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Variation and taxonomic value of some mandibular characters in red-toothed shrews of the genus *Sorex* L. (Insectivora: Soricidae)

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ABSTRACT. The variability of five mandibular characters of the long-tailed shrews of the genus *Sorex* (the position of mental foramen, the structure of mandibular/postmandibular foramina complex, the structure of condyloid process, the pattern of pigmentation of the first lower incisor i1, and the color of tooth pigment) was examined. It is shown that each of these features is characterized by a specific level of variation. It should take into account in identifying and in the formulation of taxonomic hypotheses. On the basis of the obtained data the assumption of a specific taxonomic position of *S. trowbridgii* and *S. mirabilis* in relation to the traditionally recognized subgenera *Sorex* and *Otisorex* was made.

KEY WORDS: *Sorex*, taxonomy, morphology, paleontology.

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Изменчивость и таксономическая ценность некоторых признаков нижнечелюстной кости землероек-бурозубок рода *Sorex* L. (Insectivora: Soricidae)

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РЕЗЮМЕ. Изучена вариабельность пяти признаков нижней челюсти у землероек-бурозубок рода *Sorex* L. (положения подбородочного отверстия, структуры комплекса нижнечелюстных отверстий, формы межсуставной поверхности сочленовоного отростка, характера пигментации нижнего края переднего резца, общего тона окраски зубов). Показано, что каждый из этих признаков характеризуется специфическим уровнем изменчивости, который необходимо учитывать в практической работе при диагностике и выдвижении таксономических гипотез. На основании полученных данных высказано предположение о возможном специфическом статусе *S. trowbridgii* и *S. mirabilis* по отношению к традиционно выделяемым в составе рода подродам *Sorex* и *Otisorex*.

КЛЮЧЕВЫЕ СЛОВА: *Sorex* L., таксономия, морфология, палеонтология.

Introduction

The genus *Sorex* Linnaeus, 1758 contains 74 species of red-toothed shrews distributed mainly in the boreal region of the Holarctic (Lapini & Testone, 1998; Wolsan & Hutterer, 1998; Brünner *et al.*, 2002). The Palearctic and Nearctic parts of its range differ significantly in their species composition. The species of the subgenus *Sorex* Linnaeus, 1758 are mainly distributed in the Old World. The species of the subgenus *Otisorex* De Kay, 1942, as a rule, occupy the New World territories. The taxonomy of both subgenera is primarily based on the skull and upper tooth characters (Zyll de Jong, 1978; Junge & Hoffmann, 1981; Dolgov, 1985; Yudin, 1989). The mandibular and lower tooth characters have been used rather seldom in their taxonomy (Sergeev & Kharitonova, 1987; Carraway, 1995). On the other hand, the tooth characters play an important role in the fossil species discrimination (Repenning, 1967; Reumer, 1984, 1985; Rzebik-Kowalska, 1991, 2000; Storch, 1995; Qiu & Storch, 2000; Zaitsev & Baryshnikov, 2002). As a result, the taxonomy of the recent and fossil species was created to a high degree independently, because different sets of characters were used for their diagnoses and taxonomic conclusions. Besides, the importance of common characters in the diagnostics and taxonomic conclusions is sometimes differently understood. The variation of particular diagnostic characters has not been adequately studied and only a few papers touching this question can be cited (e.g. Dannelid, 1989).

In the present paper, the prime subject of investigations is the variation study of the five mandible characters usually used in the paleontological and sometimes in the neontological research of the red-toothed shrews. They are: the position of the mental foramen, the structure of the mandibular/postmandibular foramina complex, the structure of the condyloid process, the pattern of pigmentation in the first lower incisor i1 and the color of the tooth pigment.

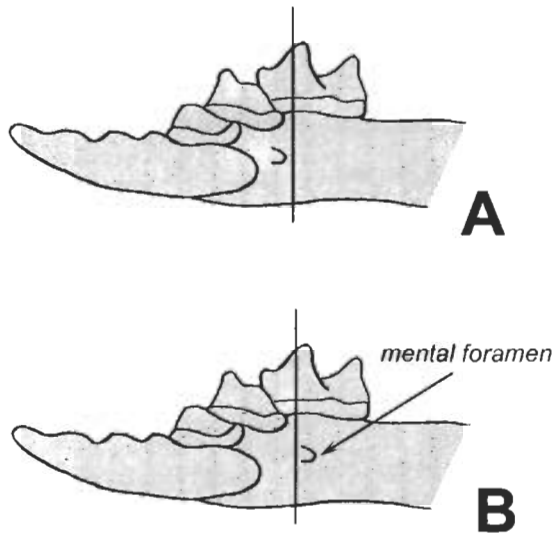

Figure 1. Position of the mental foramen in *Sorex* species. A — morphotype 1; B — morphotype 2.

Materials and methods

21 recent and four fossil species of shrews were studied. Most of them belong to the Palearctic group of the subgenus *Sorex* with the exception of one American species of this subgenus, *S. trowbridgii* Baird, 1857, which was also examined. Three Palearctic (*S. camtschaticus* Yudin, 1972, *S. leucogaster* Kuroda, 1933, and *S. portenkoi* Stroganov, 1956) and one Nearctic (*S. vagrans* Baird, 1857) representatives of the subgenus *Otisorex* were also analyzed. For each species a random sample of specimens from different localities was prepared (Appendix). The subadult specimens were preferred. The sex was not distinguished.

Three European fossil species (*S. praearaneus* Kormos, 1934, *S. runtonensis* Hinton 1911, and *S. thaleri*

Table 1. Variability of three structural features of the mandible (in %; frequencies more 90% are highlighted).

Species	Mental foramen		MPF complex			Interarticulation area		
	Morphotypes		Morphotypes			Morphotypes		
	1	2	1	2	3	1	Intermediate	2
S. araneus	0.0	**100.0**	8.0	**92.0**	0.0	16.0	60.0	24.0
S. asper	0.0	**100.0**	0.0	**100.0**	0.0	62.5	25.0	12.5
S. satunini	0.0	**100.0**	5.4	81.1	13.5	17.1	20.0	62.9
S. tundrensis	0.0	**100.0**	0.0	**100.0**	0.0	58.0	16.0	26.0
S. caecutiens	0.0	**100.0**	2.0	**96.0**	2.0	**96.0**	4.0	0.0
S. isodon	0.0	**92.0**	12.0	86.0	2.0	**100.0**	0.0	0.0
S. unguiculatus	0.0	**100.0**	0.0	**100.0**	0.0	89.6	10.4	0.0
S. roboratus	0.0	**100.0**	6.0	76.0	18.0	46.7	46.7	6.6
S. gracillimus	34.3	65.7	0.0	81.4	18.6	**94.2**	2.9	2.9
S. minutus	40.0	60.0	0.0	**92.5**	7.5	82.4	12.3	5.3
S. volnuchini	0.0	**100.0**	0.0	67.6	32.4	81.1	8.1	10.8
S. daphaenodon	0.0	**100.0**	2.0	**98.0**	0.0	22.4	23.5	54.1
S. raddei	31.8	68.20	0.0	**98.3**	1.7	89.5	10.5	0.0
S. alpinus	**96.3**	3.7	0.0	**100.0**	0.0	69.6	30.4	0.0
S. minutissimus	0.0	**100.0**	0.0	72.6	27.4	39.6	33.7	26.7
S. mirabilis	0.0	**100.0**	36.2	61.7	2.1	**100.0**	0.0	0.0
S. trowbridgii	0.0	**100.0**	9.6	49.3	41.1	88.0	12.0	0.0
S. portenkoi	0.0	**100.0**	**98.3**	1.7	0.0	**90.4**	9.6	0.0
S. leucogaster	0.0	**100.0**	**100.0**	0.0	0.0	**100.0**	0.0	0.0
S. camtschaticus	0.0	**100.0**	**100.0**	0.0	0.0	**96.9**	3.1	0.0
S. vagrans	0.0	**100.0**	**96.1**	3.9	0.0	**100.0**	0.0	0.0
† *S. paearaneus*	7.7	**92.3**	8.3	85.7	7.0	55.0	20.0	25.0
† *S. runtonensis*	0.0	**100.0**	3.8	**93.3**	2.9	18.0	62.0	21.0
† *S. thaleri*	0.0	**100.0**	40.6	46.3	3.1	6.3	28.2	65.5
† *S. doronichevi*	17.8	**82.2**	3.6	**90.9**	5.5	2.2	15.5	82.3

Jammot, 1989) were excavated in Polish Pliocene and Pleistocene localities: Zamkowa Dolna Cave A, Kielniki 3B (Late Pliocene), Kadzielnia (Pliocene/Pleistocene boundary), Kielniki 3A, Kamyk (Early Pleistocene), Kozi Grzbiet (Early/Middle Pleistocene) and Oblazowa Cave and Oblazowa Cave (site 2) (Late Pleistocene) (Rzebik-Kowalska, 1991, 1994, 2003). The single Caucasian fossil species, *S. doronichevi* Zaitsev et Baryshnikov, 2002, derives from layers 5 and 7 of the Treugolnaya Cave (Zaitsev & Baryshnikov, 2002).

In the frequency analysis the left and right mandibles were counted separately. The degree of the variability of characters was measured by means of the Shannon entropy (H):

$H = -\Sigma p_i \ln p_i$,

where pi is a probability of the morphotype distribution of the character in particular species.

The entropy can range from 0 to 0.693 for the characters with two morphotypes, and from 0 to 1.099 for the characters with three morphotypes. The minimum value (H=0) means the complete absence of the character variation, so it is observed in specimens characterized by only one morphotype. The maximum value (H=0.693; 1.099) indicates the uniform distribution of morphotypes in the specimens examined.

The most interesting is the comparison of the obtained data with the median value of entropy. Thus, the value lesser than median can be considered as low variability of the character, and the value greater than median as high variability of character. The numerical median value for two and three morphotypes equals to 0.346 and 0.550 respectively.

Results

Position of the mental foramen

General variation and patterning. In the Soricinae species the mental foramen opens on the buccal side of the mandible and is usually situated under p4 or m1. The position of the mental foramen can be traced by the location of its posterior edge. Two morphotypes were recognized (Fig. 1.).

Morphotype 1. The mental foramen is in the anterior position. Its posterior edge is situated under p4, in front of or exactly under its posterior edge, or a little backward of this edge Fig. 1A).

Morphotype 2. The mental foramen is in the posterior position. Its posterior edge is situated more backward than in the morphotype 1 (Fig. 1B).

Variation in the *Sorex* species. The frequency of morphotypes of the mental foramen position is presented in Tab. 1. It shows that the recent species (17 from 21) are characterized by its posterior position (92–100%). Moreover, in 16 of them this position is almost invariable. The first morphotype visibly prevails only in *S. alpinus* (96.3%). The entropy of the mental foramen position of all these species is very low (0–0.279) and has considerably lower median value (Fig. 5A).

Three species of the subgenus *Sorex*, *S. gracillimus* Thomas, 1907, *S. minutus* Linnaeus, 1766, and *S. raddei* Satunin, 1895 show a higher level of variation of this character. Their ratio of morphotypes is approximately 1:2. The data of H for these species are rather high (0.625–0.673) and considerably exceed the median value (Tab. 3).

Table 2. Variability of the pigmentation of teeth (in %; frequencies more 90% are highlighted).

Species	Pigmentation of lower incisor		Color of teeth pigment		Species	Pigmentation of lower incisor		Color of teeth pigment	
	Morphotypes		Morphotypes			Morphotypes		Morphotypes	
	1	2	1	2		1	2	1	2
S. araneus	**100.0**	0.0	5.5	**94.5**	*S. raddei*	**98.3**	1.7	3.4	**96.6**
S. asper	**100.0**	0.0	0.0	**100.0**	*S. alpinus*	**96.2**	3.8	16.7	83.3
S. satunini	**100.0**	0.0	0.0	**100.0**	*S. minutissimus*	**100.0**	0.0	1.2	**98.8**
S. tundrensis	**98.3**	1.7	3.3	**96.7**	*S. mirabilis*	**100.0**	0.0	0.0	**100.0**
S. caecutiens	**100.0**	0.0	10.0	**90.0**	*S. trowbridgii*	4.5	**95.5**	0.0	**100.0**
S. isodon	**100.0**	0.0	0.0	**100.0**	*S. portenkoi*	3.4	**96.6**	0.0	**100.0**
S. unguiculatus	**100.0**	0.0	0.0	**100.0**	*S. leucogaster*	0.0	**100.0**	6.2	**93.8**
S. roboratus	**96.3**	3.7	3.7	**96.3**	*S. camtschaticus*	0.0	**100.0**	3.1	**96.9**
S. gracillimus	**98.3**	1.7	0.0	**100.0**	*S. vagrans*	2.5	**97.5**	8.0	**92.0**
S. minutus	**100.0**	0.0	3.8	**96.2**	† *S. paeraneus*	**100.0***	0.0	33.3	**66.7**
S. volnuchini	**100.0**	0.0	6.6	**93.4**	† *S. runtonensis*	**100.0**	0.0	3.0	**97.0**
S. daphaenodon	**100.0**	0.0	0.0	**100.0**	† *S. thaleri*	**100.0***	0.0	3.3	**96.8**
					† *S. doronichevi*	**100.0***	0.0	2.2	**97.8**

* Data obtained on the less then 10 specimens.

Table 3. Values of entropy (*H*) in *Sorex* species (values exceeds median entropy level are highlighted).

	Mental foramen	MPF complex	Inter-articulation area	Pigmentation of I1	Color of the teeth pigment
S. araneus	0.000	0.280	**0.942**	0.000	0.213
S. asper	0.000	0.000	**0.900**	0.000	0.000
S. satunini	0.000	**0.598**	**0.916**	0.000	0.000
S. tundrensis	0.000	0.000	**0.959**	0.086	0.145
S. caecutiens	0.000	0.196	0.169	0.000	0.325
S. isodon	0.279	0.462	0.000	0.000	0.000
S. unguiculatus	0.000	0.000	0.335	0.000	0.000
S. roboratus	0.000	**0.686**	**0.891**	0.158	0.158
S. gracillimus	**0.643**	0.481	0.262	0.086	0.000
S. minutus	**0.673**	0.267	**0.573**	0.000	0.162
S. volnuchini	0.000	**0.631**	**0.614**	0.000	0.243
S. daphaenodon	0.000	0.099	**1.008**	0.000	0.000
S. raddei	**0.625**	0.087	0.337	0.086	0.148
S. alpinus	0.149	0.000	**0.615**	0.162	**0.451**
S. minutissimus	0.000	**0.588**	**1.086**	0.000	0.065
S. mirabilis	0.000	0.747	0.000	0.000	0.000
S. trowbridgii	0.000	**0.939**	0.368	0.184	0.000
S. portenkoi	0.000	0.087	0.317	0.148	0.000
S. leucogaster	0.000	0.000	0.000	0.000	0.232
S. camtschaticus	0.000	0.000	0.139	0.000	0.138
S. vagrans	0.000	0.166	0.000	0.117	0.279
† *S. paearaneus*	0.271	0.525	**0.997**	0.000	**0.636**
† *S. runtonensis*	0.000	0.292	**0.933**	0.000	0.135
† *S. thaleri*	0.000	**0.830**	**0.808**	0.000	0.142
† *S. doronichevi*	**0.468**	0.366	0.533	0.000	0.106

The fossil species also show a very low level of variability of this character. Only *S. doronichevi* from the Caucasus differs having a relatively high value of *H* (0.468).

Mandibular/postmansibular foramina complex (MPF-complex)

General variation and patterning. In the Soricinae species the mandibular and postmandibular foramina are situated on the lingual side of the ascending ramus of the mandible. As in other mammals the mandibular foramen opens into a canal running in the direction of the horizontal ramus of the mandible (morphotype 1), or it opens into a canal running in the direction of the internal temporal fossa (morphotype 3). The postmandibular foramen opens into vertical canal running to the internal temporal fossa (morphotypes 2 and 3) (Fig. 2). In the Soricidae the internal temporal fossa is deeply pocketed which may be defined as the synapomorphy. Therefore the presence of the postmandibular foramen can also be considered as the unique synapomorphy of the Soricidae. Both foramina form quite a complex structure named by the authors of the present paper the mandibular/postmandibular foramina complex (MPF-complex).

In the Soricinae there are several patterns of MPF-complex and all of them were found in species of the genus *Sorex*.

Three main morphotypes of the MPF-complex were defined (Fig. 2).

Morphotype 1. There is only one (mandibular) foramen visible (Fig. 2A), the postmandibular foramen is absent.

Morphotype 2. There are two, mandibular and postmandibular, foramina visible, approximately equal in size (Fig. 2B).

Morphotype 3. There is only one postmandibular foramen visible, the mandibular foramen is also present, but not visible from the lingual side (Fig. 2C).

Apart from three morphotypes mentioned above, one can observe one or more very small foramina situated near the mandibular and postmandibular ones running into the internal temporal fossa. All these cases were not taken into consideration.

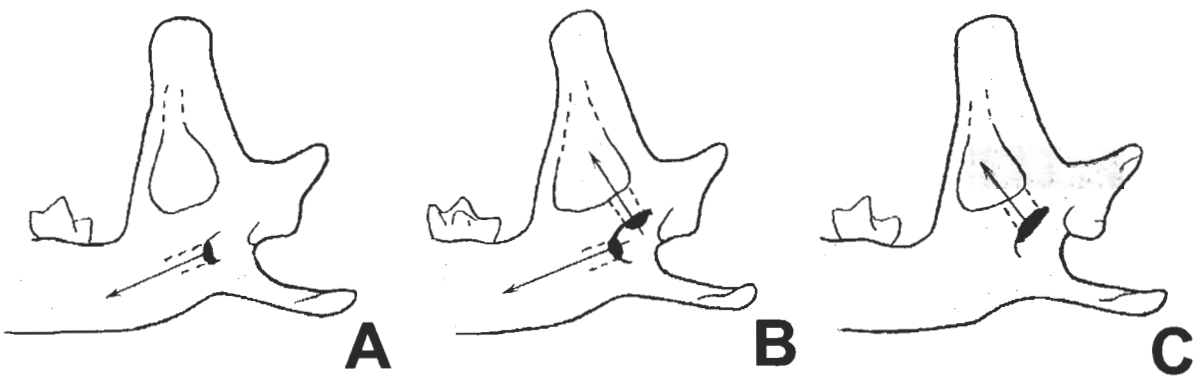

Figure 2. Structure of MPF-complex in *Sorex* species (explanation in the text).
A — morphotype 1; B — morphotype 2; C — morphotype 3.

Variation in *the Sorex* species. The frequency of the morphotypes of the MPF-complex and the value of the entropy are represented in Tabs. 1 and 3, and in Fig. 5B. They show that this character is more variable than the previous one. Among the recent shrews only about 1/3 (6) of all the examined species have H equal to 0. Five species are characterized by a moderate value of entropy that is by more or less its median level. Only *S. trowbridgii* differs having a high variation of the MPF-complex (H=0.939). It should be noted that it is a single species in which the morphotype 3 appears more frequently (41.1%). In other species is more frequent morphotype 2, whereas the morphotype 1 is observed very seldom. As a rule, it may be found in very old animals. The single exception of this rule represents *S. mirabilis* Ognev, 1937. In this species the ratio of the first two morphotypes equals 1:2.

By contrast, among the species of the subgenus *Otisorex* the first morphotype of the MPF-complex prevails (98.3–100%). The frequencies of other morphotypes are lower than the mean of statistical error.

Three from four fossil species have frequencies of the morphotypes typical of the subgenus *Sorex*. Only *S. thaleri* has 1:1 ratio of two first morphotypes that is unique in the genus *Sorex* (Tab. 1).

Shape of the interarticular area of the condyloid process

General variation and patterning. The morphology of the Soricidae condyloid process principally differs from that of other mammals. It is characterized by two (upper and lower) facets and interarticular area between them. The last structure significantly varies in the Soricidae and represents one of the main characters in their taxonomy (Repenning, 1967). In the *Sorex* species the interarticular area is relatively wide. It varies in its size and shape. Two morphotypes concerning the shape of the interarticular area can be recognized (Fig. 3).

Morphotype 1. The interarticular area is narrow in its lower part. Its lingual edge meets approximately the middle of the upper edge of the lower facet and it is straight (Fig. 3A).

Morphotype 2. Interarticular area is wide in its lower part. Its lingual edge meets approximately the end of the upper edge of the lower facet and is more or less concave.

This division corresponds roughly to the presently accepted in paleontology terms: "rectangular" and "trapezoid" (Rzebik-Kowalska, 1991).

Sometimes it is difficult to include particular specimens to one morphotype or another. For such cases the third "intermediate" morphotype was introduced (Tab. 1).

Variation in the *Sorex* species. The frequencies of morphotypes and the values of entropy of the shape of the interarticular area are shown in Tabs. 1 and 3, and in Fig. 5C. As may be seen, the variability of this character is considerably higher than in the two previous cases. Almost always half of the recent and all fossil species have H exceeding the median value. As this takes place, in many species the proportion of "intermediate" morphotype is very high, between 46.7–62.0%. Only four species, *S. isodon* Turov, 1924, *S. mirabilis*, *S. leucogaster*, and *S. vagrans* are characterized by the absence of the shape variability of the interarticular area.

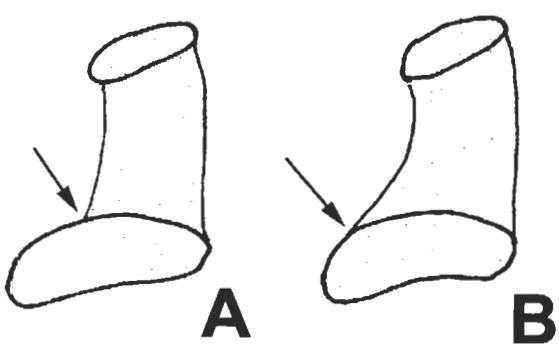

Fig. 3. Structure of interarticular region of condyloid process in *Sorex* species.
A — morphotype 1; B — morphotype 2.

Pigmentation pattern of the first lower incisor (i1)

General variation and patterning. In comparison with other mammals, the first lower incisor i1 in shrews is large and elongated in the antero-posterior direction. As a rule, in *Sorex* species its cutting edge has one or more cusps. On the buccal side of i1 the pigment spreads mainly in the anterior and upper parts of the crown. On the lingual side it covers only apex and a thin zone along the lower edge of the crown (Fig. 4). Carraway (1995) was the first who pointed to the difference in pigmentation pattern of the lingual side on i1 in some American species of shrews. In the present paper a little modification was made and two morphotypes were recognized.

Morphotype 1. A rather wide and flat crest forms the ventrolingual edge of the crown of i1. Strips of pigment on the ventrolingual and buccal sides of this tooth are approximately equal and do not exceed half of the crown length (Fig. 4A).

Morphotype 2. A rather thin and rounded crest forms the ventrolingual edge of the crown of i1. Strip of pigment on the ventrolingual side is much longer than the strip on the buccal side of the tooth and exceeds half of the crown length (Fig. 4B).

Variation in the *Sorex* species. The frequencies of morphotypes and the value of entropy of i1 pigmentation pattern are presented in Tabs. 2 and 4, and in Fig. 6A. They show that this character has a very low value of variability and may be treated as the most stable one. None of the species have the mean of H reaching ½ of the median entropy level. i1 recent and all fossil species are absolutely invariable. It should also be noted that in all shrews of the subgenus *Sorex* morphotype 1 prevails, whereas the examined species of the subgenus *Otisorex* are characterized by morphotype 2. The single exception of this rule is *S. trowbridgii*. In spite of its belonging to the subgenus *Sorex*, it has the pattern of i1 pigmentation observed in the *Otisorex* species (Tab. 2).

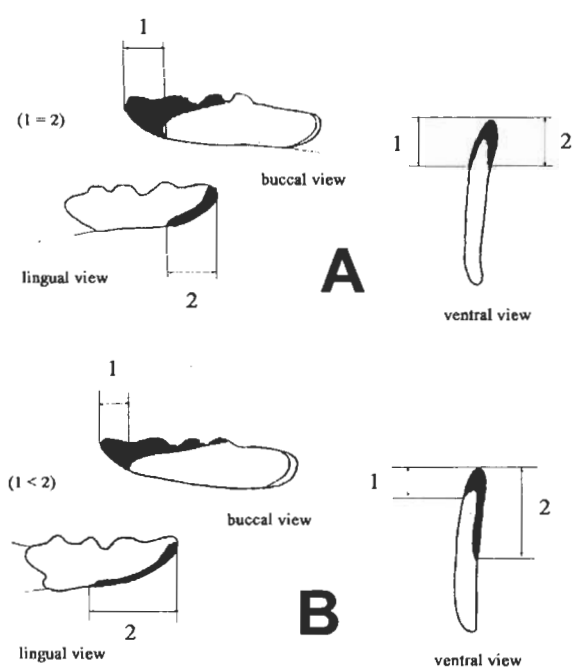

Figure 4. Types of pigmentation of the first lower incisor in *Sorex* species (explanation in the text).
A — morphotype 1; B — morphotype 2; C — morphotype 3.

Color of the tooth pigment

General variation and patterning. The red color of tooth pigment of the red-toothed shrews is due to the presence of iron in the enamel tooth (Dötsch & Koenigswald, 1978; Vogel, 1984). The intensity of the red color widely differs in various genera of the Soricinae. It may be very light yellow to very light orange (*Nectogale*), or darkish red (*Sorex, Blarina*). Among Sorcini light orange color of teeth is characteristic mainly for one fossil genus/subgenus *Drepanosorex*, but sometimes it can be also present in some specimens of various species of the

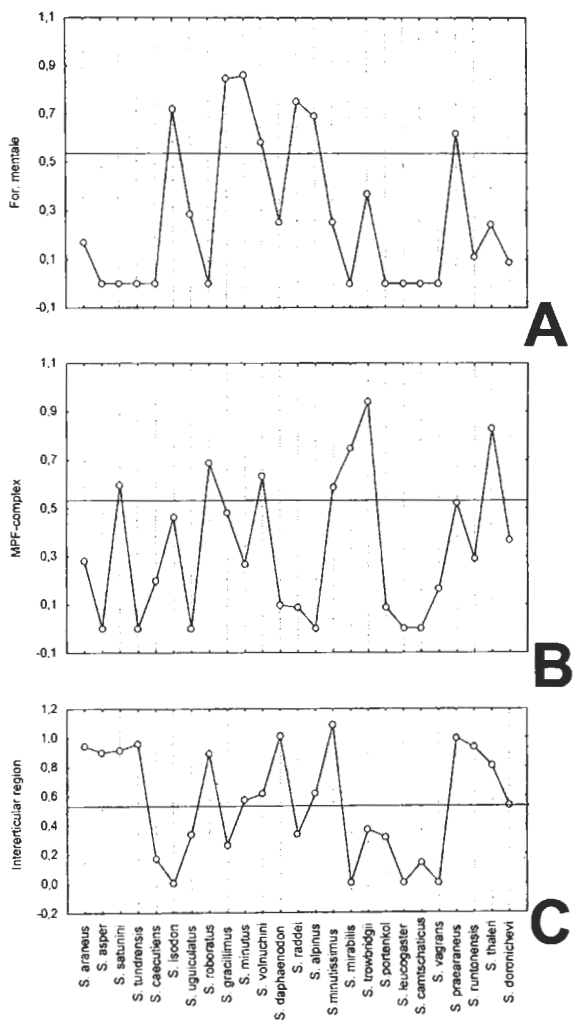

Figure 5. Values of Shannon entropy for three structural characters in *Sorex* species.
A — position of mental foramen; B — structure of MPF-complex; C — structure of interarticular region of condyloid process (horizontal line in the bar shows the median level of entropy).

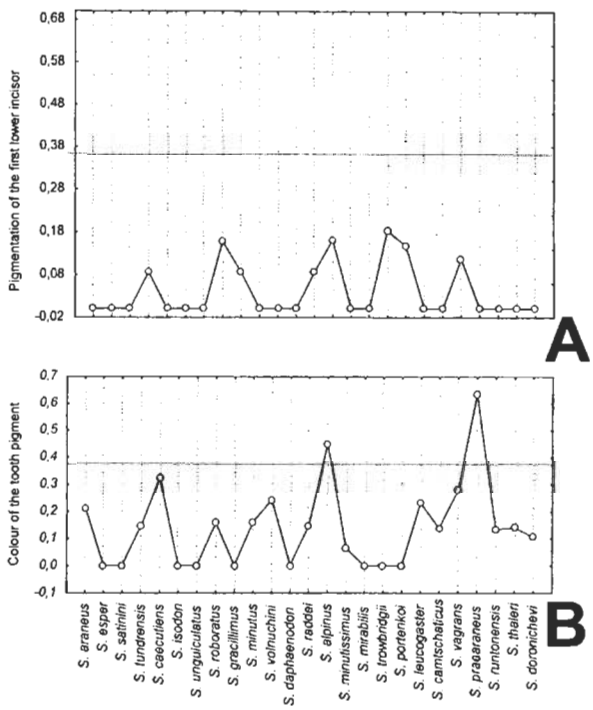

Figure 6. Values of Shannon entropy for two characters of teeth pigmentation in *Sorex* species.
A — pigmentation of the first lower incisor; B — color of the teeth pigment (horizontal line in the bar shows the median level of entropy).

red-toothed shrews. Two main morphotypes of the tooth pigmentation are recognized:

Morphotype 1. The color of the tooth pigment is light orange.

Morphotype 2. The color of the tooth pigment is light or darkish red.

Variation in the *Sorex* species. The frequencies of morphotypes and the value of entropy of tooth pigmentation in *Sorex* species are represented in Tab. 2 and 4, and in Fig. 6B. They show that the most of shrews are characterized by a relatively low level of variation of this character. Only recent *S. alpinus* and fossil *S. praearaneus* have *H* that exceeds the median entropy level. The share of morphotype 1 in these species equals to 16.7% and 33.3% of the examined specimens, respectively. In other species the share of morphotype 1 does not exceed, as a rule, 5.0%, and very seldom (in *S. isodon*, *S. volnuchini* Ognev, 1922, *S. leucogaster*, *S. vagrans*) reaches 6.2–10.0%. Morphotype 2 is more characteristic for the majority of fossil and recent species of both subgenera.

Discussion

The results presented above show that none of the characters examined may be treated as absolutely certain and informative. Each of them has a specific level of variation, which should be taken into account in preparing any taxonomic hypothesis. In this regard it should be pointed that the diagnosis of species, especially paleontological ones, that base on one character only cannot be reliable and effective. On the other hand, using a number of various characters that do not correlate in their variability may be more fruitful.

The majority of characters examined will also be available for the characteristic of various taxonomic groups. For example, as can be observed in the material presented above, the anterior position of the mental foramen is very characteristic for *S. alpinus*. However, it does not mean that other type of variability of this character could be found in this species. In the similar manner the "*alpinus*" type of the position of the mental foramen is sometimes present in other species (e.g. *S. raddei*, *S. minutus*, *S. gracillimus*).

The presence of the postmandibular foramen (morphotypes 2 and 3) is characteristic for the subgenus *Sorex*, while the absence of this foramen for the subgenus *Otisorex*. This estimation has a certain "normal" level of probability. As a rule, the variation of MPF-complex does not exceed 5% and very seldom 8-12%. So, for species that show the variation that exceeds these values mentioned above one can put a question concerning their taxonomic position. Among the *Sorex* species a great variation of the MPF-complex structure is noted in *S. trowbridgii* and *S. mirabilis*. It is quite possible that the last species are a taxonomically distant form from the most typical species of both subgenera.

Among characters studied in the present paper, the morphology of interarticular area seems to be the most variable. Besides its great level of variability it is difficult to find any regularity in the distribution of various morphotypes in different taxonomic groups of the genus. On the contrary, as it is evident from the data presented above, the pattern of pigmentation of the first lower incisor is the most stable, and may be used for diagnostics of subgenera *Sorex* and *Otisorex* (except *S. trowbridgii*).

Besides, it should be noted that the level of variation of tooth pigmentation is considerably lower than in any other morphological character. The red type of tooth pigment is characteristic for the genus *Sorex* and may be used as a good taxonomic feature together with other diagnostic ones.

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References

Brünner H., Lugon-Moulin N., Balloux F., Fumagalli L. & Hausser J. 2002. A taxonomic re-evaluation of the Valais chromosome race of the common shrew *Sorex araneus* (Insectivora: Soricidae) // Acta Theriologica. Vol.47. No.3. P.245–275.

Carraway L.N. 1995. A key to recent Soricidae of the Western United States and Canada based primarily on dentaries // Natural History Museum, The University of Kansas.

Occasional Papers. No.175. P.1–49.
Dannelid F. 1989. Medial tines on the upper incisors and other dental features used as identification characters in European shrews of the genus *Sorex* (Mammalia, Soricidae) // Zeitschrift für Säugetierkunde. Bd.54. Hf.2. P.205–214.
Dolgov V.A. 1985. [The long-tailed shrews of the Old World]. Moskva: Izdatel'stvo Moskovskogo Universiteta. 221 p. [in Russian].
Dötsch C. & Koenigswald W. von. 1978. Zur Rotfärbungvon Soricidenzähnen // Zeitschrift für Säugetierkunde. Bd.43. Hf.1. S.65–78.
Junge J.A. & Hoffmann R.S. 1981. An annotated key to the long-tailed shrews (genus *Sorex*) of the United States and Canada, with notes on Middle American *Sorex* // Natural History Museum, The University of Kansas. Occasional Papers. No.94. P.1–48.
Lapini L. & Testone R. 1998. A new *Sorex* from north-eastern Italy (Mammalia, Insectivora: Soricidae) // Gortania. Atti del Museo Friulano de Storia Naturale. Vol.20. P.231–250.
Qiu Z. & Storch G. 2000. The early Pliocene micromammalian fauna of Bilike, Inner Mongolia, China (Mammalia: Lipotyphla, Chiroptera, Rodentia, Lagomorpha) // Senckenbergiana Lethaea. Bd.80. Hf.1. P.173–229.
Repenning C A. 1967. Subfamilies and genera of the Soricidae // United States Geological Survey Professional Paper. No.565. P.1–74.
Reumer J.W.F. 1984. Ruscinian and early Pleistocene Soricidae (Insectivora, Mammalia) from Tegelen (The Netherlands) and Hungary // Scripta Geologica. No.73. P.1–173.
Reumer J.W.F. 1985. The generic status and species of *Drepanosorex* reconsidered (Mammalia, Soricidae) // Revue de Paléobiologie. T.4. No.1. P.53–58.
Rzebik-Kowalska B. 1991. Pliocene and Pleistocene Insectivora (Mammalia) of Poland. VIII. Soricidae: *Sorex* Linnaeus, 1758, *Neomys* Kaup, 1829, *Macroneomys* Fejfar, 1966, *Paenelimnoecus* Baudelot, 1972 and Soricidae indeterminate // Acta Zoologica Cracoviensia. Vol.34. No.2. P.323–424.
Rzebik-Kowalska B. 1994. Pliocene and Quaternary Insectivora (Mammalia) of Poland // Acta Zoologica Cracoviensia. Vol. 37. No.1 P.77–136.
Rzebik-Kowalska B. 2000. Insectivora (Mammalia) from the Early and early Middle Pleistocene of Betfia in Romania. I. Soricidae Fisher von Waldheim, 1817 // Acta Zoologica Cracoviensia. Vol.43. No.1. P.1–53.
Sergeev V.E. & Kharitonova N.A. 1987. [The morphological analysis of the mandible of the shrews (Soricidae) of the fauna of West Siberia] // Yudin B.S. (ed.). [Fauna, Taxonomy and Ecology of Mammals and Birds]. Novosibirsk: Nauka. P.61–66 [in Russian].
Storch G. 1995. Th Neogene Mammalian faunas of Erteme and Harr Obo in Inner Mongolia (Nei Mongol), China. — 11. Soricidae (Insectivora) // Senckenbergiana Lethaea. Vol.75. P.221–251.
Vogel P. 1984. Verteilung des roten Zahnschmelzes im Gebiss der Soricidae (Mammalia, Insectivora) // Revue Suisse de Zoologie. T.91. Fasc.3. P.699–708.
Wolsan, M. & Hutterer R. 1998. A list of the living species of shrews // Wójcik J.M. & Wolsan M. (eds.). Evolution of Shrews. Białowieza: Mammal Research Institute, Polish Academy of Sciences. P.425–458.
Yudin B.S. 1989. [Insectivore Mammals of Siberia]. Novosibirsk: Nauka. 360 p. [in Russian].
Zaitsev M.V. & Baryshnikov G.F. 2002. Pleistocene Soricidae (Lipotyphla, Insectivora, Mammalia) from Treugolnaya Cave, Northern Caucasus, Russia // Acta Zoologica Cracoviensia. Vol.45. No.2. P.283–305.
Zyll de Jong C.G. 1978. Handbook of Canadian Mammals. Ottawa: National Museum of Natural Sciences. 210 p.

Appendix. Specimens examined

Species	Number of specimens *	Number of localities	Museums	Species	Number of specimens *	Number of localities	Museums
S. araneus	50	4	1	*S. alpinus*	24	5	1, 2
S. asper	11	3	1, 2	*S. minutissimus*	64	17	1, 2
S. satunini	37	8	1, 2	*S. mirabilis*	24	2	1, 2
S. tundrensis	50	2	1	*S. trowbridgii*	146	3 (?)	1, 2, 3
S. caecutiens	50	5	1	*S. camtschaticus*	32	4	1
S. isodon	50	5	1	*S. portenkoi*	30	7	1
S. unguiculatus	50	3	1	*S. leucogaster*	16	1	1
S. roboratus	50	9	1	*S. vagrans*	52	7	2
S. gracillimus	70	6	1	† *S. praearaneus*	23	5	4
S. minutus	53	6	1	† *S. runtonensis*	111	4	4
S. volnuchini	37	5	1, 2	† *S. thaleri*	35	1	4
S. daphaenodon	99	12	1	† *S. doronichevi*	75	1	1
S. raddei	58	14	1, 2				

* The number of skulls for recent species and number of mandibles for fossil (†) species.
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Occasional Papers. No.175. P.1–49.
Dannelid F. 1989. Medial tines on the upper incisors and other dental features used as identification characters in European shrews of the genus *Sorex* (Mammalia, Soricidae) // Zeitschrift für Säugetierkunde. Bd.54. Hf.2. P.205–214.
Dolgov V.A. 1985. [The long-tailed shrews of the Old World]. Moskva: Izdatel'stvo Moskovskogo Universiteta. 221 p. [in Russian].
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Vogel P. 1984. Verteilung des roten Zahnschmelzes im Gebiss der Soricidae (Mammalia, Insectivora) // Revue Suisse de Zoologie. T.91. Fasc.3. P.699–708.
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