown to be an archeological site. Since the early 1980s, researchers of the Institute of Archeology and Ethnography of the Siberian Division of the Russian Academy of Sciences (Novosibirsk) have performed annual excavations in this locality.

The cave is located 630 m a.s.l. and 29 m above the level of the Anui River, on the right bank. It is a karst cavity in Silurian limestone. Until 1999, excavations were performed in the central part of the cave. In 1996, the excavations occupied of 9 m²; the exposed Pleistocene deposits were 6.05 m thick.

The species composition of small mammals in the Pleistocene beds exposed in Denisova Cave (beds 22.3–9.1) varies only slightly within the section. This provides evidence for a relatively continuous succession of small mammals in the valley of the Anui River, and the absence of long gaps in sedimentation.

Among fossil small mammals, the following species are absent in the Recent Altai Fauna: Eversmann's hamster (*Allocricetus eversmanni* Brandt), the gray lemming (*Lemmus*), and beaver (*Castor*). Typical members of the steppe communities, such as marmots (*Marmota*), mole voles (*Ellobius*), and steppe lemmings (*Lagurus lagurus* Pallas), are present. Inhabitants of high-mountain steppes, such as the narrow-skulled vole (*Stenocranius gregalis* Pallas) and the Asiatic high-mountain vole (*Alticola strelzovi* Kastchenko) are abundant. In the list of Recent species, members of forest assemblages, such as redbacked voles (*Clethrionomys*) and field mice (*Apodemus*), prevail in the area near Denisova Cave.

Morphological dental features of the narrow-skulled vole from the Pleistocene beds of Denisova Cave were examined on the basis of the first lower molars (M_1). Only complete teeth were measured. The proportions of certain morphotypes were estimated using isolated paraconids as well. The length and width of each tooth were measured with the aid of a binocular microscope MBS-9 at 8× and 16× magnification. Comparisons with Recent species were performed using material housed at the Mammal Laboratory of the Paleontological Institute of the Russian Academy of Sciences (PIN) and the Zoological Museum of Moscow State University (MSU).

In the layers characterized by clear bedding and abundant material, the main morphological types of M_1 were distinguished and the morphotype proportions were estimated in each temporal population of the species examined. The fossil material was analyzed in three temporal sections, top, middle, and bottom of the Pleistocene strata of Denisova Cave, including the following beds:

- (a) beds 9.1–11.1 from the upper part of the section;
- (b) bed 22.1, layers 0, 1, and 2, from the middle part of the section; and
- (c) beds 22.2 and 22.3, layers 8 to 13 inclusive, from the lower part of the section.

RESULTS AND DISCUSSION

*The Analysis of Morphological Variation of M_1 in *Stenocranius gregalis* Pallas, 1779*

Description. The teeth lack roots, the deposition of external cement in the reentrant angles is well developed. The enamel is differentiated; on the anterior walls of the triangular loops, it is thicker than on the posterior walls. The triangular loops depart perpendicular to the longitudinal tooth axis; at the endings, there are distinct hooked projections, which are characteris-

Table 1. Linear parameters of M_1 in *Stenocranius gregalis* from the Pleistocene of Denisova Cave, mm

| Population | M_1 | N | Mean | min | max | st. d |
|------------------------------|--------|-----|-----------------|------|------|--------|
| Recent | length | 52 | 2.70 ± 0.19 | 2.35 | 3.12 | 0.026 |
| | width | 52 | 1.01 ± 0.8 | 0.82 | 1.22 | 0.011 |
| Beds 9.1–11.1 | length | 150 | 2.56 ± 0.17 | 2.25 | 3.0 | 0.0135 |
| | width | 160 | 0.91 ± 0.1 | 0.35 | 1.05 | 0.08 |
| Bed 22.1, upper layers | length | 86 | 2.44 ± 0.17 | 2.05 | 2.8 | 0.018 |
| | width | 86 | 0.89 ± 0.12 | 0.75 | 1.1 | 0.008 |
| Beds 22.2–22.3, lower layers | length | 40 | 2.41 ± 0.15 | 2.15 | 2.75 | 0.025 |
| | width | 40 | 0.87 ± 0.06 | 0.75 | 1.0 | 0.01 |

tic of Recent and Late Pleistocene voles (Kochev, 1993). The protoconid, hypoconid, metaconid, and entoconid of M_1 are well developed. The paraconid complex is complicated. It consists of two isolated triangles and an anterior unpaired loop. The folds of the anterior unpaired loop (projecting angles and reentrant folds) vary within a wide range; this allows one to distinguish morphological types.

Measurements. M_1 from the lower strata of Denisova Cave (beds 22.2 and 22.3) is, on average, 2.41 mm long and 0.87 mm wide. In the middle unit, M_1 is, on average, 2.44 mm long and 0.89 mm wide; and in the upper beds, M_1 is, on average, 2.56 mm long and 0.91 mm wide (Table 1).

Table 1 gives evidence for a gradual increase in size of the narrow-skulled vole throughout the time interval studied.

Variability. As the main morphotypes were distinguished, the following parameters were taken into account: (1) variability of the anterior unpaired loop; (2) the shape of denticles (projections) at the base of the loop; and (3) the depths of the internal and external reentrant folds. The structure of the anterior unpaired loop of *Stenocranius gregalis* allows one to distinguish clearly outlined morphotypes and use them for tracing stages in the paraconid complication. The main morphotypes of M_1 occur in both Recent and extinct populations. However, the proportions of certain morphotypes vary depending on geological age. Maleeva (1977) indicated that interpopulation geographic variability of teeth in the Recent narrow-skulled vole is low, i.e., the species shows stable phenotypic characteristics throughout its range. All examined teeth are characterized by a completely formed paraconid complex, the anterior unpaired loop of which is differentiated. All M_1 morphotypes can be divided into two groups by the presence of seven or eight closed dentin lakes on the occlusal surface. The group characterized by seven lakes is more numerous. The variants of the M_1 structure in *Stenocranius gregalis* from each temporal section are shown in Fig. 1.

Characteristic features of the morphotypes possessing seven lakes are as follows:

Morphotype I. On the lingual side, at the base of the anterior unpaired loop, there is a projection with a well-pronounced pointed apex. The projection widely ranges in size from very small to large. The labial side of the anterior unpaired loop is smooth.

Morphotype II. On the lingual side, at the base of the anterior unpaired loop, there is a reentrant fold anterior to the projection. On the labial side, at the base of the anterior unpaired loop, there is a small reentrant fold. In all cases, the reentrant folds of the anterior unpaired loop of the paraconid lack external cement.

Morphotype III. On the lingual side of the anterior unpaired loop, there is a well-developed pointed projection and reentrant fold. On the labial side of the anterior unpaired loop, the reentrant fold is well developed and contains external cement.

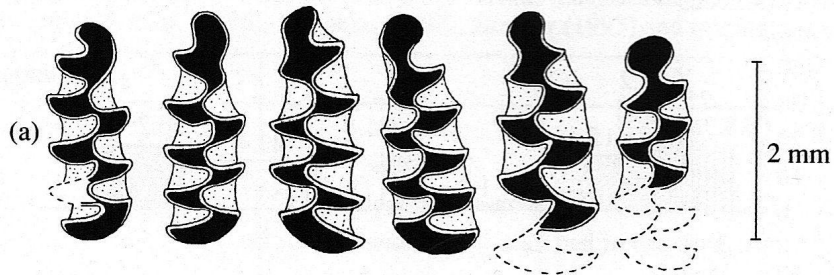
Morphotype IV. The reentrant folds at the base of the anterior unpaired loop are well-pronounced and contain external cement. A pointed projection is formed posterior to the labial fold.

Morphotype V. The paraconid is similar in structure to that of M_1 in *Microtus arvalis*, i.e., the projection on the labial side at the base of the unpaired loop is of almost the same size as the projection on the lingual side of the unpaired loop.

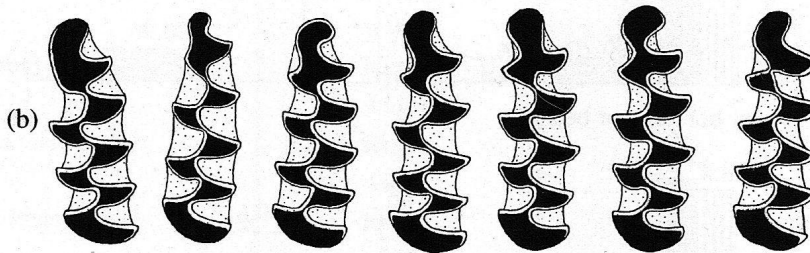
Morphotype VI. The reentrant angles of the unpaired loop of the paraconid are extremely well developed. This morphotype comprises variants VIa, VIb, and VIc (Fig. 2). The constriction at the base of the unpaired loop is narrower than the anterior part of the unpaired loop. The proportion of each variant is low; therefore, they are considered to be the same morphotype.

Characteristic features of the morphotypes possessing eight lakes are as follows:

Morphotype VII. The reentrant angles of the unpaired loop of the paraconid adjoin each other to isolate a supplementary unpaired loop in the anterior part of the paraconid. This anterior unpaired loop is not differentiated. The occlusal surface bears eight dentin lakes. This morphotype comprises two structural variants, VIIa and VIIb (Fig. 2).



Bed 22, lower horizons (22.2 and 22.3, layers 8-13 inclusive)



Bed 22, upper horizons (22.1, layers 0-2)

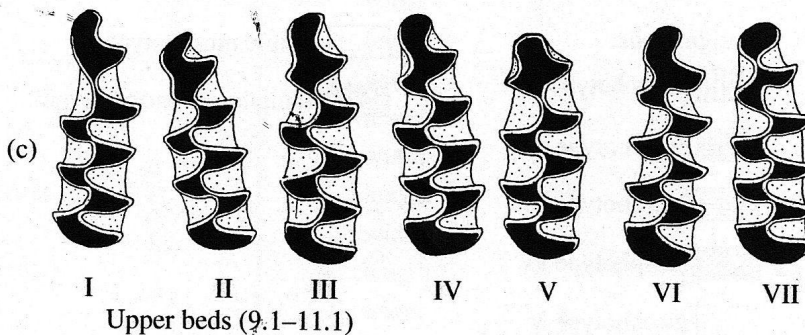


Fig. 1. Tooth morphotypes of *Stenocranius gregalis* Pallas from Denisova Cave.

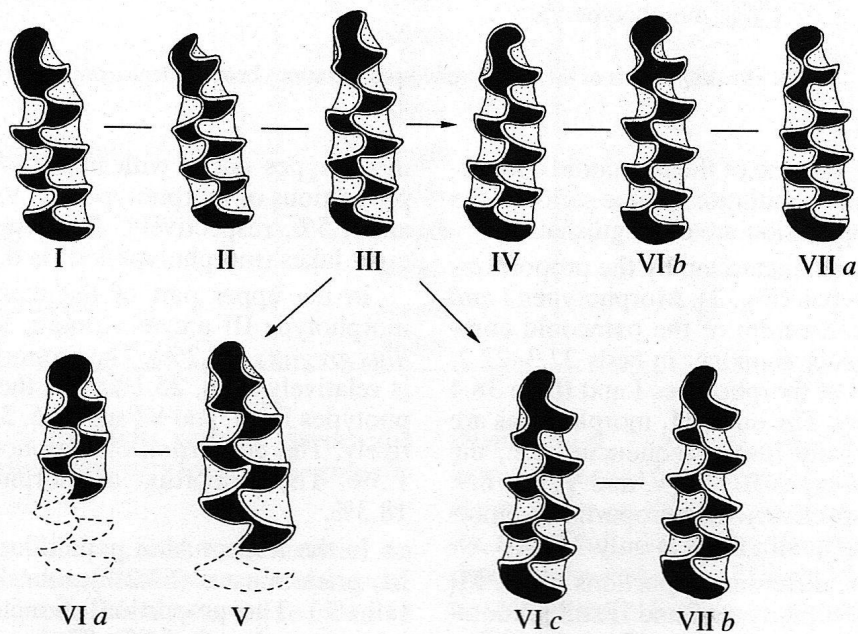


Fig. 2. The scheme of the paraconid complication in *Stenocranius gregalis* Pallas.

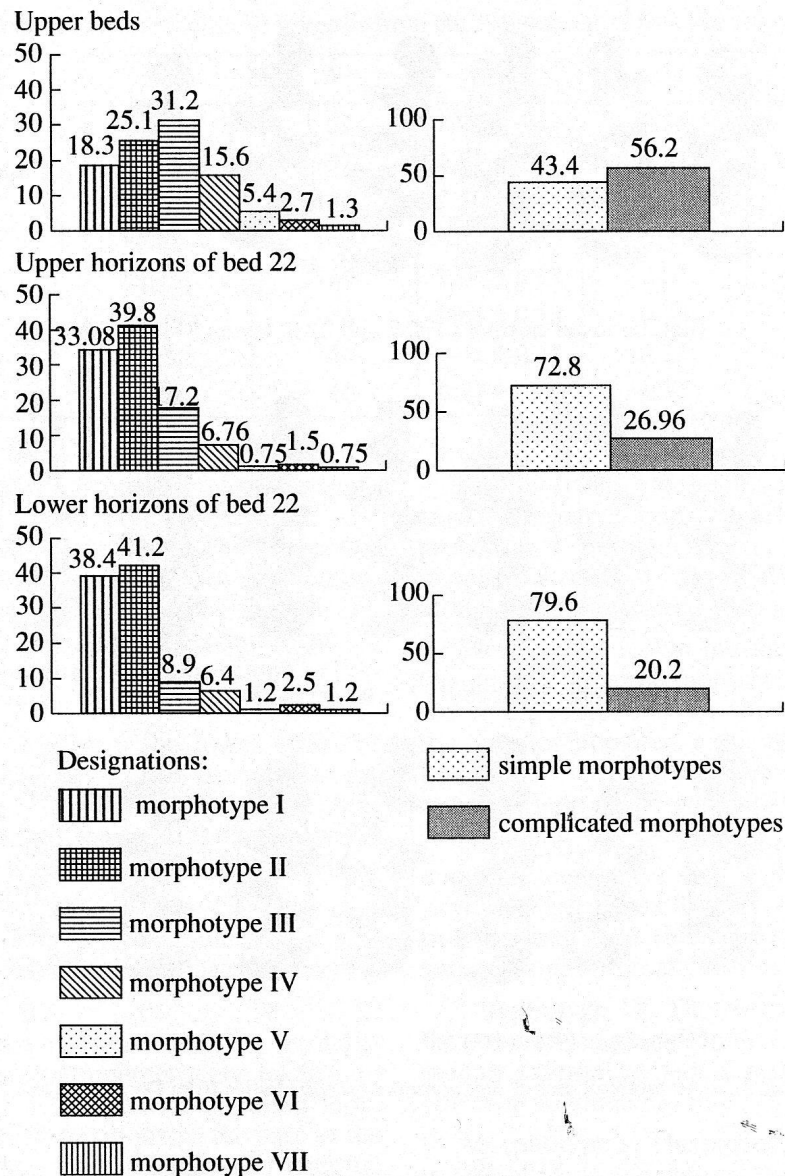


Fig. 3. The proportions of the M_1 morphotypes in various beds of Denisova Cave.

Figure 2 shows the scheme of the paraconid complication. In the *S. gregalis* populations, three series of the paraconid region complication are distinguishable.

Each population is characterized by the proportions of the above morphotypes (Fig. 3). Morphotypes I and II are of the simplest structure of the paraconid complex. Such teeth are most abundant in beds 22.3–22.2, where the proportions of morphotypes I and II are 38.4 and 41.0% respectively. The other M_1 morphotypes are present with substantially lower frequencies; i.e., the proportions of morphotypes III, IV, V, and VI are 8.9, 6.4, 1.2, and 2.5% respectively. The proportion of morphotype VII with eight dentin lakes is only 1.2%.

In the middle beds, different proportions of the M_1 morphotypes occur. Morphotypes I and II still predominate (33.08 and 39.8%) and the proportion of morphotype III substantially increases (17.2%). The other

molar types occur with much lower frequencies; the proportions of morphotypes IV, V, and VI are 6.7, 0.75, and 1.5%, respectively. The proportion of teeth with eight lakes (morphotype VII) is 0.75%.

In the upper part of the section (beds 11.1–9.1), morphotype III prevails among M_1 teeth of *Stenocranius gregalis* (31.2%). The proportion of morphotype II is relatively high, 25.1%; and the proportions of morphotypes IV, V, and VI are 15.6, 3.4, and 2.7%, respectively. The proportion of morphotype VII increases to 1.3%. The proportion of morphotype I decreases to 18.3%.

In the Recent Altai populations, morphotype IV of M_1 predominates (61.2%); morphotype VI is frequent (19.1%). The proportion of teeth with eight enamel lakes increases to 5.6%. The proportions of morphotypes I and II are low, 1.8 and 11.3%, respectively.

Table 2. Linear parameters of M₁ in *Stenocranius gregalis* from various localities of western Siberia, northeastern Europe, and Belorussia, mm, after Smirnov *et al.* (1986), Motuzko (1992), Kochev (1993) and original data

| Population | M ₁ | N | Mean |
|-------------------------------------|----------------|-----|-------------|
| Recent goltsy | length | 52 | 2.70 ± 0.02 |
| | width | | 1.01 ± 0.01 |
| Tundra (Komi Republic) | length | 45 | 3.01 |
| | width | | 1.05 |
| Steppe (Kazakhstan) | length | 30 | 2.7 ± 0.03 |
| | width | | 1.08 ± 0.02 |
| Yarsino (Late Pleistocene) | length | 79 | 2.67 |
| | width | | — |
| Ryabovo (Late Pleistocene) | length | 317 | 2.7 ± 0.02 |
| | width | | 1.03 ± 0.03 |
| Medvezh'ya Cave (Late Pleistocene) | length | 551 | 2.57 ± 0.01 |
| | width | | 0.97 ± 0.01 |
| Studenaya Cave-4 (Late Pleistocene) | length | 405 | 2.75 ± 0.05 |
| | width | | 0.99 ± 0.03 |
| Studenaya Cave-3 | length | | 2.79 ± 0.02 |
| | width | | 1.01 ± 0.02 |
| Studenaya Cave-2 | length | | 2.76 ± 0.04 |
| | width | | 1 ± 0.01 |
| Studenaya Cave-1 | length | | 2.76 ± 0.03 |
| | width | | 0.98 ± 0.02 |
| Kur'yador (Late Pleistocene) | length | 10 | 2.81 ± 0.05 |
| | width | | 1 ± 0.02 |
| Drichaluki (Late Pleistocene) | length | 3 | 2.93 |
| | width | | 0.98 |
| Yudinovo (Late Pleistocene) | length | 8 | 2.8 |
| | width | | 1.05 |
| Semeika (Middle Pleistocene) | length | 23 | 2.69 |
| | width | | — |
| Gavrilovka (Middle Pleistocene) | length | 24 | 2.7 ± 0.04 |
| | width | | 1.2 ± 0.02 |
| Zhukevichi (Middle Pleistocene) | length | 4 | 2.63 |
| | width | | 1.0 |
| Gralevo-2 (Middle Pleistocene) | length | 57 | 2.61 |
| | width | | 1.0 |
| Komintern (Middle Pleistocene) | length | 508 | 2.41 |
| | width | | 0.92 |

Thus, morphotype I is the most archaic; during the Pleistocene, it gradually disappears from the *S. gregalis* phenotype.

Comparisons. To date, extensive material on *S. gregalis* from the localities in Russia and other countries has been accumulated. This allows one to examine the trends of changes of the occlusal surface patterns against a background of general paleogeographic

development. The Pleistocene material on *S. gregalis* from Denisova Cave (lower layers) was compared with the material on this species from the Komintern locality, the Middle Volga Region (the Komintern Fauna is dated as the end of the Middle Pleistocene); the localities of western Siberia, northeastern Europe, Poland, and Hungary. The data on the extinct populations were also compared with the Recent *S. gregalis* populations

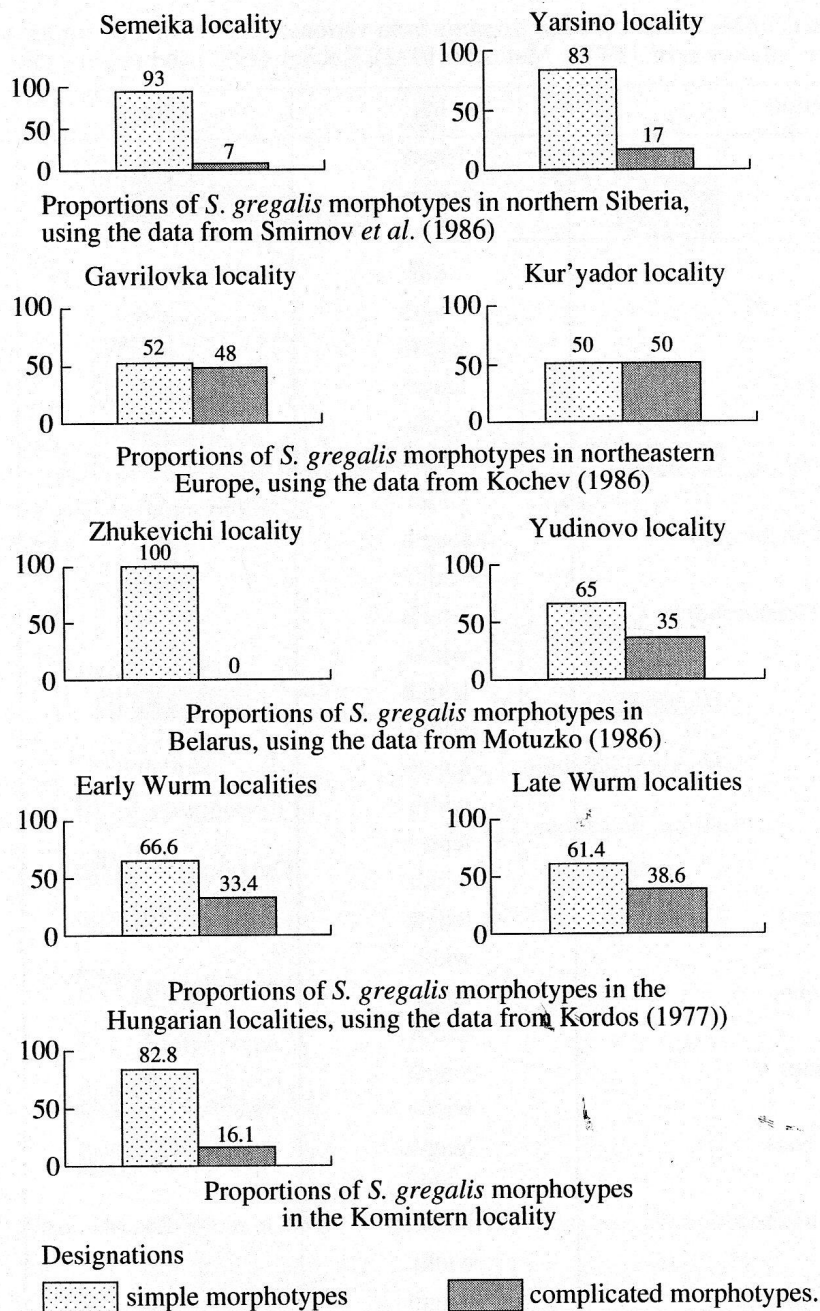


Fig. 4. The proportions of the M_1 morphotypes in various localities.

from Western Siberia, the Altai Nature Reserve, the Komi Republic, and Kazakhstan (specimens housed at the Zoological Museum of MSU). The changes of linear measurements and morphotypic variation (percentage of morphotypes) depending on time were estimated (Table 2 and Fig. 4).

A high variability of the anterior unpaired loop structure allows one to distinguish morphological types. As mentioned above, seven main morphotypes are distinguished. Previously, researchers divided the structural diversity of M_1 into a smaller number of morphotypes (Smirnov *et al.*, 1986; Motuzko, 1992;

Kochev, 1993). To compare the data on Denisova Cave with those on other localities, I used the method proposed by Motuzko (1992). The morphotypes were divided into two main groups and distinguished by the simple or complex structure of the anterior unpaired loop. The first group comprised the teeth, the labial side of the anterior unpaired loop of which is smooth or bears a very small reentrant fold lacking external cement. This corresponds to morphotypes I and II of the system proposed in this study; morphotypes I and II after Kochev (1993); gregaloid and gregaloid-microtid types after Smirnov *et al.* (1986); morphotypes I and II

after Motuzko (1992); morphotypes 1, 2, and 3 after Kordos (1977); and gregaloid and gregaloid-arvalis types after Nadachowski (1982). The second group comprises teeth possessing a differentiated anterior unpaired loop, well-developed projections, and reentrant folds. It includes morphotypes III–VII of our classification; morphotypes III–IV after Kochev (1993); the microtid type after Smirnov *et al.* (1986); morphotypes III–V after Motuzko (1992); morphotypes 4 and 5 after Kordos (1977); and the arvalis and *other* types after Nadachowski (1982).

It is well known that an animal's size and, in particular, tooth measurements depend on geographic distribution. Relatively large animals inhabit the northern parts of the range, whereas the southern forms are smaller. Presumably, animals could vary in size depending on environmental conditions. At the same time, the ratio between simple and complex morphological types allows one to judge the evolutionary advantage of each population.

For example, in Recent tundra, *S. gregalis*, M_1 is, on average, 3.01 mm long and 1.05 mm wide. Steppe voles are smaller; M_1 is 2.58 mm long and 0.98 mm wide. The ratios of teeth morphotypes also varies within the species range. In the steppe populations, the proportion of simple morphotypes is 70% (Motuzko, 1992); that of voles from the goltsy and tundra assemblages is 15%. This is attributable to the fact that the tundra populations originate from the steppe populations. This theory is corroborated by the data presented by Smirnov (1996). The narrow-skulled voles from the lower layers of Denisova Cave are most similar in tooth measurements to the Recent steppe populations (M_1 is 2.41 mm long and 0.87 mm wide).

The Komintern locality is on the left bank of the Volga River, 30 km downstream of the mouth of the Kama River. The bone horizon is in fluvial sand overlain by Mikulino paleosol. These deposits form the base of the Late Pleistocene terrace of the Volga River, alluvium of which outcrops above the section. In addition, the latter is overlain by a paleosol and loess series. The collection from the Komintern locality consists of several thousand bone specimens. Based on the species composition, the evolutionary grade of various taxa, and the position in the section, the Komintern Fauna is dated to the end of the Middle Pleistocene.

The total number of *S. gregalis* teeth from the Komintern locality is 508. The M_1 crowns are, on average, 2.41 mm long and 0.92 mm wide. The morphological diversity of the M_1 structure in this population is described by the same seven main morphotypes as in the narrow-skulled voles from Denisova Cave, and any new structural variants are not registered. Simple variants of the anterior unpaired loop prevail in the Komintern population. The proportions of morphotypes I, II, III, IV, and VI are 41.3, 41.5, 6.8, 7.8, and 1.5%, respectively. The arvalis structural variant of the anterior unpaired loop (morphotype V) is not registered. In

addition, the Komintern population includes the teeth of morphotype VII (with eight lakes), the proportion of which is, at most, 0.7%. According to the classification proposed by Motuzko (1992), simple morphotypes prevail (82.8%), whereas the proportion of evolutionarily advanced variants is low, 16.1% (see Fig. 4).

A comparison between the teeth from the Komintern locality and Denisova Cave (lower horizons of bed 22) shows that the two extinct populations are similar in the proportions of the M_1 morphotypes. The proportions of simple structural variants of the anterior unpaired loop (morphotypes I and II) are high in both the Komintern and Denisova Cave populations (82.8 and 77.4%, respectively). However, in *S. gregalis* from Denisova Cave, the proportion of morphotypes possessing eight closed lakes is somewhat higher than in the Komintern population, 1.7 and 0.7%, respectively.

A comparison between the data on the Denisova Cave and western Siberia (Smirnov *et al.*, 1986) included both Middle and Late Pleistocene localities. The Semeika locality is on the right bank of the Irtysh River, 8 km downstream of the village of Semeika (Smirnov *et al.*, 1986). Based on the morphological analysis of lemmings, the researchers assigned the Semeika locality to the Middle Pleistocene (Chem-bakchinsk Fauna). This fauna comes from the Chem-bakchinsk beds of the Tobolsk Horizon dated 500–470 thousand years BP. In the *S. gregalis* populations from the Semeika locality, simple morphotypes prevail, i.e., the proportion of the gregaloid and gregaloid-microtid types is 93% and the proportion of the microtid type is lower than 10%. The M_1 crowns are, on average, 2.69 mm long.

In the comparisons, the Late Pleistocene localities are presented by the Yarsino locality assigned to the onset of the Late Pleistocene (Smirnov *et al.*, 1986). This locality is on the left bank of the Dem'yanka River (right tributary of the Irtysh River), 500 m downstream of Izby Yarsiny (Smirnov *et al.*, 1986, p. 32). The localities of the Yarsino Fauna "belong to the Yalybinskaya Formation formed in the Kazanian (Riss–Wurm) Interglacial dated 127–115 thousand years BP" (Smirnov *et al.*, 1986, p. 32). Among M_1 teeth of *S. gregalis*, simple morphotypes prevail (83%); however, the proportion of complex morphotypes is 17%, i.e., higher than in the Middle Pleistocene. The M_1 crowns are, on average, 2.67 mm long.

The narrow-skulled vole from Denisova Cave is smaller in tooth measurements than extinct voles from western Siberia. The proportions of M_1 morphotypes in the lower horizons of the Denisova Cave are similar to those in the Late Pleistocene Yarsino locality. From the lower beds of Denisova Cave to the upper beds, the percentage of complex structural variants of the anterior unpaired loop gradually increases.

The proportions of the M_1 morphotypes in *S. gregalis* from western Siberia, Denisova Cave, and the Komintern locality differ from those of northeastern

Europe. The data on the Middle and Late Pleistocene localities obtained by Kochev (1993) were also included in the comparisons. The Gavrilovka locality was dated as the Late Pleistocene; the Ryabovo, Kur'yador, Medvezh'ya Cave, and Studenaya Cave were dated as the Middle Pleistocene.

The Gavrilovka locality is a 31-meter-high outcrop on the right bank of the Vychegoda River near the upper extremity of the village of Gavrilovka (Kochev, 1993, p. 18). The bone horizon was formed in the Late Pechora Time, i.e., 260 thousand years BP. The proportions of simple and complex morphotypes in this locality are 52 and 48%, respectively, whereas in the above-mentioned Middle Pleistocene populations, the proportion of simple morphotypes was higher than 50%. In the Late Pleistocene localities, approximately the same ratio is observed. The Ryabovo locality is an outcrop extending from 16 to 32 m above the river level on the right bank of the Vychegoda River near the village of Ryabovo of the Arkhangelsk Region, 60 km upstream of the town of Kotlas (Kochev, 1993, p. 23); the strata are dated as the Lower Laya Time. The proportions of the simple and complex morphotypes are 52 and 48%, respectively. The Kur'yador locality is a 14-meter-high outcrop on the right bank of the Vychegoda River, 6 km downstream of the village of Kur'yador (Kochev, 1993, p. 24); the bone bed is dated as 35 thousand years BP. The proportions of simple and complicated morphotypes are 50 and 50%. The Medvezh'ya Cave locality is in the entrance grotto of Medvezh'ya Cave, on the right bank of Iordanskii Ravine, open on the right bank of the Verkhnyaya Pechora River, 17 km upstream of the Sheshin cordon (Kochev, 1993, p. 25). The bone bed is dated as 31–35 thousand years BP. The proportions of teeth of simple and complicated structure of the anterior unpaired loop are 46 and 54%, respectively. Near Medvezh'ya Cave, there is Studenaya Cave. In the entrance grotto of the latter, four main horizons were distinguished. Based on the morphological variation of the Arctic lemming (*Dicrostonyx torquatus*), the beds of Studenaya Cave were dated as the interval from the onset of the Laya Stade to the beginning of the Byzovskii Stade. From the lower horizons of Studenaya Cave to the upper horizons, the percentage of complicated structural variants of the anterior unpaired loop gradually increases (Kochev, 1993).

The analysis of *S. gregalis* from Belarus was also based on the Middle and Late Pleistocene populations. The Zhukevichi and Galevo-2 localities are dated as the Middle Pleistocene; the Kobelyaki, Yudinovo, and Drichaluki localities are dated as the Late Pleistocene. The Late Valdai Faunas are associated with the Usvyatskaya Formation and dated as 25–17 thousand years BP (Motuzko, 1992). The M_1 measurements of *S. gregalis* from Belarussia increase from the Middle Pleistocene to the Late Pleistocene. In the Zhukevichi locality, the crowns are, on average, 2.63 mm long and 0.9 mm wide; in Galevo-2, 2.61 and 1 mm, respectively. In the Late Pleistocene Drichaluki locality, the

crowns become 2.93 mm long and 1 mm wide; and in the Yudinovo locality, 2.8 mm long and 1.05 mm wide. The proportion of complex morphotypes also increases during this time interval. In the Zhukevichi locality (Middle Pleistocene), the proportion of simple morphotypes is 100%; in the Galevo-2 locality, 74%. In the Late Pleistocene beds of the Yudinovo and Drichaluki localities, the proportions of simple tooth morphotypes are 35 and 50%, respectively.

Nadachowski (1982) analyzed the material from twelve cave sites in Poland. From the Early Pleniglacial to the Holocene, the tooth crowns decreased from 2.83 to 2.68 mm in length. The proportions of the morphotypes in the populations are relatively stable, i.e., within the time interval indicated, the proportion of simple structural variants of the anterior unpaired loop increased from 61.4 to 70.7%; the proportion of complex morphotypes changed from 38.6 to 29.3%.

In the Hungarian localities, in the Early to Late Wurm, the proportion of simple morphotypes increased from 66.6 to 85.5%. To the Holocene, the proportion decreased to 77% (Kordos, 1977).

Thus, the analysis of the proportions of M_1 morphotypes in *Stenocranius gregalis* from the lower horizons of Denisova Cave has shown that the proportion of simple morphotypes is high (50%); this is characteristic of the Middle Pleistocene populations. In the lower beds of Denisova Cave, the proportion of M_1 morphotypes characterized by eight closed lakes is substantially higher than in the Komintern Fauna (in the latter case, the proportion is lower than 1%). Therefore, one can propose that the Denisova Cave Fauna is of earlier geological age than the Komintern Fauna, and the fauna from the lower beds of Denisova Cave should be dated the Late Pleistocene. The superstrata of Denisova Cave are younger. The middle and upper parts of the deposits from Denisova Cave should be aged as the Upper Pleistocene.

Occurrence. In the former Soviet Union, the narrow-skulled vole (*S. gregalis*), characterized by a peculiar shape of the anterior unpaired loop, occurs in the fossil faunas of a mixed ecological pattern beginning at the Middle Pleistocene. This species is abundant in tundra–forest–steppe faunas (Dupal, 1998). At the end of the Pleistocene, it became extinct in almost the whole of Europe. Today, it inhabits an area from the Primorye tundra to lowland and highland steppes; in the forest belt, it dwells in meadow habitats.

Material. Skulls of Recent voles, 127 specimens; (PIN, nos. 4835/1–222) 222 vole teeth from beds 9–11.1 of the Denisova Cave; (PIN, nos. 4835/223–358) 136 teeth from bed 22.1, layers 0–2; and (PIN, nos. 4835/359–398) 40 teeth from beds 22.2 and 22.3, layers 8–13.

CONCLUSIONS

(1) In *Stenocranius gregalis* from the Pleistocene deposits of Denisova Cave, seven morphological types of the paraconid region of M_1 were distinguished. Mor-

photype I, characterized by seven dentin lakes on the occlusal surface and weakly developed denticles at the base of the anterior unpaired loop, is the most archaic. Morphotype VII characterized by eight lakes on the occlusal surface is the most advanced.

(2) In a successive series of extinct populations from bed 22 to the Recent, the M_1 crown of *S. gregalis* gradually became complicated.

(3) The analysis of the material from Denisova Cave and comparisons with the data on the narrow-skulled vole from other localities give evidence for the Late Pleistocene Age of the *S. gregalis* population from the Pleistocene beds of Denisova Cave.

(4) The data on various regions of northern Eurasia suggest that, throughout the Late Pleistocene, the occlusal surface of the first lower molar of *S. gregalis* gradually became complex within the entire range of the species.

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