

Late Anthropogene Insectivora from the South Urals with a Special Reference to Diagnostics of Red-Toothed Shrews of the Genus *Sorex*

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ABSTRACT.—Description of remains of insectivorous mammals (hedgehogs, moles, and shrews) from Late Pleistocene and Holocene deposits in caves of the South Urals is given. I distinguish three main types of faunas: Serpievskaya (Late Pleistocene), Ignat'evskaya (Early Holocene), and Simskaya (Late Holocene) that differ notably in abundance and species composition. A key for the identification of fossil remains of red-toothed shrews is provided.

ПОЗДНЕАНТРОПОГЕНОВЫЕ НАСЕКОМОЯДНЫЕ ИЗ ЮЖНОГО УРАЛА С УДЕЛЕНИЕМ ОСОБОГО ВНИМАНИЯ ДИАГНОСТИКЕ БУРОЗУБОК РОДА *SOREX*

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АБСТРАКТ.—Приведено описание остатков насекомоядных млекопитающих (ежей, и землероек) из позднеплейстоценовых и голоценовых отложений пещер южного Урала. Выделено три основных типа фаун: Серпиевская (поздний плейстоцен), Игнатьевская (ранний голоцен) и Симская (поздний голоцен), которые существенно отличаются друг от друга по обилию и видовому составу. Приводится система и диагностическая таблица для определения ископаемых остатков.

INTRODUCTION

One of the tasks of Quaternary paleozoology is a study of the history and dynamics of biocoenoses determined by periodic changes of the climate of the Earth throughout the Pleistocene. Until recently characterization of faunal complexes of the Pleistocene and Holocene was based primarily on data obtained as a result of a study of rodents (Order Rodentia) and large mammals (orders Carnivora, Perissodactyla, Artiodactyla, and Proboscidea). Characterization through use of these groups was undoubtedly determined by a number of factors, namely: 1) numerous remains of representatives of these groups in paleontological collections; 2) exceptional diversity of the rodent and large mammal fauna; and 3) a high level of knowledge of morphological diversity and diagnostics of recent and fossil forms.

Data from insectivorous mammals (Order Insectivora) as a whole and shrews (Family Soricidae) in particular did not have importance of their own. This was primarily because insectivore fossils are relatively few and difficult to identify. At the same time, however, it was recognized that in a number of cases insectivores can be more exact indicators of paleobiocoenoses.

In addition, study of remains of Quaternary insectivorous mammals has its own great importance. As is known, the Pliocene and Early Pleistocene insectivore fauna of Europe has been studied in detail (Bachmayer and Wilson 1970, 1978, 1980; Feifar 1961, 1966, 1983; Kowalski 1956, 1960a, b; Kretzoi 1959; Rabeder 1970; Rzebic-Kowalska 1971, 1975, 1976, 1981; Sukhov 1970, 1977; Sulimski 1959, 1962; Sulimski, Szykiewicz, and Woloszyn 1979; Topachevsky 1961, 1965). This fauna is fundamentally different in composition compared with the recent one (Sharova 1974, 1980). Study of material comparing the Pliocene and Early Pleistocene record to that of the recent time therefore would be of interest. The objective of this study is the illumination of the history of formation of the recent Insectivora fauna.

Recently obtained collections of numerous insectivores from Pleistocene - Holocene cave deposits in the South Urals collected under the direction of Dr. N. Smirnov (Institute of Plant and Animal Ecology, Russian Academy of Sciences) permits a step forward in a study of the problems noted above. One major task in this study is the development of diagnostic methods distinguishing species of shrews with reference to paleontological material. This material is most commonly mandibles recovered in cave excavations.

MATERIAL

The present study is based on the collection of fossil insectivore remains from Pleistocene - Holocene deposits in Ignatyevskaya (caves II and V), Serpievskaya I, Prizhim II, Sim II and Sim III caves in the southern Ural Mountains (Smirnov et al. 1990) as well as on the collection of recent shrews in the Zoological Institute, Russian Academy of Sciences, St. Petersburg.

A total of 14 species of recent red-toothed shrews (*Sorex*) from the Palearctic fauna have been studied, including *S. araneus*, *S. isodon*, *S. roboratus*, *S. daphaenodon*, *S. alpinus*, *S. raddei*, *S. asper*, *S. unguiculatus*, *S. caecutiens*, *S. tundrensis*, *S. minutus*, *S. garcillimus*, *S. minutissimus*, and *S. cinereus*. Presently known sibling species, including *S. araneus* (*S. araneus* - *S. caucasicus*), *S. minutus* (*S. minutus* - *S. volnuchini*), and *S. cinereus* (*S. cinereus* - *S. portenkoi* - *S. camchatica* - *S. leucogaster*), were not separated or studied separately.

METHODS

White-toothed shrews, moles, and hedgehogs were identified using conventional methods. A technique of identification of species of red-toothed shrews was developed for the first time by the author (Zaitsev 1989, 1992) on the basis of combined qualitative characteristics of the structure of individual teeth and the mandible and a number of quantitative characters. As quantitative data were compared, particular importance was attached both to the absolute values of some measurements and to their generalized index expressed in terms of the principal components analysis.

A matrix of 40 measurements of the mandible (Fig. 1) was compiled for 5 - 15 individuals of each species. Animals from different parts of the modern distribution range were used as comparative material (Dolgov 1972). For widespread species, individuals were chosen with maximal, average, and minimal skull and body size. The analyses were restricted to skulls of young animals having well-preserved, unworn teeth.

The procedure of identification of species using principal components analysis included several stages. At the first stage a matrix was made of measurements of a number of recent species, compared species, and groups of species. The number of measurements in this matrix was determined by the maximum possible

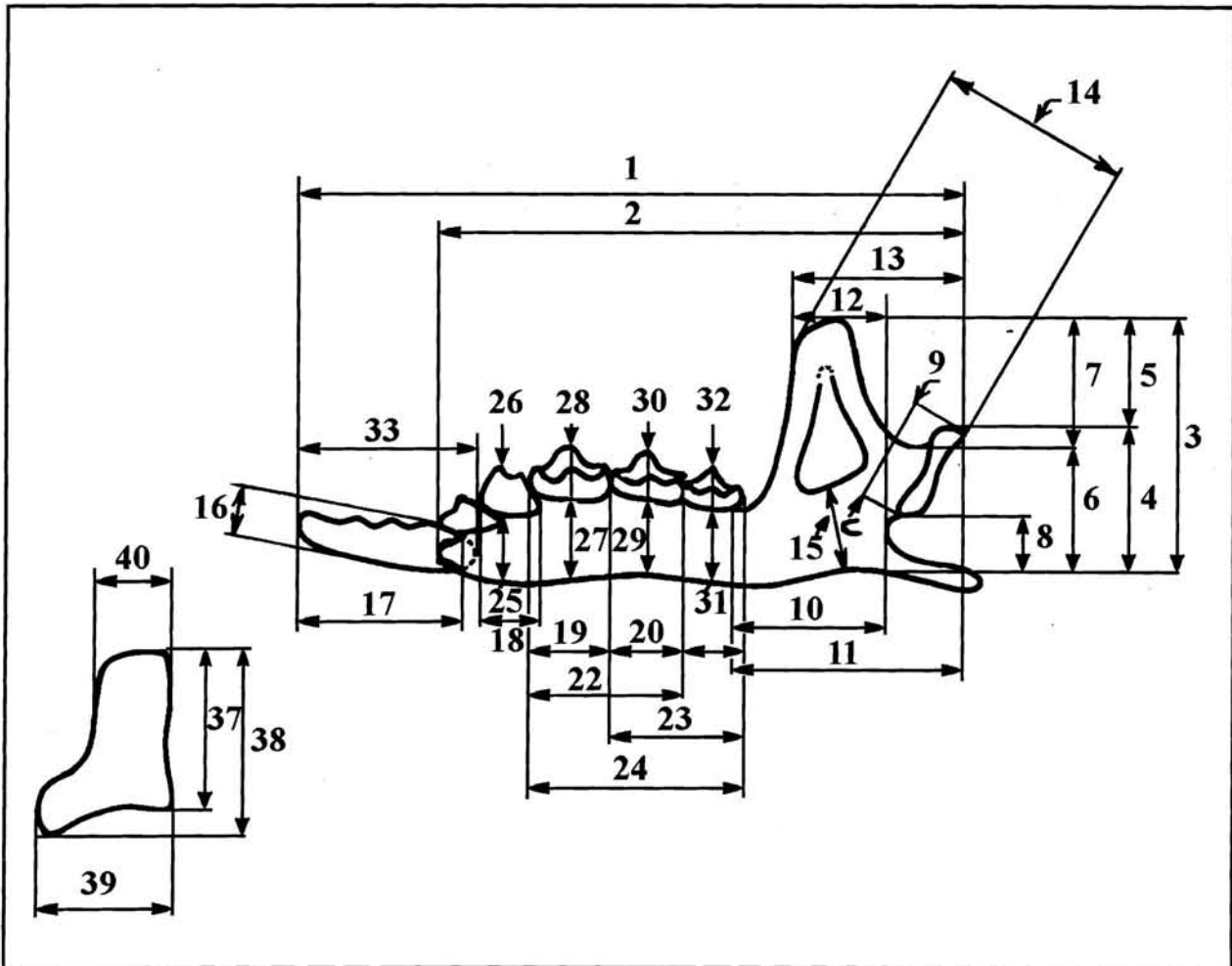


Figure 1. The scheme of measurements of *Sorex* mandibles.

number of measurements in the scheme proposed above (Fig. 1). These measurements were limited by those that could be taken from the paleontological specimen under study. The matrix was processed using a computer program for principal components analysis. As a result of this analysis I obtained a graph of arrangement in two- or three-factor space. At this stage I assessed the level of difference between compared groups of species by the set of characters that was used in the particular analysis. In the case when differences between groups were distinct, new data from paleontological specimens were added to the matrix and the analysis was conducted again. As a result I obtained a second graph combining data on recent and fossil forms. Position of the dots designating the paleontological specimen under study determined its attribution to a particular species or species group.

Measurements were obtained using an ocular micrometer of a binocular microscope (MBS) with precision of up to 0.05 - 0.1 mm.

DIAGNOSTICS OF PALEARCTIC RED-TOOTHED SHREWS OF THE GENUS *SOSEX*

Distinguishing individual species using the techniques above depends on the preservation of the fossil material. This material is often fragmentary. The most efficient means of identification of specimens to species is on the basis of both well-preserved molars and ascending mandibular ramus. Shape of the last lower premolar and the first incisor also appears to be informative in many cases.

Diagnoses of subgenera

The first step in identification of fossil material is the placement of the specimen in one of the subgenera of the genus *Sorex*, i.e., subgenus *Sorex* or subgenus *Otisoorex*. The most reliable criterion is the presence (subgenus *Sorex*) or absence (subgenus *Otisoorex*) of the postmandibular canal (Fig. 2).

- 1 (2) Postmandibular canal in the lower jaw is present.....3 (subgenus *Sorex*)
- 2 (1) Postmandibular canal in the lower jaw is absent.....subgenus *Otisoorex* (*S. cinereus*)

Diagnoses of species

The second step in the identification of species in the subgenus *Sorex* is the placement of the specimen under study in a particular size group. Three size classes are distinguished: A) shrews of small size (*S. minutus*, *S. minutissimus*, *S. gracillimus*), B) shrews of average size (*S. caecutiens*, *S. tundrensis*); and C) shrews of large size (*S. araneus*, *S. isodon*, *S. alpinus*, *S. roboratus*, *S. daphaenodon*, *S. raddei*, *S. asper*, *S. unguiculatus*).

Shrews of small size may be separated on the basis of absolute measurements.

- 3 (4) a) Length of row M_1 - M_3 (m24) is less or equal to 3.2 mm,
b) Length of row M_1 - M_2 (m22) is less or equal to 2.2 mm,
c) Length of M_1 (m19) is less or equal to 1.0 mm,
d) Height of ascending ramus of mandible (m3) is less or equal to 3.4 mm.....5 (size group A)
- 4 (3) a) Length of row M_1 - M_3 (m24) is greater than 3.2 mm,
b) Length of row M_1 - M_2 (m22) is greater than 2.2 mm,
c) Length of M_1 (m19) is greater than 1.0 mm,
d) Height of ascending ramus of mandible (m3) is greater than 3.4 mm.....9 (size groups B, C)

Identification is subsequently performed in each of the size groups separately.

Group A (shrews of small size). Group A includes three species of recent red-toothed shrews: *S. minutissimus* Zimmermann, 1780; *S. minutus* L., 1766; and *S. gracillimus* Thomas, 1907.

A preliminary identification of remains of these species can be made using the following key:

- 5 (6) a) Height of ascending ramus of mandible (m3) is less or equal to 2.6 mm,
b) Height of processus articularis (m5) is less or equal to 1.3 mm,
c) Length of M_1 - M_3 (m24) is less than 2.8 mm,
d) Length of M_1 - M_2 (m22) is less than 2.0 mm*S. minutissimus* Zimm.
- 6 (5) a) Height of ascending ramus of mandible (m3) is greater than 2.6 mm,
b) Height of processus articularis (m5) is greater than 1.3 mm,
c) Length of M_1 - M_3 (m24) is more than 2.8 mm,
d) Length of M_1 - M_2 (m22) is more than 2.0 mm7
- 7 (8) a) The cingulum of M_1 has a distinct notch,
b) Processus coronoideus is wide in its upper part (Fig. 3 a)*S. gracillimus* Thomas
- 8 (7) a) On the cingulum of M_1 the notch is lacking,
b) Processus coronoideus is narrow in its upper part (Fig. 3 b) *S. minutus* L.

Each of the three Group A species differs in the complex of measurements in the factor space. Figure 4 shows the results of diagnoses of fossil shrews of Group A from Serpievskaya I and Sim II-III caves and from the third horizon of Prizhim II Cave.

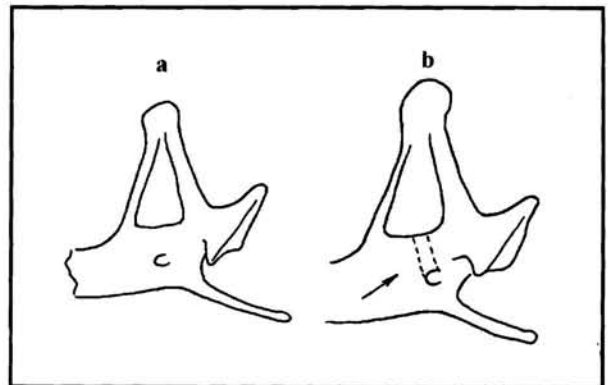


Figure 2. The ascending ramus of the mandible of *Sorex* (*Otisoorex*) *cinereus* (a) and *Sorex* (*Sorex*) *caecutiens* (b).

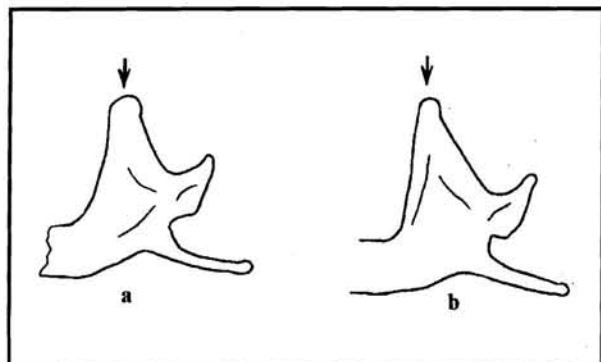


Figure 3. The ascending ramus of the mandible of *Sorex minutus* (a) and *Sorex gracillimus* (b).

Groups B and C (shrews of average and large size). Approximately 80% of the mandibles of groups B and C may be referred to each on the basis of the length of the processus articularis:

- 9 (10) Length of processus articularis (m9) is less than or equal to 1.9 mm 11 (size group B)
- 10 (9) Length of processus articularis (m9) is greater or equal to 1.9 mm 13 (size group C)

Placement of specimens into size classes may be more vital if principal components analysis is used. This analysis may be conducted also in cases where the length of the processus articularis indicated above is 1.9 mm, or in cases where the processus articularis is lacking.

The sample of fossil remains from Pleistocene - Holocene deposits of the South Urals included 68 mandibles belonging to size groups B and C. Identification of 20 specimens was made on the bases of key sections 9 (10) and 10 (9) above. Identification of other remains was made using factor analysis. As a result, 23 additional specimens were placed in size group B or size group C using different sets of 11 characters, including m3, m6 - m10, m12, m14, m15, m19, and m24 (Fig. 1). One of the results of analysis is presented in Figure 5.

With the material under study now separated into groups, the identification of species can begin.

Size group B (shrews of average size) includes two species: *S. caecutiens* Laxmann, 1788 and *S. tundrensis* Merriam, 1900.

The most significant diagnosis is obtained using the method of principal components analysis. In the Pleistocene - Holocene material from the South Urals, I found 17 lower jaws belonging to this size group. Using six measurements (m3, m6, m7, m10, m14, m15), I made a significant identification of 13 specimens (Fig. 6).

In addition, the following qualitative characters can be used that permit a more or less significant separation of *S. caecutiens* and *S. tundrensis*:

- 11 (12) a) Second lower incisor low, elongated in sagittal direction (Fig. 7 a),
b) Height of the first lower incisor (m16) does not exceed 0.8 mm,
c) Posterior edge of the processus articularis viewed from the buccal side is situated approximately at right angles to the longitudinal axis of the mandible (Fig. 8 a).....*S. caecutiens*
- 12 (11) a) Second lower incisor is high, triangular in shape (Fig. 7 b),
b) Height of anterior lower incisor (m16) is greater than 0.8 mm,
c) Posterior edge of the processus articularis, viewed from the buccal side is situated at an acute angle to the longitudinal axis of the mandible (Fig. 8 b)..... *S. tundrensis*

Size group C (shrews of large size) includes most of the Palearctic species, including *S. araneus* L., 1758; *S. isodon* Turov, 1924; *S. roboratus* Hollister, 1913; *S. unguiculatus* Dobson, 1890; *S. daphaenodon* Thomas, 1907; *S. raddei* Satunin, 1895; *S. asper* Thomas, 1914; and *S. alpinus* Schinz, 1837. The group may also include the largest specimens of *Sorex tundrensis*.

Identification of species within Group C begins with analysis of the structure of the anterior lower molar:

- 13 (14) a) Pyramidal funnels on masticatory surface of lower molars are absent,
b) Length of trigonids in M_1 and M_2 is less than length of talonids (Fig. 9 a)
.....*S. daphaenodon* Thom.
- 14 (13) a) Pyramidal funnels on masticatory surface of lower molars are distinct;
b) Length of trigonids in M_1 and M_2 is greater or equal to length of talonids (Fig. 9 b-d)
..... 15

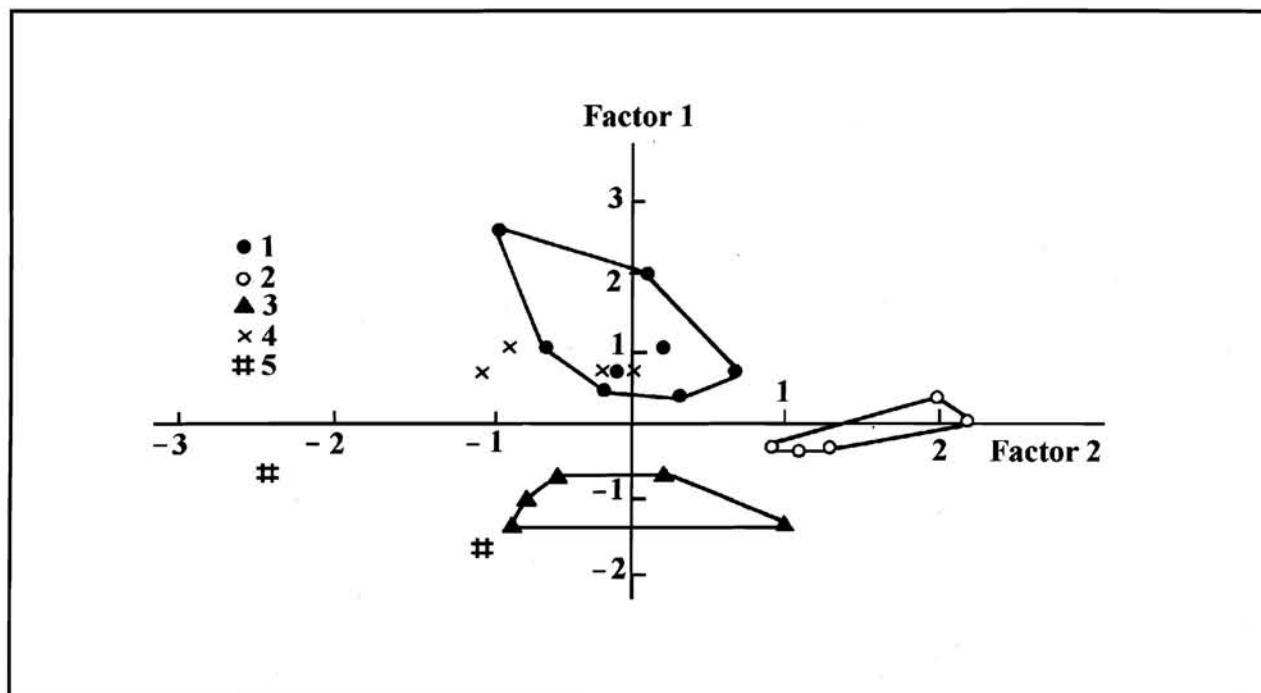


Figure 4. Principal components analysis of recent *Sorex minutus* (1), *S. minutissimus* (3), and *Sorex gracillimus* (2) and fossil remains (4, 5).

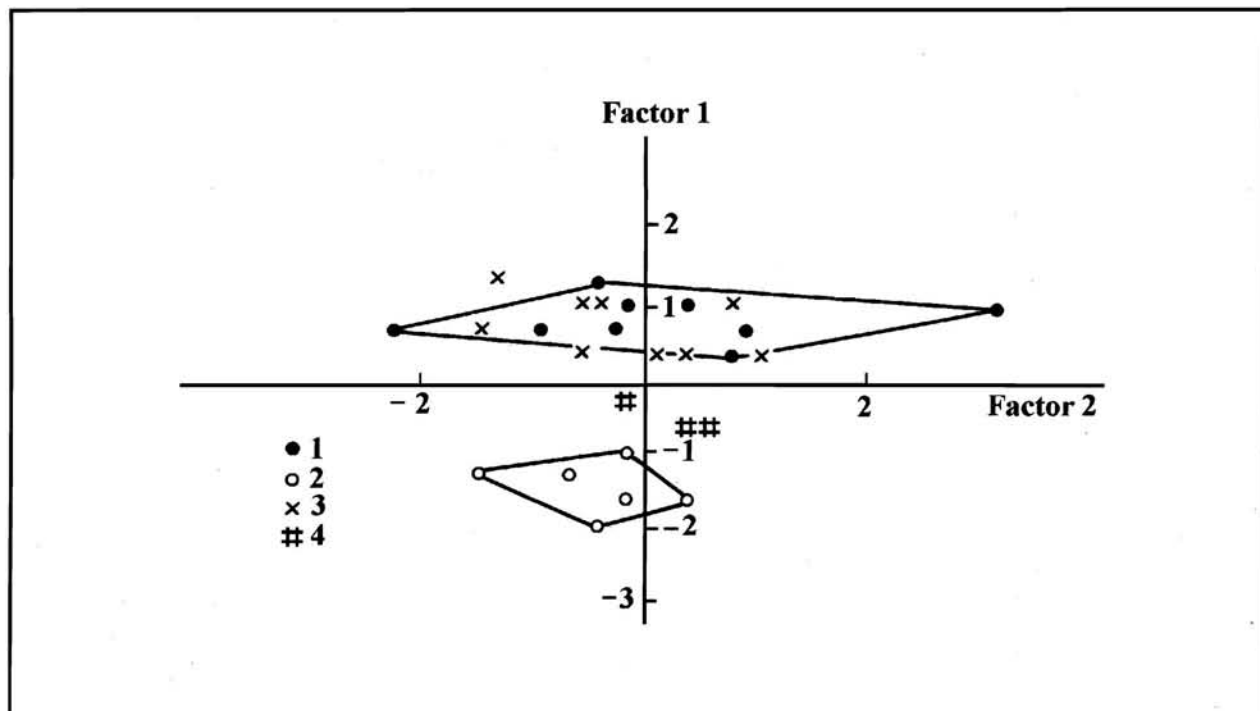


Figure 5. Principal components analysis of identified Holocene shrews of groups B (2), C (1) and Pleistocene remains (3, 4).

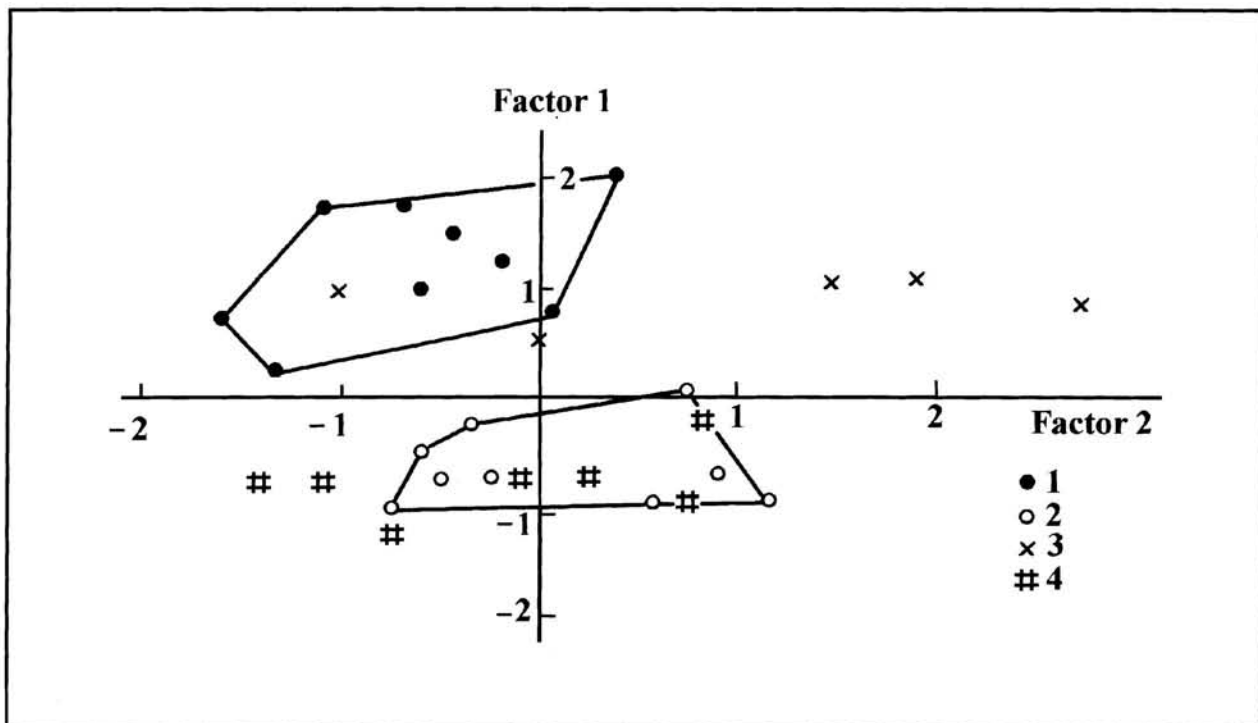


Figure 6. Principal components analysis of recent *Sorex tundrensis* (1) and *Sorex caecutiens* (2) and fossil remains (3, 4).

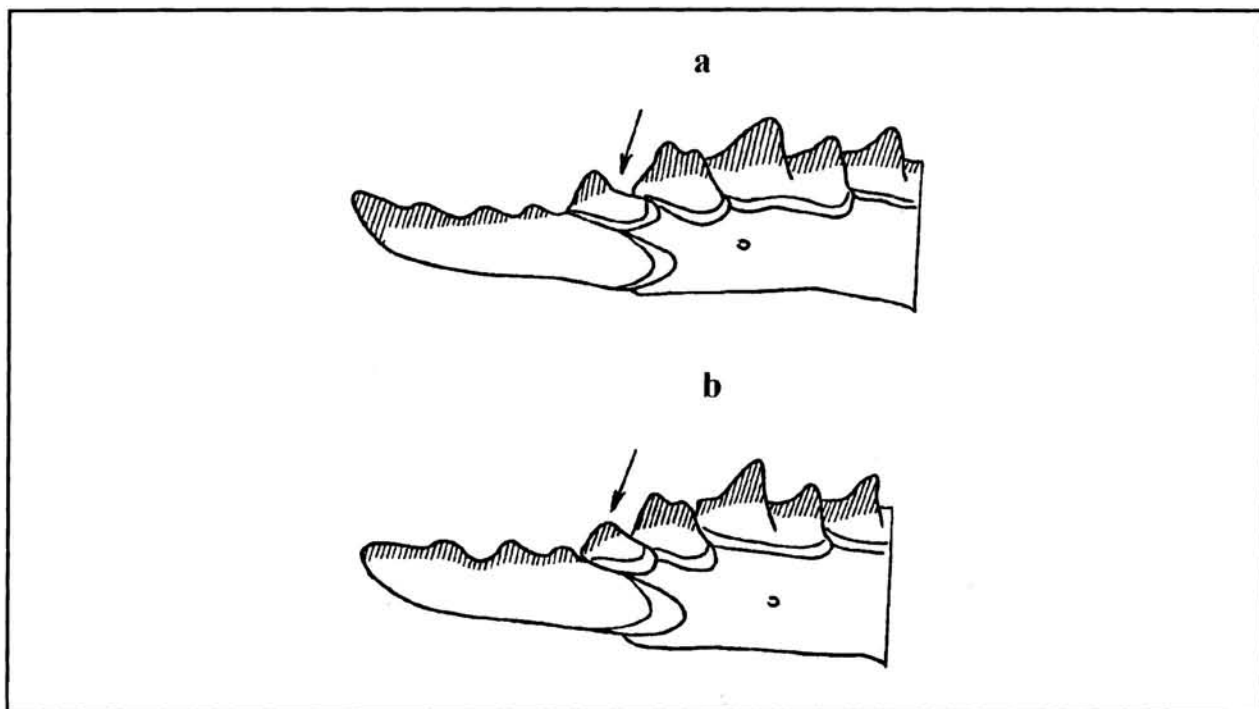


Figure 7. The morphology of the second lower incisor in *Sorex caecutiens* (a) and *Sorex tundrensis* (b).

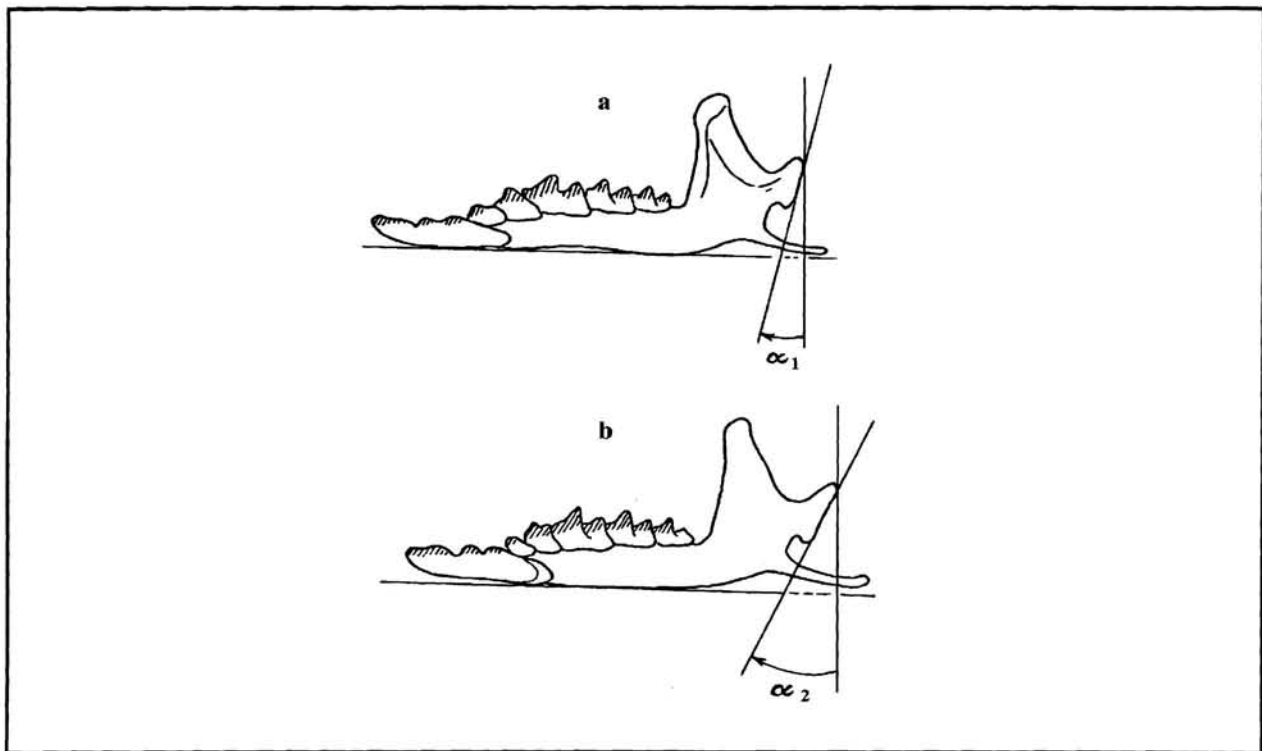


Figure 8. The morphology of the mandible of *Sorex caecutiens caecutiens* (a) and *Sorex tundrensis* (b).

15 (18) Cingulum of M_1 has marked notch
(Fig. 9 c, d) 16

16 (17) a) Mental foramen is located under the middle
of M_1 (Fig. 9 c),

b) Second lower incisor of triangular shape
with one apex or with two apices, but in
this case the second apex is notably smaller
than the first one (Fig. 9 c)
..... *S. roboratus* Holl.

17 (16) a) Mental foramen is located beneath anterior
root of M_1 , or on the level of the posterior
edge of crown of P_4 (Fig. 9 d),

b) Second lower incisor is elongated in sagittal
direction with two well-developed apices
(Fig 9 d)..... *S. alpinus* Schinz.

18 (15) There is no marked notch on the cingulum of
 M_1 (Fig. 9 b) 19

19 (20) Length of the processus articularis (m9) is
greater, equal, or less than 0.3 mm inferior to
length of the processus coronoideus
(m7)..... 23
(*S. isodon*, *S. unguiculatus*, *S. tundrensis*)

20 (19) Length of the processus coronoideus (m7)
exceeds the length of the processus articularis
(m9) by more than 0.3 mm 27
(*S. araneus*, *S. raddei*, *S. asper*)

This feature also separates the above-mentioned three species of shrews and can be used for checking their diagnoses. Thus the ratio of the lengths of the processus coronoideus and the processus articularis typical of *S. isodon* and *S. unguiculatus* is also observed in *S. daphaenodon* and *S. roboratus*, but in *S. alpinus* this ratio is similar to *S. araneus*, *S. raddei*, and *S. asper*.

The largest specimens of *S. tundrensis* placed in group C (m9 = 2.0 mm) are separated from *S. isodon* and *S. unguiculatus* on the basis of the following features:

The remaining portion of species in group C is divided significantly into two subgroups on the basis of the following character:

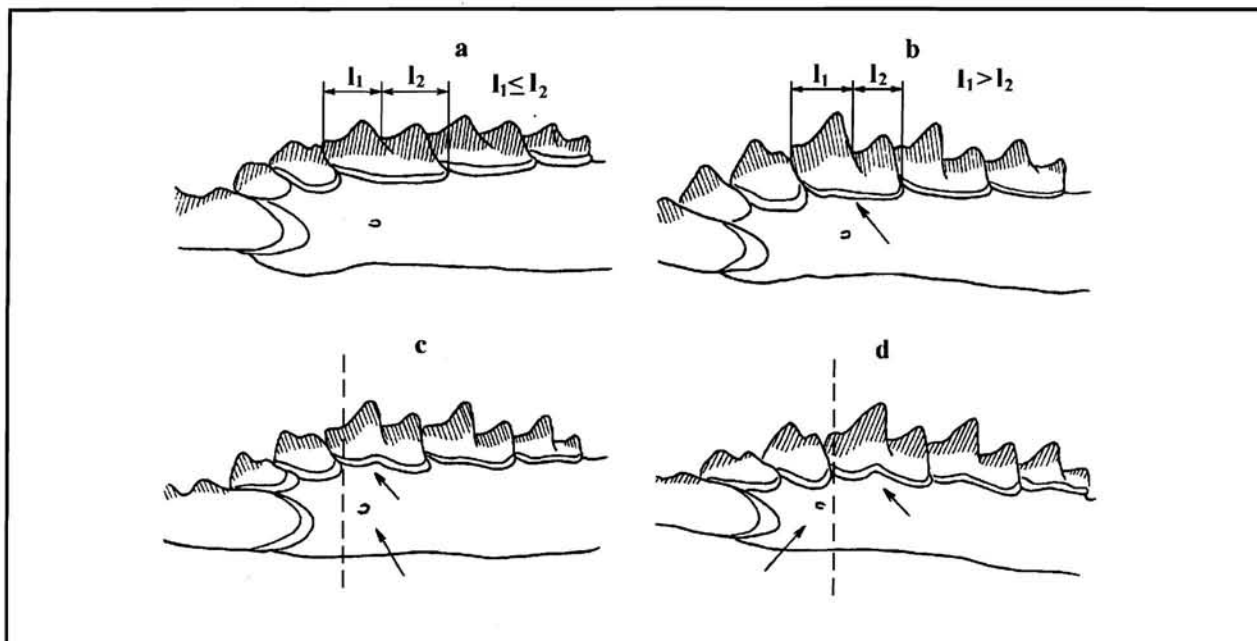


Figure 9. The morphology of the first lower molar in *Sorex daphaenodon* (a), *Sorex araneus* (b), *Sorex roboratus* (c), and *Sorex alpinus* (d).

- 23 (24) Distance from the posterior edge of alveoli of M_3 (m11) to the posterior edge of the processus articularis less than 3.9 mm *S. tundrensis* Merr.
- 24 (23) Distance from posterior edge of alveoli of M_3 to the posterior edge of the processus articularis (m11) is larger or equal to 3.9 mm 25
- 25 (26) Posterior apex of first lower incisor can be compared in size with the second apex of this tooth (Fig. 10a)..... *S. unguiculatus* Dobs.
- 26 (25) Posterior apex of anterior lower incisor is notably smaller than second apex of this tooth (Fig. 10 b)..... *S. isodon* Turov

To present significant diagnoses of *S. asper*, *S. araneus*, and *S. raddei* is much more difficult, and for the latter two species is nearly impossible:

- 27 (28) a) Second lower incisor is elongated vertically with a wide base and rounded apex;
- b) Length of talonid of M_3 is less than length of trigonid *S. asper* Thom.

- 28 (27) a) Second lower incisor is triangular in outline with sharpened apex;
- b) Length of talonid of M_3 is greater or equal to length of trigonid *S. araneus*
S. raddei

FOSSIL FAUNA OF INSECTIVOROUS MAMMALS OF THE SOUTH URALS

The main stages in the development of the rodent fauna in the Late Pleistocene and Holocene of the Urals have been described by Smirnov (this volume) and by Smirnov and his co-authors (1990). Here I present information on the Insectivora.

Fauna of the Late Pleistocene

The earliest fauna, termed Serpievskaya, is represented by remains from the ninth horizon of Ignatyevskaya Cave V and from the third horizon of Serpievskaya Cave I. Composition of the Serpievskaya fauna is very different from both the modern and the Middle - Late Holocene faunas of the region (Table 1). Of recent species, only *Sorex minutus*, *S. tundrensis*, and *S. araneus* are represented in the Serpievskaya fauna. Remains of recent species constitute only 36.9% of the total number of insectivore remains identified. The other identified species do not have analogues among the modern fauna.

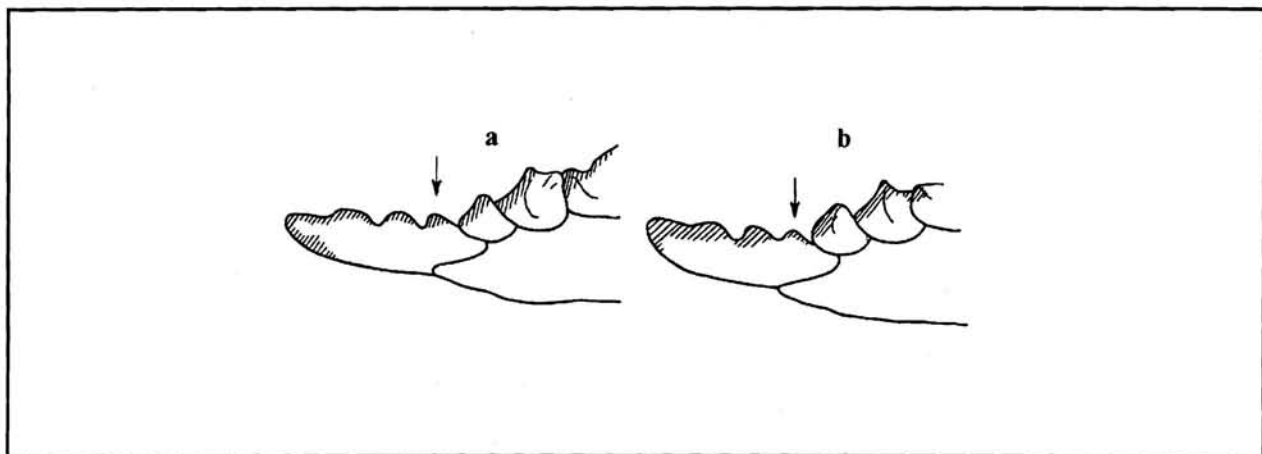


Figure 10. The morphology of the first lower incisor in *Sorex unguiculatus* (a) and *Sorex isodon* (b).

Insectivores in the Serpievskaya fauna include remains of hedgehogs (*Erinaceus* sp.) and moles (*Talpa* sp. nov. 1) and the possible presence of the Russian desman (*Desmana* sp.). Some shrew material, e.g., the water mole *Neomys*, and two new species of red-toothed shrews - *Sorex* sp. nov. 1 and *Sorex* sp. nov. 2 have also been found. In mandibular size and proportions the latter two species are close to the group *S. tundrensis*. In addition to *Sorex tundrensis*, *Sorex runtonensis* Hinton, *Sorex praeareneus* Kormos, *S. subareneus* Heller, *S. araneoides* Heller, and *S. pachyodon* Pasa are also placed in this group. Taxonomic relationships in the *S. tundrensis* group can be established only through a direct comparison of the material. Therefore, I refrain from specifying the status of the described species in the present paper.

An analogous situation is observed with the white-toothed shrews of the genus *Crocidura* known from Serpievskaya faunal localities, e.g., *Crocidura* sp. nov. 2, which in morphological features is close to the group conditionally termed *C. leucodon-rusula*. White-toothed shrews of the *leucodon-rusula* group are known from Pleistocene - Holocene deposits of different age in Europe and Asia (Besenecker, Spitzberger, and Storch 1972; Jammout 1973; Janossy 1986; Rzebik 1968; Zazhigin 1980). Determination of taxonomic relationships of the latter and the white-toothed shrews from the South Urals is only possible if the specimens are compared directly.

Fauna of the Early Holocene

The succeeding Ignatyevskaya insectivore fauna, from the second horizon and layers 2 - 8 of Ignatyevskaya Cave II, the third horizon of Serpievskaya Cave, and layers 1 - 8 of the Prizhim II locality, differs in being very poor, both in species composition and in the total number of remains. Among shrews of the genus *Sorex*, *S. tundrensis* (41.7%) predominates. The Ignatyevskaya fauna typically contains a number of East Palearctic species, e.g., *S. daphaenodon* and *S. roboratus*, that are absent in the recent fauna of the South Urals. West Palearctic boreal species, e.g., *S. araneus* and *S. minutus*, are few and constitute not more than 9% of recovered remains. *Neomys* and *Crocidura* are rare (Table 1).

A peculiar feature of the Early Holocene is the lack of hedgehogs and presence of few mole remains. Among the latter two isolated specimens of *Talpa europea* are known from layer 1 of Prizhim II Cave. These differ from the other Early Holocene remains by a lighter coloration and they could have been redeposited from more recent layers. Other remains of moles identified as *T. cf. fossilis* and *Talpa* sp. are similar in their features to recent *Talpa altaica* and European Pliocene-Pleistocene *Talpa fossilis* Petenyi and *T. minor* Freudentberg (Kowalski 1956; Janossy 1969, 1986; Sulimski 1959). The small number of specimens and their fragmentary nature precluded a significant assessment of taxonomic status and taxonomic position of these other mole remains.

Table 1. Changes in the insectivore fauna of the South Urals from the Late Pleistocene to the Holocene.

Taxa	Middle - Late Holocene	the end of the Late Pleistocene	the first half of the Late Pleistocene
<i>Erinaceus cf. europaeus</i>	2	-	-
<i>Erinaceus sp.</i>	-	-	-
<i>Talpa europaea</i>	25	2	-
<i>T. cf. europaea</i>	69	-	-
<i>T. cf. fossilis</i>	-	5	-
<i>Talpa sp.</i>	-	2	-
<i>Talpa sp. nov. 1</i>	-	-	1
? <i>Desmana sp.</i>	-	-	1
<i>Sorex minutus</i>	26	1	4
<i>S. minutissimus</i>	3	-	-
<i>S. caecutiens</i>	12	1	-
<i>S. tundrensis</i>	5	5	1
<i>S. araneus</i>	36	1	1
<i>S. cf. araneus</i>	6	-	-
<i>S. roboratus</i>	-	1	-
<i>S. daphaenodon</i>	-	1	-
<i>S. isodon</i>	2	-	-
<i>Sorex sp. nov. 1</i>	-	-	2
<i>Sorex sp. nov. 2</i>	-	-	5
<i>Sorex sp.</i>	53	44	42
<i>Neomys cf. fodiens</i>	6	-	-
<i>Neomys sp.</i>	-	1	1
<i>Crocidura cf. suaveolens</i>	1	-	-
<i>Crocidura sp. nov. 1</i>	1	1	-
<i>Crocidura sp. nov. 2</i>	-	-	5

The presence of the white-toothed shrew *Crocidura* sp. nov. 1 in the upper layer of Prizhim II Cave does not conform well to the general type of fauna otherwise indicated for the Early Holocene. It is possible that remains of these animals, as in the case of *T. europea*, may be extrusive from younger deposits.

Fauna of the Late Holocene

The youngest fauna, Simskaya, is represented by material from deposits of Middle and Late Holocene age in the first horizon of Serpievyskaya cave and in the first and second layers of the Sim II and III localities. Insectivores and other mammals are represented primarily by recent species. Predominant among shrews are *Sorex araneus* (39.1%) and *Sorex minutus* (28.3%). *Sorex caecutiens* occurs less frequently (13.0%). Other species of red-toothed shrews, including *S. tundrensis*, are few. Their contribution to the shrew fauna does not exceed 6%. *Neomys* remains are relatively few and those of *Crocidura* are rare. The shrew fauna of the Middle and Late Holocene as a whole is similar in species composition and relative abundance to that of the recent (Sharova 1980).

It is typical of the Middle - Late Holocene that common moles are numerous recovered and constitute slightly less than one half of the total number of insectivore remains. It should be noted, however, that such marked predominance of moles may have been determined to a large extent by the burial conditions and fragmentary nature of the material. As previously noted, isolated teeth constitute the larger portion of remains of moles whereas shrews are represented more commonly by complete mandibles or by their major portions. Remains of hedgehogs and white-toothed shrews in this late fauna are of great interest. The hedgehogs differ from the recent forms by being of large sizes and are perhaps to be placed in a separate subspecies. Among *Crocidura* I distinguish *C. cf. suaveolens* and *Crocidura* sp. nov. 1. The latter is a form that is absent from the recent fauna and undoubtedly close to the widely-distributed group *C. suaveolens*, particularly to this group's larger representatives *C. caspica* and *C. sibirica*. A number of characters, however, suggest *Crocidura* sp. nov. 1 is also similar to *C. leucodon*.

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