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Fossil insectivorous mammals (Eulipotyphla) of the southern Pre-Urals (Bashkortostan, Russia)

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ABSTRACT

Seven species of red-toothed shrews (*Sorex araneus, Sorex isodon, Sorex tundrensis, Sorex caecutiens, Sorex minutus, Sorex minutissimus, Neomys fodiens*), white-toothed shrews (*Crocidura* sp.), moles (*Talpa* sp.) and hedgehogs (*Erinaceus* sp.) were found in Late Pleistocene and Holocene deposits of the southern part of the western slope of the Ural Mountains. In the Late Pleistocene and Early Holocene deposits, the red-toothed shrews were dominated by *S. tundrensis*. This species disappeared from the area by the Late Holocene, when *S. araneus* became the predominant species. Smaller mandibular sizes have been registered for *S. araneus* in the Middle and Late Holocene, as compared to the sizes of older samples. The morphometric criteria have been established for a species differential diagnosis of the Late Pleistocene – Early Holocene mandibular samples of *S. araneus* and *S. tundrensis*, found in local deposits of the southern Pre-Urals area studied.

1. Introduction

Insectivorous mammals (Eulipotyphla, Mammalia) are one of the least studied mammal groups within the Ural region (Sharova, 1992; Bolshakov et al., 1996). The development history for the communities of this mammal group in the Urals over the period from the Late Pleistocene to the present day has been studied in varying degrees of detail for two local territories only (north of the South Urals, Zaitsev, 1992; and north of the Middle Pre-Urals, Fadeeva, 2016). In the majority of studies, the bone remains have only been classified to the genus. Modern representatives of this order are mainly identified by features of the skull and upper teeth (Zaitsev et al., 2014), which are relatively poorly preserved in the fossil state. The vast majority of bone remains of insectivorous mammals in the Quaternary sediments are mandibles and their fragments. The variability of qualitative and quantitative mandibular traits in representatives of recent geographically remote populations of red-toothed shrews of the Ural has hardly been studied, which prevents an objective interpretation of paleontological results (see Tables 1–4).

Biostratigraphic reconstructions of the Late Pleistocene and Holocene development history of the natural environment in the southern part of the western slope of the Ural Mountains (the latitudinal course of the Belaya River in Bashkortostan) are based on detailed studies of the spore-pollen spectra and fossil remains of animal species (mollusks, reptiles, amphibians, rodents, and large mammals) (Danukalova et al., 2002, 2011, 2020; Yakovlev et al., 2003, 2004, 2006; Yakovleva and Yakovlev, 2011; Osipova and Danukalova, 2021). The same southern group of caves of the southern Pre-Urals includes the Imanay Cave on the latitudinal section of the Nugush River (Yakovlev et al., 2016; Gimranov et al., 2016; Silaev et al., 2018, 2020; Gimranov and Kosintsev, 2020; Fadeeva et al., 2022). In the cold periods of the geological time scale (from the end of the Late Pleistocene to the Early Holocene), forest-steppes were common in this area, which were partially covered by forest vegetation in warmer periods (Middle to Late Holocene); modern mountain mixed forests emerged as recently as in the Late Holocene (Danukalova et al., 2011). Remains of insectivorous mammals were found in the deposits at various locations within the study area; their morphological features, paleoecological and biostratigraphic significance are discussed in this paper.

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2. Background

The caves and grottoes (Yurmash 3, Yurmash 4, Bajslan-Tash, Tugai-Chishma, Azan-Tash and Mujnak-Tash caves, as well as Archaeologists, Maksyutovsky, and Tashmurun grottoes) (Fig. 1) located in the valley of the Belaya River in the southern part of the western slope of the Ural mountains (between 52°57′ N, 56°36′ E and 52°58′ N, 57°00′ E) had been studied as part of the field work between 1999 and 2002 (Danukalova et al., 2011). The excavation sites at these locations were established in the entrance areas and designed to search for archaeological artifacts and remains of vertebrate animals. Bone accumulation in the deposits of these grottoes and caves was due to the activity of birds of prey and mammals (Yakovleva and Yakovlev, 2011). The available radiocarbon dating data (Tabl. 1) suggests that the Bajslan-Tash cave and Maksyutovsky grotto deposits studied date back to the end of the Late Pleistocene, Early, Middle, and Late Holocene (Yakovlev et al., 2006; Danukalova et al., 2011; Kosintsev and Bachura, 2013; Meiri et al., 2018). The archaeological artifacts discovered in the deposits of the Archaeologists and Tashmurun grottoes date back to the Eneolithic Age (3rd–2nd millennium B.C.), the Early Iron Age (1st millennium B.C.) and the Middle Ages (X–XIV centuries) (Yakovlev et al., 2003; 2004). The relative age of the deposits of the Yurmash 3, Yurmash 4, Tugai-Chishma, Mujnak-Tash, and Azan-Tash caves was established by analogy with the species composition of the remains of small mammals dating back to the Middle Holocene and Late Holocene faunas of the southern Urals (Danukalova et al., 2002).

The Imanay cave (53°02′ N, 56°26′ E) is located approximately 15 km northwest of the Yurmash 3 cave (Fig. 1). Excavations at the deposits of the Imanay cave were conducted in 2016. There is a corridor-type cave, approximately 100 m long, ending with a grotto measuring 5 × 6 × 5.6 m. This cave grotto contains an excavation site with a total area of 9.5 m^2. Numerous bones of large cave lions and cave bears were found in the cave deposits (Gimranov et al., 2016). Remains of small mammals from the deposits of squares “G4” (Fadeeva et al., 2022) and “B4” have been studied so far. The bones of small mammals are highly fragmented. The zoogenic deposits were formed as a result of the activity of predatory mammals (fox, arctic fox), which used the inner grotto of the cave as a temporary shelter. Judging by the radiocarbon dating data (Tabl. 1), the lower and middle parts of the deposits of the Imanay cave were formed in the Late Glacial period (Fadeeva et al., 2022). The small mammal fauna of the upper part of the deposits is similar to the fauna from the dated deposits of the Bajslan-Tash cave of the end of the Late Pleistocene and Early Holocene.

3. Materials and methods

209 maxillary bones and 751 mandibles of insectivorous mammals were discovered in the deposits of the ten caves and grottoes studied (Tabl. 2). There are no complete skulls in the collection: no intermediate teeth have been preserved in the maxillary bone fragments. All mandibles are fragmented to a varying degree.

Species identification for the mandibles of representatives of the Soricinae was based on a number of cumulative morphodiagnostic features (the shape of the fourth premolar (p4), the shape of the articular process, the location of the mental foramen, the sizes of the mandibles and teeth), as described in the methods section of previous works (Zaitsev, 1992, 1998; Zaitsev et al., 2014; Fadeeva, 2016). Considering the absence of skull elements, generally used for species identification (Zaitsev et al., 2014), red-toothed shrew maxillary bone fragments were only identified down to subfamily. The remains of representatives of the Erinaceidae and Talpidae and the Crocidurinae were identified to the genus.

We follow Reumer’s (1984) anatomical nomenclature.

Species identification for the remains of representatives of Soricinae was most difficult in terms of mandible differentiation for *S. araneus* and *S. tundrensis*, the total share of which in the samples studied amounted to approximately 85% of the number of remains identified down to the species. Differential visual diagnosis for part of the mandibles of the common red-toothed shrew and the tundra red-toothed shrew from the Bajslan-Tash cave (the red-toothed shrew remains of the cave are relatively well preserved) was conducted based on the shapes of the fourth premolar and/or articular process (Fig. 2).

Mandible measurements for these species-identified samples were used to establish species-specific morphometric indicators, to be subsequently used for species identification of mandibles with p4 premolars and the articular process missing or damaged. The following measurements were taken (Fig. 3): **L p4** = buccal length p4, **L m1** = buccal length m1, **L m1-m2** = buccal length m1-m2, **L m1-m3** = buccal length m1-m3, **L i-art** = buccal length from the base of the incisor alveolus to the apex of the articular process, **Hp4** = buccal height p4, **H m1 pr** = buccal height protoconid m1, **H m1 hyp** = buccal height hypoconid m1, **H m2 pr** = buccal height protoconid m2, **H m2 hyp** = buccal height hypoconid m2, **L m1-m3 alv** = lingual length of alveoli m1-m3, **L m3-art** = lingual length from the posterior edge of the alveolus m3 to the apex of the articular process, **H asc** = lingual height ascending ramus, **H cor** = lingual height coronoid process, **H desc. p4** = lingual height descending ramus behind p4, **H desc. m3** = lingual height descending ramus behind m3. All measurements (mm) were taken with an MBC-10 stereoscopic microscope (8X eyepiece with a scale).

In order to clarify the effects of the age variability factor, the mandible samples were differentiated by conditional age groups using respective existing methods (Conaway,1952; Dapson, 1968). The relevant protoconid and hypoconid height data was summarized for the teeth that have been preserved in the fossil mandibles: the fourth premolar (p4) and the first and second molars (m1, m2).

The principal component method was used to establish the morphometric species identification characteristics for mandibles in local single-period samples of *S. araneus* and *S. tundrensis*. Since multivariate analysis requires the use of a complete data set for each specimen, a limited amount of material (13 and 69 mandibles, respectively) from all Late Pleistocene – Early Holocene samples of the study locations was used in identifying such mandibular features for *S. araneus* and *S. tundrensis*.

Temporal variability analysis has only been conducted for the

Table 1
^{14}C chronology of studied deposits.

Location	Laboratory code	Layer/horizon	Material	^{14}C yr BP	Reference
Bajslan-Tash Cave	GIN-10852	layer 2 (5)	Wood coal	1600 ± 50	Yakovlev et al. (2006);
	OxA - 22168	layer 2 (6)	*Cervus elaphus* bone	2095 ± 28	Kosintsev and Bachura, 2013;
	GIN-10854	layer 3 (11–13)	Bone of small mammals	7140 ± 170	Meiri et al. (2018); this article
	IEMEA-1369	layer 3 (15)	*Lepus timidus* ("*tanaiticus*") bone	8216 ± 344	
	IEMEA-1340	layer 4 (15)	Bone of large mammal	9616 ± 62	
	SPb-367	layer 4 (17)	Bone of small mammals	11450 ± 150	
	GIN-10854	layer 4 (18)	Bones of small mammals	13560 ± 250	
Maksyutovsky Grotto	SOAN-7755	layer 2	*Bison priscus* bone	15650 ± 150	Danukalova et al. (2011)
Imanay Cave	IGAN 9116	horizon G4-6	Bones of small mammals	13255 ± 60	Fadeeva et al. (2022)
	IGAN 9117	horizon G4-11		17100 ± 50	

Table 2
The list of insectivorous mammal species (number of mandibles – bold font , number of maxillae – usual font , + – isolated teeth) represented in deposits of the southern group of karst cavities of the southern Pre-Urals, latitudinal sections of the valleys of the Belaya and Nugush rivers, Bashkortostan, Russia.

Location/Period	Late Pleistocene-Early Holocene																	Middle Holocene			Late Holocene									∑
	Imanay[a]																													
Layer or horizon	12	11	10	9	8	7	3	4	6	5	4	3	2	1	B-T 1	M 1	Yu-4 1–2	B-T 2	B-T 1	Yu-3 1, 3	T-Ch 7	T 1	Ar 1,3,4	M-T 1	A-T 1	
Erinaceus sp.	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	+
Talpa sp.	2	1	-	1	1	1	-	1	1	1	2	-	1	2	-	2	1	7	3	1	-	1	3	-	-	32
	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	2
Crocidura sp.	2	1	-	-	-	-	-	5	-	-	-	-	2	1	3	-	-	2	2	-	-	-	1	-	-	19
	-	-	-	-	-	-	-	3	-	-	-	2	-	2	2	-	-	1	-	-	-	-	-	1	-	11
Neomys fodiens	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	2	1	-	-	5
Sorex araneus	-	-	-	-	1	1	-	23	5	10	-	3	10	19	12	9	1	26	5	2	2	4	21	-	-	154
Sorex isodon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	3
Sorex tundrensis	2	5	7	3	4	2	1	110	11	11	4	4	11	28	16	4	-	9	14	-	-	-	-	-	-	246
Sorex caecutiens	1	1	-	1	-	-	-	3	-	-	-	-	-	-	1	1	2	8	-	-	-	1	5	-	-	24
Sorex minutus	-	-	-	-	-	-	-	1	1	-	1	-	3	-	3	4	-	7	9	-	-	2	7	-	-	38
Sorex minutissimus	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	3
Sorex sp.	2	9	13	4	4	7	-	30	12	24	13	11	30	36	7	2	2	12	3	-	-	-	6	-	-	227
Soricinae	-	4	2	-	1	1	-	81	8	15	4	1	8	21	14	10	-	15	5	-	1	-	3	-	2	196
∑	9	22	22	9	11	12	1	259	38	61	24	21	65	110	58	32	6	91	42	3	3	10	48	1	2	960
	664														96			200								

[a] **Imanay** – Imanay Cave; **M** – Maksyutovsky Grotto; **B-T** – Bajslan-Tash Cave; **Yu-4** – Yurmash 4 Cave; **Yu-3** – Yurmash 3 Cave, **Ar** – Archaeologists Grotto, **T-Ch** – Tugai-Chishma Cave, **T** – Tashmurun Grotto, **M-T** – Mujnak-Tash Cave, **A-T** –Azan-Tash Cave.

S. araneus genus, the remains of which were found in relatively large quantities in the deposits of all considered time periods of the Late Pleistocene – Early Holocene at the locations studied. The material analyzed was divided into three conditional time groups (Late Pleistocene – Early Holocene (LP-EH), Middle Holocene (MH), Late Holocene (LH)) in accordance with the geological age of the deposits established by radiocarbon dating and assumed from indirect data. The LP-EH time group was identified due to the fact that Early Holocene material is present only in a mixture with Late Pleistocene material among the mammal remains of the deposits of the Bajslan-Tash (layer 4) and Imanay (upper horizons) caves studied.

The dating process for sample SPb-367 (Tabl. 1) was conducted at the laboratory of the Department of Geology and Geoecology Herzen State Pedagogical University (St.Petersburg, Russia). For 14C dating of bones, collagen extraction was carried out according to the standard procedures of Arslanov and Svezhentsev (1993). For liquid scintillation counting (LSC), benzene cocktails were measured on a Quantulus 1220 liquid scintillation counting system.

The material was photographed using a Stemi 508 (Zeiss) stereomicroscope with a Zeiss Axiocam 208 multi-purpose color digital camera. The results were plotted using the ggplot2 package (Wickham, 2011) in the R environment (version 4.3.1) using RStudio (version 2022.07.2 + 576). Statistical processing of the results was carried out using Statistika (version 10).

4. Results

4.1. The species list

The largest number of mandibles of insectivorous mammals was found in deposits of the **end of the Late Pleistocene** to **Early Holocene** (Tabl. 2). Species of red-toothed shrews (*S. araneus* Linnaeus 1758*, S. tundrensis* Merriam, 1900*, S. caecutiens* Laxmann, 1785*, S. minutus* Linnaeus, 1766*, S. minutissimus* Zimmermann, 1780*, Neomys fodiens* Pennant, 1771), white-toothed shrews (*Crocidura* sp.), and moles (*Talpa* sp.) were registered in Late Glacial deposits (Lateglacial transition (MIS 2/1): Imanay Cave (horizons 6–12), Bajslan-Tash Cave (layer 4), Maksyutovsky Grotto (layer 3)). Remains of a member of Erinaceinae were also found in the deposits of this period in the Bajslan-Tash Cave (Yakovlev et al., 2006). During this period, the Tundra shrew (*S. tundrensis*) dominated the study area. The Eurasian common shrew (*S. araneus*) was the second most common species among the remains of insectivorous mammals. The deposits of presumably the Early Holocene (Imanay Cave (horizons 1–5)) are still dominated by the Tundra shrew; however, the share of the Eurasian common shrew remains is growing.

Few remains of insectivorous mammals were found in the **Middle Holocene** deposits at various locations within the study area. These include four species of red-toothed shrews (*S. araneus, S. tundrensis, S. caecutiens, S. minutus*) in addition to white-toothed shrews and moles. At this point, the dominant role already passed from the Tundra shrew to the Eurasian common shrew (Maksyutovsky Grotto, layer 1).

The **Late Holocene** deposits of the Bajslan-Tash Cave (layer 1–2) are relatively rich in terms of the number of species of insectivorous mammals (white-toothed shrews, mole, hedgehog, seven species of red-toothed shrews (*S. araneus, S. tundrensis, S. caecutiens, S. minutus, S. minutissimus, S. isodon* Turov, 1924*, Neomys fodiens*). The largest number of remains classified to species are of *S. araneus* and *S. tundrensis*. In the Late Holocene deposits of other locations within the study area, however, only the Eurasian common shrew had a clear quantitative advantage. No Tundra shrew remains were found in the deposits of the Subatlantic period of the Holocene at the Archaeologists Grotto (Yakovlev et al., 2003) or in the Late Holocene deposits of the Tashmurun Grotto, Yurmash 3, Azan-Tash, Mujnak-Tash and Tugai-Chishma Caves (Danukalova et al., 2002, 2011; Yakovlev et al., 2004).

4.2. Morphometric characteristics of fossil mandibles of S. tundrensis and S. araneus

4.2.1. Conditional ontogenetic groups

Within the *S. tundrensis* (n = 51) and *S. araneus* (n = 18) red-toothed shrew mandible samples found at the deposits of the Bajslan-Tash cave with their p4, m1 and m2 preserved, three conditional age groups were identified by the degree of attrition: group I with the sum of conid heights (Hp4+Hm1pr + Hm1hyp + Hm2pr + Hm2hyp) ≥5.0 mm; group II with 4.0–4.9 mm; and group III with ≤3.9 mm (Fig. 4, A). Within the same mandible samples and the mandible samples with only m1 preserved (*S.tundrensis* (n = 29) and *S. araneus* (n = 16)), conditional age group boundaries were established according to the degree of wear of m1 conids (I – with the sum of conid heights (Hm1pr + Hm1hyp) ≥ 2,05 mm, II – with 1,65 to 2,05 MM, III – with ≤1,65 mm) (Fig. 4, B). Statistical analysis of the main morphometric characteristics of the mandibles (length and height) within these species samples of different conditional age groups has shown significant differences in interspecific comparisons and the lack of differences between these indicators within single-species samples (Fig. 4C and D). An interspecific analysis of morphometric characteristics may therefore include combined species samples of mandibles and ignore the tooth wear.

4.2.2. Interspecific differentiation by morphometric characteristics

Multidimensional analysis of morphometric characteristics of *S. araneus* and *S. tundrensis* mandibles has identified six components in the local single-period samples, the first two of which explain 79.6% of the total variability (Tabl. 3). The first component is associated with the variability of the mandibular ramus height. The second component describes the variability in the coronoid process ramus height and the length of the first lower root tooth. Intraspecific samples of mandibles differ little in these parameters, as evidenced by the insignificant scatter of points for the first component (Fig. 5). Interspecific differences are well-expressed for the first component: the mandibles of *S. araneus* have larger ramus heights (H asc and L m3-art). The mandibles of the species do not differ in the features of the second component (Lm1 and H cor). This and previous analyses have identified that the mandibular ramus height (H asc) and the distances between the posterior parts of the incisor tooth and last molar alveoli and the articular process (L i-art, L m3-art) are therefore the morphometric species-identifying features for local single-period samples of the red-toothed shrew species (*S. tundrensis* and *S. araneus*) most represented in the Late Pleistocene – Early Holocene deposits. No other morphometric features analyzed in this study are species-specific (Tabl. 4).

4.2.3. Temporal variability of mandibular parameters

Significant metric differences in average values of mandibular parameters were observed between the Late Pleistocene – Early Holocene and Middle – Late Holocene mandibular samples for *S. araneus*. In particular, the average distance between the posterior part of the third molar and the articular process (Fig. 6, A) and the mandibular height behind the last premolar (Fig. 6, E) for older mandibles exceeded those observed in the Middle and Late Holocene samples. When assessing three additional morphometric features, the older samples were significantly larger than those of the Late Holocene (Fig. 6, B, F) and Middle Holocene (Fig. 6, C).

Table 4
Values (min–mean ± std–max [n], mm) of selected morphometric features of mandibles (*S. tundrensis*, *S. araneus*) from Late Pleistocene-Early Holocene sediments of locations in the southern Pre-Urals.

Measurements (mm)/ species	*Sorex araneus*	*Sorex tundrensis*
L p4	1.25–1.33 ± 0.06–1.40 [26]	0.95–1.13 ± 0.07–1.30 [93]
L m1-m3	3.75–4.01 ± 0.14–4.20 [7]	3.40–3.73 ± 0.11–3.95 [41]
L m1-m2	2.85–3.03 ± 0.10–3.20 [19]	2.60–2.83 ± 0.08–3.05 [109]
L m1	1.6–1.79 ± 0.07–1.90 [37]	1.50–1.64 ± 0.07–1.80 [161]
L m1-m3 alv	3.50–3.75 ± 0.10–3.95 [43]	3.10–3.48 ± 0.09–3.70 [178]
H desc. p4	1.35–1.48 ± 0.06–1.55 [31]	1.15–1.32 ± 0.06–1.50 [124]
H desc. m3	1.25–1.43 ± 0.08–1.60 [55]	1.00–1.27 ± 0.06–1.40 [207]
H asc	4.65–4.97 ± 0.17–5.30 [29]	3.90–4.31 ± 0.11–4.50 [118]
L i-art	8.45–8.91 ± 0.25–9.20 [8]	7.30–7.80 ± 0.19–8.10 [46]
H cor	2.50–2.78 ± 0.14–3.00 [35]	1.45–2.42 ± 0.15–2.70 [135]
L m3-art	4.25–4.59 ± 0.17–4.85 [28]	3.65–4.01 ± 0.12–4.30 [122]

5. Discussion

Remains of *S. tundrensis* dominate in the Late Pleistocene and Early Holocene deposits of the locations studied in the southern part of the western slope of the Ural Mountains. Modern representatives of the species prefer open and shrubby habitats and avoid forested areas (Zaitsev et al., 2014). At the end of the Late Pleistocene and in the beginning of the Holocene, periglacial forest-steppes with a predominance of Asteraceae, Chenopodiaceae, Poaceae, Ranunculaceae, Apiaceae, Polypodiaceae, as well as *Pinus*, *Tilia*, *Betula* and *Alnus* in open woodlands, were common in the valley of the Belaya River. Numerous remains of steppe species of rodents, such as steppe lemmings (*Lagurus lagurus*), narrow-skulled voles (*Microtus* (*Stenocranius*) *gregalis*), and pikas (*Ochotona* sp.), were discovered in cave deposits formed during these periods (Danukalova et al., 2002, 2011; Yakovlev et al., 2006; Fadeeva et al., 2022).

By the Middle Holocene, *S. araneus* gradually becomes the dominant species among the red-toothed shrews in the territory of the southern Pre-Ural Region. The vegetation of the Middle Holocene interval was different from that of the Early Holocene: its open woodlands consisted of *Pinus*, *Betula*, *Tilia*, *Alnus*, *Picea*, *Quercus*, *Ulmus*, *Corylus*, and its open landscapes were dominated by Polypodiaceae, herbs, Asteraceae, *Artemisia* and other non-arboreal plants (Danukalova et al., 2011). Judging by the relatively higher proportion of forest species in the fauna of small mammals (Danukalova et al., 2002; Yakovlev et al., 2006), the area studied is undergoing gradual afforestation. In the first half of the Middle Holocene, steppe species of rodents still dominated the area. The

Table 3
Correlation of the main components (PC 1 – PC 6) with the quantitative values of the original variables.

Measurements/PC	PC1	PC2	PC3	PC4	PC5	PC6
L m1	−0.387	**−0.599**	−0.114	−0.474	−0.473	0.173
L m1-m3	−0.408	−0.200	−0.542	0.001	**0.707**	−0.029
H desc. m3	−0.381	−0.244	**0.814**	0.112	0.339	0.076
H cor	−0.373	**0.700**	0.067	−0.546	0.045	0.256
H asc	**−0.465**	0.167	−0.002	0.125	−0.256	−0.821
L m3-art	**−0.428**	0.157	−0.161	**0.669**	−0.308	0.473
Percentage of explained variances	69.3	10.3	8.1	6.2	4.7	1.4

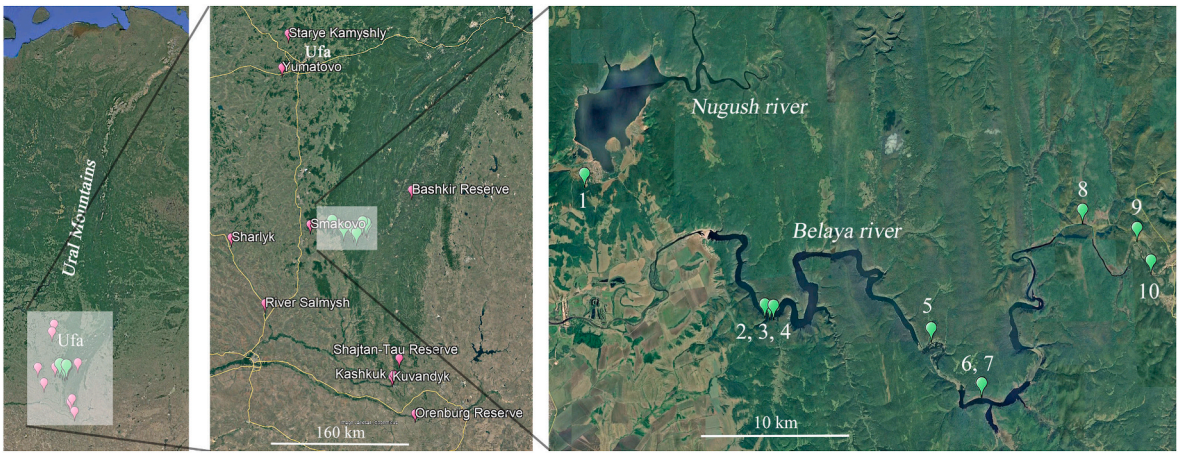

Fig. 1. The geographical position of fossil (green) and modern (pink) localities of insectivorous mammals in the southern Pre-Urals. 1 – Imanay Cave, 2 – Yurmash 3 Cave, 3 – Yurmash 4 Cave, 4 – Azan-Tash Cave, 5 – Mujnak-Tash Cave, 6 – Bajslan-Tash Cave, 7 – Archaeologists Grotto, 8 – Tugai-Chishma Cave, 9 –Maksyutovsky Grotto, 10 – Tashmurun Grotto.

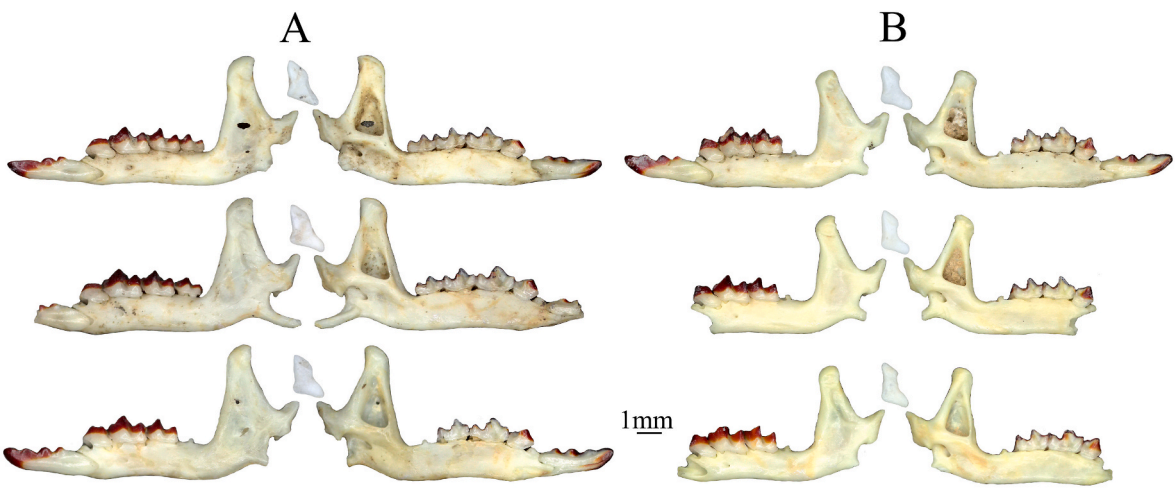

Fig. 2. Fragments of fossil mandibles (from buccal and lingual sides) and articular processes of *S. araneus* (A) and *S. tundrensis* (B) from sediments of Baislan-Tash cave.

predominance of remains of red-backed voles (*Myodes* sp.) was also already visible in the rodent fauna from the Middle Holocene deposits of the Yurmash 4 cave (Danukalova et al., 2011).

In most Late Holocene deposits, red-toothed shrews are dominated by *S. araneus*. These deposits contain remains of the even-toothed shrew (*S. isodon*), which is evidence of the spread of dark coniferous forests in the study area. Intensive foresting of the area in the second half of the Late Holocene is the presumable cause for the disappearance of *S. tundrensis*. Forest-steppe vegetation existed in this area up until the Late Holocene, however its coniferous part (*Pinus*) was significantly reduced and *Betula* and *Tilia* predominated. It is for this period that the fossil fauna of rodents is sharply dominated by the remains of red-backed voles (Danukalova et al., 2011).

Similar trends in changes in the composition and structure of the faunas of insectivorous mammals at the end of the Late Pleistocene and in the Holocene are observed in other territories of the Urals. The predominance of Tundra shrew remains was recorded for cave deposits of the second half of the Late Pleistocene in the northern part of the southern Urals (Zaitsev, 1992) and the Late Glacial in the north of the Middle Pre-Ural region. The same trend is observed with the predominance of remains of *S. araneus* in the Middle and Late Holocene deposits of certain locations in the north of the South Urals (Zaitsev, 1992), while the bone remains of *S. tundrensis* are very few. In the northeastern part of the Middle Pre-Ural region, Tundra shrews were present up to the boreal period of the Holocene and then disappeared from the communities of insectivorous mammals; the prevalence of the Eurasian common shrew is recorded for later periods (Fadeeva, 2016).

The history of modern mixed forests in the Belaya River valley therefore begins in the Late Holocene and, according to the relevant research data (Kozheva et al., 1973), bank (*Myodes glareolus*) and northern (*Myodes rutilus*) red-backed voles were the predominant mammal species in this area in the XX century. The area studied is currently part of a botanical-geographic region of broad-leaved forests (Gorichev, 2015). The following species of insectivorous mammals have been observed in the western part of this area (village Smakovo, Meleuzovskiy district, Bashkortostan, Fig. 1): *Erinaceus europaeus, Talpa europaea, S. araneus, S. caecutiens, S. minutus, Neomys fodiens* (Kozheva et al., 1973). The nearest eastern point to the area with a studied composition of insectivorous mammal species is in an area of light coniferous forests (Bashkir Reservation, Burzyanskiy district, Bashkortostan, Fig. 1). This nature reserve is home to four species of red-toothed shrews *S. araneus, S. caecutiens, S. minutus, S. isodon* (Snegirevskaya, 1947; Puchkovskiy, 1976). According to L. P. Sharova (1992), *S. tundrensis* was found approximately 170 km south of the study area, in the floodplain of the Sakmara River, near the village of Kashkuk, Kuvandyksky District, Orenburg Region (see Fig. 1). *S. tundrensis*, however, is

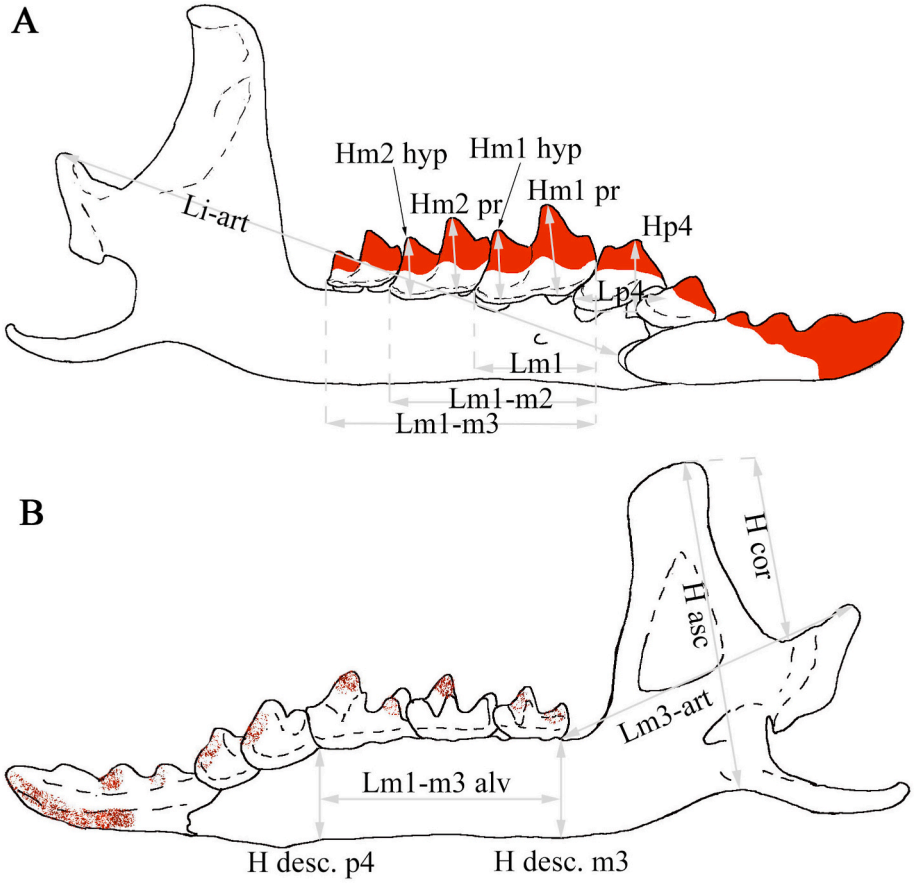

Fig. 3. Measurements of the mandible and teeth (buccal (A) and lingual (B) projections).

not found in the summary of capture results (1960–2016) for small mammals of the Guberlinsky hillocky area (Kuvandyksky District) (Vasilyev et al., 2017).

The distribution history and current habitat of *Crocidura* representatives in the territory of the southern Pre-Ural region have been studied extremely poorly as compared to those of red-toothed shrews. Fragments of the skulls and mandibles of white-toothed shrews (*Crocidura* sp.) were found in the Imanay, Bajslan-Tash, and Mujnak-Tash Caves and the Archaeologists Grotto in the deposits of all periods of the Late Pleistocene and Holocene considered. All fossil mandibles of white-toothed shrews studied had rather large mandibular ramus heights (L asc) (4.75–5.15 mm), which is not typical for *C. suaveolens*, most commonly having "L asc" of up to 4.4 mm in males and 4.2 mm in females (Zaitsev et al., 2014). B. S. Yudin (1989) noted that "L asc" for *C. suaveolens* found in Siberia does not exceed 4.6 mm. The fourth upper premolars (P4) in the shrew skull fragments studied are variable in shape. The species of modern white-toothed shrew skulls were identified by the structure of the P4 premolar masticatory surface (absence/presence of anterior lingual notch, protocone notch, anterior margin shape) (Poitevin et al., 1986; Zaitsev, 1991; Rolland, 2008; Tovpinets, 2012; Zaitsev et al., 2014). However, the shape of the anterior margin of this tooth varies within the same species (Jenkins, 1976). The degree of development of the anterior lingual notch is also questionable in terms of species identification, since, within a population of one species, this trait "has a varying degree of expression and may be asymmetric or even transitional …" (Bannikova et al., 2001). In order to identify the species of the fossil remains of shrews, additional studies of the recent material are required.

Only fragmented data is available on the current distribution of shrews in the southern Urals. *C. leucodon* and *C. suaveolens* were registered near the village of Kashkuk (Sharova, 1992). Individual young specimens of the latter species were identified erroneously in the field and in fact represent *C. leucodon* (Vasilyev et al., 2022). This species was also found in Orenburg and Shaitan-Tau nature reserves (Fig. 1) (Bystrov and Khuzhakhmetova, 2021). *C. suaveolens* was registered near the villages of Yumatovo and Starye Kamyshly (Fig. 1) in the southwestern Pre-Ural region (Yakovlev and Valuev, 2015; Yakovlev and Naumova, 2020).

Very few fossil remains of hedgehogs (*Erinaceus*) are currently known, found at several locations in the Urals (Zaitsev, 1992; Yakovlev et al., 2003, 2006; Fadeeva et al., 2020; Kosintsev et al., 2022). It is commonly known that fossil remains of *E. europaeus* are indications of temperate climatic conditions (Sommer, 2007), however species identification of fossil remains of hedgehogs is generally complicated and based on the structural features of mandibles (Holz, Niethammer, 1990a, b). The information on the modern habitat of representatives of the *Erinaceus* genus in the Urals requires revision. The southern hedgehog (*E. roumanicus*) is found in the south of the southern Urals (Kashkuk (Fig. 1) (Vasilyev et al., 2017), near the village of Sharlyk, in the valley of the Salmysh River (Fig. 1) (Debelo et al., 2016)). The northern boundary of the natural habitat for this species of hedgehogs, however, has not been precisely established (Lisovskiy et al., 2019); the region may have sympatry of natural habitats of two species of hedgehogs (*E. roumanicus* and *E. europaeus*). Overall, *E. europaeus* and *E. roumanicus* demonstrate no significant differences in their environmental preferences, however the former species is less sensitive to low temperatures (Holz, Niethammer, 1990a, b).

For the deposits studied, mandibles of the Common red-toothed shrew and Tundra red-toothed shrew predominated in the remains of insectivorous mammals, morphotypic characteristic-based species identification for which is extremely limited. These species are included in different size groups of red-toothed shrews (large-sized and medium-

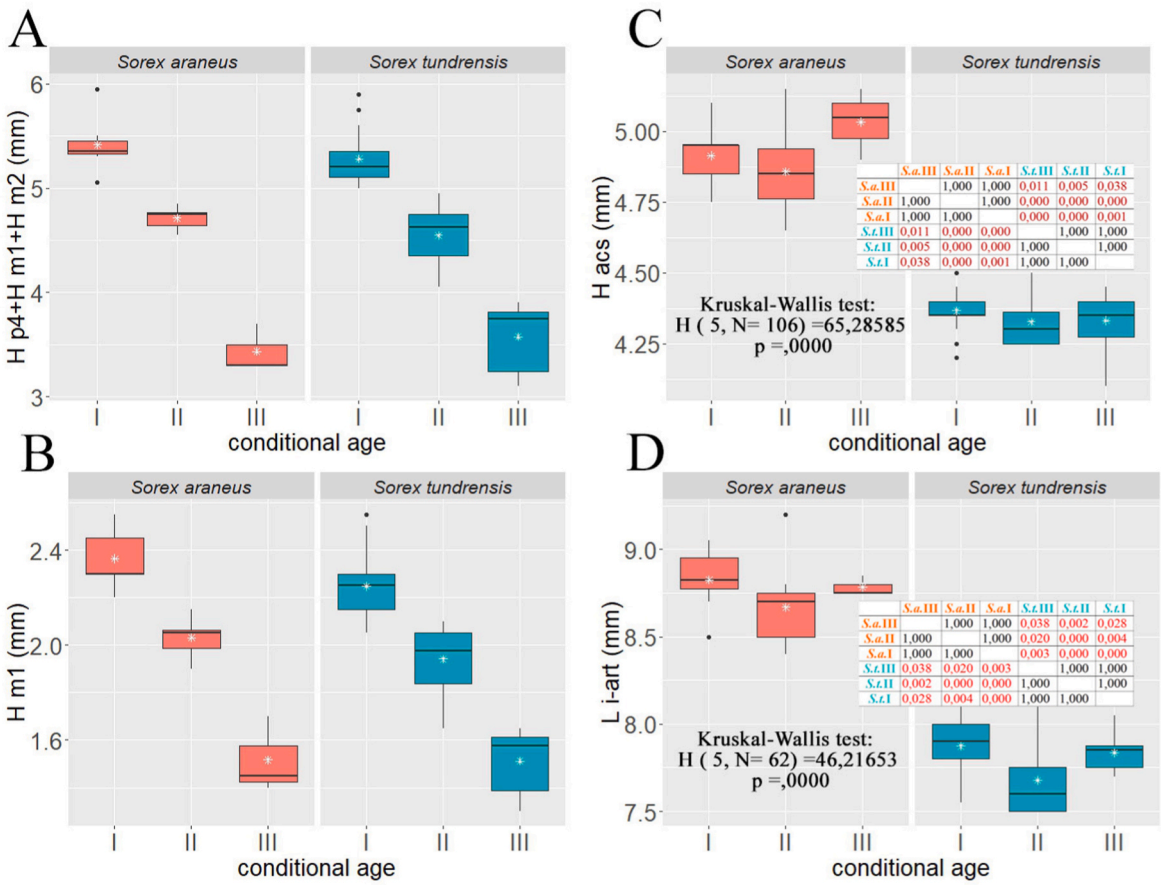

Fig. 4. Dimensions of teeth and mandibles of different ontogenetic groups of the shrews *S. tundrensis, S. araneus*. Cave Bajslan-Tash Cave.

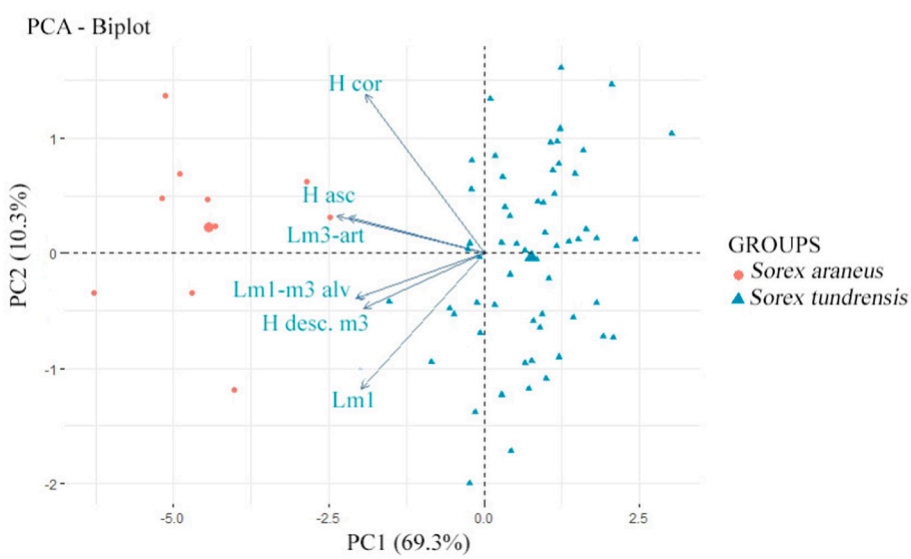

Fig. 5. Scatter diagram and factor loadings (6 measurements of mandibles of *S. tundrensis* and *S. araneus*) from Late Pleistocene-Early Holocene deposits of the southern Pre-Urals localities).

sized, respectively). The large-sized group may also include the largest specimens of *S. tundrensis* (Zaitsev, 1998); some morphometric characteristics of the skulls and mandibles of the two species may overlap. There is wide variability in morphometric craniological characteristics of both species within the modern habitats (e.g. Okulova et al., 2007; Bobretsov et al., 2008, 2012; Schipanov et al., 2011).

Do morphometric characteristics of mandibles change with age? It is known that the size of the skull in shrews depends on the season (Lazaro et al., 2021). Researchers disagree on age-related changes in mandibles of modern red-toothed shrews (Pucek, 1965; Homolka, 1980; Searle and Thorpe, 1987; Novakova and Vohralik, 2017). Certain differentiation methods (Conaway,1952; Dapson, 1968) are available to eliminate the effects of the age variability factor for the mandibles within each sample. These are based on quantitative tooth wear data (the summed heights of

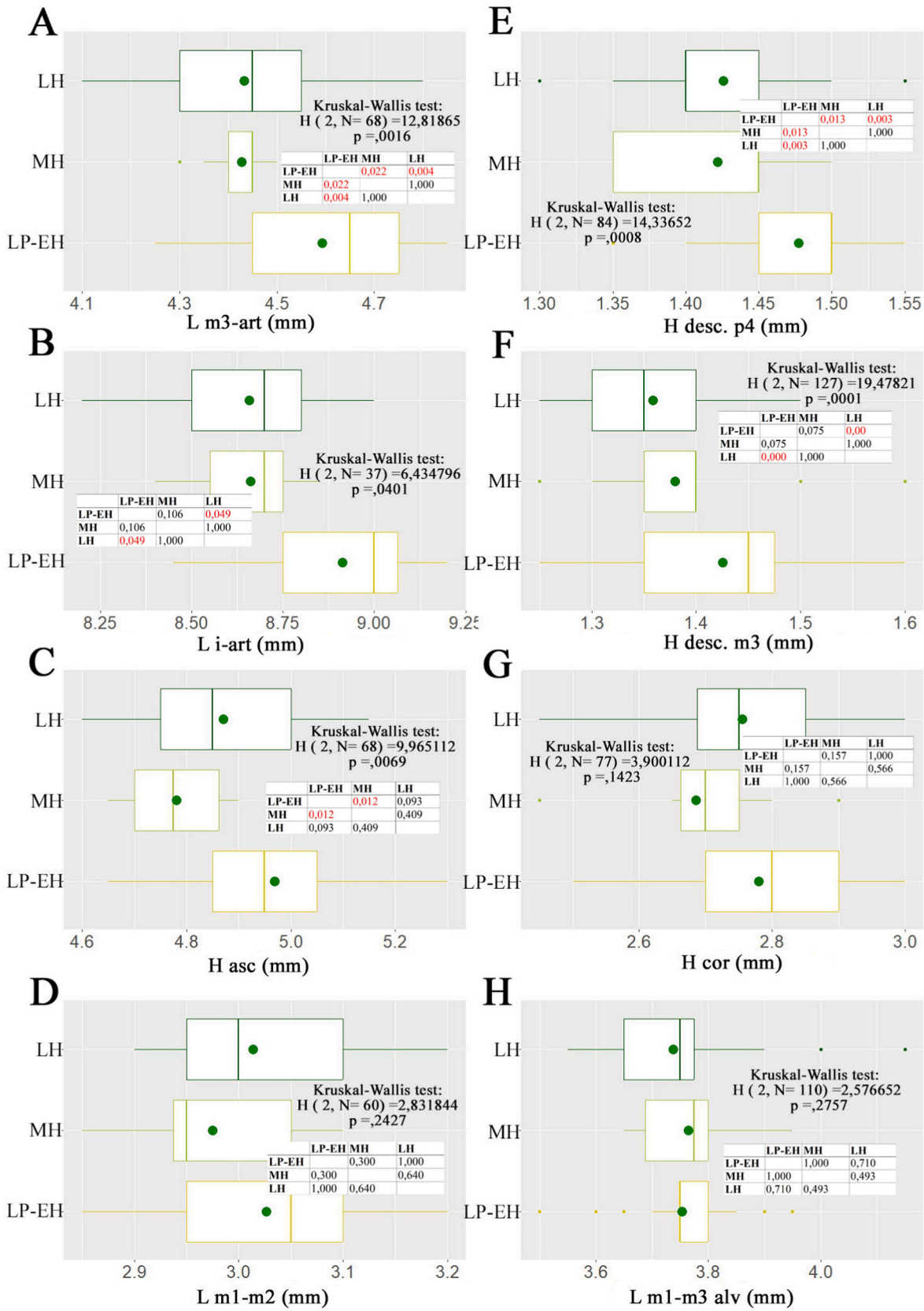

Fig. 6. Mandible sizes from different time samples of *S. araneus*. LP-EH – Late Pleistocene-Early Holocene; MH – Middle Holocene; LH – Late Holocene. Summarized samples of mandibles from localities of fossil insectivorous mammals, the southern Pre-Urals.

the medial and distal buccal cusps of the teeth) and allow avoiding subjectivity when establishing mandible age using the descriptive tooth wear assessment approach. These methods, used to study age variability of fossil specimens of red-toothed shrews, are well-justified and enable an objective analysis of the morphometric data in species identification.

The morphometric characteristic limit data obtained for the fossil mandibles of *S. araneus* and *S. tindrensis* found in the deposits of certain locations in the southern part of the southern Pre-Ural region suggest a preliminary conclusion that these populations had larger sizes as compared to those of representatives of fossil northern populations of the species. The maximum values (L asc) are higher for the samples studied than for the Late Pleistocene – Early Holocene samples of *S. araneus* and *S. tundrensis* (4.40–4.73 ± 0.21–5.10 mm [8] and 3.75–4.11 ± 0.15–4.30 mm [56], accordingly) obtained at the locations in the north of the Middle Pre-Ural region (Fadeeva, 2016).

It is known that body size of *S. araneus* negatively correlates with geographic latitudes: representatives of the species found in northern latitudes are noticeably smaller (Ochocinska and Taylor, 2003; Schipanov et al., 2011; Bobretsov et al., 2012). The mandibles of *S. araneus* are larger in the Late Pleistocene and Early Holocene deposits at the locations studied, as compared to those in the Middle and Late Holocene deposits. Changes in the structure of small mammal faunas by the Late Holocene, with a significant decrease in the proportion of species of semi-desert and steppe biotopes and the predominance of forest species, were due to the development of forest vegetation in the area, which was undoubtedly the result of the likely climatic trend of decreasing temperatures and higher humidity. The mandibles of *S. araneus* are larger in the Late Pleistocene and Early Holocene deposits at the locations studied, as compared to those in the Middle and Late Holocene deposits. The question now arises of whether the increase in the size of the South Urals *S. araneus* was due to the change in the habitat or is indicative of the morphological characteristics of different chromosomal races of the species, whose representatives might have lived in the same territory in different time periods. To answer this question, further analysis of samples of fossil mandibles of the species from other territories of the Southern and Middle Urals is required, which will allow establishing certain trends that were typical of the local populations of *S. araneus* in the Late Pleistocene and Holocene.

6. Conclusion

The study of the remains of insectivorous mammals obtained from the deposits of the Late Pleistocene and Holocene at various locations in the southern Pre-Urals (at the latitudinal course of the Belaya and Nugush Rivers) has identified the study area as a former habitat of seven species of red-toothed shrews (*S. araneus, S. isodon, S. tundrensis, S. caecutiens, S. minutus, S. minutissimus, Neomys fodiens*), white-toothed shrews (*Crocidura* sp.), moles (*Talpa* sp.), and hedgehogs (*Erinaceus* sp.). It has been demonstrated that *S. tundrensis* was the dominant species in the fauna of insectivorous mammals at the end of the Late Pleistocene and in the Early Holocene. By the second half of the Holocene, *S. araneus* began dominating the fauna, while *S. tundrensis* gradually disappeared from the area studied. These changes in the insectivore fauna coincided with the changes in the rodent fauna in this area: by the late Holocene, forest species began to dominate, while steppe and semi-desert species became rare (Danukalova et al., 2011). Considering that modern representatives of *S. tundrensis* prefer open and shrubby habitats and representatives of *S. araneus* are widespread in forest habitats, including in broad-leaved forests (Zaitsev et al., 2014), it becomes obvious that, by the late Holocene, environmental conditions in the study area had changed towards higher humidity and more extensive forestation.

In places where red-toothed shrews cohabitate, it may be difficult to distinguish between *S. araneus* and *S. tundrensis* (Zaitsev et al., 2014). In order to establish accurate diagnostic mandibular features for specific fossil local populations of these species, the degree of age and temporal variability were assessed. Late Pleistocene and Early Holocene *S. araneus* and *S. tundrensis* are well differentiated by mandibular ramus heights and by the distances between the posterior parts of the incisor and last molar alveoli and the articular process. According to the preliminary data, red-toothed shrews of these two species, inhabiting the area studied and the north of the Middle Pre-Ural region, differed in size in the late Pleistocene and early Holocene (the southern red-toothed shrews were larger). Temporal variability was traced within the samples of mandibles of *S. araneus*, which populated the study area in all periods of the Late Pleistocene and Holocene analyzed. Larger mandible sizes for this species were found in the Late Pleistocene – Early Holocene samples, as compared to the Middle and Late Holocene samples.

CRediT authorship contribution statement

Tatyana Fadeeva: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft. **Anatoliy Yakovlev:** Investigation, Resources, Writing - original draft. **Dmitriy Gimranov:** Investigation, Resources, Writing - original draft. **Pavel Kosintsev:** Investigation, Resources, Writing - original draft. **Kristina Cheremiskina:** Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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