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ARTICLE

Ground squirrels of the genus *Spermophilus* from the Pleistocene and Holocene localities of the Middle and South Urals and Trans-Urals region: the dental features

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ABSTRACT

The dental features of fossil *Spermophilus* from eleven Pleistocene and Holocene localities of the Middle and South Urals and Trans-Urals region are described. The comparison with the recent species *S. major, S. fulvus* and *S. pygmaeus* from the same region was carried out. The most important features of the recent and fossil *S. pygmaeus* are: small and medium sizes; metaloph of P4-M2 bear constrictions or interruptions, metaconule is well pronounced and rounded; anterostyle often is well developed in P4; high frequency of meso- and metastylid in m1-3. In M3 the anterior inner and posterior roots are close together and tend to merge with each other in their upper parts. Also, *S. major* was a part of the Late Pleistocene and Holocene faunas. The most important features of *S. major* are: medium and large sizes; a small number of P4-M2 with the occlusal cusps, among them the most significant is the presence of parastyle; in m1-2 mesostylid commonly occurs. The tendency to complication of the root part of M3 of *S. superciliosus* is revealed from Late Pleistocene to Holocene. The comparison with the fossil *S. superciliosus* from Eastern Europe was carried out. No significant differences between *S. superciliosus* and *S. major* were found.

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Introduction

The problem of the extinction of mammalian species at the end of the Late Pleistocene and at the beginning of the Holocene is in the focus of modern research due to the accumulation of a large volume of paleontological material and the development of the dating methods. *Spermophilus superciliosus* is one of the problematic species. This large extinct ground squirrel appeared in the Middle Pleistocene and persist during the Late (?) Pleistocene (Gromov et al. 1965; Popova 2006). It is a probable ancestor of *S. major*, which formed as an independent species in the Holocene (Gromov et al. 1965). At the same time, some authors state the synchronous existence of *S. superciliosus* and *S. major* (Topachevsky et al. 2000). Perhaps, these contradictions come from the difficulties of species identification of the fossil remains without the detailed description of the variability of cranial and dental features in the entire area.

The most complete description of the recent and fossil representatives of this genus is given in the monograph of Gromov et al. (1965). But the description focuses on the skull features, the information about molar morphology is extremely fragmentary, as well as about the molar dimensions. Therefore, an accurate species definition of *Spermophilus* molars is difficult. So, it is a common practice to name ground squirrel as *Spermophilus* sp. in the fauna list.

The earliest remains of *Spermophilus* were dated as Eopleistocene (= Olduvai?) (Stefanovsky and Borodin 2002). The most northern findings (outside the modern area) are known from the caves in 59 ′N in the interval from the Late Pleistocene to the beginning of the Early Holocene, while in the case of southern part of the Middle Trans-Urals – until the middle Holocene. At the South Trans-Urals *Spermophilus* occurs from the Late Pleistocene to the Late Holocene (Smirnov et al. 2016).

Four ground squirrels species are living in the Urals and surrounding areas at present (Kryštufek and Vohralík 2012): *Spermophilus fulvus* Lichtenstein, 1823, *Spermophilus major* Pallas, 1779, *Spermophilus pygmaeus* Pallas, 1778, *Spermophilus brevicauda* Brandt, 1843. The species *Spermophilus brevicauda* is one of so-called 'red-cheeked' ground squirrels. The habitat area of this species is not clearly defined, variability is not studied. Only a few people consider it a separate species, most researchers consider it a subspecies of *S. erythrogenys* (for example, Kryštufek and Vohralík 2012). So we have excluded *S. brevicauda* from the study for now. But perhaps this species was also represented like as *S. fulvus, S. major, S. pygmaeus* in the Late Pleistocene and Holocene faunas.

By the moment, the remains of ground squirrels from the South Urals localities were referred to *S. major* and *S. pygmaeus* (Kuzmina 2006, 2009), and the remains from Middle and South Trans-Urals – to *S. superciliosus* (Maleeva 1976; Pogodina 2006; Chemagina et al. 2017). Here, we provide an analysis of dental variability of the recent and fossil representatives of the genus *Spermophilus* from the Middle and South Urals and Trans-Urals and surrounding areas in order to 1) reveal common and specific features of molars of the recent species; 2) try to assess their implementation on the fossil material for species identification.

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Material and methods

Fossil remains of the genus *Spermophilus* described here are deposited in the Museum of the Institute of Plant and Animal Ecology, Ural Branch of Russian Academy of Sciences, Ekaterinburg, Russia (collections of E.A. Kuzmina, A.G. Maleeva and T.V. Strukova). Fossils consist of isolated teeth. The specimens have been collected from eleven Pleistocene and Holocene localities in the Middle and South Urals and Trans-Urals (Russia) (Figure 1):

Middle Trans-Urals: Nitsinskoye (the end of the Middle Pleistocene); Parenkino (Late Pleistocene); Mal'kovo (31,800 ± 350 BP (GIN–5337)); Nizhnyaya Tavda (24,820 ± 750 BP (SOAN – 4535)); Pershinskaya Cave (7380 ± 150 BP (SOAN –3824)).

South Urals and Trans-Urals: Verhnyaya Alabuga (the first half of the Late Pleistocene); Zverinogolovskoye (Late Pleistocene); Smelovskaya-II Cave (Late Pleistocene); Syrtinskaya Cave ((22,050 ± 200 BP (SBRAS–5133)); Alekseevskaya Cave (8450 ± 200 BP (GIN–11,334)); Khudolaz (Late Holocene).

Detailed information for these localities can be found in (Maleeva 1976; Maleeva and Stefanovsky 1988; Strukova 2003; Kuzmina 2006, 2009; Pogodina and Strukova 2013). The species identification of the material is given in accordance with the one which was published earlier (Maleeva 1976; Kuzmina 2006, 2009; Pogodina 2006; Chemagina et al. 2017).

For comparison the teeth of *Spermophilus superciliosus* Kaup, 1839 from Podbaba (Late Pleistocene) Praga, Central Bohemian Region (Zoological Institute of Russian Academy of Science, St. Petersburg, Russia), and *Spermophilus superciliosus birulai* Gromov, 1961 (Late Pleistocene) from Adzhy-Koba, Crimea (Zoological Institute of Russian Academy of Science, St. Petersburg, Russia), were used. Also, the teeth of extant *Spermophilus* species, living in the Urals and surrounding areas, were used. *Spermophilus fulvus* Lichtenstein, 1823, Kyzylorda, Kazakhstan; Samarkand, Bukhara, Uzbekistan; Balkanabat, Turkmenistan (Zoological Museum of Moscow University, Moscow, Russia); *Spermophilus major* Pallas, 1778, Ekaterinburg, Russia (collection of E.S. Nekrasov, Zoological Museum of Ural Federal University, Ekaterinburg, Russia); *Spermophilus pygmaeus* Pallas, 1778, Aktobe, Kazakhstan (collection of E.A. Kuzmina, Museum of the Institute of Plant and Animal Ecology, Ural Branch of Russian Academy of Sciences, Ekaterinburg, Russia). All recent material is taken out of hybridisation zones (Kryštufek and Vohralík 2012). Generic rank of *Spermophilus* follows Helgen et al. (2009).

Upper premolars and molars are denoted as P3, P4, M1, M2, M3, and lower ones as p4, m1, m2, m3.

Figure 1. Geographic locations of *Spermophilus*-bearing fossil localities discussed in the text. Cross indicate the Middle Pleistocene site, circles indicate the Late Pleistocene site, triangles indicate the Holocene sites. 1 – Pershinskaya Cave; 2 – Nitsinskoye; 3 – Parenkino; 4 – Mal'kovo; 5 – Nizhnyaya Tavda; 6 – Verhnyaya Alabuga; 7 – Zverinogolovskoye; 8 – Smelovskaya-II Cave; 9 – Syrtinskaya Cave; 10 – Alekseevskaya Cave; 11 – Khudolaz.

Measurements of fossil and recent specimens were taken to the nearest 0.01 mm with a Leica EZ 4 binocular microscope. Dimensions of P4-M3 and p4-m3 were measured at the occlusal surface, as described by Weerd van de (1976); the P3 measurements represent greatest crown dimensions taken parallel (width) and perpendicular (length) to protoloph. The teeth of juvenile individuals were excluded.

Terminology for dental structures follows Sinitsa and Pogodina (2019). In order to minimise age variability, which can decrease the number of observed signs, the teeth of old individuals were excluded.

The variability of the root part of M3 and p4 was studied (the principle is stated in Pogodina 2006). Not only teeth with intact lower parts have been studied, but also fragments of maxillae with the alveoli. We examined all fossil remains, all M3 and p4 of recent *S. major*, three M3 of *S. pygmaeus*.

Statistical analysis was performed using STATISTICA 8 package (StatSoft, Inc. 2007. STATISTICA (data analysissoftware system), version 8.0. www.statsoft.com). Analysis of variance (ANOVA) was used to test for significant differences between mean values of the teeth length (L) and width (W).

Results

The dental features of recent ground squirrels

Dimensions of S. pygmaeus, S. major and S. fulvus

The smallest is *S. pygmaeus*, medium – *S. major*, the biggest is *S. fulvus*. The averages of their sizes are different (see Appendix A), but areas of tooth size variability overlap: *S. pygmaeus* with *S. major, S. major* with *S. fulvus*. Area of tooth size variability is the widest for the *S. major*. The dimensions of m3 of *S. fulvus* show the most clear-cut differences: this molar is the widest (see Appendix B). The p4 of *S. fulvus* also are the biggest. The proportions of p4 are approximately the same in all species: its posterior width (W2) is slightly less than the anterior (W1) and the coefficient W2/W1 of all species shows similar values (see Appendix A). The proportions of M3 do not differ much, but *S. fulvus* shows a slightly larger relative length (see Appendix B). M2 is larger than M1, and m2 is larger than m1 in all species.

Teeth morphology (dental structures) of S. pygmaeus, S. major and S. fulvus

Spermophilus pygmaeus. The structure of metaloph is one of the most significant features of *S. pygmaeus*. The metaloph in P4-M2 often bears one (labial) (15.3% P4, n = 26), more often two (57.6% P4, 61.5% M1–2, n = 50) constrictions or interruptions, that delimits the metaconule swelling labially and lingually. When gaps are present, metaconule is well pronounced and rounded.

Also, *S. pygmaeus* differs from *S. fulvus* and *S. major* by the presence of some additional cusps of P4. The anterostyle is variably present at the anteroloph. In near one-fourth P4 (26.9%, n = 26) it is present as detached, well-developed rounded cusp. The hypocon in the posteroloph appears only in single P4 (3.8%, n = 26).

The mesostyl occurs in near one-fifth (19.2%, n = 52) of M1-2. The second metaconule (7.7% P4, n = 26; 3.8% M1-2, n = 52), parastyle (3.8% P4, n = 26, 1.9% M1-2, n = 52) appears only in single P4–M2.

The mesostylid is developed in the main part (96% m1-2, n = 57; 82.7% m3, n = 29) of lower molars. This cusp varies in size from large elongated to small rounded. The metastylid also occurs (25% m1-2, n = 56; 72.4% m3, n = 29). It varies from moderate to small and almost indistinct. Meso- and metastylid are located close to each other. Ectostylid (3.5%) and mesoconid (5.3%) are rare (n = 56) in m1-2. Ectostylid appears only in single m3 (3.4%, n = 29). Mesoconid in m3 occurs more frequently (38%, n = 29).

Three roots present in all studied (n = 3) M3. There are no well-marked crests in the bottoms of these M3.

Spermophilus major

The *S. major* is characterised by the small number of upper teeth with the occlusal cusps. But nevertheless some main crests cusps in P4 (n = 48) and M1-2 (n = 142) occur: parastyle (12.5% P4, 16% M1-2), paraconule (16.6% P4, 8.3% M1-2), the second metaconule (4.2% P4; 18% M1-2) and mesostyl (20.1% M1-2). These structures are present as small rounded or oval cusps at the anteroloph, labial protoloph and labial metaloph, respectively. As you can see the frequency of occurrence of each of these structures is relatively low and does not exceed 20% of the total sample.

The mesoconid (as swelling of ectolophid) (2.8%) and ectostylid (as noticeable rounded cusp) (2.1%) are rare in m1-2 (n = 143).

The mesostylid as detached, well-protrusive rounded cusp is variably present at m1-2 (35.6%, n = 143) and m3 (36.5%, n = 41). Metastylid presents sometimes (12.2%, n = 41) near mesostylid only in m3. It is smaller and is shifted towards the metaconid.

Some recent M3 (40.3%, n = 72) bear three roots (a simple variant of the structure of the roots) (Figure 2). The posterior root is expanded upwards. There is a hollow in the upper section of the posterior root. It can be shallow and unobtrusive or deep. Significant part of recent teeth (59.7%), bear complicated variants of the structure of the roots. There are different variants of complication: the splitting of the posterior root, the presence of additional roots near the external anterior root (Figure 2), or both. There are three low, but defined crests in the bottoms of all these M3. They extend to the main roots from the centre of the bottom (Figure 2). Two free posterior roots are present in all p4 (100%, n = 51).

Spermophilus fulvus

Parastyle, paraconule and second metaconule are absent in the upper teeth.

The protostyle occurs in antesinus of P4 (7.1%, n = 28). The hypostyle appears in sinus of M1-2 (3.6%, n = 56). These structures look like sharpened noticeably knobby.

The mesostyl occurs more often than in *S. major*. It is present in M1-2 (42.8%, n = 56).

The mesostylid in m1-2 is rarer than at *S. major* (35.7%, n = 56). More than a half of m1-2 bear ectostylid (57%, n = 56). Mesostylid and ectostylid are quite well expressed and much larger than that at *S. major*.

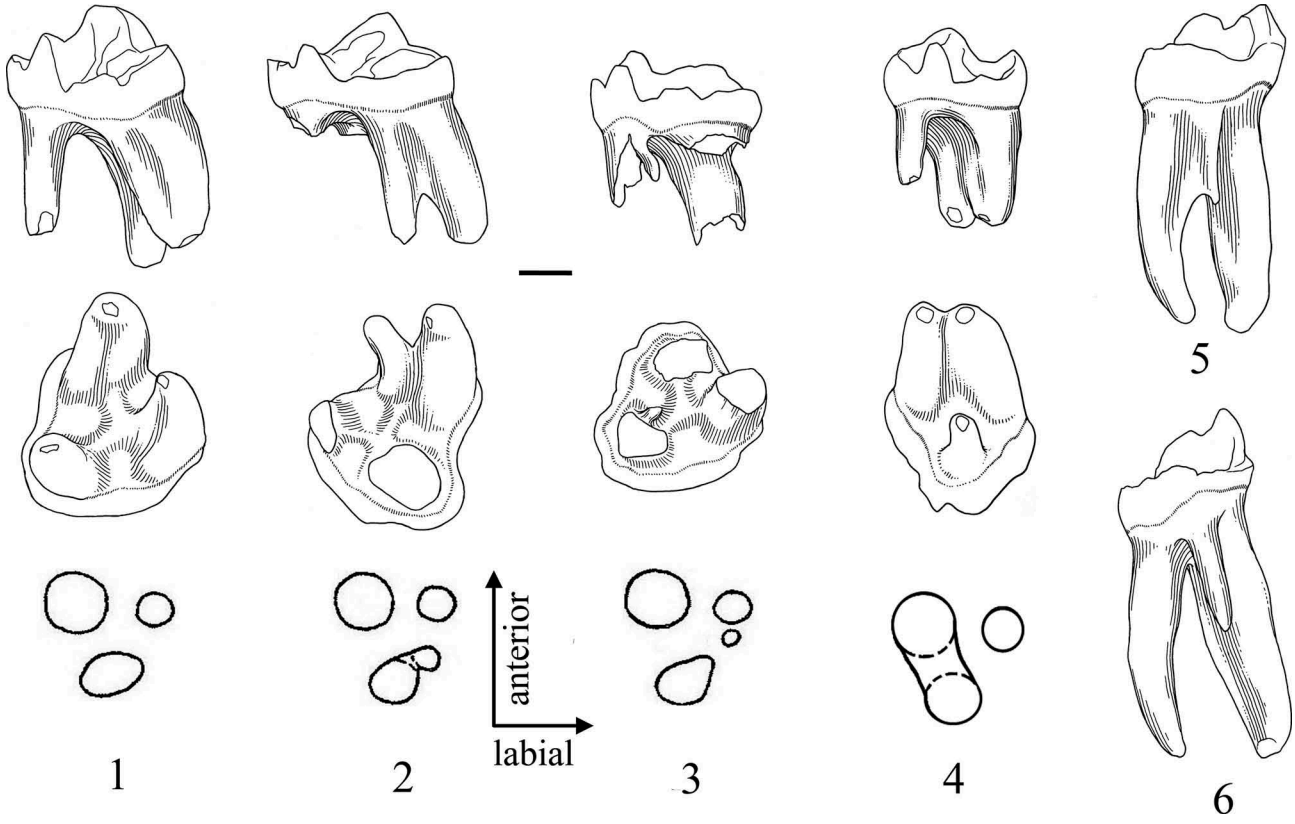

Figure 2. Root part of M3 and p4: 1 – M3 with three roots (Mal'kovo, *S. superciliosus*); 2 – M3 with four roots, additional posterior root (Nitsinskoye, *S. superciliosus*); 3 – M3 with four roots, additional root near anterior external root (Khudolaz, *S. pygmaeus*); 4 – M3 with two roots; (Smelovskaya-II Cave, *S. pygmaeus*); 5 – p4 with inner root merged with the outer in almost the entire length (Pershinskaya Cave, *S. superciliosus*); 6 – p4 with free inner root (Pershinskaya Cave, *S. superciliosus*). 1–4, lover row: schema of roots holes, anterior and labial directions are shown with arrows. 5, 6 – posteriolabial view.

The dental features of fossil ground squirrels

Spermophilus pygmaeus

The teeth show small and medium sizes (Figure 3, see Appendix B). The sizes of all fossil *S. pygmaeus* fall in the area of tooth size variability of the same recent species (see Appendices A and B). Significant differences between the studied fossil samples and the recent ones were revealed for M1-2 and m1-2. It could be an effect of the joining together of the different categories (the firth and the second molars (see Appendix A). The largest sample from Syrtinskaya Cave shows the largest range of values.

Over half P4-M2 bear constrictions or interruptions of the metaloph (Figure 4), metaconule is well pronounced and rounded: in the case of the single M1-2 from Verhnyaya

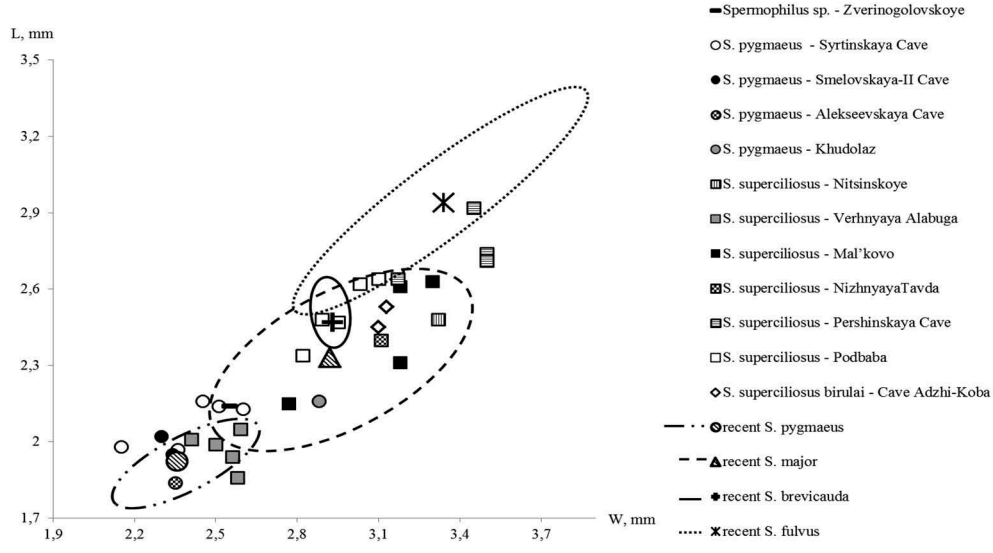

Figure 3. Dimensional characters of P4.

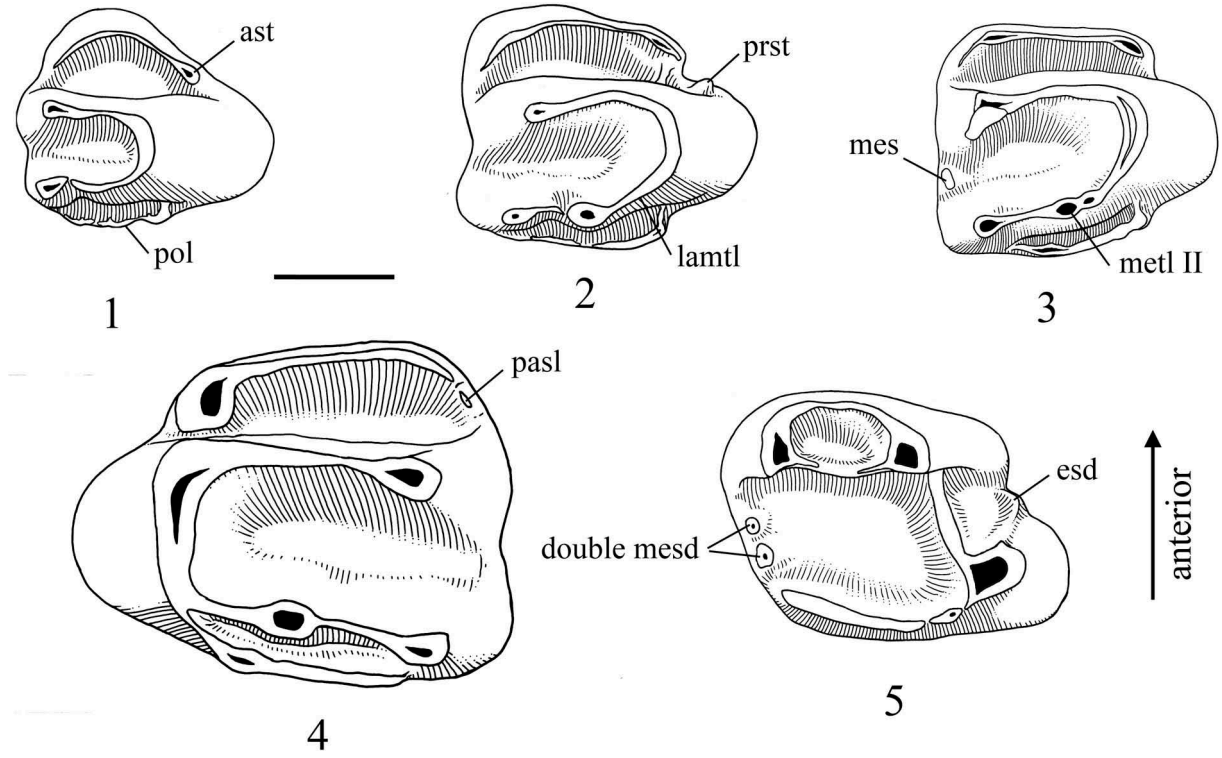

Figure 4. Occlusal view of cheek teeth: 1 – *S. pygmaeus*, Syrtinskaya Cave, P4; 2 – *S. pygmaeus*, Smelovskaya-II Cave, M1-2; 3 – *S. superciliosus*, Nizhnyaya Tavda, M1-2; 4 – *S. superciliosus*, Pershinskaya Cave, M1-2; 5 – *S. superciliosus*, Mal'kovo, m1-2. Abbreviations: ast – anterostyle; esd – ectostylid; lamtl – labial metaloph; mes – mesostyl; double mesd – double mesostylid; metl II – second metaconule; pasl – parastyle; pol – posteroloph. Anterior direction is shown with arrow.

Alabuga, 1 out of 2 P4 (50%), all M1-2 (100%, n = 2) from Smelovskaya-II Cave, 2 out of 5 P4 (40%), all (100%, n = 6) M1-2 from Syrtinskaya Cave, 1 out of 3 M1-2 (33.3%) from Alekseevskaya Cave. The anterostyle is well developed in 1 out of 5 P4 (20%) from Syrtinskaya Cave (Figure 4). The mesostyl occurs in 1 out of 5 P4 (20%) from Syrtinskaya Cave and in near one-third of the fossil M1-2 (2 of the 6 (33.3%) from Syrtinskaya Cave and one out of the three M1-2 (33.3%) from Alekseevskaya Cave). The cusps of additional crests present in some P4-M2 – hypostyle present in 1 out of 5 P4 (20%) and 1 out of 6 M1-2 (16.6%) and protostyle – in 1 out of 6 M1-2 (16.6%) from Syrtinskaya Cave. There is a reduction of the posteroloph or its splitting on separated tubercles in some P4 from Syrtinskaya Cave (Figure 4). In this case, hypocone can be detached and well developed like in 1 out of 6 P4 (16.6%) from Syrtinskaya Cave. The second metaconule occurs in 1 out of 5 P4 (20%), parastyle – in 2 out of 5 P4 (40%) and in 1 out of 6 M1-2 (16.6%) from Syrtinskaya Cave.

The mesostylid present in 5 out of 7 of m1-2 (71.4%), all m3 (100%, n = 2) from Alekseevskaya Cave, all m3 (100%, n = 2) from Syrtinskaya Cave and metastylid – in 2 out of 7 m1-2 (28.6%), 1 out of 3 m3 (33.3%) from Alekseevskaya Cave, all m3 (100%, n = 2) from Syrtinskaya Cave. Ectostylid present in 3 out of 7 of m1-2 (42.8%) teeth from Alekseevskaya Cave: small and weakly defined in the first two, and well pronounced and rounded in the third.

The construction of the root part of M3 is similar to recent teeth. Three roots present in the main part of fossil M3 (5 out of the 6, 83.3%). The anterior inner and posterior roots of the three ones are close together and tend to merge with each other in their upper parts. One tooth from Smelovskaya-II Cave bear two roots – the anterior inner and posterior root are fused with each other (Figure 2).

Two out of three p4 (66.6%) bear one posterior root: the internal posterior root is completely reduced. The third p4 possesses the stepped outgrowth on the single posterior root as a vestige of the inner root. A similar structure of roots was described (Gromov et al. 1965) for Eastern populations of *S. pygmaeus*.

Spermophilus major

The teeth show relatively small and medium sizes. The sizes of fossil *S. major* fall in the area of tooth size variability of the recent *S. major* (see Appendix B).

Significant differences between the studied fossil samples and the recent ones were revealed for M1-2, M3 and m3 (see Appendix A). However, no significant differences were found between the sizes of M3 of Late Holocene and recent samples ($F_{2,47} = 1.86$; $p = 0.18$).

Dimensions of P4 and M1-2 show it best of all (Figure 3, see Appendix B).

The metaloph bears constrictions between metacone and metaconule in some P4-M2 from south localities: in 3 out of 5 M1-2 (60%) from Smelovskaya-II Cave; in 2 out of 6 M1-2 (33.3%) from Syrtinskaya Cave, in a single M1-2 from Alekseevskaya Cave and in 1 out of 2 M1-2 (50%) from Khudolaz.

The parastyle and mesostyl are the most common cusps in fossil M1-2 (Figure 4). The parastyle presents in 1 out of 6 M1-2 (16.6%) from Syrtinskaya Cave; in 1 out of 2 M1-2

(50%) from Khudolaz. The mesostyl presents in 2 out of 6 M1-2 (33.3%) from Syrtinskaya Cave; in 1 out of 5 M1-2 (20%) from Smelovskaya-II Cave. The dual mesostyl occurs in single M1-2 from Alekseevskaya Cave.

The well-developed hypocone occurs in 1 out of 5 M1-2 (20%) from Smelovskaya-II Cave. The protostyle occurs in 1 out of 5 M1-2 (20%) from Smelovskaya-II Cave (Figure 4).

The mesostylid is the most common cusp in fossil m1-3 (Figure 4). It presents in 3 out of 6 m1-2 (50%), in single m3 from Syrtinskaya Cave; in 3 out of 4 of m1-2 (75%) from Alekseevskaya Cave; in 3 out of 4 of m1-2 (75%), in all m3 (100%, n = 2) from Khudolaz.

The ectostylid (Figure 4) is rare, it presents only in one locality: in 1 of 2 m3 (50%) from Smelovskaya-II Cave.

Few teeth: 1 out of 2 M3 (50%) from Syrtinskaya Cave, the single M3 from Smelovskaya-II Cave and the single M3 from Alekseevskaya Cave bear three roots like some recent *S. major*. Some M3 bears complicated variants of the structure of the roots (1 out of 2 M3 (50%) from Syrtinskaya Cave, the single M3 from Khudolaz). There are three low, but defined crests in the bottoms of all these M3. They extend to the main roots from the centre of the bottom (Figure 4).

Two posterior roots are present in fossil p4, the inner root is significantly shorter than the outer, free along the entire length (3 out of 7, 42.8%) (Figure 2) or merged with the outer in almost the entire length (4 out of 7, 57.1%) (Figure 2).

Spermophilus superciliosus

The teeth show relatively small, medium and relatively large sizes. The sizes of fossil *S. superciliosus* fall in the area of tooth size variability of the recent *S. major* (see Appendices A and B). The smallest are the teeth from Verhnyaya Alabuga. Sizes of P4 and M1-2 show it best of all (Figure 3, see Appendix B). On the average, the teeth from Mal'kovo and Pershinskaya Cave are larger than the other. The proportions of some fossil p4 are slightly different from those of the recent *S. major*: in the teeth from Mal'kovo and Pershinskaya Cave the posterior width (W2) is a little bigger than the anterior (W1), in the teeth from Verhnyaya Alabuga, Parenkino and Nizhnyaya Tavda W1 and W2 are approximately equal (see Appendix B).

No significant differences between the studied fossil Late Pleistocene and Holocene samples were revealed (see Appendix A), except m3.

The metaloph bears constriction between metacone and metaconule only in 1 out of 5 P4 (20%) from Verhnyaya Alabuga.

The parastyle and mesostyl are the most common cusps in fossil P4-M2. The parastyle presents in the single P4 from the Middle Pleistocene Nitsinskoye; in the single M1-2 from Parenkino; in 1 out of 5 P4 (20%), and in 6 out of 20 M1-2 (30%) from Mal'kovo; in 1 out of 4 P4 (25%), and in 3 out of 38 M1-2 (7.9%) from Pershinskaya Cave (Figure 4). The mesostyl presents in the single M1-2 from Nitsinskoye; in 1 out of 5 P4 (20%), and in 8 out of 20 M1-2 (40%) from Mal'kovo; in the single P4 and in the single M1-2 from Nizhnyaya Tavda (Figure 4); in 19 out of 40 (47.5%) M1-2 from Pershinskaya Cave.

The paraconule and detached, well-developed rounded hypocone appears only in single P4-M2. The paraconule occurs in 1 out of 5 P4 (20%) from Verhnyaya Alabuga; in 1 out of 20 M1-2 (5%) from Mal'kovo. The well-developed hypocone occurs in the single P4 from Nizhnyaya Tavda. The second metaconule presents only in M1-2. It occurs in 2 out of 3 (66.6%) from Verhnyaya Alabuga; in 1 out of 20 (5%) from Mal'kovo; in the single M1-2 from Nizhnyaya Tavda (Figure 4); in 2 out of 40 (5%) from Pershinskaya Cave.

The mesostylid is the most common cusp in fossil m1-3. It presents in 3 out of 7 m1-2 (42.8%) (in one (14.3%) – also with metastylid) from Nitsinskoye; in 16 out of 21 m1-2 (76.2%) (in two (9.5%) – also with metastylid), in 1 out of 11 m3 (9.1%) from Mal'kovo (Figure 4); in 22 out of 23 m1-2 (95.6%) (in three (13%) – also with metastylid), in 7 out of 10 m3 (70%) (in three (30%) – also with metastylid) from Pershinskaya Cave. The mesoconid appears only in 1 out of 21 of m1-2 (4.7%) from Mal'kovo. The ectostylid (Figure 4) also is rare: it present in 1 out of 21 of m1-2 (4.7%), in 2 out of 11 m3 (18.2%) from Mal'kovo; in 3 out of 23 of m1-2 (13%), in 2 out of 10 of m3 (20%) from Pershinskaya Cave.

The structure of the root part of M3 and p4 is similar to that described for *S. major*.

The main part (6 out of 7, 85.7%) of the Late Pleistocene M3, half of Holocene (14 out of 25, 56%) bear three roots like recent *S. major* (Figure 5). Some Late Pleistocene M3, near the half of Holocene (11 out of 25, 44%) bears complicated variants of the structure of the roots. In a single whole middle Pleistocene M3 (Nitsinskoye) the posterior root is split (complicated variant) (Figure 2).

Two posterior roots are present in fossil p4, the inner root is significantly shorter than the outer, free along the entire length (19 out of 22, 86.3%) (Figure 2), merged with the outer in almost the entire length (2 out of 22, 9.1%) (Figure 2) or slightly merged with the outer in the upper part (1 out of 22, 4.5%).

Spermophilus sp

The teeth from Zverinogolovskoye show medium sizes, some teeth are as the largest recent *S. pygmaeus* or the smallest *S. major*, and some – as the most part of the recent *S. major*. And only one of two p4 is relatively large (see Appendix B). It is a little bigger than the largest recent *S. major*, but smaller than the recent *S. fulvus* (see Appendix B).

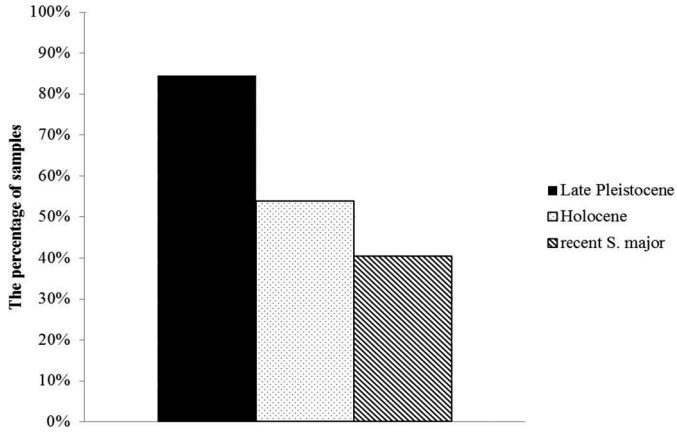

Figure 5. Percentage of M3 with three roots of *S. superciliosus* and recent *S. major*.

The anterostyle is well developed in the single P4 from Zverinogolovskoye. The parastyle and mesostyl present in the single M1-2 from Zverinogolovskoye. The mesostylid present in the single m3 from Zverinogolovskoye.

Discussion

The study of teeth from Zverinogolovskoye showed the presence of both *S. pygmaeus* and *S. superciliosus* in this locality. One specimen (single P4) was indicated as *S. pygmaeus*: it falls into the size range of the recent *S. pygmaeus* and also bears anterostyle. Other specimens (P3, M1-2, p4, m3) were defined as *S. superciliosus*.

Analysis of the dimensional and morphological variability of the fossil *S. pygmaeus* from the Urals, in comparison with the recent one, allowed us to confirm the diagnosis previously made (Kuzmina 2006, 2009; Popova et al. 2019). The most important characteristics of its teeth were chosen. At first, it is the small and medium sizes of the teeth. Then, it is a combination of morphological features: metaloph of P4-M2 bear constrictions or interruptions, metaconule is well pronounced and rounded; anterostyle often is well developed in P4; high frequency of meso- and metastylid in m1-3. In M3 the anterior inner and posterior roots are close together and tend to merge with each other in their upper parts.

The mid-size ground squirrels previously described as *S. major* and *S. superciliosus* (Kuzmina 2006, 2009; Chemagina et al. 2017, 2018; Popova et al. 2019) were compared with the recent *S. major*. Analysis of the dimensional variability of these species showed that they fall in size range of the recent *S. major*.

But there is some difference in size between the Late Pleistocene and Holocene teeth of *S. superciliosus* and *S. major* (see Appendices A and B). Significant differences were found between Late Pleistocene *S. superciliosus* from the Middle Urals and *S. major* from the South Urals for M3 and m3. On the average, M3 and m3 of *S. superciliosus* from the Middle Urals (Mal'kovo) are larger, and M3 and m3 of *S. major* from the South Urals (Syrtinskaya Cave, Smelovskaya-II Cave) are smaller. No significant differences were found between Holocene *S. superciliosus* from the Middle Urals (Pershinskaya Cave) and *S. major* from the South Urals (Alekseevskaya Cave, Khudolaz) (see Appendices A and B).

All teeth from Verhnyaya Alabuga are small and it distinguishes them from *S. superciliosus* from other studied localities. It may be a geographic variability, and it is an occasion for analysis of molars of *S. superciliosus* from other south localities. Ground squirrel from Nitsinskoye possesses the largest P3.

The small amount of the studied fossil material, the lack of material from age-synchronous localities, the lack of detailed information about the limits of morphological variability of *S. major* do not allow us to give an explanation for the revealed differences in size in certain categories of teeth both between Late Pleistocene *Spermophilus superciliosus* and *Spermophilus major*, and between the fossil and recent *Spermophilus major*.

The morphological variability of the dental structures of *S. superciliosus* and fossil *S. major* is also similar to that of the recent *S. major*. These species are characterised by the small number of upper teeth with the occlusal cusps. The presence of parastyle in the fossil P4-M2 is the most significant and brings them together with *S. major*. Commonly occurring in m1-2 mesostylid brings them together with *S. major*. Thus, no significant differences of the studied fossil *S. major* and *S. superciliosus* from the recent *S. major* were revealed. And there are also some morphological peculiarities: second metaconule presents only in M1-2 of *S. superciliosus*; metaloph bears constrictions between metacone and metaconule only in some P4-M2 fossil *S. major*.

To address the issue of belonging of the Ural mid-size fossil ground squirrel to the *S. superciliosus*, the comparison of recent *S. major*, fossil *S. major* and *S. superciliosus* from the Urals and *S. superciliosus* from Eastern Europe (localities Podbaba and Adzhi-Koba Cave) also was carried out.

The sizes of fossil *S. superciliosus* from Podbaba fall in the area of tooth size variability of the recent *S. major* (see Appendix B). The sizes of all teeth of *S. superciliosus birulai* from Adzhy-Koba are little bigger than *S. superciliosus* from Podbaba. The average dimensions of *S. superciliosus birulai* are larger than those of recent *S. major*, but they are smaller than those of recent *S. fulvus*. Recent *S. major* shows a wide range of all teeth size variability even within the same area of the Ural (see Appendix B). The size variability of *S. superciliosus* is not so wide.

The parastyle presents in all M1-2 (100%, n = 8) from Adzhy-Koba and all M1-2 (100%, n = 7) from Podbaba. The mesostyl presents in 2 out of 7 M1-2 (28.6%) from Podbaba. The mesostylid presents in all m1-2 (100%, n = 4) from Podbaba. The single M3 from Adzhy-Koba bears 3 roots.

The comparison was performed with literary data of *S. superciliosus* (Storch von 1980; Heinrich 1983; Andreasen 1997). This study made us sure that Pleistocene and Holocene teeth from the localities of the Middle and South Urals and Trans-Urals are in average close in size to *S. superciliosus* from Europe, although there are specimens that exceed them or are smaller.

No significant difference in morphology was found. The dimensions of the teeth were also similar, except P3: this premolar of the ground squirrels from Podbaba, Adzhi-Koba Cave (Eastern Europe) and Nitsinskoye (Middle Trans-Urals) is slightly larger (see Appendix B). Gromov et al. (1965, p. 303) defined S. *superciliosus* as a large ground squirrel that was very similar to *S. major* in size, but possessed relatively large P3. Tooth characteristic of *S. superciliosus* was close to *S. fulvus*.

The above allows us to confirm the diagnosis previously made for fossil *S. major* (the localities Smelovskaya-II Cave, Syrtinskaya Cave, Alekseevskaya Cave and Khudolaz), and compels us to raise the question of clarifying the species status of fossil *S. superciliosus* (the localities Parenkino, Mal'kovo, Nizhnyaya Tavda, Pershinskaya Cave and Verhnyaya Alabuga).

It should be noted that there are some differences between fossils and modern mid-sized ground squirrels from the Urals: the tendency to complication of the root system of M3 is revealed from Late Pleistocene to Holocene. This contradicts the notions of Gromov et al. (1965), who pointed to the reduction in the number of roots in the lineage *S. superciliosus* – *S. major*, and is an occasion for a detailed analysis of the roots variability within the genus *Spermophilus*.

L.V. Popova notes (2016) that the presence of protostyle is the very important feature of the recent *S. fulvus* and the fossil *S. superciliosus* (fulvoid pattern of bunodonty). This observation was confirmed by our study on *S. fulvus*. But protostyle was not found in any tooth of a middle- large-sized ground squirrel from the Urals.

An important and unresolved issue today is the reconstruction of the *S. superciliosus* area. Remains of middle- large-sized ground squirrel have repeatedly been found in the loose sediments of Central Europe. They have been described under different names: *Spermophilus altaicus, Citellus rufescens, Citellus major, Citellus superciliosus* (Storch von 1980; Heinrich 1983; Andreasen 1997; Popova et al. 2019). T.N. Andreasen (1997) states a doubt that *S. superciliosus* is a true species. He believes that *S. superciliosus* may be only one of the subspecies of *S. major*. Further research such as extensive analysis of cranial and dental features of both fossil large Pleistocene ground squirrel and *S. major*, as well as the analysis of fossil DNA, can clarify the status of *S. superciliosus*.

Conclusion

The previously made determination of small-sized ground squirrel from South Urals (Smelovskaya-II Cave, Syrtinskaya Cave, Alekseevskaya Cave, Khudolaz; Late Pleistocene – Late Holocene) as *S. pygmaeus* is confirmed. The most important features of its teeth are: small and medium sizes; metaloph of P4-M2 bear constrictions or interruptions, metaconule is well pronounced and rounded; anterostyle often is well developed in P4; high frequency of meso- and metastylid in m1-3. In M3 the anterior inner and posterior roots are close together and tend to merge with each other in their upper parts.

The previously made determination of mid- and large-sized ground squirrel from South Urals (Smelovskaya-II Cave, Syrtinskaya Cave, Alekseevskaya Cave, Khudolaz; Late Pleistocene – Late Holocene) as *S. major* is confirmed. Fossil *S. superciliosus* from the Middle and South Trans-Urals (Parenkino, Mal'kovo, Nizhnyaya Tavda, Pershinskaya Cave and Verhnyaya Alabuga; Late Pleistocene – Late Holocene) is similar to *S. major*. The most important features of its teeth are: medium and large sizes; a small number of P4-M2 with the occlusal cusps, among them the most significant is the presence of parastyle; in m1-2 mesostylid commonly occurs. The tendency to complication of the root system of M3 is revealed from Pleistocene to Holocene.

The study of teeth from Zverinogolovskoye (South Trans-Urals, Late Pleistocene) showed the presence of both *S. pygmaeus* and *S. superciliosus* in this locality.

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Appendix A. Table A1–A7. ANOVA results

Table A1. Repeated measures analysis of variance of the teeth length (L) and width (W) of the recent ground squirrels (*Spermophilus major, S. pygmaues, S. fulvus*).

	Effect					Error		
Category of teeth	SS	DF	MS	F	p	SS	DF	MS
P3	4.54	2	2.27	21.64	**0.00**	7.03	67	0.10
P4	12.14	2	6.07	59.87	**0.00**	7.10	70	0.10
M1	18.04	2	9.02	62.57	**0.00**	10.81	75	0.14
M2	17.33	2	8.67	70.11	**0.00**	9.64	78	0.12
M3	16.97	2	8.49	57.75	**0.00**	11.46	78	0.15
p4	19.21	2	9.61	49.97	**0.00**	14.99	78	0.19
m1	22.61	2	11.31	68.60	**0.00**	14.34	87	0.16
m2	25.89	2	12.95	71.31	**0.00**	17.61	97	0.18
m3	42.65	2	21.33	123.04	**0.00**	14.04	81	0.17

Note: SS – sum of squares, DF – degrees of freedom, MS – mean square, F – Fisher's statistic, p – probability values. Significant differences are highlighted in bold.

Table A2. Repeated measures analysis of variance of the teeth length (L) and width (W) of the fossil and recent *Spermophilus pygmaues.*

	Effect					Error		
Category of teeth	SS	DF	MS	F	p	SS	DF	MS
P4	0.07	2	0.03	1.081	0.35	0.95	30	0.03
M1-2	0.46	4	0.12	4.606	**0.00**	1.40	56	0.03
M3	0.20	1	0.20	2.34	0.14	2.50	29	0.09
p4	0.20	1	0.20	2.34	0.14	2.50	29	0.09
m1-2	1.22	2	0.61	6.51	**0.00**	5.70	61	0.09
m3	0.97	2	0.48	3.21	0.05	4.67	31	0.15

Table A3. Repeated measures analysis of variance of the teeth length (L) and width (W) of the fossil and recent *Spermophilus major.*

	Effect					Error		
Category of teeth	SS	DF	MS	F	p	SS	DF	MS
M1-2	1.9760	3	0.66	3.87	**0.01**	9.01	53	0.17
M3	2.2050	2	1.11	7.63	**0.00**	7.51	52	0.14
p4	0.3138	2	0.16	0.68	0.51	11.94	52	0.23
m1-2	0.1697	2	0.08	0.42	0.66	10.86	54	0.201
m3	1.8792	2	0.94	5.08	**0.01**	8.87	48	0.18

Table A4. Repeated measures analysis of variance of the teeth length (L) and width (W) of *Spermophilus superciliosus* and recent *Spermophilus major.*

	Effect					Error		
Category of teeth	SS	DF	MS	F	p	SS	DF	MS
P4	0,051	1	0,051	0,34	0,56	7,82	52	0,15
M1-2	0.18	1	0.18	1.09	0.30	10.38	63	0.17
M3	0.15	1	0.15	0.93	0.34	10.32	63	0.16
p4	0.00	1	0.00	0.001	0.97	13.21	63	0.21
m1-2	0.21	1	0.21	1.01	0.32	13.25	63	0.21
m3	0.004	1	0.004	0.02	0.89	11.51	63	0.18

Table A5. Repeated measures analysis of variance of the teeth length (L) and width (W) of the Late Pleistocene and Holocene *Spermophilus superciliosus* from the Middle Trans-Urals.

	Effect					Error		
Category of teeth	SS	DF	MS	F	p	SS	DF	MS
P4	0.18	1	0.18	1.85	0.22	0.57	6	0.10
M1-2	0.03	1	0.02	0.23	0.63	2.51	25	0.10
M3	0.068	2	0.03	0.22	0.81	4.15	28	0.15
p4	0.00	1	0.00	0.00	0.97	2.86	18	0.16
m1-2	0.14	2	0.07	0.50	0.61	3.57	26	0.14
m3	1.32	2	0.66	4.21	**0.03**	3.44	22	0.16

Table A6. Repeated measures analysis of variance of the teeth length (L) and width (W) of the Late Pleistocene *Spermophilus superciliosus* and *Spermophilus major*.

	Effect					Error		
Category of teeth	SS	DF	MS	F	p	SS	DF	MS
M1-2	1.54	2	0.77	7.51	**0.00**	2.25	22	0.10
M3	0.97	1	0.97	14.84	**0.01**	0.46	7	0.07
p4	0.24	1	0.24	1.22	0.29	2.19	11	0.20
m1-2	0.08	1	0.08	1.45	0.25	0.84	16	0.05
m3	1.48	1	1.48	11.34	**0.01**	1.43	11	0.13

Table A7. Repeated measures analysis of variance of the teeth length (L) and width (W) of the Holocene *Spermophilus superciliosus* and *Spermophilus major*.

	Effect					Error		
Category of teeth	SS	DF	MS	F	p	SS	DF	MS
M1-2	0.01	1	0.01	0.08	0.77	0.87	13	0.07
M3	0.48	1	0.48	3.55	0.07	3.38	25	0.14
p4	0.06	1	0.06	0.47	0.53	1.70	12	0.14
m1-2	0.12	1	0.12	0.56	0.47	2.82	13	0.22
m3	0.18	1	0.18	1.19	0.30	1.35	9	0.15

Appendix B. Table B1–B7. Dental dimensions (min – average – max, SE) of the fossil and recent *Spermophilus*

Table B1. Dental dimensions of P3.

Species	Locality	n	L	W	L/W
Spermophilus pygmaeus Pallas, 1778	Syrtinskaya Cave	1	1.62	1.85	87.56
recent *S. pygmaeus*		16	1.27 – 1.60 – 1.88 ± 0.04	1.32 – 1.67 – 2.06 ± 0.04	87.01 – 95.82 – 100.62 ± 1.00
S. superciliosus Kaup, 1839	Nitsinskoye	1	2.27	2.28	99.56
	Verhnyaya Alabuga	1	1.71	1.90	90.00
	Pershinskaya Cave	1	1.87	1.94	96.39
S. superciliosus	Podbaba, Czech	5	1.90 – 1.98 – 2.18 ± 0.06	2.00 – 2.06 – 2.20 ± 0.03	91.78 – 96.18 – 99.09 ± 1.21
S. superciliosus birulai	Cave Adzhi-Koba, Crimea	1	2.10	2.12	99.05
Spermophilus sp.	Zverinogolovskoye	1	2.11	2.26	93.36
recent *S. major* Pallas, 1778		46	1.42 – 1.86 – 2.20 ± 0.03	1.26 – 1.97 – 2.41 ± 0.04	85.48 – 94.51 – 127.12 ± 1.12
recent *S. fulvus* Lichtenstein, 1823		6	2.11 – 2.35 – 2.71 ± 0.09	1.98 – 2.37 – 2.60 ± 0.12	82.02 – 99.64 – 108.58 ± 4.06

Table B2. Dental dimensions of P4.

Species	Locality	n	L	W	L/W
Spermophilus pygmaeus Pallas, 1778	Syrtinskaya Cave	5	1.97 – 2.07 – 2.16 ± 0.06	2.15 – 2.41 – 2.60 ± 0.10	81.9 – 86.18 – 92.09 ± 1.64
	Smelovskaya-II Cave	2	1.95	2.3	83.33
			2.02	2.34	87.82
	Alekseevskaya Cave	1	1.84	2.35	78.29
	Khudolaz	1	2.16	2.81	76.87
recent *S. pygmaeus*		26	1.75 – 1.92 – 2.07 ± 0.02	2.1 – 2.36 – 2.67 ± 0.02	74.9 – 81.36 – 90.27 ± 0.73
S. superciliosus Kaup, 1839	Nitsinskoye	1	2.48	3.32	74.69
	Verhnyaya Alabuga	5	1.87 – 1.97 – 2.05 ± 0.03	2.41 – 2.52 – 2.59 ± 0.03	72.09 – 78.00 – 83.4 ± 1.90
	Mal'kovo	4	2.15 – 2.42 – 2.63 ± 0.11	2.77 – 3.10 – 3.30 ± 0.11	72.64 – 78.00 – 82.07 ± 2.00
	NizhnyayaTavda	1	2.40	3.11	77.17
	Pershinskaya Cave	4	2.64 – 2.75 – 2.92 ± 0.05	3.17 – 3.40 – 3.50 ± 0.07	77.42 – 80.90 – 84.63 ± 1.79
S. superciliosus	Podbaba, Czech	5	2.34 – 2.51 – 2.64 ± 0.05	2.82 – 2.95 – 3.10 ± 0.04	82.97 – 84.83 – 86.46 ± 1.25
S. superciliosus birulai	Cave Adzhi-Koba, Crimea	2	2.45	3.10	80.83
			2.53	3.13	79.03
Spermophilus sp.	Zverinogolovskoye	1	2.14	2.55	83.92
recent *S. major* Pallas, 1778		40	1.95 – 2.33 – 2.75 ± 0.03	1.97 – 2.92 – 3.42 ± 0.04	67.94 – 79.60 – 95.55 ± 1.13
recent *S. fulvus* Lichtenstein, 1823		6	2.54 – 2.94 – 3.42 ± 0.12	2.82 – 3.34 – 3.84 ± 0.15	83.54 – 88.17 – 90.08 ± 0.97

Table B3. Dental dimensions of M1-2.

Species	Locality	n	L	W	L/W
Spermophilus pygmaeus Pallas, 1778	Verhnyaya Alabuga	1	2.01	2.60	77.31
	Syrtinskaya Cave	6	1.85 – 1.95 – 2.02 ± 0.02	2.42 – 2.45 – 2.50 ± 0.01	76.13 – 79.68 – 83.47 ± 1.15
	Smelovskaya-II Cave	2	1.80	2.23	80.71
			1.86	2.33	79.82
	Alekseevskaya Cave	3	1.80	2.43	74.07
			2.03	2.65	76.60
			2.10	2.85	73.68
	Khudolaz	1	1.72	2.10	81.90
recent *S. pygmaeus*	M1	26	1.70 – 1.95 – 2.18 ± 0.02	2.43 – 2.57 – 2.86 ± 0.02	69.11 – 75.92 – 80.77 ± 0.59
	M2	24	1.75 – 2.03 – 2.20 ± 0.02	2.43 – 2.65 – 3.06 ± 0.03	70.59 – 76.75 – 82.40 ± 0.68
S. superciliosus Kaup, 1839	Nitsinskoye	1	2.27	3.30	81.25
	Verhnyaya Alabuga	3	2.14	2.73	78.38
			2.15	2.75	78.18
			2.17	2.86	75.87
	Mal'kovo	14	2.10 – 2.48 – 2.78 ± 0.05	2.85 – 3.39 – 3.97 ± 0.08	66.57 – 73.48 – 77.99 ± 0.91
	Parenkino	1	2.45	3.26	75.15
	NizhnyayaTavda	1	2.27	3.30	67.47
	Pershinskaya Cave	13	2.30 – 2.54 – 2.77 ± 0.04	3.10 – 3.41 – 3.92 ± 0.06	68.58 – 74.61 – 79.35 ± 0.96
S. superciliosus	Podbaba, Czech (M1)	6	2.27 – 2.43 – 2.56 ± 0.04	3.07 – 3.24 – 3.47 ± 0.06	73 – 74.97 – 76.68 ± 0.96
	Podbaba, Czech (M2)	5	2.34 – 2.63 – 2.98 ± 0.12	3.12 – 3.47 – 3.68 ± 0.1	71.25 – 75.67 – 80.97 ± 1.91
S. superciliosus birulai	Cave Adzhi-Koba, Crimea (M1)	4	2.43 – 2.52 – 2.58 ± 0.03	3.16 – 3.29 – 3.42 ± 0.05	74.31 – 76.98 – 80.06 ± 1.35
	Cave Adzhi-Koba, Crimea (M2)	4	2.41 – 2.71 – 3.06 ± 0.13	3.28 – 3.49 – 3.78 ± 0.12	71.15 – 77.58 – 84.75 ± 3.17
Spermophilus sp.	Zverinogolovskoye	1	2.38	3.18	74.84
S. major Pallas, 1778	Syrtinskaya Cave	6	2.13 – 2.28 – 2.58 ± 0.06	2.58 – 2.87 – 3.13 ± 0.08	72.2 – 79.69 – 85.65 ± 2.40
	Smelovskaya-II Cave	5	2.13 – 2.28 – 2.41 ± 0.05	2.49 – 2.95 – 3.35 ± 0.14	68.65 – 76.49 – 86.74 ± 3.04
	Alekseevskaya Cave	1	2.60	3.52	73.86
	Khudolaz	2	2.49	3.56	69.94
			2.53	3.50	72.29
recent *S. major*	M1	45	1.94 – 2.41 – 2.96 ± 0.04	2.69 – 3.42 – 4.26 ± 0.05	61.81 – 70.52 – 82.04 ± 0.67
	M2	49	2.00 – 2.52 – 3.28 ± 0.04	2.85 – 3.39 – 3.96 ± 0.04	63.25 – 74.40 – 87.03 ± 0.83
recent *S. fulvus* Lichtenstein, 1823	M1	7	2.49 – 2.81 – 3.04 ± 0.08	3.17 – 3.57 – 3.99 ± 0.13	75.18 – 78.82 – 85.15 ± 1.3
	M2	8	2.38 – 2.93 – 3.26 ± 0.04	3.29 – 3.70 – 4.11 ± 0.12	72.26 – 79.11 – 86.33 ± 1.79

Table B4. Dental dimensions of M3.

Species	Locality	n	L	W	L/W
Spermophilus pygmaeus Pallas, 1778	Syrtinskaya Cave	4	2.51 – 2.69 – 2.80±0.06	2.40 – 2.50 – 2.60±0.04	104.58 – 107.79 – 111.11 ± 1.42
	Smelovskaya-II Cave	1	2.67	2.50	106.80
	Alekseevskaya Cave	1	2.72	2.43	111.93
recent *S. pygmaeus*		27	2.41 – 2.81 – 3.30 ± 0.04	2.45 – 2.71 – 3.40 ± 0.04	92.94 – 103.77 – 115.35 ± 1.06
S. superciliosus Kaup, 1839	Nitsinskoye	2	3.31	2.62	126.82
			3.61	3.20	100.84
	Verhnyaya Alabuga	1	3.30	3.04	108.55
	Mal'kovo	5	3.27 – 3.45 – 3.88 ± 0.11	2.90 – 3.29 – 3.52 ± 0.10	95.91 – 105.11 – 112.76 ± 2.98
	Pershinskaya Cave	24	2.61 – 3.37 – 3.84± 0.06	2.71 – 3.20 – 3.71± 0.05	91.37 – 105.17 – 116.51 ± 1.14
S. superciliosus	Podbaba, Czech	3	3.51	3.37	104.15
			3.52	3.34	105.38
			3.58	3.37	106.23
S. superciliosus birulai	Cave Adzhi-Koba, Crimea	4	3.69 – 3.99 – 4.26± 0.13	3.57 – 3.79 – 4.08± 0.1	102.12 – 105.18 – 110.84 ± 1.94
S. major Pallas, 1778	Syrtinskaya Cave	4	2.89 – 3.08 – 3.22± 0.08	2.57 – 2.73 – 2.91± 0.07	102.48 – 112.93 – 125.29 ± 4.70
	Smelovskaya-II Cave	1	3.23	3.12	103.53
	Khudolaz	3	2.91	2.94	98.97
			3.02	2.98	101.34
			3.16	2.91	108.59
recent *S. major*		48	2.87 – 3.43 – 4.17± 0.04	2.82 – 3.29 – 4.05 ± 0.04	90.12 – 104.36 – 111.25 ± 0.60
recent *S. fulvus* Lichtenstein, 1823		7	3.52 – 3.99 – 4.64 ± 0.14	3.29 – 3.69 – 4.27 ± 0.15	98.21 – 108.65 – 114.47 ± 2.05

Table B5. Dental dimensions of p4.

Species	Locality	n	L	W1	W2	W2/W1	W2/L
Spermophilus pygmaeus Pallas, 1778	Syrtinskaya Cave	3	1.69 1.81 1.83	1.38 1.94 1.84	1.66 1.68 1.77	120.28 86.59 96.19	98.22 92.81 96.72
	Alekseevskaya Cave	3	1.83 1.96	1.96 2.03	1.86 1.9	94.89 93.59	101.63 96.93
recent *S. pygmaeus*		28	1.47 – 1.84 – 2.30 ± 0.03	1.61 – 1.97 – 2.42 ± 0.03	1.49 – 1.87 – 2.38 ± 0.04	78.3 – 95.2 – 107.69 ± 1.22	86.45 – 101.8 – 113.58 ± 1.16
S. superciliosus Kaup, 1839	Nitsinskoye	1	2.50	2.62	2.69	102.67	107.6
	Verhnyaya Alabuga	1	1.90	2.08	2.06	99.03	108.42
	Mal'kovo	9	1.90 – 2.25 – 2.48 ± 0.06	2.00 – 2.37 – 2.72 ± 0.08	1.90 – 2.40 – 2.83 ± 0.09	92.13 – 101.39 – 112.5 ± 2.37	100.00 – 106.75 – 117.92 ± 2.05
	Parenkino	1	2.07	2.26	2.24	99.11	108.21
	Nizhnyaya Tavda	1	2.20	2.34	2.31	98.71	105.00
	Pershinskaya Cave	11	1.85 – 2.12 – 2.40 ± 0.06	2.06 – 2.44 – 2.91 ± 0.08	2.00 – 2.48 – 2.94 ± 0.25	90.63 – 102.03 – 115.74 ± 2.10	106.95 – 117.14 – 128.2 ± 2.29
S. superciliosus	Podbaba, Czech	2	2.20 2.30	2.55 2.67	2.55 2.79	100.00 104.49	115.9 126.81
Spermophilus sp.	Zverinogolovskoye	2	2.53 2.68	2.62 2.75	2.56 2.67	97.70 97.09	101.58 99.62
S. major Pallas, 1778	Syrtinskaya Cave	4	2.13 – 2.39 – 2.53 ± 0.08	1.96 – 2.60 – 2.96 ± 0.22	2.06 – 2.56 – 2.91 ± 0.18	95.13 – 98.92 – 105.1 ± 2.16	96.71 – 106.62 – 117.34 ± 4.27
	Alekseevskaya Cave	1	2.10	2.01	1.91	95.02	90.95
	Khudolaz	3	2.22 2.28 2.45	2.61 2.39 2.55	2.53 2.35 2.61	96.93 98.33 102.35	114.48 103.07 106.53
recent *S. major*		50	1.72 – 2.28 – 2.61 ± 0.03	1.55 – 2.46 – 2.98 ± 0.04	1.61 – 2.31 – 2.93 ± 0.04	82.50 – 94.22 – 119.19 ± 1.12	88.8 – 101.25 – 123.04 ± 1.10
recent *S. fulvus* Lichtenstein, 1823		8	2.82 – 3.13 –3.46 ± 0.06	3.01 – 3.29 – 3.54 ± 0.07	2.80 – 3.13 – 3.61 ± 0.1	89.31 – 95.04 – 102.68 ± 1.51	91.27 – 100.15 – 114.66 ± 3.47

Table B6. Dental dimensions of m1-2.

Species	Locality	n	L	W	L/W
Spermophilus pygmaeus Pallas, 1778	Syrtinskaya Cave	1	2.05	2.41	85.06
	Alekseevskaya Cave	7	1.86 – 1.96 – 2.07 ± 0.03	2.71 – 2.89 – 3.1 ± 0.04	65.03 – 68.12 – 73.8 ± 0.94
recent *S. pygmaeus*	m1	29	1.43 – 1.87 – 2.24 ± 0.04	1.97 – 2.56 – 3.2 ± 0.05	64.37 – 73.39 – 83.4 ± 0.83
	m2	28	1.70 – 2.06 – 2.42 ± 0.04	2.18 – 2.76 – 3.48 ± 0.05	68.64 – 75.08 – 86.23 ± 0.79
S. superciliosus Kaup, 1839	Nitsinskoye	6	2.26 – 2.53 – 2.74 ± 0.06	2.70 – 3.04 – 3.24 ± 0.08	80.00 – 83.34 – 88.43 ± 1.25
	Verhnyaya Alabuga	3	1.99 2.01 2.22	2.78 2.37 3.02	71.58 84.81 73.50
	Mal'kovo	12	2.17 – 2.46 – 2.74 ± 0.04	3.05 – 3.29 – 3.64 ± 0.05	64.56 – 74.87 – 82.87 ± 1.39
	Nizhnyaya Tavda	1	2.20	2.62	83.90
	Pershinskaya Cave	11	1.83 – 2.5 – 3.11 ± 0.11	2.41 – 3.05 – 3.64 ± 0.11	69.38 – 81.95 – 93.04 ± 3.06
S. superciliosus	Podbaba, Czech (m1)	2	2.23 2.41	3.41 3.51	65.39 68.66
	Podbaba, Czech (m2)	2	2.38 2.47	3.53 3.58	67.42 68.99
S. superciliosus birulai	Cave Adzhi-Koba, Crimea (m2)	1	2.86	3.67	77.92
S. major Pallas, 1778	Syrtinskaya Cave	6	2.32 – 2.45 – 2.64 ± 0.05	2.78 – 3.11 – 3.40 ± 0.09	69.70 – 79.24 – 84.3 ± 2.14
	Alekseevskaya Cave	4	2.11 – 2.24 – 2.49 ± 0.08	2.84 – 3.12 – 3.65 ± 0.18	68.22 – 72.23 – 75.35 ± 1.52
	Khudolaz	4	2.32 – 2.38 – 2.43 ± 0.02	3.08 – 3.48 – 3.69 ± 0.13	63.41 – 68.65 – 75.32 ± 2.58
recent *S. major*	m1	52	1.61 – 2.25 – 3.02 ± 0.04	2.28 – 3.22 – 3.96 ± 0.06	60.25 – 69.97 – 88.27 ± 0.75
	m2	63	2.06 – 2.53 – 3.22 ± 0.03	2.77 – 3.59 – 4.48 ± 0.05	61.72 – 70.86 – 86.03 ± 0.71
recent *S. fulvus* Lichtenstein, 1823	m1	9	2.78 – 2.93 – 3.18 ± 0.04	3.44 – 3.89 – 4.24 ± 0.08	69.70 – 75.52 – 81.03 ± 1.43
	m2	9	2.90 – 3.12 – 3.29 ± 0.04	3.84 – 4.14 – 4.54 ± 0.09	71.19 – 75.55 – 81.66 ± 1.12

Table B7. Dental dimensions of m3.

Species	Locality	n	L	W	L/W
Spermophilus pygmaeus Pallas, 1778	Syrtinskaya Cave	2	2.51	1.82	137.91
			2.70	1.87	144.38
	Alekseevskaya Cave	3	2.84	2.54	111.81
			2.95	2.26	130.53
			3.18	2.74	116.05
recent *S. pygmaeus*		29	2.06 – 2.88 – 3.51 ± 0.06	2.01 – 2.56 – 3.1 ± 0.05	97.28 – 112.69 – 124.43 ± 1.34
S. superciliosus Kaup, 1839	Nitsinskoye	6	2.90 – 3.41 – 3.96 ± 0.16	2.71 – 2.96 – 3.38 ± 0.09	101.75 – 115.26 – 133.78 ± 4.91
	Verhnyaya Alabuga	1	2.97	2.76	107.60
	Mal'kovo	11	3.31 – 3.91 – 4.61 ± 0.11	2.91 – 3.27 – 3.62 ± 0.07	100.55 – 120.08 – 137.66 ± 3.94
	Pershinskaya Cave	8	3.37 – 3.89 – 4.92 ± 0.16	2.98 – 3.16 – 3.55 ± 0.06	110.70 – 122.89 – 138.59 ± 3.64
S. superciliosus	Podbaba	2	3.63	3.26	111.34
			3.65	3.24	112.65
S. superciliosus birulai	Cave Adzhi-Koba, Crimea	1	4.23	3.81	111.02
Spermophilus sp.	Zverinogolovskoye	1	3.61	2.85	126.67
S. major Pallas, 1778	Syrtinskaya Cave	1	3.25	2.76	117.75
	Smelovskaya-II Cave	2	3.31	2.83	116.96
			2.91	2.68	108.58
	Alekseevskaya Cave	1	3.34	3.05	109.51
	Khudolaz	3	3.62	3.17	114.19
			3.68	2.96	124.32
			3.78	2.77	136.46
recent *S. major*		46	3.08 – 3.77 – 4.78 ± 0.05	2.77 – 3.37 – 4.08 ± 0.04	92.98 – 112.13 – 139.76 ± 1.4
recent *S. fulvus* Lichtenstein, 1823		9	3.94 – 4.26 – 4.67 ± 0.07	4.03 – 4.30 – 4.69 ± 0.07	94.14 – 99.03 – 106.90 ± 1.27