

Is there Sexual Size Dimorphism in Shrews? A Case Study of Six European Species of the Family Soricidae

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Abstract: The morphological differences between sexes of six soricid species belonging to two subfamilies, Crocidurinae (*Crocidura suaveolens* and *C. leucodon*) and Soricinae (*Neomys anomalus*, *N. fodiens*, *Sorex araneus* and *S. minutus*), were studied on the basis of 39 cranial, mandibular and tooth measurements. Different patterns regarding sexual differences in size were recorded in the two subfamilies. The two white-toothed shrew species exhibited clear male-biased sexual size differences, which were better expressed in *C. suaveolens* compared to *C. leucodon* as well as in Southeastern Europe compared to Central Europe. Conversely, red-toothed shrews did not display distinct sexual differences in size. In *N. fodiens*, *N. anomalus*, *S. araneus* and *S. minutus*, some measurements were larger in males, others were larger in females, while certain measurements did not differ between sexes. Furthermore, differences between samples of one species were observed. The characters that showed the most significant sex variations differed among the species. As a great overlap exists among the ranges of the measurements, it is more correct to speak of size differences between sexes rather than of a distinct sexual size dimorphism.

Keywords: Soricidae, *Crocidura*, *Neomys*, *Sorex*, craniometry, sexual size dimorphism

Introduction

Sexual size dimorphism (SSD) has controversial origin and complex nature, which have been objects of numerous studies since the works of Darwin till now. There are two major theories explaining the origin of SSD: the first is based on the concept of sexual selection (DARWIN 1871, LINDENFORS *et al.* 2007), while the second is based on the concept of natural selection, *i.e.* different interactions of each sex with its environment (see review in LOVICH, GIBBONS 1992).

Sexual size dimorphism is recorded in many mammalian taxa. It is more often male-biased (FERGUSON, LARIVIÈRE 2008, LINDENFORS *et al.* 2007) and associated with the mating system (LINDENFORS *et al.* 2007, WECKERLY 1998). The classical explanation for the larger size in males is the sexual selection in polygynous species: fitness is greater in larger males, *i.e.* they obtain better access to mates

and give more offspring. According to LINDENFORS *et al.* (2007), “reproductive rate is lower for larger females, indicating that fecundity selection selects for smaller females in mammals”. However, recent studies stated that sexual selection is not in all cases and/or is not the only force leading to SSD.

Sexual dimorphism could be influenced by a number of population and environmental characteristics related to the amount of the available resources (mainly food): population density, latitudinal and seasonal variation, disease, etc. Males and females often differ substantially in the direction and magnitude of selection on shared traits (COX, CALSBEEK 2009). Sexual size dimorphism is associated with sexual differences in feeding habits, habitat use, growth rates and growth strategies (see review in ISAAC 2005). FERGUSON, LARIVIÈRE (2008) asserted that SSD can increase due to lower primary produc-

tivity, which leads to greater home ranges and lower population density, respectively.

It is found that sex differences in sensitivity to the environment during growth can lead to SSD as well as to spatial and temporal variation in SSD prompted by the heterogeneity and changeability of the environment (BADYAEV 2002, TRUBENOVÁ *et al.* 2010). The degree of SSD is found to be related to the mating systems. According to FERGUSON, LARIVIÈRE (2008), it is higher in polygynous species, lower in monogamous species and the lowest in multi-male species. After BOONSTRA *et al.* (1993), SSD should again be the greatest in strongly polygynous species, intermediate in promiscuous species and the least in monogamous species. TRIVERS (1972) stated that male-biased SSD is “especially likely in species where males provide little or no parental investment, as males in these species can increase their reproductive success directly by competing for matings”. However, male-biased SSD may not be always attributed to the polygynous mating system. For example, SCHULTE-HOSTEDDE *et al.* (2002) found no relationship between the male reproductive success and body size in the yellow-pine chipmunks. After Rensch’s rule (RENSCH 1950), across species within a lineage, size dimorphism will increase with increasing body size when the male is the larger sex, and decrease with increasing average body size when the female is the larger sex. According to LINDENFORS *et al.* (2007), this rule applies to the mammals as a whole, but is observed only in some mammalian orders, excluding Eulipotyphla.

The results of a comparative analysis of the sexual size dimorphism in mammalian orders (LINDENFORS *et al.* 2007) show tendency males to be larger in all of them with the exception of orders Lagomorpha and Chiroptera. Insectivores display slight and non-significant male-biased sexual differences.

Although male-biased SSD is assumed to be the common pattern in mammals, a considerable number of mammalian species display female-biased SSD (LINDENFORS *et al.* 2007, RALLS 1976, SCHULTE-HOSTEDDE, MILLAR 2000). According to RALLS (1976), this phenomenon is rarely a result of sexual selection acting upon the female sex but is probably “associated with the fact that a big mother is often a better mother and resulting from more intense competition among females for some resource than among males”. The author assumed that the phenomenon is not correlated with an unusually large degree of male parental investment, polyandry, greater aggressiveness in females than in males, greater development of weapons in females, female dominance, or matriarchy.

Some authors suggest that the degree of sexual dimorphism, indicative of strong sexual selection, is greater in larger species (McLAIN 1993, WECKERLY 1998). In this context, the extremely small body size in soricids should be associated with a low degree or absence of sexual dimorphism, including in size. In fact, the investigations on SSD in soricids have displayed varied results; moreover, only few of them have examined a great number of cranial and tooth traits, which can present a comprehensive view on the shrews’ sexual variability in size in the context of the models for sexual and natural selection.

The reports on SSD in soricids are contradictory, in some cases even within a single species. According to a number of studies on shrew species, males and females do not differ in size or weight (BALČIAUSKAS 2004, BERNAL 2010, HOMOLKA 1980, MISHTA 2007, MOTOKAWA *et al.* 1996, PANKAKOSKI 1989, RYCHLIK *et al.* 2006, SEARLE, THORPE 1987). However, male-biased sexual size differences are recorded in several species of soricids, both white-toothed (Crocidae) and red-toothed (Soricidae) (BALÁŽ, AMBROS 2006, BOUTEILLER-REUTER C., N. PERRIN 2005, KITCHENER *et al.* 1994, MOTOKAWA *et al.* 2003, NISTREANU 2000). Only a few studies indicate larger measurements in females: concerning the weight in *N. fodiens* (RYCHLIK *et al.* 2006) and the condylo-basal length in *Crocidae shantungensis* (MOTOKAWA *et al.* 2003).

Although the sexual size differences are recorded in a certain degree in some species of shrews, there are no reports for incontestable and strongly expressed sexual size dimorphism. The degree of differences between males and females is always comparatively low. For instance, VASILEV, SHAROVA (1992) found that sexual dimorphism accounts for the only 2.8% of morphological variability in *Sorex araneus*, while its geographical variability is as much as 30 times more.

The complex nature of SSD makes it difficult to be studied. The absence of consensus about it in soricids could probably be explained by intraspecific spatial and/or temporal variation regarding that pattern, as well as by methodological differences among studies, such as the division of age groups and the choice of variables to be investigated. Furthermore, the selection of an inappropriate variable can lead to erroneous conclusions regarding SSD (LOVICH, GIBBONS 1992). The usage of large number of metric characters for the analysis of SSD could provide a comprehensive view of the morphometric structures influenced by the sexual differences in exploitation of the environment and strategies for achieving maximum fitness.

Therefore, the aim of this study is to contribute to the knowledge of the SSD in mammals, using identical methods of approach on several soricid species as suitable objects for a comparative investigation of that phenomenon. The species chosen for the study represent the two subfamilies of the family Soricidae, i.e. Crocidurinae and Soricinae. Although they share many features (the small size, invertebrate diet, high metabolism rate in comparison with most of the other mammal species, the comparatively short lifespan, low breeding rates compared to most other small mammals, etc.), the shrews of Crocidurinae and Soricinae differ vastly in their mating system, territorial and intraspecific behaviour, individual development, metabolism, etc. Crocidurinae shrews are characterised by territoriality in breeding pairs, a monogamous mating system, low metabolic rate and low energy demands, tolerance toward conspecifics, sometimes even communal nesting. Soricinae shrews have stable (*Sorex araneus* and *S. minutus*) or shifting (*Neomys fodiens*) territories (with the exception of *N. anomalus*, which is non-territorial beyond the reproductive period), a promiscuous mating system, very high metabolic rate and great energy demands, and agonistic behaviour toward conspecifics, which is occasionally manifested in cannibalism and infanticide.

As teeth are believed to evolve substantially independently from jaws (SMITH 2003), both skull and tooth characters are relevant to be used in the analyses of SSD. This was decisive in choosing the characters in the present study.

Material and Methods

The sexual variability in six soricid species (*C. suaveolens*, *C. leucodon*, *N. anomalus*, *N. fodiens*, *S. araneus*, and *S. minutus*) was examined on the basis of 39 cranial, mandibular and tooth measurements taken by means of a sliding caliper (0.1 mm accuracy) or a low-power stereo microscope (0.01 mm accuracy). In order to minimise the possibility of measuring errors, all the specimens were measured by a single person. The obtained measurements were grouped according to their anatomical and functional relevance (Fig. 1).

The cranium materials for this study were from the collections of small mammals at the Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Natural History Museum Vienna (Austria) and the Hungarian Natural History Museum.

Since the preliminary discriminant analyses showed some geographic and altitudinal variability (much higher than that in the sexual respect), the species samples for further analyses were differentiated on the basis of the geographic location and the altitude of the localities of the materials; the following abbreviations (Table 1) are further used for these samples: SEE-low (South-Eastern Europe lowland samples), SEE-middle (South-Eastern Europe middle-mountain samples), SEE-high (South-Eastern Europe high-mountain samples), CE-low (Central Europe lowland samples) and CE-high (Central Europe high-mountain samples). No significant differences were found between the specimens of *S. minutus* from the high and the middle mountains in Southeastern Europe. Consequently, these materials were pooled into one sample in order to obtain a larger sample for the analyses of SSD.

The preliminary analyses also showed an age variability concerning some of the characters. Therefore, for eliminating the influence of the age variation, only subadult individuals (with unworn or slightly worn teeth corresponding to sexually immature current year animals) were used in this study. The comparison of the sexual size differences between subadults and adults was possible only in *N. anomalus* from SEE-low, because of the small numbers of adult specimens in the available materials from the other species.

A total of 617 skulls were used for the analyses. Sample sizes are presented in Table 2.

A graphic method proposed by SIMPSON (1941) was used to illustrate the differences in the obtained measurements between the two sexes for each species. The sample of females was chosen as a standard in the diagram. The horizontal scale of the diagram presents the differences between the \log_{10} of the variables' means in males and those in females. All the metric characters are represented on the vertical scale.

The size dimorphism index (SDI) proposed by LEVENSON (1990) was used for quantifying SSD. Thus, the degree of SSD was calculated by the formula $[(\text{mean female body measurement} / \text{mean male body measurement}) - 1.000] \times 100$. The overall value of sex differences is presented by the sum of SDI of all characters for each sample. Sexual differences in each character and locality were checked with *t*-test for independent samples ($p \leq 0.05$), which was possible because of the distribution of the variables being close to normal.

All statistical calculations were implemented using STATISTICA 7.0 for Windows (STATSOFT 2004).

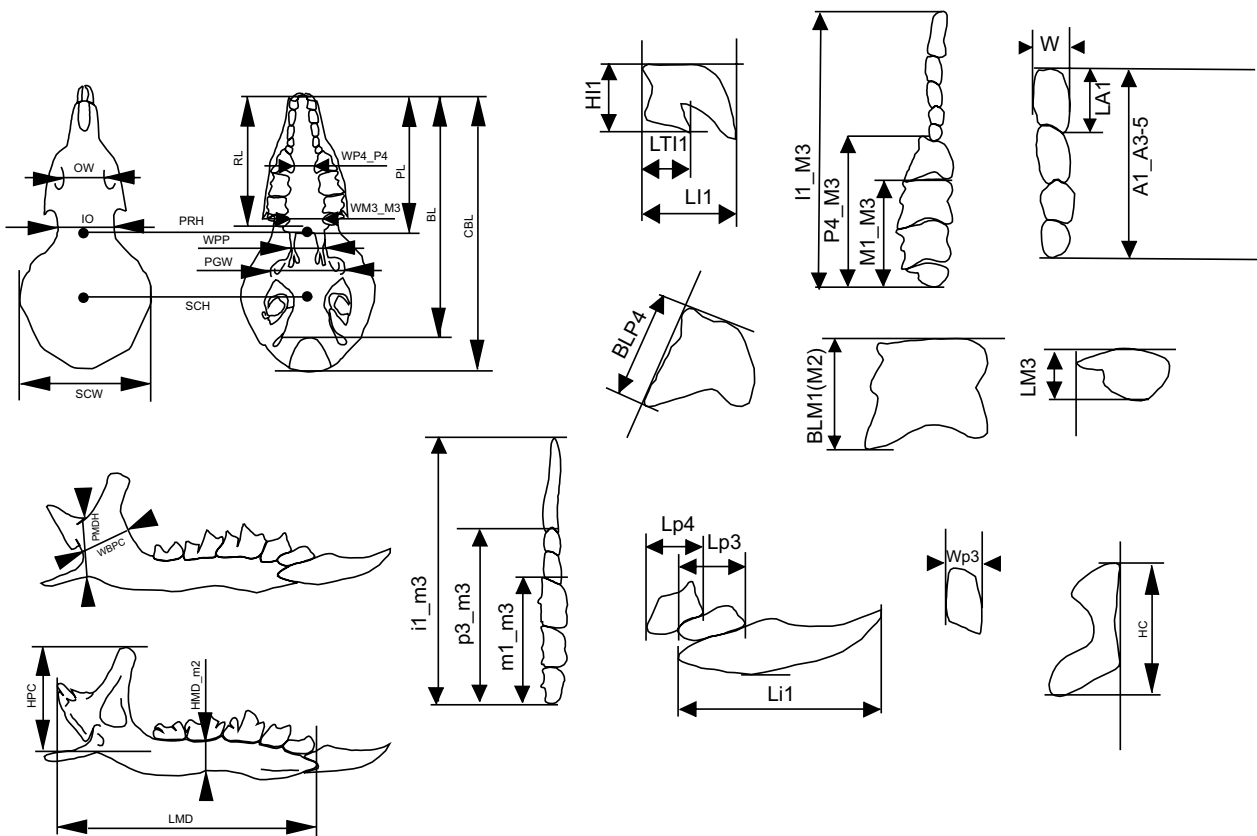


Fig 1. Cranial, mandibular, and dental variables used in this study.

Cranium width: SCW - skull case width; OW - orbital width; IO - infraorbital width; PGW - postglenoid width; WP4_P4 - width between P4's; WM3_M3 - width between M3's; WPP - width between processi hamulari; **Cranium length:** CBL - condylobasal length; BL - basal length; PL - palatal length; RL - rostral length; **Cranium height:** SCH - skull case height; PRH - post-rostral height; **Upper tooth rows:** I1_M3 - length of I1 - M3; P4_M3 - length of P4 - M3; M1_M3 - length of M1-M3; A1_A3-5 - length of antemolars; **Upper teeth:** LI1 - length of upper incisive; LTI1 - upper incisive talon length; HI1 - height of upper incisive; LA1 - length of the first antemolar; WA1 - width of the first antemolar; BLP4 - buccal length of P4; BLM1 - buccal length of M1; BLM2 - buccal length of M2; LM3 - length of M3; **Mandibula:** LMD - length of mandible; PMDH - distance from the lowest positioned point between proc. coronoideus and proc. articularis to the ventral edge of the mandibulae in front of proc. angularis; WBPC - minimal width of ramus mandibulae (behind proc. angularis and below proc. coronoideus) HPC - height of coronoid process; HMD_m2 - distance from the lower fringe of the m2 alveolus to the ventral edge of the mandibula (lingual view); HC - height of condyle; **Lower tooth rows:** i1_m3 - length of i1-m3; p3_m3 - length of p3-m3; m1_m3 - length of m1-m3; **Lower teeth:** Li1 - length of lower incisive; Lp3 - length of p3; Lp4 - length of p4; Wp3 - width of p3.

Table 1. Description of the samples used in the analyses of sexual size differences of shrews

Geogr. region	Sample abbreviation	Country	Relief	Altitudinal range [m a.s.l.]	Species
Southeastern Europe	SEE-low	Bulgaria	Lowland	5-355	<i>C.s., C.l., N.a.</i>
	SEE-middle	Bulgaria	Middle mountain	650-1400	<i>N.a., N.f.</i>
	SSE-high	Bulgaria	High mountain	1400-2000	<i>N.f., S.a., S.m.</i>
Central Europe	CE-low	Austria and Hungary	Lowland	80-630	<i>C.s., C.l., N.a., N.f., S.a.</i>
	CE-high	Austria	High mountain	1000-1980	<i>N.f., S.a.</i>

Results

Simpson's diagrams

As shown in the Simpson's diagram (Fig. 2), the males were larger than females in almost all studied metric characters in *C. suaveolens*. *C. leucodon* also exhibited male-biased sex differences in most of the measurements; however, this tendency was not as strong as in *C. suaveolens*. In both white-toothed species, this pattern was obvious in the specimens from Southeastern Europe (SEE) and from Central Europe (CE), but was better manifested in those from SEE.

In all four studied red-toothed species, Simpson's diagrams did not show clear trends in size differences between sexes. Nevertheless, a slight tendency to female-biased sex differences in most variables was observed in the sample of adult *N. anomalus*. In *N. fodiens*, *S. araneus* and *S. minutus*, some of the measurements were larger in males, others were larger in females, while the rest did not differ between sexes. Furthermore, some differences between samples of the same species were observed.

Levenson SDI's

The degree of sex differences for all the measured characters was quantified by SDI values (Tables 2-7). SDI had the greatest values (above 4) in some measurements from the SEE specimens of white-toothed soricids, namely: WP4_P4, SCH, LI1, HI1, WA1 and HMD_m2 in *C. suaveolens* as well as LTI1, LM3, and HMD_m2 in *C. leucodon*. There were only several characters with comparatively great SDI values in the remaining samples from all species.

The overall values of sex differences, as presented by the sum of SDI of all variables in each sample (Tables 2 and 3), clearly proved the presence of sexual differences in size in both *Crocridura* species. SEE samples of *C. suaveolens* and *C. leucodon* were found as the most sexually dimorphic, followed by the sample of *C. suaveolens* from CE. These results confirmed the trends displayed by Simpson's diagrams.

The summarised Levenson indexes for each sample of water shrews (Tables 4 and 5) showed that slightly female-biased sexual differences in size are present in both species. They were better pronounced in the samples from CE lowland and SEE mountains in *N. fodiens* and in the lowlands of CE and SEE in *N. anomalus*. The overall values of Levenson indexes in *S. araneus* (Table 6) showed that males are slightly larger in CE low-

land, while the females are slightly larger in CE and SEE mountains. The males and females from the single sample of *S. minutus* (Table 7) did not differ in size excepting for some particular characters (see text below).

t-test

Crocridurinae

Approximately 44% of the investigated metric characters of the skulls in *C. suaveolens* from SEE were significantly larger in males than in females (t-test, $p < 0.05$; Table 2). These characters included: cranium width (WP4_P4, WM3_M3), cranium length (CBL, PL, RL), cranium height (SCH), upper tooth rows (I1_M3, M1_M3, A1_A3), upper teeth (LI1, HI1, WA1), massiveness of the mandibula (LMD, WBPC, HPC, HMD_m2), and lower tooth row (il_m3). In CE, the males were significantly larger only in two variables, both associated with incisive massiveness: HI1 and LI1.

Approximately 10% of the examined characters of *C. leucodon* from SEE showed statistically significant sex differences, being again larger in males. These characters were related to the cranium width (PGW) and upper teeth (M1_M3, BLP4, and LM3). Although not significant, there were quite a few variables which were characterised by relatively high values of Levenson SDI (Table 3), which could be an evidence of certain size differences between the males and females. Only two measurements in the sample from CE were significantly larger in males (SCH and Wp3).

Soricinae

The results of t-test for the red-toothed soricid species were contradictory and not as consistent as in the white-toothed species (Tables 4-7). There were significant sex differences only in a few characters in each soricine species. Differences were found (the degree and direction of SSD, as well as in the significance of the differences) both between species and between samples of the same species.

In the case of the subadult *N. anomalus*, only one variable (LI1) showed significant female-biased sex differences in the SEE-low sample, while in the CE-low such differences were found in two variables (WA1 and Wp3). On the other hand, two characters (PRH and HMD_m2) were significantly larger in the males from SEE-low. Wp3 was the only measurement, significantly larger in the males from the sample of adult *N. anomalus*. At the same time, HMD_m2 was larger (although not always significantly) in the males from all samples.

Eight characters showed significant sex differences in *N. fodiens*: I1_M3, LI1, WA1, HPC, IO, Li1, SCH and PRH. Most of them were larger in females (the exceptions being SCH and LI1).

S. araneus showed significant sex differences only in the CE samples. They concern BL, I1_M3, LI1, i1_m3 and HPC in lowland samples and WA1, BLM2 and PMDH in the mountains. Some of the measurements (BL, I1_M3, LI1, i1_m3, BLM2) had larger values in males, while others (HPC, WA1, PMDH) in females.

In the sample of *S. minutus*, only two variables showed significant differences: SCW was larger in males while IO in females.

Discussion

Comparison between the subfamilies Soricinae and Crocidurinae

The results of this study argue for low degree of SSD in soricids. According to the arbitrary categories, proposed by COX, CALSBEEK (2009), the SSD is low for most of the studied characters, moderate for a small part of the characters and reaches high values for most of the characters in *C. suaveolens*, followed by *C. leucodon*. As there is a great overlap in the ranges of measurements (Table 2), it is more correct to interpret them as size differences between sexes instead of distinct sexual size dimorphism.

According to our results, different patterns regarding SSD are observed in Crocidurinae and Soricinae shrews. The two white-toothed shrew species show clear male-biased sexual size differences, which are better expressed in *C. suaveolens* compared to *C. leucodon*. Conversely, the red-toothed shrews do not manifest distinct sexual differences in size. Although there are particular variables, which have significantly greater values in the one or the other sex, it could be generalised that the males and females in the investigated Soricinae species are approximately of the same size. However, some tendency for female-biased sexual differences in size in regard to several measurements is observed in the genus *Neomys*.

The results of this study disagree with the widely-held view that the degree of male-biased SSD should be lower in monogamous species in comparison with polygynous and promiscuous species (BOONSTRA *et al.* 1993, FERGUSO, LARIVIÈRE 2008). At the same time, the better expressed male-biased differences in size in the smaller white-tooth species, *C. suaveolens*, in comparison with the larger *C. leucodon*, support the statement of LINDENFORS *et al.*

(2007) that Rensch's rule is not observed in order Eulipotyphla.

The natural selective forces is thought to give advantage to the smaller size in shrews (OCHOCIŃSKA, TAYLOR 2003) in order to minimise their energy demands since they have extremely high metabolism rate in comparison with other mammalian species. On the contrary, sexual selection should select for larger size since it assures social dominance and gives advantage in the defense of the territory and access to mates and food resources. Thus, the larger individuals are more successful parents, which provide their offspring with more protection and resources. Obviously, these two selective forces (natural and sexual) combine their influences in different ways in the two subfamilies of shrews. The approximately equal size of males and females in the Soricinae species agree with the hypothesis of ISAAC (2005) that female-female competition for dominance and resources may select for an increased female size. In contrast to Crocidurinae species, the Soricinae shrews have a promiscuous mating system and higher level of intraspecific aggressiveness. The absence of male-biased SSD in the examined *Sorex* and *Neomys* species, unlike *Crocidura* spp., could be related to the agonistic behaviour, cannibalism and infanticide in the species of the subfamily Soricinae (and absent in the Crocidurinae). Females should be large enough to protect their offspring from attacks of adult males and subadults as well as to defend territories needed for providing food and shelter for the young. On the other hand, the Crocidurinae shrews are monogamous and males actively defend the territory of the breeding pair. Apparently, this may be the reason for the larger size of males in *C. suaveolens* and *C. leucodon*. Similar results are reported for *Crocidura russula* by BOUTEILLER-REUTER, PERRIN (2005), who believed that males are heavier than females, because of the stronger sexual selection.

It could be concluded that the patterns of SSD in shrews are a result of a fragile balance between natural selection (selecting for smaller size) and sexual selection (selecting for larger size) in the context of different mating systems. In the promiscuous Soricinae shrews, sexual selection prevails over natural selection in both sexes. In the monogamous Crocidurinae species, sexual selection is stronger in males than in females.

Variability of characters and functional significance

The characters that show significant sex differences in the greatest number of the studied six species (3 or 4 of them) are I1_M3, SCH, LI1, WA1,

Table 2. Skull measurements and Levenson index of all samples of *Crocidura suaveolens* (significant sex differences are marked in bold)

Sample	SEE-low						CE-low							
	females			males			IL	females			males			IL
	Mean	SD	N	Mean	SD	N		Mean	SD	N	Mean	SD	N	
SCW	8.03	0.25	11	8.15	0.28	10	-1.47	7.94	0.24	26	8.04	0.14	20	-1.24
OW	3.17	0.11	16	3.17	0.09	18	0.00	3.15	0.05	27	3.13	0.08	21	0.64
IO	3.95	0.12	17	4.01	0.10	18	-1.50	3.87	0.10	27	3.89	0.10	21	-0.51
CBL	16.18	0.54	13	16.70	0.52	13	-3.11	16.19	0.47	26	16.37	0.46	20	-1.10
BL	14.64	0.59	10	14.88	0.43	12	-1.61	14.52	0.46	26	14.71	0.42	19	-1.29
I1_M3	7.47	0.20	17	7.64	0.23	18	-2.23	7.38	0.22	25	7.46	0.23	21	-1.07
PL	6.69	0.17	17	6.81	0.18	17	-1.76	6.75	0.24	27	6.84	0.24	21	-1.32
RL	6.42	0.18	17	6.60	0.25	18	-2.73	6.41	0.21	26	6.50	0.23	21	-1.38
P4_M3	4.54	0.12	17	4.63	0.17	18	-1.94	4.38	0.12	27	4.40	0.15	21	-0.45
M1_M3	2.84	0.07	17	2.91	0.11	18	-2.41	2.98	0.09	27	3.01	0.09	21	-1.00
A1_A3-5	2.04	0.06	17	2.10	0.09	18	-2.86	2.12	0.08	27	2.16	0.09	20	-1.85
PGW	5.76	0.24	16	5.86	0.15	15	-1.71	5.67	0.16	27	5.74	0.14	21	-1.22
WP4_P4	0.98	0.06	17	1.06	0.08	18	-7.55	1.10	0.08	27	1.11	0.06	21	-0.90
WM3_M3	1.79	0.10	16	1.86	0.06	18	-3.76	1.97	0.09	27	1.97	0.09	19	0.00
WPP	2.19	0.12	16	2.18	0.09	16	0.46	2.33	0.09	27	2.34	0.12	21	-0.43
SCH	4.23	0.31	11	4.48	0.21	12	-5.58	4.27	0.19	26	4.28	0.12	19	-0.23
PRH	3.29	0.10	16	3.35	0.14	18	-1.79	3.28	0.14	27	3.32	0.09	21	-1.20
LI1	1.63	0.06	17	1.72	0.07	17	-5.23	1.70	0.05	25	1.73	0.06	21	-1.73
LTI1	0.79	0.04	17	0.80	0.06	18	-1.25	0.77	0.04	27	0.79	0.06	21	-2.53
HI1	1.10	0.04	17	1.17	0.04	18	-5.98	1.12	0.04	26	1.16	0.05	21	-3.45
LA1	1.10	0.05	17	1.13	0.04	18	-2.65	1.15	0.04	26	1.16	0.04	20	-0.86
WA1	0.67	0.03	17	0.70	0.03	18	-4.29	0.70	0.03	26	0.72	0.04	20	-2.78
BLP4	1.64	0.05	17	1.67	0.06	18	-1.80	1.70	0.05	27	1.71	0.06	21	-0.58
BLM1	1.31	0.04	17	1.34	0.08	18	-2.24	1.40	0.05	27	1.41	0.04	21	-0.71
BLM2	1.14	0.04	17	1.16	0.05	18	-1.72	1.23	0.04	26	1.22	0.05	21	0.82
LM3	0.58	0.03	17	0.60	0.02	18	-3.33	0.60	0.03	27	0.60	0.03	21	0.00
LMD	9.12	0.27	17	9.32	0.28	18	-2.15	8.92	0.42	27	9.02	0.30	21	-1.11
i1_M3	6.99	0.13	17	7.11	0.19	18	-1.69	6.78	0.15	26	6.87	0.20	21	-1.31
p3_m3	5.37	0.10	17	5.44	0.16	18	-1.29	5.11	0.12	26	5.15	0.15	21	-0.78
m1_m3	3.67	0.16	17	3.76	0.17	18	-2.39	3.59	0.08	27	3.62	0.12	21	-0.83
PMDH	2.02	0.07	17	2.07	0.09	18	-2.42	1.98	0.16	27	2.01	0.15	21	-1.49
WBPC	1.84	0.08	17	1.91	0.08	18	-3.66	2.03	0.11	27	2.05	0.12	21	-0.98
HPC	4.13	0.17	17	4.28	0.12	18	-3.50	4.02	0.18	27	4.09	0.15	21	-1.71
Li1	2.96	0.12	17	3.01	0.09	17	-1.66	2.91	0.09	27	2.97	0.11	21	-2.02
Lp3	1.07	0.05	17	1.07	0.06	18	0.00	1.08	0.05	26	1.10	0.04	21	-1.82
Lp4	1.11	0.04	17	1.12	0.04	18	-0.89	1.10	0.04	26	1.11	0.04	21	-0.90
HMD_m2	1.07	0.08	17	1.14	0.09	18	-6.14	1.17	0.06	26	1.18	0.06	21	-0.85
HC	1.50	0.10	17	1.52	0.11	18	-1.32	1.61	0.09	27	1.66	0.11	21	-3.01
Wp3	0.57	0.03	17	0.58	0.04	18	-1.72	0.59	0.03	27	0.61	0.05	21	-3.28
Summarized Levenson index:							-98.88	Summarized Levenson index:						-46.48

Legend: SD – standard deviation; N – sample size; IL – Index Levenson

Table 3. Skull measurements and Levenson index of all samples of *Crocidura leucodon* (significant sex differences are marked in bold). For abbreviations see Table 2

Sample	SEE-low						CE-low						IL	
	females			males			IL	females			males			
	Mean	SD	N	Mean	Std.dev.	N		Mean	SD	N	Mean	SD		N
SCW	9.09	0.31	9	9.17	0.19	5	-0.87	8.98	0.23	23	9.05	0.28	24	-0.77
OW	3.66	0.11	10	3.74	0.10	6	-2.14	3.63	0.12	24	3.66	0.14	25	-0.82
IO	4.43	0.17	10	4.53	0.13	6	-2.21	4.36	0.14	24	4.39	0.15	25	-0.68
CBL	19.01	0.64	9	19.17	0.28	6	-0.83	18.58	0.49	24	18.74	0.68	24	-0.85
BL	16.88	0.57	9	17.10	0.13	5	-1.29	16.53	0.48	23	16.65	0.58	23	-0.72
I1_M3	8.86	0.26	9	9.02	0.16	6	-1.77	8.78	0.23	24	8.75	0.27	25	0.34
PL	7.78	0.28	10	7.91	0.13	6	-1.64	7.87	0.30	24	7.84	0.27	25	0.38
RL	7.40	0.27	10	7.49	0.07	6	-1.20	7.40	0.24	24	7.40	0.24	25	0.00
P4_M3	5.13	0.15	10	5.27	0.08	6	-2.66	5.05	0.13	24	5.04	0.15	24	0.20
M1_M3	3.21	0.09	10	3.31	0.07	6	-3.02	3.44	0.09	24	3.41	0.10	24	0.88
A1_A3-5	2.45	0.08	9	2.42	0.09	6	1.24	2.54	0.08	22	2.54	0.11	23	0.00
PGW	6.63	0.20	10	6.88	0.15	6	-3.63	6.42	0.22	24	6.41	0.21	24	0.16
WP4_P4	1.11	0.09	9	1.13	0.09	6	-1.77	1.13	0.07	24	1.12	0.08	24	0.89
WM3_M3	2.26	0.06	10	2.25	0.08	6	0.44	2.37	0.10	24	2.36	0.08	24	0.42
WPP	2.42	0.16	10	2.50	0.08	6	-3.20	2.52	0.10	24	2.54	0.13	23	-0.79
SCH	4.72	0.20	9	4.81	0.05	4	-1.87	4.58	0.17	23	4.71	0.25	23	-2.76
PRH	3.62	0.18	10	3.74	0.07	6	-3.21	3.63	0.14	24	3.65	0.12	25	-0.55
LI1	2.22	0.06	9	2.29	0.08	5	-3.06	2.25	0.09	24	2.29	0.09	24	-1.75
LTI1	1.01	0.05	9	1.07	0.06	6	-5.61	1.04	0.06	23	1.07	0.07	23	-2.80
HI1	1.31	0.08	9	1.36	0.05	6	-3.68	1.37	0.05	23	1.37	0.07	24	0.00
LA1	1.36	0.06	9	1.36	0.08	6	0.00	1.46	0.04	24	1.47	0.06	24	-0.68
WA1	0.79	0.06	9	0.81	0.09	6	-2.47	0.87	0.03	24	0.88	0.04	24	-1.14
BLP4	1.89	0.06	10	1.96	0.03	6	-3.57	2.03	0.09	24	2.06	0.07	24	-1.46
BLM1	1.51	0.05	10	1.55	0.03	6	-2.58	1.65	0.06	24	1.63	0.07	24	1.23
BLM2	1.28	0.05	10	1.29	0.02	6	-0.78	1.39	0.06	24	1.39	0.06	24	0.00
LM3	0.58	0.03	10	0.62	0.03	6	-6.45	0.62	0.03	24	0.61	0.03	24	1.64
LMD	10.50	0.41	10	10.73	0.34	6	-2.14	10.24	0.31	24	10.35	0.30	25	-1.06
i1_M3	8.17	0.26	9	8.32	0.12	6	-1.80	8.11	0.19	24	8.09	0.25	25	0.25
p3_m3	6.15	0.15	10	6.28	0.13	6	-2.07	6.04	0.12	23	6.00	0.19	24	0.67
m1_m3	4.30	0.11	10	4.40	0.08	6	-2.27	4.26	0.09	24	4.26	0.13	24	0.00
PMDH	2.43	0.12	9	2.49	0.05	6	-2.41	2.32	0.18	24	2.31	0.14	24	0.43
WBPC	2.20	0.09	9	2.24	0.08	6	-1.79	2.42	0.13	24	2.47	0.13	24	-2.02
HPC	5.04	0.22	9	5.18	0.12	6	-2.70	4.80	0.18	24	4.86	0.18	25)	-1.23
Li1	3.58	0.14	8	3.67	0.13	6	-2.45	3.63	0.13	24	3.63	0.16	24	0.00
Lp3	1.24	0.05	9	1.27	0.06	6	-2.36	1.27	0.05	23	1.24	0.06	24	2.42
Lp4	1.27	0.06	9	1.30	0.06	5	-2.31	1.34	0.05	23	1.32	0.05	24	1.52
HMD_m2	1.34	0.08	10	1.40	0.06	6	-4.29	1.39	0.09	24	1.43	0.08	24	-2.80
HC	1.78	0.10	10	1.83	0.06	6	-2.73	1.88	0.08	24	1.89	0.12	24	-0.53
Wp3	0.67	0.07	9	0.68	0.07	6	-1.47	0.73	0.03	22	0.75	0.03	21	-2.67
	Summarized Levenson index:						-88.62	Summarized Levenson index:						-14.66

Table 4. Skull measurements and Levenson index of all samples of *Neomys anomalus* (significant sex differences are marked in bold). For abbreviations see Table 2

Sample Sex Measure- ment	SEE-low			SEE-middle			CE-low			SEE-low (ads)			IL								
	females		males	females		males	females		males	females		males									
	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N									
SCW	10.23	0.16	24	10.33	0.19	20	10.10	0.29	13	10.00	0.21	16	1.00	10.13	0.24	28	10.09	0.19	30	0.40	
OW	3.39	0.09	24	3.42	0.11	20	3.23	0.10	13	3.25	0.07	16	-0.62	3.23	0.10	28	3.21	0.08	31	0.62	
IO	4.41	0.11	24	4.41	0.12	20	4.27	0.11	13	4.24	0.16	16	0.71	4.18	0.10	28	4.19	0.10	31	-0.24	
CBL	20.40	0.46	24	20.42	0.49	20	20.17	0.49	13	19.99	0.32	16	0.90	20.30	0.52	28	20.30	0.43	31	0.00	
BL	17.97	0.42	24	18.04	0.34	20	17.70	0.57	13	17.59	0.34	16	0.63	17.79	0.49	28	17.86	0.36	30	-0.39	
II_M3	10.00	0.22	24	9.96	0.14	20	9.92	0.31	13	9.87	0.28	16	0.51	9.83	0.23	28	9.84	0.17	31	-0.10	
PL	9.81	0.31	24	9.76	0.21	20	9.75	0.35	13	9.77	0.33	16	-0.20	9.32	0.25	28	9.32	0.21	31	0.00	
RL	9.26	0.29	24	9.16	0.18	20	9.23	0.34	13	9.23	0.31	16	0.00	8.80	0.23	28	8.80	0.19	31	0.00	
P4_M3	5.54	0.13	24	5.48	0.12	20	5.58	0.14	13	5.55	0.13	16	0.54	5.32	0.13	28	5.30	0.11	31	0.38	
M1_M3	3.91	0.09	24	3.87	0.09	20	3.88	0.10	13	3.87	0.10	16	0.26	3.79	0.10	28	3.75	0.09	31	1.07	
A1_A3-5	3.54	0.13	24	3.51	0.10	20	3.46	0.17	13	3.45	0.14	16	0.29	3.46	0.10	28	3.47	0.09	31	-0.29	
PGW	5.94	0.21	24	5.93	0.23	20	5.87	0.22	13	5.84	0.19	16	0.51	5.85	0.18	28	5.82	0.13	31	0.52	
WP4_P4	1.41	0.10	24	1.44	0.09	20	1.43	0.10	13	1.40	0.10	16	2.14	1.38	0.09	28	1.38	0.09	31	0.00	
WM3_M3	2.65	0.10	24	2.69	0.13	20	2.64	0.10	13	2.62	0.11	16	0.76	2.61	0.10	28	2.61	0.10	31	0.00	
WPP	2.63	0.11	24	2.64	0.10	20	2.53	0.12	13	2.58	0.15	16	-1.94	2.90	0.11	28	2.91	0.11	31	-0.34	
SCH	5.59	0.13	24	5.67	0.22	20	5.63	0.19	13	5.65	0.17	16	-0.35	5.66	0.18	28	5.65	0.20	29	0.18	
PRH	3.79	0.11	24	3.89	0.15	20	3.67	0.10	13	3.63	0.13	16	1.10	3.56	0.10	28	3.58	0.11	31	-0.56	
LI1	1.77	0.05	24	1.78	0.07	20	1.77	0.09	13	1.78	0.12	16	-0.56	1.87	0.06	28	1.85	0.07	31	1.08	
LTI1	0.79	0.04	24	0.79	0.04	20	0.00	0.77	0.04	13	0.77	0.07	16	0.00	0.85	0.05	28	0.84	0.06	31	1.19
HI1	1.27	0.05	24	1.25	0.05	20	1.29	0.07	13	1.29	0.07	16	0.00	1.24	0.05	28	1.22	0.04	31	1.64	
LA1	1.35	0.04	24	1.33	0.05	20	1.34	0.07	13	1.32	0.07	16	1.52	1.30	0.05	28	1.30	0.05	31	0.00	
WA1	0.76	0.03	24	0.76	0.02	20	0.00	0.75	0.04	13	0.76	0.04	16	-1.32	0.73	0.02	28	0.71	0.03	31	2.82
BLP4	1.90	0.05	24	1.89	0.06	20	1.95	0.06	13	1.93	0.09	16	1.04	1.82	0.06	28	1.81	0.04	31	0.55	
BLM1	1.70	0.05	24	1.67	0.04	20	1.68	0.07	13	1.68	0.05	16	0.00	1.62	0.04	28	1.61	0.03	31	0.62	
BLM2	1.53	0.05	24	1.53	0.04	20	1.51	0.04	13	1.51	0.05	16	0.00	1.49	0.04	28	1.47	0.05	31	1.36	
LM3	0.88	0.05	24	0.87	0.03	20	0.86	0.04	13	0.86	0.04	16	0.00	0.84	0.04	28	0.83	0.04	31	1.20	
LMD	11.27	0.30	24	11.29	0.27	20	10.93	0.29	13	10.87	0.27	16	0.55	10.91	0.35	28	10.98	0.25	31	-0.64	
i1_M3	9.34	0.21	24	9.29	0.18	20	9.30	0.26	13	9.23	0.23	16	0.76	9.15	0.21	28	9.16	0.17	31	-0.11	
p3_m3	6.37	0.17	24	6.35	0.15	20	6.36	0.15	13	6.35	0.20	16	0.16	6.14	0.14	28	6.12	0.13	31	0.33	
m1_m3	4.48	0.10	24	4.44	0.11	20	4.54	0.11	13	4.47	0.13	16	1.57	4.40	0.10	28	4.38	0.08	31	0.46	
PMDH	2.60	0.07	24	2.59	0.09	20	2.59	0.13	13	2.57	0.12	16	0.78	1.96	0.11	28	1.95	0.09	30	0.51	
WBPC	4.50	0.13	24	4.49	0.14	20	4.52	0.18	13	4.51	0.17	16	0.22	4.35	0.12	28	4.33	0.10	30	0.46	
HPC	4.47	0.07	24	4.40	0.06	20	4.44	0.16	13	4.51	0.19	16	-1.55	4.29	0.16	28	4.26	0.13	31	0.70	
Li1	1.33	0.07	24	1.31	0.06	20	1.33	0.08	13	1.35	0.11	16	-1.48	1.25	0.04	28	1.25	0.05	31	0.00	
Lp3	1.33	0.04	24	1.32	0.06	20	1.32	0.06	13	1.31	0.05	16	0.76	1.27	0.04	28	1.27	0.04	31	0.00	
Lp4	1.35	0.09	24	1.41	0.11	20	1.29	0.06	13	1.33	0.08	16	-3.01	1.34	0.05	28	1.36	0.06	31	-1.47	
HMD_m2	2.56	0.08	24	2.58	0.13	20	2.42	0.11	13	2.44	0.08	16	-0.82	2.55	0.11	28	2.52	0.08	31	1.19	
HC	0.69	0.03	24	0.69	0.04	20	0.70	0.04	13	0.71	0.05	16	-1.41	0.68	0.02	28	0.66	0.03	31	3.03	
Wp3													3.44							16.17	
													1.94							16.11	
													Summarized Levenson index:							Summarized Levenson index:	

Table 5. Skull measurements and Levenson index of all samples of *Neomys fodiens* (significant sex differences are marked in bold). For abbreviations see Table 2

Sample Sex Measure- ment	SEE-middle						SEE-high						CE-low						CE-high												
	females			males			IL			females			males			IL			females			males			IL						
	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N				
SCW	10.69	0.16	19	10.64	0.22	26	0.47	10.65	0.17	11	0.00	10.84	0.23	12	10.86	0.30	9	-0.18	10.62	0.41	13	10.56	0.34	7	0.57						
OW	3.40	0.10	19	3.39	0.12	26	0.29	3.36	0.11	11	0.60	3.45	0.10	12	3.46	0.16	9	-0.29	3.37	0.13	13	3.29	0.07	8	2.43						
IO	4.62	0.15	19	4.54	0.13	26	1.76	4.42	0.12	11	0.23	4.56	0.14	12	4.62	0.21	9	-1.30	4.50	0.16	13	4.38	0.08	8	2.74						
CBL	21.03	0.35	19	21.00	0.37	26	0.14	20.97	0.22	13	0.77	21.53	0.14	11	21.42	0.54	9	0.51	20.97	0.54	13	20.98	0.40	8	-0.05						
BL	18.46	0.31	19	18.41	0.35	26	0.27	18.43	0.30	13	1.10	19.06	0.67	12	18.86	0.54	9	1.06	18.51	0.51	12	18.38	0.40	8	0.71						
I1_M3	10.51	0.19	19	10.47	0.17	26	0.38	10.31	0.21	11	1.75	10.59	0.12	12	10.51	0.38	9	0.76	10.35	0.33	13	10.46	0.16	8	-1.05						
PL	10.36	0.24	19	10.36	0.22	26	0.00	9.82	0.26	13	-0.20	10.09	0.15	12	10.05	0.41	9	0.40	9.86	0.30	13	9.77	0.17	8	0.92						
RL	9.79	0.21	19	9.79	0.23	26	0.00	9.27	0.28	13	0.11	9.46	0.13	12	9.36	0.36	9	1.07	9.26	0.31	13	9.22	0.15	8	0.43						
P4_M3	5.79	0.11	19	5.79	0.11	26	0.00	5.66	0.08	13	0.71	5.66	0.11	12	5.60	0.16	9	1.07	5.59	0.18	13	5.62	0.14	8	-0.53						
M1_M3	4.00	0.09	19	4.00	0.09	26	0.00	3.94	0.06	13	0.51	3.92	0.08	12	3.88	0.09	9	1.03	3.86	0.12	13	3.83	0.08	8	0.78						
A1_A3-5	3.69	0.10	19	3.65	0.09	26	1.10	3.64	0.07	13	1.96	3.74	0.08	12	3.69	0.21	9	1.36	3.66	0.09	13	3.64	0.09	8	0.55						
PGW	6.15	0.18	19	6.14	0.20	26	0.16	6.20	0.15	13	1.14	6.42	0.14	12	6.39	0.23	9	0.47	6.08	0.22	13	5.99	0.15	8	1.50						
WP4_P4	1.50	0.10	19	1.46	0.09	26	2.74	1.45	0.12	13	2.84	1.49	0.07	12	1.55	0.11	9	-3.87	1.44	0.09	13	1.45	0.05	8	-0.69						
WP3_M3	2.73	0.11	19	2.69	0.14	26	1.49	2.73	0.10	13	1.11	2.81	0.07	12	2.86	0.12	9	-1.75	2.75	0.11	13	2.68	0.05	8	2.61						
WPP	2.43	0.13	19	2.46	0.10	26	-1.22	2.45	0.08	13	1.24	3.14	0.19	12	3.16	0.23	9	-0.63	2.92	0.15	13	2.92	0.11	8	0.00						
SCH	5.83	0.08	19	5.83	0.18	26	0.00	5.73	0.21	13	-2.72	6.11	0.16	11	6.04	0.19	9	1.16	5.98	0.24	12	5.85	0.27	7	2.22						
PRH	3.78	0.08	19	3.79	0.14	26	-0.26	3.83	0.09	13	0.26	3.91	0.12	12	3.88	0.17	9	0.77	3.70	0.16	13	3.56	0.09	8	3.93						
LH1	2.02	0.07	19	2.01	0.06	26	0.50	2.04	0.05	13	0.99	2.17	0.11	12	2.11	0.13	9	2.84	2.04	0.08	12	2.12	0.06	8	-3.77						
LTI1	0.87	0.05	19	0.85	0.05	26	2.35	0.86	0.06	13	1.18	0.95	0.07	12	0.92	0.08	9	3.26	0.88	0.06	12	0.91	0.06	8	-3.30						
H11	1.50	0.05	19	1.48	0.05	26	1.35	1.42	0.05	13	-2.74	1.47	0.04	12	1.42	0.09	9	3.52	1.35	0.09	13	1.35	0.08	8	0.00						
LA1	1.42	0.05	19	1.41	0.06	26	0.71	1.40	0.05	13	2.94	1.45	0.04	12	1.41	0.06	9	2.84	1.40	0.04	13	1.43	0.05	8	-2.10						
WA1	0.85	0.04	19	0.84	0.03	26	1.19	0.81	0.03	13	3.85	0.85	0.03	12	0.83	0.05	9	2.41	0.79	0.04	13	0.77	0.04	8	2.60						
BLP4	2.04	0.07	19	2.04	0.07	26	0.00	1.96	0.03	13	-1.51	2.01	0.05	12	1.98	0.07	9	1.52	1.94	0.06	13	1.98	0.05	8	-2.02						
BLM1	1.78	0.04	19	1.78	0.05	26	0.00	1.77	0.05	13	0.57	1.71	0.05	12	1.71	0.08	9	0.00	1.68	0.05	13	1.67	0.03	8	0.60						
BLM2	1.57	0.05	19	1.54	0.05	26	1.95	1.55	0.04	13	0.65	1.46	0.04	12	1.46	0.03	9	0.00	1.49	0.05	13	1.46	0.04	8	2.05						
LM3	0.87	0.04	19	0.87	0.03	26	0.00	0.86	0.03	13	2.38	0.85	0.04	12	0.85	0.04	9	0.00	0.78	0.05	13	0.82	0.03	8	-4.88						
LMD	11.49	0.24	19	11.49	0.23	26	0.00	11.37	0.23	13	0.62	11.93	0.23	12	11.78	0.25	9	1.27	11.33	0.38	13	11.28	0.19	8	0.44						
i1_M3	9.73	0.17	19	9.71	0.17	26	0.21	9.73	0.13	13	1.14	9.80	0.12	12	9.66	0.31	9	1.45	9.58	0.31	13	9.63	0.20	8	-0.52						
p2_m3	6.71	0.15	19	6.66	0.15	26	0.75	6.60	0.13	13	0.92	6.69	0.11	12	6.62	0.26	9	1.06	6.49	0.23	13	6.49	0.09	8	0.00						
m1_m3	4.69	0.11	19	4.66	0.11	26	0.64	4.59	0.09	13	0.00	4.65	0.06	12	4.58	0.15	9	1.53	4.56	0.16	13	4.59	0.10	8	-0.65						
PMDH	2.74	0.11	19	2.75	0.11	26	-0.36	2.71	0.12	13	1.12	2.59	0.28	12	2.61	0.34	9	-0.77	2.62	0.09	13	2.60	0.08	8	0.77						
WBPC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
HPC	4.84	0.12	19	4.85	0.11	26	-0.21	4.84	0.08	13	4.09	5.10	0.13	12	5.06	0.24	9	0.79	4.69	0.14	13	4.64	0.12	8	1.08						
L11	4.82	0.19	19	4.79	0.13	26	0.63	4.74	0.16	11	1.50	4.82	0.12	12	4.59	0.20	9	5.01	4.64	0.19	13	4.78	0.15	7	-2.93						
Lp3	1.50	0.08	19	1.50	0.07	26	0.00	1.43	0.06	13	2.14	1.55	0.08	12	1.50	0.13	9	3.33	1.45	0.08	13	1.46	0.05	8	-0.68						
Lp4	1.38	0.04	19	1.37	0.05	26	0.73	1.34	0.05	13	0.75	1.37	0.05	12	1.38	0.08	9	-0.72	1.34	0.04	13	1.33	0.06	8	0.75						
HMD_m2	1.43	0.08	19	1.43	0.08	26	0.00	1.47	0.05	13	2.80	1.59	0.06	12	1.56	0.09	9	1.92	1.40	0.07	13	1.36	0.07	8	2.94						
HC	2.60	0.10	19	2.61	0.08	26	-0.38	2.60	0.08	13	1.56	2.77	0.14	12	2.68	0.12	9	3.36	2.55	0.14	13	2.50	0.09	8	2.00						
Wp3	0.79	0.03	19	0.77	0.03	26	2.60	0.71	0.04	13	1.43	0.77	0.04	12	0.76	0.04	9	1.32	0.72	0.03	13	0.70	0.05	8	2.86						
						Summarized Levenson index:	19.98							Summarized Levenson index:	37.77							Summarized Levenson index:	37.57							Summarized Levenson index:	12.32

Table 6. Skull measurements and Levenson index of all samples of *Sorex araneus* (significant sex differences are marked in bold). For abbreviations see Table 2

Sample	SEE-high							CE-low							CE-high						
	females			males			IL	females			males			IL	females			males			IL
	Mean	SD	N	Mean	SD	N		Mean	SD	N	Mean	SD	N		Mean	SD	N	Mean	SD	N	
SCW	9.36	0.23	31	9.32	0.26	23	0.43	9.37	0.19	8	9.36	0.24	8	0.11	9.56	0.17	8	9.54	0.23	8	0.21
OW	2.72	0.09	44	2.69	0.10	30	1.12	2.69	0.09	8	2.67	0.07	8	0.75	2.73	0.09	8	2.72	0.10	8	0.37
IO	3.87	0.13	44	3.84	0.13	30	0.78	3.81	0.13	8	3.74	0.11	8	1.87	3.90	0.05	8	3.91	0.06	8	-0.26
CBL	18.92	0.36	38	18.83	0.38	29	0.48	18.85	0.32	8	18.99	0.16	8	-0.74	19.59	0.22	8	19.53	0.39	8	0.31
BL	16.43	0.33	42	16.41	0.37	30	0.12	16.36	0.30	8	16.68	0.16	8	-1.92	17.06	0.22	8	17.03	0.44	8	0.18
I1_M3	8.45	0.20	44	8.41	0.24	30	0.48	8.54	0.15	8	8.70	0.13	8	-1.84	8.92	0.13	8	8.86	0.22	8	0.68
PL	8.34	0.24	44	8.28	0.26	30	0.72	8.08	0.10	8	8.19	0.12	8	-1.34	8.43	0.13	8	8.32	0.16	8	1.32
RL	7.96	0.22	44	7.92	0.26	30	0.51	7.67	0.14	8	7.76	0.09	8	-1.16	8.00	0.12	8	7.96	0.15	8	0.50
P4_M3	4.84	0.10	44	4.80	0.13	30	0.83	4.74	0.10	8	4.77	0.06	8	-0.63	4.79	0.12	8	4.79	0.10	8	0.00
M1_M3	3.33	0.07	44	3.30	0.10	30	0.91	3.23	0.08	8	3.25	0.06	8	-0.62	3.28	0.09	8	3.29	0.07	8	-0.30
A1_A3-5	2.95	0.10	44	2.96	0.11	30	-0.34	2.95	0.07	8	3.03	0.10	8	-2.64	3.18	0.06	8	3.13	0.14	8	1.60
PGW	5.66	0.18	43	5.64	0.22	28	0.35	5.62	0.11	8	5.66	0.15	8	-0.71	5.65	0.15	8	5.52	0.15	8	2.36
WP4_P4	1.31	0.10	44	1.28	0.07	30	2.34	1.33	0.06	8	1.29	0.09	8	3.10	1.27	0.07	8	1.28	0.06	8	-0.78
WM3_M3	2.17	0.11	43	2.16	0.09	30	0.46	2.21	0.06	8	2.21	0.04	8	0.00	2.12	0.05	8	2.17	0.06	8	-2.30
WPP	2.57	0.13	42	2.58	0.14	28	-0.39	2.58	0.06	8	2.55	0.08	8	1.18	2.52	0.09	8	2.52	0.13	8	0.00
SCH	5.19	0.23	32	5.19	0.22	25	0.00	5.29	0.18	8	5.23	0.23	8	1.15	5.43	0.17	8	5.41	0.15	8	0.37
PRH	3.51	0.13	44	3.50	0.12	29	0.29	3.51	0.07	8	3.53	0.11	8	-0.57	3.58	0.07	8	3.61	0.06	8	-0.83
LI1	1.84	0.08	40	1.87	0.09	24	-1.60	1.73	0.06	8	1.82	0.06	8	-4.95	1.81	0.08	8	1.83	0.05	8	-1.09
LTI1	0.99	0.06	44	1.00	0.07	29	-1.00	0.94	0.06	8	0.99	0.05	8	-5.05	1.01	0.07	8	0.99	0.05	8	2.02
HI1	1.26	0.04	44	1.25	0.05	27	0.80	1.20	0.05	8	1.21	0.03	8	-0.83	1.24	0.05	8	1.23	0.04	8	0.81
LA1	0.90	0.05	44	0.89	0.05	30	1.12	0.89	0.03	8	0.91	0.03	8	-2.20	0.96	0.06	8	0.95	0.03	8	1.05
WA1	0.80	0.05	44	0.78	0.06	30	2.56	0.83	0.03	8	0.85	0.03	8	-2.35	0.84	0.02	8	0.81	0.03	8	3.70
BLP4	1.63	0.05	44	1.62	0.05	30	0.62	1.55	0.04	8	1.58	0.04	8	-1.90	1.58	0.05	8	1.55	0.04	8	1.94
BLM1	1.48	0.04	44	1.48	0.05	30	0.00	1.44	0.02	8	1.45	0.03	8	-0.69	1.48	0.05	8	1.50	0.03	8	-1.33
BLM2	1.28	0.04	44	1.28	0.04	30	0.00	1.26	0.03	8	1.27	0.04	8	-0.79	1.27	0.04	8	1.31	0.03	8	-3.05
LM3	0.72	0.03	44	0.71	0.04	30	1.41	0.72	0.02	8	0.72	0.03	8	0.00	0.72	0.02	8	0.71	0.02	8	1.41
LMD	9.89	0.20	44	9.87	0.20	30	0.20	9.95	0.29	8	9.98	0.13	8	-0.30	10.20	0.18	8	10.28	0.26	8	-0.78
i1_M3	8.00	0.15	43	7.99	0.17	30	0.13	7.94	0.12	8	8.08	0.07	8	-1.73	8.26	0.13	8	8.23	0.18	8	0.36
p3_m3	5.57	0.14	44	5.57	0.14	30	0.00	5.45	0.08	8	5.52	0.07	8	-1.27	5.59	0.11	8	5.62	0.11	8	-0.53
m1_m3	3.89	0.08	44	3.89	0.08	30	0.00	3.84	0.05	8	3.84	0.06	8	0.00	3.86	0.07	8	3.89	0.07	8	-0.77
PMDH	2.28	0.09	7	2.22	0.04	4	2.70	2.26	0.04	8	2.25	0.11	8	0.44	2.26	0.11	8	2.15	0.08	8	5.12
WBPC	2.08	0.10	7	2.15	0.12	4	-3.26	2.15	0.09	8	2.18	0.09	8	-1.38	2.23	0.09	8	2.23	0.10	8	0.00
HPC	4.68	0.15	44	4.69	0.12	30	-0.21	4.73	0.10	8	4.61	0.12	8	2.60	4.79	0.12	8	4.70	0.14	8	1.91
Li1	3.78	0.14	43	3.74	0.15	30	1.07	3.74	0.18	8	3.84	0.04	8	-2.60	3.94	0.09	8	3.86	0.11	8	2.07
Lp3	1.10	0.06	44	1.11	0.07	30	-0.90	1.09	0.06	8	1.11	0.05	8	-1.80	1.15	0.07	8	1.14	0.05	8	0.88
Lp4	1.25	0.06	44	1.24	0.05	30	0.81	1.23	0.04	8	1.27	0.04	8	-3.15	1.27	0.05	8	1.29	0.06	8	-1.55
HMD_m2	1.31	0.06	44	1.30	0.09	30	0.77	1.38	0.05	8	1.38	0.06	8	0.00	1.29	0.04	8	1.32	0.06	8	-2.27
HC	1.89	0.09	44	1.92	0.11	30	-1.56	1.88	0.10	8	1.85	0.09	8	1.62	1.82	0.10	8	1.90	0.10	8	-4.21
Wp3	0.63	0.05	44	0.62	0.04	30	1.61	0.69	0.04	8	0.70	0.03	8	-1.43	0.68	0.02	8	0.66	0.02	8	3.03
	Summarized Levenson index:						14.36	Summarized Levenson index:						-31.74	Summarized Levenson index:						12.12

HPC, and Li1. Obviously, the sexual selection in soricids affects most frequently the massiveness of incisors, first antemolar and procesus coronoideus as well as the height of the braincase. The most sexually variable characters differ among the species. Variables with the greatest sex differences (the largest Levenson SDI) are WP4_P4, SCH, LI1, HI1 and

HMD_m2 in *C. suaveolens*, LTI1 and LM3 in *C. leucodon*, PMDH in *S. araneus* and Li1 in *N. fodiens*.

As the sizes of the body and skull in *C. suaveolens* and *C. leucodon* are always correlated to a certain extent (MICHALAK 1989), the general skull size is indicative of the overall body size. Most of the characters examined here, associated with the

Table 7. Skull measurements and Levenson index of all samples of *Sorex minutus* (significant sex differences are marked in bold). For abbreviations see Table 2

Sample	SEE-high						IL
	females			males			
	Mean	SD	N	Mean	SD	N	
SCW	7.59	0.19	23	7.71	0.18	20	-1.56
OW	2.16	0.06	26	2.15	0.06	21	0.47
IO	3.22	0.21	25	3.12	0.09	21	3.21
CBL	15.77	0.31	22	15.81	0.36	19	-0.25
BL	13.62	0.32	23	13.66	0.25	21	-0.29
I1_M3	6.71	0.14	26	6.68	0.14	21	0.45
PL	6.77	0.23	26	6.75	0.16	21	0.30
RL	6.41	0.20	26	6.40	0.14	21	0.16
P4_M3	4.00	0.08	26	3.98	0.07	21	0.50
M1_M3	2.84	0.06	26	2.84	0.05	21	0.00
A1_A3-5	2.29	0.07	26	2.30	0.07	21	-0.43
PGW	4.49	0.14	25	4.46	0.22	21	0.67
WP4_P4	0.88	0.06	26	0.88	0.07	21	0.00
WM3_M3	1.73	0.08	26	1.73	0.06	19	0.00
WPP	2.27	0.06	25	2.26	0.11	21	0.44
SCH	4.25	0.19	22	4.18	0.16	18	1.67
PRH	2.77	0.10	25	2.77	0.10	21	0.00
LI1	1.29	0.06	25	1.32	0.06	20	-2.27
LT11	0.70	0.05	25	0.73	0.06	21	-4.11
HI1	0.91	0.04	25	0.91	0.03	19	0.00
LA1	0.64	0.02	26	0.65	0.03	21	-1.54
WA1	0.60	0.04	26	0.60	0.03	21	0.00
BLP4	1.33	0.03	26	1.32	0.05	21	0.76
BLM1	1.22	0.04	26	1.23	0.04	21	-0.81
BLM2	1.09	0.03	26	1.09	0.04	21	0.00
LM3	0.66	0.02	26	0.66	0.02	21	0.00
LMD	7.98	0.18	25	7.99	0.17	21	-0.13
i1_M3	6.30	0.14	26	6.31	0.10	21	-0.16
p3_m3	4.51	0.10	26	4.51	0.07	21	0.00
m1_m3	3.25	0.06	26	3.22	0.07	21	0.93
PMDH	1.58	0.07	11	1.56	0.04	10	1.28
WBPC	1.56	0.07	11	1.59	0.09	10	-1.89
HPC	3.28	0.11	25	3.30	0.08	21	-0.61
Li1	2.84	0.08	26	2.85	0.08	21	-0.35
Lp3	0.81	0.05	26	0.81	0.05	21	0.00
Lp4	0.98	0.04	26	0.98	0.03	21	0.00
HMD_m2	0.82	0.04	26	0.80	0.04	21	2.50
HC	1.59	0.07	24	1.58	0.07	20	0.63
Wp3	0.46	0.04	25	0.46	0.03	21	0.00
Summarized Levenson index:							-0.43

cranium and mandibula massiveness, actually show significant sex differences in the SEE sample of *C. suaveolens* (Table 2). Body size is usually related to environmental factors, such as climate and habitat productivity. Since a number of authors consider that bite force and prey size as positively correlated with the body size in shrews (CARRAWAY, VERTS 1994,

CHURCHFIELD 1991, 1994, CHURCHFIELD, SHEFTEL 1994, DICKMAN 1988), the sexual differences in the overall body size of *C. suaveolens*, as reported in this study, may probably be ascribed both to the sensitivity to the environment and to the feeding habits. Furthermore, some tooth characters show larger values, especially regarding I1, in the males of both white-toothed species. The upper incisor contributes to the prey gripping, but could also be related to some aspects of the intraspecific behaviour, namely the agonistic interactions between the male white-toothed shrews during the breeding season – the larger upper incisors are probably better weapons or at least a serious threat against conspecific intruders. Prey gripping and intraspecific behaviour could also be related to the size of the lower incisor, which is significantly larger in females of *N. fodiens* from CE-low sample (Table 5).

The variation in size of the late-ossifying mandibular region (the ramus of the mandible) in *Sorex* species is closely associated with both the bite force and muscle activity (YOUNG, BADIYAEV 2010, YOUNG *et al.* 2007). The main muscles responsible for the prey crushing and grinding in soricids are musculus temporalis and m. masseter, which attach to this part of the lower jaw. YOUNG, BADIYAEV (2010) state that epigenetic regulation of bone growth in soricid shrews may enable both development of local adaptations and evolutionary divergence in mandibular morphology. That divergence could lead to species diversity, as well as to diversity within species expressed by SSD or geographic variability. If sexes differ in their foraging strategy, this could reflect the size and shape of their mandibles. According to YOUNG, BADIYAEV (2010), the morphology of late-maturing mandible components are more affected by functional requirements (local functional demands of foraging), compared to the early-ossifying parts. Consequently, the measurements as HPC, WBPC and PMDH, should be more influenced by the functional demands from the environment than the measurement as HMD_m2, where the measured part is located in the early maturing region of the mandible. Therefore, the sexual difference in the foraging strategy is a possible explanation for the observed differences in the ramus of the mandible in *Crocidura* spp. (larger values in males), *S. araneus* (larger HPC and PMDH in females, larger WBPC in males), and *N. fodiens* (larger HPC in females).

Geographic variation of sexual size differences and comparison with other investigations

Most of the published data on SSD in red-toothed shrews are in agreement with the results of

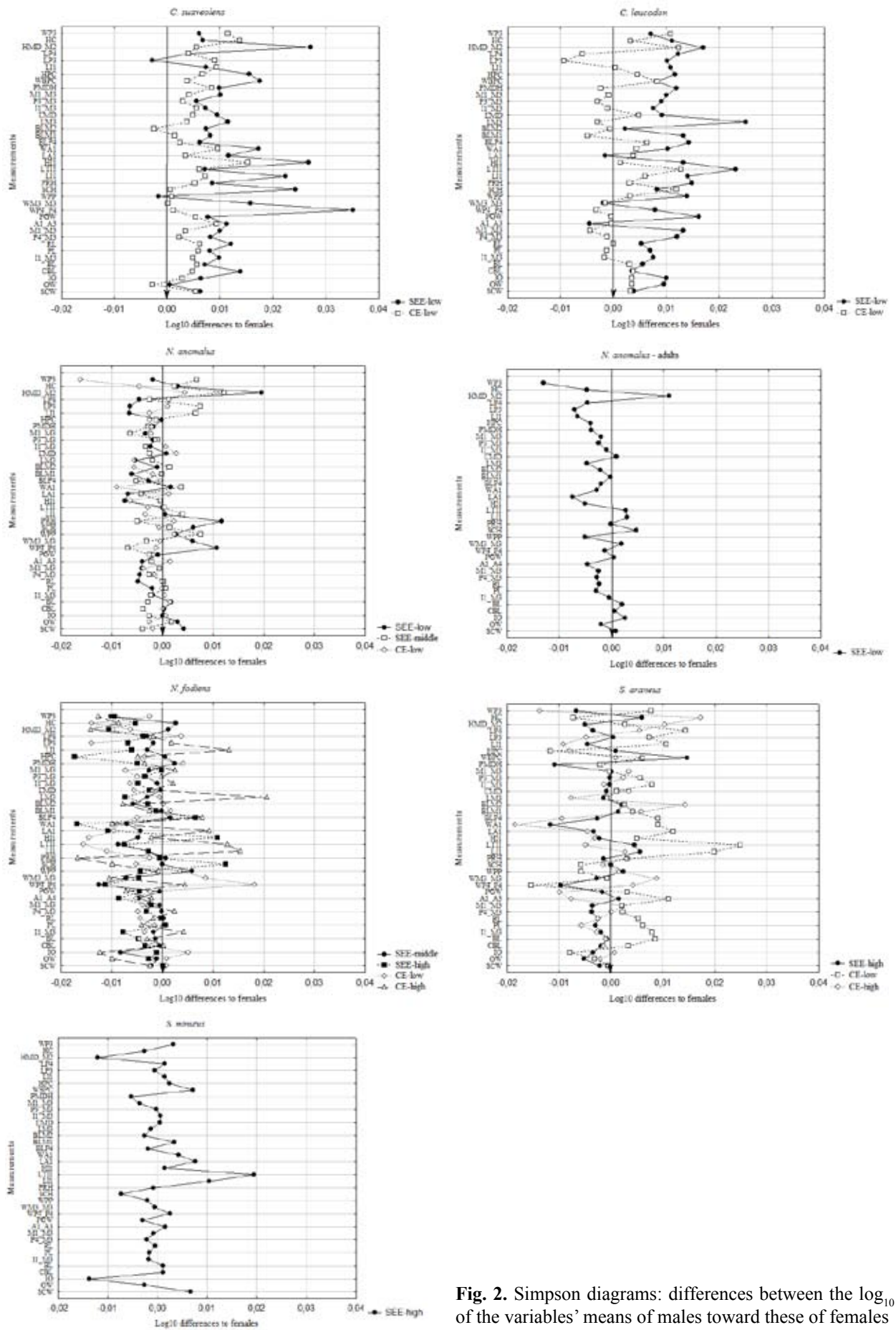


Fig. 2. Simpson diagrams: differences between the \log_{10} of the variables' means of males toward these of females

this study, in showing absence of SSD or low degree of mainly female-biased sexual differences. RYCHLIK *et al.* (2006) has found that females are heavier than males in *N. fodiens* but has proved no dimorphism in the other size variables studied. Most of the authors report absence of SSD in the studied *Sorex* and *Neomys* species (BALČIAUSKAS 2004, BERNAL 2010, HOMOLKA 1980, MISHTA 2007, PANKAKOSKI 1989, RYCHLIK *et al.* 2006, SEARLE, THORPE 1987), or extremely low degree of SSD (OKULOVA *et al.* 2007). However, some studies found male-biased SSD in terms of size and weight in the same species of the Soricinae (BALÁŽ, AMBROS 2006, NISTREANU 2000). SPITZENBERGER (2001) has found sexual differences only in several body and skull measurements in the samples of adults in the Soricinae species from Austria and no SSD in the two species of *Crociodura*. In this study, the variables in subadults do not differ between sexes with the exception of mandibula length in *N. fodiens*. NISTREANU (2000) demonstrated a male-biased sexual dimorphism in some body and skull measurements in *S. araneus*, *S. minutus*, *Neomys fodiens*, *N. anomalus* and *C. leucodon* from Romania but found no sexual differences in *C. suaveolens*. Conversely, according to our results, *C. suaveolens* show the greatest sexual differences in size amongst the six species of shrews in both sampling regions (SEE and CE). The differences between the results of this study and other investigations are probably due to the spatial and temporal variation in SSD, the degree and direction of which is known to differ among the populations of the same species as well as temporally (see review in LOVICH, GIBBONS 1992, TRUBENOVÁ *et al.* 2010). MOTOKAWA *et al.* (2003) have found this phenomenon in another shrew species, *Crociodura shantungensis*. Further possible reasons for the contradictory results are some methodological differences of the studies: the trapping period, different division of age groups, number and choice of variables to be investigated, etc.

Similarly, the different intensity of SSD within SEE and CE samples in this study (especially in *Crociodura* spp.) could result from the geographic and (or) temporal variability due to different climatic and ecological conditions. The sex differences in both Crocidurinae species are better pronounced in the SEE samples in comparison with the CE samples. This tendency is hard to be explained since there are not sufficient data about all the parameters of the environment and resources in the sample localities.

Probably, the density of Crocidurinae populations is higher in SEE as the environment there is closer to the optimal conditions for those species, compared with that in CE. The higher density could lead to a higher level of intraspecific aggressiveness and thus, to a higher degree of sexual differences in size. A possible explanation for the stronger expression of the sexual differences in size in the SEE samples of *Crociodura* spp. may also be the greater spatial homogeneity of these samples in comparison with those from CE.

Apparently, the patterns of sexual craniometric variability in shrews differ among the species and, in some cases, among the populations of a single species. They are influenced by a number of abiotic and biotic factors. The various skull and teeth structures show different sensitivity to the environment and the intraspecific interactions. Future investigations, by using standardized methodology, on a greater number of cranium and tooth measurements from many populations and species of soricids would give us a better view on the sexual variability in size of that taxon.

Conclusions

Different patterns regarding sexual differences in size are recorded in the two subfamilies of shrews, Crocidurinae and Soricinae. The two white-toothed shrew species show clear male-biased sexual size differences, which are better expressed in *C. suaveolens* compared to *C. leucodon* as well as in Southeastern Europe compared to Central Europe. Conversely, the red-toothed shrews do not manifest distinct sexual differences in size. In *N. fodiens*, *N. anomalus*, *S. araneus* and *S. minutus*, some of the measurements were larger in males, others were larger in females, while the rest did not differ between the sexes.

Because of the great overlap of the measurement ranges, it is more correct to speak of size differences between sexes rather than of a distinct sexual size dimorphism.

Acknowledgements: I would like to express my sincere gratitude to Dr. Vasil Popov for his constructive advices and notes on the manuscript, as well as for the cranium material from Bulgaria. The access to the material from Central Europe was possible thanks to the funding from Synthesys programme (AT-TAF-2826 and HU-TAF-2845). I also thank an anonymous referee for the useful comments.

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Received: 14.04.2014
Accepted: 04.09.2014