Pleistocene Soricidae (Lipotyphla, Insectivora, Mammalia) from Treugolnaya Cave, Northern Caucasus, Russia

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Abstract. Ten species of Soricidae, among them three new ones: Sorex doromchevi n. sp., Drepanosorex rupestris n. sp., and Neomys hintoni n. sp. are described from the Middle Pleistocene of Treugolnaya Cave in Northern Caucasus, Russia. The systematic position of the above-mentioned taxa, their measurements, and illustrations are given.

Key-words: fossil mammals, Insectivora, Lipotyphla, Soricidae, Pleistocene, Caucasus, Russia.

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1. INTRODUCTION

The fossil fauna of Soricidae from the Caucasus is almost unknown. There is only one reference (VERESTCHAGIN 1959) concerning two species of the genus Crocidura [C. rassula (HERMANN, 1780) and C. hucodon (HERMANN, 1780)] from the Late Pliocene Binagady fauna (Apsheron Peninsula, Transcaucasia) but the author did not give a detailed description of these species. Moreover, only one subspecies of insectivores, the hedgehog Erinaceus europaeus binagadensis ZAIDOVA-IRBRAGIMOVA, 1974 was described in more detail.

The history of the Caucasus fauna, however, seems to be very important. It is commonly known that the Caucasus was one of the main refuges during the Pleistocene. A high level of endemism is characteristic of the recent fauna of this region. It includes nine species of Soricidae belonging to four genera: Crocidura WAGLER, 1832, Suncus EHRENB. 1832, Sorex LINNAEUS, 1758, and Neomys KAUP, 1829.

Among Crocidurinae only C. leucodon is distributed in the Northern Caucasus and Transcaucasia. Outside the Caucasus region, this species is common in South and Central Europe and in Asia Minor. Suncus etruscus SAVI, 1822 has a similar distribution (except Central Europe) but is less common. The extensive range of Crocidura suaveolens PALLAS, 1811 reaches from the Atlantic to the Pacific coasts of Eurasia. In the Caucasus, however, it is restricted to its northern part only. Contrary to C. suaveolens, C. gudelniapetri PALLAS, 1811 is known only from the Transcaucasia. In should be pointed out, however, that the taxonomy of this species is controversial. The majority of
investigators (e.g. CATZEFIS et al. 1985, HUTTERER 1993) consider it as a parapatric form or a sub-
species of *C. suaveolens*. Others (GRAFODATSKY et al. 1988, SOKOLOV and TEMBOTOV 1989, ZAITSEV
1993) are of the opinion, that it is a separate species. Outside the Caucasus (on Eastern Medi­
teanean Islands, in Turkey and Israel), *C. suaveolens* is morphologically similar to *C. Gueldertsiadeti*.

*C. pergrisea* MILLER, 1913 is a very rare species. In the Caucasus it was found only in two lo­
calities of Armenia. It is related rather to several desert and mountain taxa of the "pergrisea" group
from Asia Minor (ZAITSEV 1993).

In the Caucasus and adjacent territories all Soricinae species are endemic. *Sorex raddei*
SATUNIN, 1895 is probably an autochthon of this region, whereas *S. satunini* OGNEV, 1922 and *S.
volnuchini* OGNEV, 1922 are sibling species of the European *S. araneus LINNAEUS, 1758* and *S.
minor* LINNAEUS, 1766.

The only species of the genus *Neomys, N. scheikovnikovi* SATUNIN, 1913, by its morphological
characters has an intermediate position between *N. fodiens* PENNANT, 1771 and *N. anomalus*
CABRERA, 1907 (ZAITSEV 1999).

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GOLOVANOVA and Vladimir DORONICH (St. Petersburg) for the possibility of collecting fossil
material in Treugolnaya Cave. They are also obliged to Prof. Barbara RZEBIK-KOWALSKA (Institute
of Systematics and Evolution of Animals, Cracow), who made available her collections during the
visit of one of the authors (M. ZAITSEV) in Poland and also for the discussion of the results and for
help in editing the present work. They are indebted to Prof. Adam NADACHOWSKI and Prof. Kazim­
ierze KOWALSKI for their support and help during the stay in Cracow. Authors are also grateful to Galina BARANOVA and
Vera OSIPOVA who did the work of cleaning fossil specimens and preparing them for the study. The
Russian Fund of Basic Researches supported the investigation devoted to extinct Soricidae of the
Caucasus (Grant N. 00-04-48452).

II. MATERIAL

Treugolnaya Cave is situated within the limits of the Skalistyi Khrebet (Rocky Ridge) of
Baranakha Plate in the basin of the river Urup, 8 km north-east of the village Pregradnaya (43°57'
N, 41°11' E). Dr V. B. DORONITCHEV, from Saint Petersburg, was the first to discover this cave in

Treugolnaya Cave lies 1510 m above sea level, in the zone of mountain birch forests and sub-
alpine meadows. It represents a karst cavity; its length is 12 m, breadth 3 m, while height reaches 4
m. The excavation area amounts to 20 m² (DORONICHEV 1991, BARYSHNIKOV 1993).

Cave deposits consist of grey, brownish, and orange brown clayed sand and light loams includ­
ing corroded lime detritus. Total thickness of deposits reaches 3 - 4.5 m. Bone remains are mineral­
ized to various degree. Their colour varies considerably even within the same layer, from light
brown to greenish-yellow, often with black spots to entirely black.

Seven lithological layers can be distinguished. Layer 1 is dated to the Late Holocene, layer 2 to
the end of the Pleistocene or the Holocene. Layers 3a and 3b represent the last (Valdai) glaciation,
while layers 4a-c and 5a-b are also of the Late Pleistocene but more ancient and correspond to the
second half of the Palaeolithic. The oldest layers, 6 and 7a, are dated to the beginning of the Middle
Pleistocene (BARYSHNIKOV 1993).

The age of sediments was determined by two absolute dates obtained by electron paramagnetic
resonance of two layers; 393,000 ± 2,700 for layer 5 and 583,000 ± 25,000 years for layer 7a (Table I).

The studied material is summarized in Table I. It was figured and measured under ZEISS-Stemi
SR and MBS-2 microscopes. The pigmented parts of teeth are not shown in the figures because they
have no essential significance for the species diagnosis. The general pattern of measurements of
mandible and lower teeth was especially developed for the diagnosis of both fossil and recent spe­
cies (Fig. 1). It is based on the scheme identical to that used earlier for the genus *Sorex* (ZAITSEV
1998). This pattern includes 58 measurements, but only 21 of them were used in the present work
(Table II).

The identification of specimens was carried out by means of the traditional characters used in
palaontological research and new methods developed for the recent species of the genus *Sorex*
Table 1

Chronological position of Treugolnaya Cave sediments and material examined. Numbers indicate quantity of remains of particular species.

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All the specimens are housed in the Department of Taxonomy (T.) of the Laboratory of Mammalogy at the Zoological Institute (ZISP) of the Russian Academy of Sciences (Saint Petersburg, Russia).

III. SYSTEMATIC PART

Family Soricidae FISHER VON WALDHOF, 1817

Subfamily Soricinae FISHER VON WALDHOF, 1817

Tribe Soricini FISHER VON WALDHOF, 1817

Genus Sorex LINNAEUS, 1758

Sorex cf. minutissimus ZIMMERMANN, 1780

(Fig. 2)

Material. One fragment of mandible with M1 and coronoid and condyloid processes (see Table 1).

Description. Mandible. The horizontal ramus is very thin and delicate. The ascending ramus is low and the coronoid process thin. The upper part of this process is inclined slightly for-
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**Table II**

Dimention of mandible and lower dentition (in mm). The top of columns – no. of dimension (see Fig. 1). In line – for each dimension (from above) number of specimens, average and minimum/maximum.
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(continued)
wards, the posterior edge is straight, the anterior one slightly concave. The external temporal fossa is narrow and deep, with a well-developed anterior longitudinal bar. The bar runs parallel to the posterior edge of the coronoid process. The coronoid spicule is moderately protruding. The internal temporal fossa is high and distinctly triangular in shape. It extends almost up to the apex of the coronoid process. There is no horizontal bar. The condyloid process is high. Its interarticular area is relatively broad, the upper facet cylindrical and obliquely set, the lower facet larger, and its upper margin slightly concave. It is not inclined to the same degree as the upper one. The mental foramen is situated under the protoconid of M₁. There is one mandibular and one postmandibular foramen,
which is typical of all species of the subgenus Sorex sensu stricto. Both foramina are connected by a relatively deep depression.

**Measurements.** See Table II.

**Systematic position and comparison.** A very small size permits the inclusion of the specimen above described to *S. minutissimus*. It differs distinctly from *S. volnuchini* and *S. aff. minutus* in its measurements (see Table II) and in the morphology of its ascending ramus which in the specimen from Treugolnaya Cave is similar to *S. minutissimus* from Belfa VII’3 (RZEB{K-KOWALSKA 2000). It should be noted, however, that the majority of recent *S. minutissimus* are smaller and have no such deep external temporal fossa.

*Sorex volnuchini* OGNÉV, 1922

(Figs. 3 and 4A)

**Material.** 26 fragments of mandible with all types of teeth and processes, except angular ones (see Table I).

**Description.** Mandible. The horizontal ramus is relatively narrow, and the ascending one relatively wide. The coronoid process is triangular in shape with straight posterior and slightly concave anterior edges. Its apex is relatively wide, rounded, and inclined slightly forward. The length of the upper inclined part does not exceed one third of the coronoid process height. The axis of the anterior edge of the coronoid process runs through its apex (Fig. 4A). The external temporal fossa is wide and not very deep. It begins near the anterior edge of the coronoid process and runs down at least to the level of the upper sigmoid notch. The coronoid spicule is slightly protruding. The internal temporal fossa is triangular with rounded angles. It does not reach the apex of the coronoid process. The condyloid process is high and its interarticular area broad and centrally depressed. The upper articular facet is narrow and cylindrical, the lower one is wide and its upper margin rounded. The two facets are inclined approximately to the same degree and run parallel to one another. The mental foramen is situated below the trigonid of M1 and its posterior edge below the tip of the protoconid of this tooth.

Lower dentition. The lower incisor, I1, is distinctly tricuspidate. Its first cusp is distinctly separated from the apex, while the last one is shifted forward in relation to the first lower antemolar. A) This tooth (A1) is very low and long and its posterior dorsal edge is distinctly concave. It is compressed between I, and P4 but the gap between the crowns of T1 and P4 is relatively wide. In the buccal view the posterior edge of A1 lies not far from the posterior edge of I. Some specimens of A1 have a tendency to be bicuspidate.
Fig. 3. *Sorex m. volnuchini* from Treugolnaya Cave. A - fragment of left mandible with $P^+$ - Mj (buccal view), spec. no. T7a-2/87, B - condyloid process (posterior view), spec. no. T7a-132/87, C - fragment of mandible with Eax- Mj (buccal view), spec. no. T5v- 82/87.

Fig. 4. Recent *Sorex m. volnuchini* (A) and *Sorex m. m. minuchini* (B, C) from Treugolnaya Cave. A - fragment of right mandible with Mt (lingual view), spec. no. 7a-132/87, B - fragment of right mandible (lingual view), C - condyloid process (posterior view), spec. no. T7a-2/87.
The second lower antemolar, P4, is typical in the shape and proportions of the *Sorex* species. It overlaps one-third to half of the crown of Ai. Its postero lingual edge is well developed and its posterolingual basin quite deep.

The lower molars have narrow buccal and comparatively wide lingual cingula. The buccal base of the crown of Mi is straight or slightly undulated. The mesoconid, if present, is better developed in M. than in Mi. In most specimens, the metaconid is shifted closer to the entoconid than to the paracoid, but this shift is never very distinct. The entoconid crest is very high.

**Measurements.** See Table II.

**Systematic position and comparison.** No examined specimens differ from recent *S. volnuchini* in dimensions or in morphological characters of teeth and mandible. They are, however, smaller than recent specimens of *S. minutus* from East Europe and Siberia.

*Sorex aff. minutus* LINNAEUS, 1766

(Figs. 4B, C)

**Material.** One fragment of mandible with M1, M2 and coronoid process (see Table I).

**Description.** Small-sized shrew. Mandible. The coronoid process is very narrow, especially in its upper part. Its posterior edge is straight, the anterior one also straight in its upper part (it runs parallel to the posterior edge), but in one third of its height it bends forward, so that the upper and lower parts of the anterior edge form an obtuse angle. The length of this upper inclined part slightly exceeds one-third of the height of the coronoid process. The apex of the coronoid process is rectangular. It is considerably inclined forwards. The axis of the anterior edge of the coronoid process runs behind the apex of this process (Fig. 4B). The coronoid spicule is situated low. The external temporal fossa is relatively deep, provided with an anterior longitudinal bar. This bar runs parallel to the posterior edge of the coronoid process. The mental foramen is placed below the trigonid of Mi.

Lower teeth. Only the two first lower molars, Mi and M2, are present. They do not differ in the morphology from the teeth of *S. minutus* from other known localities. It should be pointed out that the mesoconids are also well developed in both molars.

**Measurements.** See Table II.

**Systematic position and comparison.** The taxonomy of the small fossil *Sorex* species similar to *S. minutus* (*S. subminutus* SULIMSKI, 1962, *S. praeminutus* HELLER, 1963, *S. biharicus* TERZEA, 1970) was discussed by RZEBIK-KOWALSKA (1991, 2000) and does not need repetition. As concerns the specimen of *S. aff. minutus* from Treugolnaya Cave it should only be noted that its size does not differ from that of recent *S. minutus* and is slightly smaller than in fossil and extant *S. volnuchini*. On the other hand, it differs from both these species in the morphology of the coronoid process. It is narrower, more inclined forwards, and its apex appears more rectangular. Also its coronoid spicule is different, similar to this structure in *Neomys* species. However, the poor material does not permit an answer to the question, as to what degree these characters are sufficient to describe a new species or whether they only represent the intraspecific variability of *S. minutus* or *S. Volnuchini*.

*Sorex cf. runtonensis* HINTON, 1911

(Fig. 5)

**Material.** 54 fragments of mandible with all types of teeth and processes except angular ones (see Table I).

**Description.** Middle-sized shrews. Mandible. The horizontal ramus of the mandible is comparatively narrow and slightly concave under M. The ascending ramus and the coronoid process are also narrow and delicate. The latter one is shifted anteriorly and thus situated close to the tooth row. Its upper part is moderately wide and slightly inclined forward. The posterior edge of the coronoid process is straight, the anterior one also being straight in its upper part and running parallel to the posterior edge. It makes its apex look more square than in other middle-sized species of shrews. The coronoid spicule is moderately developed. It does not protrude much and is not visible in lingual view. The external temporal fossa is fairly deep and as a rule provided with two longitudinal bars. The internal temporal fossa is high. It extends almost to the apex of the coronoid process. In
general it has no distinct horizontal bar but in some specimens a deep internal apical fossa may be present. The condyloid process is very narrow and high. The interarticular area is rectangular, in some specimens with a slightly concave lingual edge. The upper facet is narrow and cylindrical, the lower one wide, drop-shaped. The mental foramen is situated under the re-entrant valley of Mi. The mandibular and postmandibular foramina lie in a deep depression.

Lower teeth. The lower incisor, I₁ is relatively short and thick. It is tricuspid but its cusps are low and slightly differentiated. Its lower edge is slightly concave in its middle part. The first lower antemolar, A₁ is comparatively small and low. Its length is notably less than that of P₁. It is considerably shifted forwards. In buccal view the distance between the posterior edges of Ai and Ii is greater than that between the posterior edge of Ii and the paraconid of Mi (Fig. 5, D). The main cusp of Ai is shifted forwards. The posterodorsal edge of its crown is concave. The P₄ is higher and wider than Ai. Its two cusps are rounded. Its posterolingual crest is slightly developed and does not reach the lingual cingulum. The posterolingual basin is quite deep. The lower buccal edge of Mi is slightly concave and that of M₂ flat. The metaconids in Mi and M₂ are curved. They are wider and higher than entoconids. In Mi the metaconid is situated much closer to the entoconid and in M₂ it lies at an equal distance from the paraconid and entoconid. In Mi and M₂ the buccal cingulum is narrow but protruding, while the lingual one is wider but flatter. In some specimens the lingual cingulum in both lower molars is almost invisible.
Measurements. See Table II.

Systematic position and comparison. \( S. \) runtonensis belongs to the group of medium-sized long-tailed shrews which are smaller than \( S. \) araneus but larger than \( S. \) minutus. Among extant species \( S. \) runtonensis is similar in size to the Siberian species \( S. \) caecutiens LAXMANN, 1788 and \( S. \) tundrensis MERRIAM, 1900. Unfortunately no correct comparison of all these species has been carried out and it is difficult to evaluate the phylogenetic value of characters used for identification of all the above-listed forms. A specific revision of this group of shrews is needed.

At present it can only be noted, that in most characters the specimens from Treugolnaya Cave do not differ greatly from other European populations of \( S. \) runtonensis, although in some details insignificant differences may be found. Moreover, specimens from the Caucasus are larger than \( S. \) runtonensis from most European fossil localities.

Sorex satunini OGnev, 1922

(Fig. 6)

Material. Eight mandibles with all types of teeth (except for incisor, Ii) and coronoid and condyloid processes (See Table I).

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Fig. 6. Sorex satunini from Treugolnaya Cave (A, B, C) and recent specimen (D). A - fragment of right mandible with M1 - M2 (lingual view), B - the same (buccal view), C - condyloid process (posterior view), spec. no. T4g-1/87, D - fragment of left mandible with P4 - M1 (buccal view), spec. no. ZISP T.31575.
**Description.** Mandible. The horizontal ramus of the mandible is relatively wide. Its lower margin is slightly concave between Mi and M2. The ascending ramus is fairly wide. It bends slightly lingually and anteriorly. The apex of the coronoid process is slightly inclined backwards. It begins under the coronoid spicule and does not reach the anterior edge of the coronoid process. Its anterior longitudinal bar runs parallel to the posterior edge of the coronoid process and ends slightly below the level of the upper sigmoid notch. The internal temporal fossa is triangular and rather high. The pterygoid spicule may be developed or not. The condyloid process is wide and not very high. Its interarticular area is trapezoidal and in some specimens centrally depressed. The upper articular facet is cylindrical and moderately inclined, the lower one being wide, drop-shaped. The mental foramen is situated under the protoconid of Mi and its posterior edge at the level of the trigonid/talonid boundary of this tooth. Both mandibular foramina are typical of *Sorex.*

**Lower teeth.** The lower incisor, I1, is absent in the material under study, but in living shrews of this species it is quite large, distinctly tricuspid, while its first cusp is separated from the apex by a moderately deep groove. Ai is quite large, triangular in shape. Its length is slightly less than that of P4, its posterodorsal edge usually being straight, although in some specimens it may be slightly concave. This tooth is not shifted forwards. In buccal view the distance between the posterior edges of Ii and Ai is always equal to or smaller than the distance between the posterior edge of Ii and the paraconide of Mi. P4 is massive and its posterolateral basin deep. The lingual ridge of this basin runs down to the posterolateral corner of the crown but does not reach the lingual cingulum. P4 overlaps one-third to half of A1. Mi and M2 are quite large. Their metaconids are narrower than entoconids and they are slightly curved backwards. The entoconid crests are rather low, the lingual cingula wider and more protruding than the buccal ones while the mesoconids are absent.

**Measurements.** See Table II.

**Systematic position and comparison.** There is no doubt that *S. satunini* from Treugolnaya Cave, its recent population, and fossil *S. subaraneus* HELLER, 1958 belong to the *S. araneus* group. This group also includes such European taxa as *S. coronatus* MILLET, 1882, *granarius* MILLER, 1909, Asiatic *S. tundrensis* MERRIAM, 1900, *S. csper* THOMAS, 1914 and probably *S. daphaenodon* THOMAS, 1907 as well as North American *S. arcticus* KERR, 1792. *S. satunini* practically does not differ in size and morphology from *S. subaraneus.* The latter species was described by HELLER (1958) from the Late Biharian German locality Eipfingen, and then found in many Late Pliocene to Late Pleistocene localities in Europe (RZEBIK-KOWALSKA 1998). A slight difference between these two taxa concerns the morphology of Ai. This tooth seems to be heavier in *S. satunini* and has no additional small cusp. It is quite possible that *S. subaraneus* may be ancestral to some extant species of the *Sorex araneus* group in Europe (JAMMOT 1977). As the question of the taxonomy of the *Sorex araneus* group as well as that of the synonymy of *S. satunini* and *S. subaraneus* requires a special additional studies, for the time being both specific names have been retained. From the recent *S. satunini* of southern Europe and the Russian Plain both fossil forms, *S. satunini* from Treugolnaya Cave and *S. subaraneus,* differ in their smaller size (DOLGOV 1985).

*Sorex raddei* SATUNIN, 1895

(Fig. 7)

**Material.** One upper incisor, I1, and three toothless mandibles with all processes (see Table I).

**Description.** Large-sized shrew. Upper teeth. The unique upper incisor, I1, can without any doubt be referred to *S. raddei.* It is characterized by small size and reduced talon. In frontal view a trace of strongly reduced medial line is visible.

Mandible. The horizontal ramus is high and massive. The ascending ramus is very high. The coronoid process is wide and only slightly broadens from its tip to the base. Its anterior edge is straight, the posterior one straight or slightly concave. The apex of the coronoid process is broad and rounded. It is considerably oblique and bends distinctly inside. The external temporal fossa is wide and two distinctive longitudinal bars, which run parallel to the posterior edge of the coronoid process, border it anteriorly and posteriorly. The depth of this fossa is variable and it seems that it de-
Pleistocene Soricidae from Russia

The internal temporal fossa is relatively small. It has the shape of a triangle with rounded angles and does not reach the apex of the coronoid process. As a rule, the internal apical fossa is not developed. In many specimens the dorsolingual edge of the coronoid process is transformed into a longitudinal ridge, which extends to the apex. Together with the dorsal longitudinal edge of the external temporal fossa, they form a flat dorsal area of the coronoid process. The condyloid process is relatively high and massive. In general, the interarticular area is rectangular, with no considerable depression in its middle part. The upper articular facet is narrow and cylindrical, while the lower one is variable in width and has a rounded upper margin. The two facets are inclined to equal degree and run parallel to one another. The mental foramen is shifted anteriorly. It is situated considerably nearer to the posterior edge of P₄ than to the protoconid of Mi.

Lower teeth. The lower incisor, I₁ is large and distinctly tricuspidate. The lower antemolar, A² is very large and massive. Its length is equal to or in some specimens exceeds the length of P₄. The posterodorsal edge of the crown of A₁ is straight, but there are also numerous specimens with additional cusp. P₄ is not very large, it overlaps A₁ in less than one-third of its length. The depth of its posterolingual basin varies. The lingual ridge of this basin is usually well developed. It extends from the tip of the crown to its posterolingual corner and very often reaches the cingulum. In some
specimens a small additional cusp is present on this ridge. The lingual cingulum of P4 is wide and relatively rounded. All molars have very narrow buccal and rather broad lingual cingula. Their metaconids are approximately equal with the entoconids in their height and width.

Measurements. See Table II.

Systematic position and comparison. *S. raddei* is one of the largest *Sorex* species. In size it is similar to the recent European and Siberian *S. araneus* as well as to the extinct *S. polonicus* RZEBIK-KOWALSKA, 1991 and *S. praearaneus* [by many authors considered as *S. (Drepanosorex)praearaneus* KORMOS, 1934, see RZEBIK-KOWALSKA 1998]. The relationship of *S. raddei* with other species of the genus *Sorex*, however, is not quite clear because it reveals similarities with species absolutely different in taxonomic respect. It is interesting that there are numerous characters, e.g. morphology of an upper part of the coronoid and of the interarticular area of the condyloid processes, which it shares with *S. runtonensis*. Its large size, anterior position of the mental foramen, and the morphology of the posterior edge of the condyloid process are similar to these features in the genus *Drepanosorex* KRETZOL, 1941. Others of its characters (a very large A1 with additional cusp and an anterior position of a mental foramen) are also characteristic for *alpinus-group* species, such as *S. alpinus* SCHINZ, 1837 and *S. praealpinus* HELLER, 1930. It is evident that many of these characters may be plesiomorphic. In this case *S. raddei* might be considered as one of the ancient forms closely related to the ancestral ones. It seems very strange, however, that the fossil remains of *S. raddei* were found only in the upper layers of the Treugolnaya Cave and not in older deposits.

*Sorex doronichevi* n. sp.

(Fig. 8)

Etymology. The species is named in honour of Dr Vladimir DORONICHEV who discovered and investigated Treugolnaya Cave.

Holotype. ZISP T. 85191 - left lower mandible with coronoid and condyloid processes and all teeth, P3 - M3 (layer 7).

Paratypes. ZISP T.85192 - ZISP T.85195; four fragments of mandibles with all types of teeth and processes, except angular process (layers 7 and 5).

Other material. 477 fragments of maxillae, mandibles, and isolated teeth mainly from layer 7 and 5. They include all types of upper and lower teeth, and coronoid and condyloid processes of the ascending ramus of the mandible (see Table I).

Type locality. Treugolnaya Cave, Northern Caucasus, Russia.

Type horizon. Layer 7a, Middle Pleistocene.

Diagnosis. Relatively large shrew. The coronoid process narrow and high, its tip rounded and wide. The external temporal fossa very deep. It descends to the level of the upper sigmoid notch. The internal temporal fossa very high, triangular, without a horizontal bar. The condyloid process low and wide. Its lower facet oriented under the right angle to the vertical axis of the process. The mental foramen situated under trigonid of M1. The postmandibular canal present, the postmandibular foramen quite large. The teeth heavily pigmented, dark-red. A1 relatively large, but in its length and breadth essentially smaller than P4. P4 high with a deep posterolingual basin. Its lingual cingulum wide and protruding, its upper edge rather straight, forming a right or acute angle with the upper wall of the crown.

Differential diagnosis. *S. doronichevi* n. sp. differs from similar in size *S. polonicus*, *S. praearaneus*, *S. raddei*, and *S. araneus* in several morphological features. From *S. polonicus* it differs in a relatively narrow coronoid process with wide tip, the internal temporal fossa without horizontal bar and relatively small A1 from *S. praearaneus* in more posterior position of the mental foramen and in higher ascending ramus, from recent *S. raddei* in the same characters as from *S. praearaneus* and also in the large apex and low situated tines in 11 and from *S. araneus* in morphology of upper unicuspids, relatively shorter horizontal ramus of the mandible, and wider and lower condyloid process.

Description. Upper jaw. It is characterized by a deep depression above unicuspids with the deepest part situated above A3 - A4. The infraorbital foramen is triangular with rounded edges. It begins slightly behind the paracone of P5 and reaches the level of the mesostyle of M1. The lacinial foramen is situated between the mesostyle and metastyle of M1.
Teeth are usually heavily pigmented, dark-red. Upper teeth. The upper incisor, $I_1$, is of medium size. Its length equals $A_1$-$A_2$ length. It is practically not fissident. Its medial tines are very small (visible only under strong magnification) and situated very low. The talon of $I_1$ is quite large, comparable in size with the apex. The lower edge of the apex is straight, the depression between the apex and the talon is clearly visible. The posterior edge of the tooth is fairly straight, inclined slightly backwards. The posterior cingulum wide and protruding, reaches to the dorsal part of the crown. The antero-dorsal edge is gently sloping. In relation to the axis of the upper unicuspids, $I_1$ is strongly inclined upwards.

There are five upper unicuspids. They show a tendency to exoeadentonty. In occlusal view they are rounded and bulbous. The length of their crowns does not exceed their breadth. The buccal and lingual cingula are well developed. The lingual ridge, running from their apex to the lingual cingulum, may be seen in the first three teeth but it does not differ in colour from other regions of the apex. The second unicuspibid, $A_3$, is the largest and is more massive than the first one. The anterolingual corner of the $A_1$ crown is not rounded but forms an acute angle. $A_3$ is strongly compressed in the antero-posterior direction. In occlusal view this tooth is considerably smaller than $A$ and even $A_2$. $A_3$ is shifted lingually and in the dominant part is not visible from the buccal side.

![Fig. 8. Sorex doronochevi n. sp. from Treugolnaya Cave. A - fragment of left maxilla with $A_1$ - $M_2$ (buccal view), spec. no. T5v-52/87. B - fragment of left maxilla with $A_1$ and $A_3$ (buccal view), spec. no. T5v-110/87. C - right $I_1$ (anterior view), spec. no. T5v-112/87. D - $A_1$-$P_4$ (occlusial view), spec. no. ZISP T.85193 (paratype). E - left mandible with $I_1$-$M_3$ (buccal view), spec. no. ZISP T.85195 (paratype). F - fragment of left mandible with $A_1$-$P_4$ (lingual view), G - the same (buccal view), spec. no. ZISP T.85195 (paratype).]
$P^2$ has a medium-sized parastyle. It is not protruding and its vertical axis runs approximately parallel to the axis of the protocone. The parastylar crest is short and rather high. The L-shaped protocone is not very strong, the hypocone is very small and the valley between the protocone and hypocone is open and wide. The hypoconal flange is rounded and moderately concave. The buccal cingulum is usually high but very thin. It may be visible only in the anterior part of the tooth, and practically disappears behind the tip of the protocone.

$M^1$ and $M^2$ are characterized by a well-developed crest which extends backward up to the level of the hypocone. Therefore, the protocone-hypocone valley is rather narrow and deep. In $M^1$ a small and low metaloph separates the trigon valley from the talon. In $M^2$ the metaloph is not developed. In both molars the hypoconal flange is slightly concave.

**Mandible.** The horizontal ramus of the mandible is short and relatively massive. The ascending ramus is high and narrow. The posterior edge of the coronoid process is straight or slightly concave. In comparison with the length of $M^3$, the apex of the coronoid process is rather broad. The coronoid spicule is distinct. The external temporal fossa is not very deep and reaches the level of the upper sigmoid notch. Its anterior longitudinal bar is weak, the posterior one not developed. The internal temporal fossa is high and extends almost to the tip of the coronoid process. The horizontal bar is absent. The condyloid process is low and broad. The shape of the interarticular area is variable, trapzoid, or rectangular.

Its anteromedial corner is situated near the level of the lower sigmoid notch. The upper facet is oval and distinctly inclined in relation to the vertical axis of the condyloid process. The lower facet is larger and wide, slightly concave. It meets the vertical axis at a right or slightly obtuse angle. The pterygoid spicule is absent. The mandibular and postmandibular foramen open in the common distinct depression directly in front of the condyloid process. As a rule, the mental foramen is situated under the trigonid of $M^1$. Its posterior edge ends not much forward of the tip of the protoconid of $M^2$ or back of the re-entrant valley. In some specimens, however, it may be shifted not far from these limits.

Lower teeth. The lower incisor, $I^1$, is tricuspidate, with wide, round cusps and straight apex (not hooked dorsally). A shallow notch weakly separates the apex and the first cusp. This notch disappears in even slightly worn teeth and then only two cusps are clearly visible. The lower edge of $I^1$ is straight (without any concavity). The buccal cingulum is slightly developed.

The first lower antemolar $A^1$ is large but smaller than the second one, $P^4$. It is triangular in shape, single-cusped, without additional cusp on the dorsal edge of the crown. Its posterodorsal ridge is straight. The buccal and lingual cingula are very well developed.

$P^4$ is moderate in size, distinctly two-cusped. It overlaps the crown of $A^1$ on more than one-third of its length. The posterior edge of the crown is straight, formed by a high crest provided with distinct additional cusp. This cusp is usually situated at the point of contact of $P^4$ and $M^1$ and is visible in lingual view. The posterolingual basin is well developed and deep. Its lingual ridge runs from the tip to the posterior border of the tooth, which makes an impression of the depth of the basin and height of the ridge. Its buccal and lingual cingula are wide and protruding. The upper edge of the lingual cingulum is fairly straight and it forms an acute or nearly right angle with the dorsal wall of the $P^4$ crown. This tooth lies below the axis of the molar row.

The first lower molar, $M^2$, is typical of the Sorex species. Its trigonid is distinctly larger than talonid and the buccal edge of its crown is almost straight. The buccal cingulum is thin but quite protruding, the lingual one very wide and also protruding. The oblique crest in unworn teeth is usually straight, but in some specimens it is inclined downward. The metaconid is well developed, comparable in breadth with entoconid but higher. $M^1$ meets $P^4$ at the dorsal edge of its crown, which causes that the posterolingual angle of $P^4$ lies below the tooth row’s axis. The second lower molar, $M^2$, looks like a small copy of $M^1$. The third lower molar does not differ from $M^3$ in other Sorex species.

**Measurements.** See Table II.

**Systematic position and comparison.** *S. doronichevii*, sp. is similar to one of the extinct Pleistocene species, *S. praearaneus*, and especially to *S. praearaneus praetetragonurus* MEZHHERIN and SVISTUN, 1996, described from the alluvial deposits of the Dnieper and dated to the Late Pleistocene and Early Holocene (MEZHHERIN 1972, MEZHHERIN and SVISTUN 1966). This form is considered by some authors (REUMER 1984,1985, RZEBIK-KOWALSKA 1991, 1998, 2000) to belong to the subgenus Drepanosorex. Both species are characterized by relatively a short horizontal ramus of the mandible, a specific shape of the coronoid process, and a moderate exoedodonty. On the other hand, the structure of its $P^4$ is more
similar to this structure in representatives of the *Sorex araneus* group from Asia. In all of them $P^4$ has a deep posterolingual basin, distinctive internal ridge, and a straight cingulum, which forms the right angle with the posterior edge of its crown. In the proportions of the ascending ramus and in the length of the posterior part of the mandible *S. doronichevi* n. sp. resembles recent species, *S. daphaenodon* and *S. asper*, and in the morphology of unicuspids (especially in the structure of $A$) it is similar to *S. Asper*.

Genus *Drepanosorex* Kretzoi, 1941

*Drepanosorex rupestris* n. Sp.

(Fig. 9)

*Etymology:* from Latin *rupestris* = cliff. The species is described from the Cliff Ridge on the Baranakha Plateau where Treugolnaya Cave is situated.

![Figure 9: Drepanosorex rupestris n. sp. from Treugolnaya Cave.](image)

*Fig. 9. Drepanosorex rupestris* n. sp. from Treugolnaya Cave. A - right $P^4$ (lingual view), B - the same (buccal view), C - fragment of left mandible with $P^4$ - $M_1$ (lingual view), D - the same (buccal view), spec. no. ZISP T 85198 (paratype), E - fragment of right mandible with $A$ - $M_3$ (buccal view), spec. no. ZISP T 85197 (paratype), F - fragment of right mandible with $M_1$ and $M_2$ (buccal view), spec. no. ZISP T 85196 (holotype), G - fragment of left mandible with condyloid and coronoid processes (posterior view), spec. no. ZISP T 85198 (paratype).
H o l o t y p e : ZISP T. 85196 — right mandible with Mi and M2.
Paratypes: ZISP T. 85197 — fragment of the right mandible with A + M3; ZISP T. 85198 — fragment of the left mandible with P4 and Mi.
Other material: 21 fragments of mandibles from layer 7 and two fragments from layer 5. The mandibles contain the coronoid and condyloid processes and all types of teeth with the exception of I1. One isolated I1 from layer 7 probably also belongs to this species (see Table I).

Type locality: Treugolnaya Cave, North Caucasus, Russia.
Type horizon: Middle Pleistocene (layer 7a).

Diagnosis. Extremely large species of the genus *Drepanosorex*. The coronoid process very high and provided with an internal longitudinal crest situated on its lingual side. The apex of the coronoid process rounded and wide. The external temporal fossa also wide but not very deep. It is clearly visible only in the upper part of the coronoid process. The internal temporal fossa deep, not very large, in the shape of a triangle with rounded angles. It is distinctly separated from the upper part of the coronoid process which, in some specimens, suggests the presence of a shallow apical fossa. The mental foramen is situated under the posterior edge of P4. The postmandibular foramen absent. The pigmentation of teeth pale orange. A1 very large, bicuspulate, longer than P4 and only slightly shorter than Mj. P4 high and massive and M3 considerably (not less than 1.5 times) smaller than Mj.

Differential diagnosis. *D. rupestris* n. sp. differs from other species of the genus *Drepanosorex* in its large size and a very high coronoid process. Moreover, in comparison with *D. savini*, it has a relatively high and thin coronoid process. It also differs from *S. praearaneus* and from recent large species *S. raddei*, by the distinctly fissident I1, absence of the postmandibular foramen, and a pale colour of the tooth pigmentation.

Description. Upper teeth. Unfortunately only one clearly fissident I1, most probably belonging to *D. rupestris* n. sp. on the ground of its medial tines on the inner side of its crown. It is not very large. Its apex is curved and its lower edge is concave. The talon is very small. The posterior edge of the crown is slightly inclined backwards and has a deep notch. Its cingulum is well developed and extends to the dorsal part of the crown.

Mandible. The horizontal ramus of the mandible is massive. Its height under M2 is considerably larger than the length of this tooth. The ascending ramus is high and it widens weakly from its apex towards the base. The apex of the coronoid process is wide, rounded, and slightly oblique. Its anterior and posterior edges are straight. The coronoid spicule is moderately protruding. The external temporal fossa is wide but not very deep. It is clearly visible only in its upper part. The anterior longitudinal bar bordering this fossa runs obliquely to the posterior edge of the coronoid process. The posterior longitudinal bar is well developed only in the upper part of this process. It runs upward to the coronoid process apex and together with the internal longitudinal ridge forms a deep posterodor-sal platform of this process. The internal temporal fossa is deep but not very large. Its shape is triangular with rounded angles. Its upper angle reaches only to half of the coronoid process height. The shallow, but distinctly visible, apical fossa is present in the upper part of the coronoid process. The mental foramen is situated always under P4. Its posterior edge lies below the posterior edge of the crown of A1. Only one mandibular foramen is present. The postmandibular foramen and postmandibular canal are lacking. The condyloid process is large. Its upper part is cylindrical, the large lower one has its upper margin significantly concave. The interarticular area is very wide.

Lower teeth. The first lower antemolar A1 is very large, two-cusped and bulbous. The length of the tooth exceeds the length of P4 and is only slightly smaller than the length of the first lower molar M1. Its buccal cingulum is barely visible, the lingual one is very weak. P4 is high and also bulbous. Both its cusps are rounded and lie near to one another. Its buccal and lingual cingula are wide but not very protruding. The posterolingular basin is deep and distinct, its lingual edge is very well developed. It reaches the cingulum in the posterolingular corner of the crown. M1 has a massive trigonid. Its metaconid, wide and low, is similar in size to the entoconid. The entoconid crest is not very high. The buccal cingulum is thin and moderately protruding, the lingual one is weak. The lower margin of M1 crown is slightly undulated. M2 is a smaller copy of M1. M3 is very small. Its length equals approximately half the length of M1.

Measurements. See Table II.

Systematic position and comparison. The taxonomy of the genus *Drepanosorex* is one of the most confused among the subfamily Soricinae. The name was intro-
duced by KRETZOI (1941) for a new taxon of an ambiguous Soricinae species Sorex (Drepanosorex n. gen.) tasnadii. The description of Drepanosorex given by KRETZOI consists of characters of which some appeared to be variable and not useful for the identification of the genus. Some new characters were added to the diagnosis of the genus in subsequent revisions (HORACEK and LOZEK 1988, KRETZOI 1965, KOENIGSWALD 1972, RABEDER 1972, REUMER 1984, 1985, RZEBIK-KOWALSKA 1991, 2000). At the same time a number of a new species, which were earlier described as belonging to the genus Sorex sensu stricto were included into the genus Drepanosorex. They were Sorex savini HINTON, 1911, & margaritodon KORMOS, 1930, S. praearaneus KORMOS, 1934, S. austriacus KORMOS, 1937, and S. pachyodon PASA, 1947. Moreover, some new unnamed forms were also included to Drepanosorex (RZEBIK-KOWALSKA 1991) which made its diagnosis still less precise. In 1985 REUMER demonstrated that the characters that distinguish Drepanosorex from other taxa of shrews are only of subgeneric level. Other authors (see above) followed this opinion.

So far, four Plio-Pleistocene species of Europe have usually been include with the genus or subgenus Drepanosorex. They are: D. savini, D. margaritodon, D. praearaneus, and D. austriacus. Three other taxa, D. tasnadii, D. pachyodon, and D. postsavini HORACEK and LOZEK, 1988 are, as a rule, considered as synonyms of the above mentioned species.

The specimens from Treugolnaya Cave were identified as belonging to the genus Drepanosorex on the grounds of their large size, the presence of fissident I1, and the exoedanodonty and orange colour of their teeth. Moreover, they have only one mandibular foramen, and the mental foramen situated in the anterior position.

D. rupestris n. sp. differs very much from earlier described Drepanosorex species, including the largest D. austriacus, in its large size (see Tab. II). The structure of its coronoid and condyloid process is more similar to those described from Betfia (Romania) as D. margaritodon (type 2) (RZEBIK-KOWALSKA 2000) and some specimens of S. praearaneus from Tegelen, The Netherlands (REUMER 1984), than to the typical D. savini described from West Runton in England (HINTON 1911). Its relationship with other species of the genus is not clear. A taxonomic revision of the genus/subgenus Drepanosorex is necessary.

Tribe Neomyini REPENNING, 1967

Genus Neomys KAUP, 1829

Neomys schelkovnikovi SATUNIN, 1913

Material. One fragment of left maxilla with I1 and A (see Table I).

Description and comparison. The size and morphology of the above mentioned teeth do not differ from those of the recent Caucasus species Neomys schelkovnikovi.

Neomys newtoni HINTON, 1911

(Fig. 10 C,D)

Material. One fragment of mandible with Mi - M3, and probably 1 lower incisor Ii (see Table I).

Description. Mandible. Small species of Neomys. The horizontal ramus of the mandible is relatively massive in comparison with the thin and delicate coronoid process. The ascending ramus is relatively low, and its buccal surface smooth. The external temporal fossa is weak and shallow. Its deepest part is situated above the coronoid spicule. The coronoid spicule is distinct, and situated in two-thirds of the height of the coronoid process. The condyloid process has thin articular facets and an extremely narrow interarticular area. The mental foramen is situated under the talonid of Mi. The mandibular and postmandibular foramina are present.

Lower teeth. The isolated lower incisor Ii found in the same layer as a single mandibular fragment of N. newtoni probably also belongs to this species. This tooth is monocuspulate, relatively long and thin. Its lower margin is slightly concave. The ratio of its overall length to the length of the anterior concave part (between the apex and the single cusp) is 1.77. The buccal cingulum is absent. Mi - M, have the metaconids slightly curved backwards. They are higher and thinner than the ento-
Fig. 10. Neomys hintoni n. sp. (A, B) and N. newtoni from Treugolnaya Cave (C, D). A - fragment of left mandible (buccal view), B - the same (posterior view), spec. no. ZISP T-85199 (holotype), C - fragment of left mandible (buccal view), D - the same (posterior view), spec. no. T-5L-91/87.

Measurements. See Table II.

Systematic position and comparison. The morphology of the above described fragment of the mandible corresponds almost exactly to Neomys newtoni from the type locality West Runton in England although it has two mandibular foramina, while in N. newtoni from West Runton one of them, postmandibular foramen, is lacking. As concerns size, N. newtoni from Treugolnaya Cave is a little smaller than specimens from the type locality and from other known specimens of this species (RZEBIK-KOWALSKA 1991, 2000). It is also smaller than the extant N. anomalus. As the latter form, N. newtoni from Caucasus also has distinctive mandibular and post-mandibular foramina but differs in the morphology of the condyloid process: greatly reduced inter-articular area and relatively thinner and longer lower articular facet. Two mandibular foramina are also present in N. newtoni from Kozi Grzbiet in Poland (RZEBIK-KOWALSKA 1991).
Neomys hintoni n. sp.

(Fig. 10A, B)

Etymology. The species is named in honour of Dr Martin A. C. HINTON who described the first two species of the genus Neomys from the Early Pleistocene of England.

Holotype. ZISP T.85199 - fragment of the left mandible with M_2+M_3.

Paratypes. ZISP T. 85200-85201; three fragments of mandibles with the coronoid and condyloid processes and with Mi (See Table I).

Type locality. Treugolnaya Cave, Northern Caucasus, Russia.

Type horizon. Layer 7a, Middle Pleistocene.

Diagnosis. Small species of the genus Neomys comparable in size to N. newtoni. The buccal side of the ascending ramus characterized by a deep depression (fossa) situated between its upper and lower sigmoid notches. Only one mandibular foramen present.

Differential diagnosis. From N. shelkovnikovi and from N. fodiens the new species of Neomys differs in its smaller size and from all other Neomys species in the presence of a buccal fossa on the surface of the ascending ramus and the absence of lingual cingula on lower molars.

Description. Mandible. It is characterized by the presence of a deep fossa situated on the buccal side of the ascending ramus, between its upper and lower sigmoid notches. It is a continuation of the external temporal fossa with its deepest part at the level of the lower sigmoid notch, slightly above the condyloid process. The condyloid process has an extremely narrow interarticular area and relatively short and wide lower facet. The mental foramen is situated under the middle of the first lower molar, Mi. There is only one mandibular foramen.

Lower teeth. There are no characteristic features in the morphology of lower molars, differentiating particular species of the genus Neomys. However, contrary to the remaining species of Neomys, Mi and M_2 in N. hintoni are characterized by the absence of the lingual cingula and well-developed mesoconids, especially in the first molar Mi.

Measurements. See Table II.

Systematic position and comparison. Contrary to other Soricinae (e.g. Drepanosorex), the taxonomic position of the genus Neomys is unquestionable. On the other hand, the species status of the recent as well as the fossil species in this genus is not fixed. The main reason of this situation is the lack of distinct morphological characters which could be used for the identification of particular species. Especially the species rank of the Caucasus extant water-shrew, N. shelkovnikovi, is called in question (RUTTERER 1993). As concerns fossils, only three species of Neomys: N. newtoni, N. browni HINTON, 1911 and N. intermedius BRUNNER, 1952 were described from the Pliocene and the Pleistocene of Europe and only the first one seems to be valid as a separate species (JAMMOT 1977, RZEBIK-KOWALSKA 1991,1998).

Table III

Frequencies of morphotypes of the structure of mandibular/postmandibular foramina complex in recent Neomys species

<table>
<thead>
<tr>
<th>Species</th>
<th>Locality</th>
<th>N</th>
<th>Mandibular foramen (%) only</th>
<th>Mandibular and postmandibular foramen (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>N. anomalus</td>
<td>Balkans and Russian Plain</td>
<td>54</td>
<td>7.44</td>
<td>92.56</td>
</tr>
<tr>
<td>N. shelkovnikovi</td>
<td>Caucasus</td>
<td>30</td>
<td>20.0</td>
<td>80.0</td>
</tr>
<tr>
<td>N. fodiens</td>
<td>Balkans and Central Europe</td>
<td>73</td>
<td>91.78</td>
<td>8.22</td>
</tr>
<tr>
<td></td>
<td>Russian Plain</td>
<td>112</td>
<td>72.72</td>
<td>27.28</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>185</td>
<td>83.78</td>
<td>16.22</td>
</tr>
</tbody>
</table>
There is no doubt that *N. hintoni* belongs to the group of small-sized water-shrews such as *N. anomalus* and *N. newtoni*. All its measurements are close to those of the Polish *N. newtoni* specimens from the Early - earliest Middle Pleistocene locality Kozi Grzbiet (RZEBIK-KOWALSKA 1991). However, the unique structure of the buccal side of the ascending ramus of *J. hintoni* allows its consideration as a new species. This surface is almost smooth in all the remaining *Neomys* species, including *Tv. scheffelkoni* from Caucasus. Moreover, in comparison with *Tv. newtoni*, *N. hintoni* has the mental foramen situated more anteriorly, and in comparison with *N. newtoni* from Treugolnaya Cave (layer 5a), it is a little larger. Contrary to *N. newtoni* from Kozi Grzbiet (Poland) and the extant *N. anomalus*, it has only one mandibular foramen. As mentioned above, the single mandibular foramen is present in *N. newtoni* from West Runton (England). One foramen is also usually present in extant *N. fodiens* (Table III).

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