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Finding of Molars of the Archaic Vole *Lasiopodomys* (*Stenocranius*) *Gregaloides* (Hinton, 1923) (Mammalia, Rodentia, Cricetidae) in the Late Pleistocene of the Southern Urals

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Abstract—A total of 1250 lower first molars (m1) of voles (Arvicolini) were studied from Late Pleistocene deposits (the radiocarbon dates from rodent bones: 17 100 ± 50 $IGAN_{AMS}$-9117; 13 255 ± 60 $IGAN_{AMS}$-9116) of the Imanay Cave (southern Urals, 53°02' N, 56°26' E). Of these, 24 m1 of voles of the subgenus *Stenocranius* were found to have broadly connected triangles T4 and T5 (*Pitymys*–Rhombus) at the base of the anteroconid. This structure is characteristic of lower m1 of *Lasiopodomys (Stenocranius) gregaloides* (Hinton, 1923) from faunas of the second half of the Early Pleistocene and the first half of the Middle Pleistocene. Molars with such morphology have not been found so far in the Late Pleistocene and Holocene locations of Europe and the Urals.

Keywords: *Lasiopodomys* (*Stenocranius*) *gregaloides*, Arvicolini, Rodentia, Late Pleistocene, Ural, Imanay Cave

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Distinct, chronologically consecutive changes in the shape of the chewing surface of the first molar (m1) have been observed in certain phyletic lineages of a group of vole genera (Arvicolini) [1]. The lineages are among the most important biostratigraphic markers, which have been used to reconstruct the biochronology of the Pleistocene. The set includes the lineage *Lasiopodomys* (*Stenocranius*) *hintoni* (Kretzoi, 1941)–*L.* (*S.*) *gregaloides* (Hinton, 1923)–*L.* (*S.*) *gregalis* (Pallas, 1779). In Europe, the first form emerged at the end of the Early Pleistocene (approximately 1 million years ago). The second form replaced the first one in the early Middle Pleustocene (approximately 0.75 million years ago), and the modern species *L.* (*S.*) *gregalis* arose in the middle of the Middle Pleistocene (approximately 0.6 million years ago) [2]. Thus, the vole lineage has existed for approximately 1 million years. The species had a broad geographic distribution. The range of *L.* (*S.*) *hintoni* and *L.* (*S.*) *gregaloides* included Europe and West Siberia, and the *S. gregalis* range included a major part of Europe and North Asia up to Transbaikalia in the Pleistocene [3, 4]. This broad spatial and temporal distribution was associated with a distinct chronological and geographic variation in tooth size and morphotypes [2, 3, 5]. However, the variation has not been studied for a number of regions and chronological periods. Here we describe the new findings of the phyletic lineage from the Imanay Cave of the southern Urals.

Loose deposits were examined in the Imanay Cave (Meleuz District, Bashkortostan Republic, Russia; 53°02′ N, 56°26′ E). There are two layers in the deposits. Layer 1 is 0.6 m deep and consists of grayish clayish soil with chalkstone debris; single flint artifacts are found. Layer 2 is 0.6 m deep and consists of brown clayish soil with single chalkstone boulders [6]. The deposits were excavated by 0.1-m conventional layers. In addition to bones of larger mammals [7], 15 430 teeth and jaws were found to belong to small mammals of the orders Euliphotyphla, Chiroptera, Lagomorpha, and Rodentia. The collection is stored in the museum of the Institute of Ecology (Ural Branch, Russian Academy of Sciences) under no. 2284.

Two radiocarbon dates were obtained using collagen of small mammalian bones: 17 100 ±

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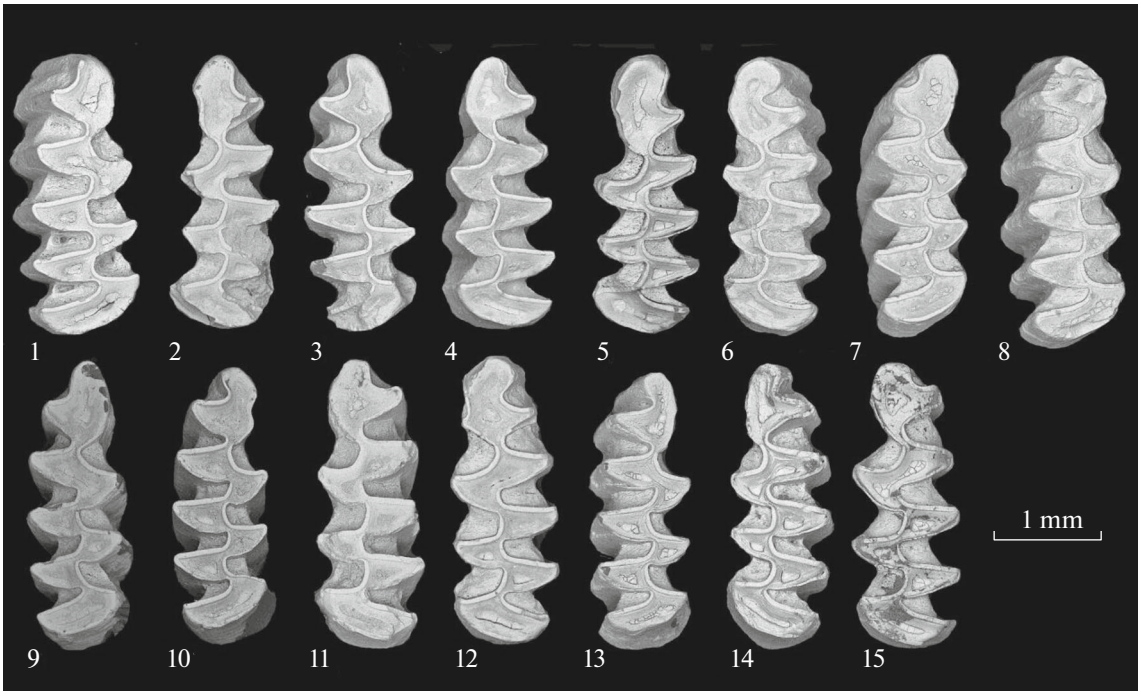

Fig. 1. Vole teeth from square G4 deposits of the Imanay Cave. *Lasiopodomys* (*Stenocranius*) *gregaloides* (Hinton, 1923) teeth were found at a depth of (1, 2) 40–50, (3–5) 50–60, (6–8) 70–80, (9, 10) 80–90, (11) 90–100, (12–14) 100–110, and (15) 110–120 cm.

50 $IGAN_{AMS}$-9117 (depth 100–110 cm) and 13255 ± 60 $IGAN_{AMS}$-9116 (depth 50–60 cm). The radiocarbon dates are uncalibrated. Remains of small mammals accumulated in mid-MIS 2, the late glacial period. All remains of small mammals showed the same degree of fossilization. Terminology, measurements, and morphotypes of common vole teeth are as in [8, 9].

The small mammalian fauna of the Imanay Cave includes mole (*Talpa* sp.), white-toothed shrew (*Crocidura* sp.), common shrew (*Sorex araneus*), tundra shrew (*S. tundrensis*), even-toothed shrew (*S. isodon*), brown bid-eared bat (*Plecotus auritus*), northern bat (*Eptesicus nilssonii*), pika (*Ochotona* sp.), ground squirrel (*Spermophilus* sp.), southern birch mouse (*Sicista subtilis*), great jerboa (*Allactaga major*), dwarf fat-tailed jerboa (*Pygeretmus pumilio*), common hamster (*Cricetus cricetus*), Eversmann's hamster (*Allocricetulus eversmanni*), gray hamster (*Cricetulus migratorius*), northern mole vole (*Ellobius talpinus*), grey red-backed vole (*Craseomys rufocanus*), bank vole (*Myodes glareolus*), northern red-backed vole (*M. rutilus*), yellow steppe lemming (*Eolagurus luteus*), steppe lemming (*Lagurus lagurus*), water vole (*Arvicola amphibius*), narrow-headed vole (*Lasiopodomys gregalis*), tundra vole (*Alexandromys oeconomus*), common vole (*Microtus arvalis*), field vole (*Microtus agrestis*), and forest vole (*Sylvaemus* sp.). *Lasiopodomys gregalis* and *Laurus lagurus* greatly predominate in the fauna. The fauna is generally similar in composition and structure to postglacial faunas found in deposits of other south Ural caves [10].

Among the 1250 m1 teeth of voles of the tribe Arvicolini, we found five whole teeth (Fig. 1) and nine fragments of cement-containing unrooted m1 teeth of the subgenus *Stenocranius* with broad connection of the first triangles (T4–T5) (*Pitymys*-Rhombus connection) at the base of the anteroconid (Table 1). This triangle connection is specific to *L. gregaloides* and differs the species from *L. gregalis*. Substantial external cement deposits were observed on the teeth. The enamel thickness was appreciably lower on the convex walls of folds; gaps in enamel were observed only on the buccal side of the head of the first unpaired loop. There is a reentrant angle on the lingual side of the head, varying in depth. A reentrant angle is small, if any, on the buccal side of the head. The head of the unpaired loop is separated from anteroconid triangles (T4–T5), which are fused together. The anteroconid varies in shape and occurs in three morphotypes, which were isolated in *L.* (*S.*) *gregaloides* [9]: "gregaloides" (a convex side of the head of the anteroconid), "gregalis" (an even buccal side of the head), and "gregaloides-arvalidens" (the buccal side of the head is concave and forms a reentrant angle). Six teeth were assigned to the gregaloides morphotype (with a convex buccal side of the anteroconid head); 11 teeth, to the gregalis morphotype; and seven teeth, to the gregaloides-arvalidens morphotype.

Table 1. Dimensions (mm) and proportions (%) of the lower first molar (m1) of *Lasiopodomys* (*Stenocranius*) *gregaloides*

Parameter	Locality*				
	Vyatkino, layer 7 ($n = 25$) **	Bol'shevik-2 ($n = 9$)	Kozi Grzbiet, layer a ($n = 15$); layers *b* and *c* ($n = 17$)	West Runton ($n = 35$)	Imanay ($n = 15$)
L (m1 length)	2.3–**2.54**–2.75	2.45–**2.54**–2.75	layer (*a*) 2.36–**2.61**–2.81 layer (*b.c*) 2.50–**2.73**–2.92	2.19–**2.40**–2.77	2.30–**2.48**–2.64
A (anteroconid length)	1.1–**1.3**–1.45	1.2–**1.29**–1.45	–	–	1.24–**1.32**–1.40
C (width of anteroconid triangle connection)	–	0.12–**0.17**–0.25	–	–	0.09–**0.13**–0.18
W (oblique width of anteroconid triangles)	–	0.8–**0.89**–0.95	–	–	0.74–**0.83**–0.93
A/L (×100)	–	48.0–**51.4**–57.3	–	48.50–**52.56**–56.60	50.38–**53.22**–56.28
C/W (×100)	–	15.0–**19.2**–27.8	–	–	10.23–**15.83**–21.69

* Data sources: Vyatkino, [11]; Bol'shevik-2, [3]; Kozi Grzbiet, [8]; West Runton, [10]; Imanay, this work.

** Minimal–**mean**–maximal values are shown.

The findings demonstrate that Middle Pleistocene *L.* (*S.*) *gregaloides* occurred along with *L.* (*S.*) *gregalis* in the Late Pleistocene rodent fauna of the Imanay Cave. The latter was widespread in Europe [2, 3, 9, 11]; its remains have been found in the southern Trans-Urals [1] and Altai [14]. The species was found together with *L.* (*S.*) *gregalis* in certain Middle Pleistocene deposits of Eastern Europe [3, 5]. However, m1 teeth with a broad connection of the anteroconid triangles, which are characteristic of *L.* (*S.*) *gregaloides,* have not been detected in European faunas of the Late Pleistocene and Holocene [3, 5, 15]. Teeth of the gregaloides morphotypes have been found in Late Pleistocene *L. gregalis* samples from the central and southern Trans-Urals and modern Asian samples of the species [1].

The finding of *L.* (*S.) gregaloides* in the Late Pleistocene fauna of the Imanay Cave indicates that geographic and chronological asynchrony was characteristic of the morphological transformation of teeth in the phyletic lineage *Stenocranius hintoni–S. gregaloides–S. gregalis*. Archaic *S. gregaloides* forms were preserved in certain regions, predominantly in the eastern part of the species range.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflict of interest.

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