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Sexual dimorphism of craniological characters in Eurasian badgers, *Meles* spp. (Carnivora, Mustelidae)

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Abstract

An analysis of 30 craniological characters of Eurasian badgers (*Meles* spp.) revealed different levels of sexual size dimorphism (SSD) and geographic variation in the three different species. SSD is displayed mostly in the general size of the skull (condylobasal length, zygomatic width, width of rostrum, and cranial height) and mandible (height of the vertical mandibular ramus, total length of the mandible, and length between the angular process and infradentale), and in some dental characters (length of the upper molar M^1). The most stable size dimorphism is manifested in the size of the canines, which is pronounced in all studied samples. SSD is not apparent in the length of the auditory bulla, the postorbital width, the minimum palatal width, the length of the lower molar M_2, and the talonid length of the lower carnassial tooth M_1.

In both the European badgers, *Meles meles*, and the Asian badgers, *Meles leucurus*, two geographic forms that differ in the degree of SSD have been found. The most pronounced SSD of cranial characters is found in the Transcaucasian form of *Meles meles* and the Far-Eastern form of *Meles leucurus*. In the large European form of *Meles meles*, SSD is less pronounced in both absolute and relative criteria than in the smaller Transcaucasian form. An analogous situation is observed in the larger Siberian and smaller Far-Eastern forms of *Meles leucurus*. In the Japanese badgers, *Meles anakuma*, a downsizing of the skull is accompanied by a decrease in SSD (except in canine size) in comparison to the continental species. The significant differences in the manifestation of SSD in the Eurasian badgers support an earlier hypothesis (Abramov, 2001. Proc. Zool. Inst. Russ. Acad. Sci. 288, 221–233; Abramov, 2002. Russ. J. Theriol. 1 (1), 57–60; Abramov, 2003. Small Carnivore Conserv. 29, 5–7) that *Meles meles*, *Meles leucurus*, and *Meles anakuma* are separate species. The differences in the level of SSD among and within these three species of badgers may be attributed not to differences in the diet or social structure, but to the history of speciation events and formation of intraspecific distribution ranges.

Keywords: *Meles meles*; *Meles leucurus*; *Meles anakuma*; Badgers; Sexual size dimorphism; Skull

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1. Introduction

The Eurasian badgers (*Meles* spp.) have a wide Palaearctic distribution from the British Islands and Iberian Peninsula in the west to the Japanese Islands in the east, and from Scandinavia and Western Siberia in the north to Palestine, Iran, and South China in the south. The geographic variation of craniological and external characters in badgers is significant, but opinions concerning the species composition of this genus vary. Depending on the authors, one to three species are accepted. Recently, several studies have shown that European and Asian badgers represent separate species (Baryshnikov and Potapova 1990; Abramov 2001, 2002; Baryshnikov et al. 2003). Some additional data also suggest that Japanese badgers are distinctly different from other Asian badgers (Abramov 2001, 2002; Kurose et al. 2001; Abramov and Medvedev 2003). Overall, the differences among the European, Asian and Japanese badgers are clear and unmistakable in several characters, such as the shape and proportions of their first upper molar, the relative length of the root and the size of their second lower premolar, and the frequency of the loss of their first premolars (Baryshnikov and Potapova 1990; Baryshnikov et al. 2003); the size and proportions of their skull and the shape of their auditory bulla (Abramov 2001; Abramov and Puzachenko in press); the colouration of their head "mask" pattern (Abramov 2003); and the morphology of their baculum (Abramov 2002).

In this paper, the taxonomy of *Meles* follows Abramov (2001, 2002, 2003): The European badger *Meles meles* (Linnaeus, 1758), the Asian badger *Meles leucurus* (Hodgson, 1847), and the Japanese badger *Meles anakuma* Temminck, 1844 (Fig. 1). The European badger *M. meles* is widespread throughout Europe west of the Volga River (Russia), the Caucasus, Iran, Iraq, Israel, the southern mountains of Middle Asia (Kopet Dagh Mountains, the South and West Tien Shan Mountains), Crete, Rhodes, Ireland, and the British Isle. The Asian badger *M. leucurus* is distributed east of the Volga River (Russia) throughout Siberia, Kazakhstan, and Middle Asia to China and Korea; and south to Tibet. The third species, the Japanese badger *M. anakuma*, inhabits at least the larger Japanese Islands of Honshu, Kyushu, and Shikoku, but is absent from Hokkaido.

Intraspecific variation in the genus *Meles* is currently under revision. Studies of phenotypical and size variation of the teeth of Eurasian badgers (Baryshnikov et al. 2003) and of craniological characters (Abramov and Puzachenko in press) allow the recognition of two morphologically distinct forms (probably having subspecies rank) within the European species: The European badger (i.e., the European badger proper) inhabiting most of Europe and the Transcaucasian

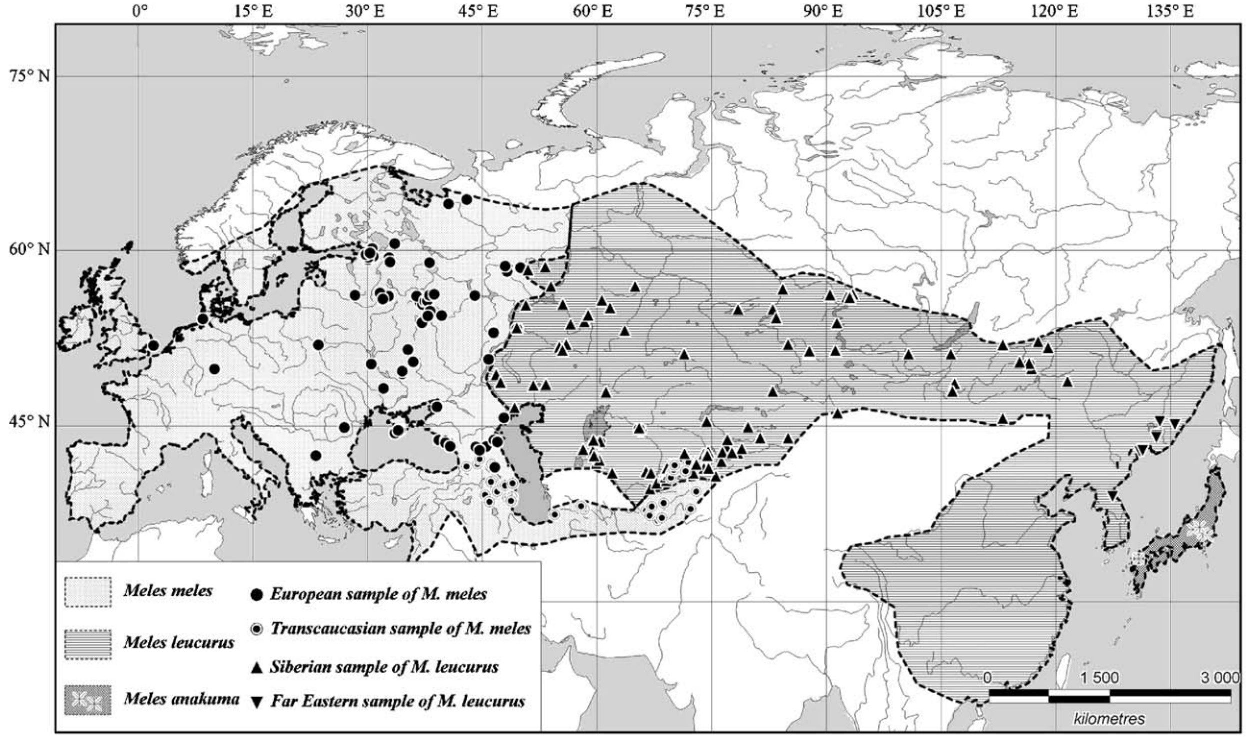

Fig. 1. Distribution ranges of the Eurasian badgers (*Meles meles, Meles leucurus,* and *Meles anakuma*) and the locations from where the materials used in this study were collected.

badger, which occurs from Transcaucasia to the Pamir-Alai Mountains (i.e., the Caucasus-Pamir badger). The Asian species can also be divided into two forms: The widely distributed Siberian badger (i.e., the Asian badger proper) and the Far-Eastern badger inhabiting the Russian Far East and Korea (Abramov 2001, 2003; Baryshnikov et al. 2003). Because the taxonomic revision of the genus *Meles* is not yet completed, we have not assigned subspecific names to these forms.

To further clarify the taxonomy of badgers, an examination of any variation of sexual size dimorphism (SSD) in Eurasian badgers appeared promising. SSD in animals is presumably a result of genes that control basic aspects of growth and their sex-biased expression during ontogeny, although the mechanisms that enable the genetically identical sexes to have divergent growth are not well understood (Haqq and Donahoe 1998). According to numerous recent investigations of both mammals and birds, SSD provides an opportunity for more or less rapid modifications in response to changes in environmental factors, such as population density, seasonality, climate change, diet, etc. (Badyaev 2002). Geographical (Sikes and Kennedy 1993), temporal (LeBlanc et al. 2001) and socially dependent (Lindenfors and Tullberg 2002) variability in SSD have also been detected.

Most previous studies of sexual dimorphism of cranial characters in badgers have examined variation only within a single area, such as Norway (Hysing-Dahl 1954; Wiig 1986), Switzerland (Lüps and Roper 1988), Slovakia (Hell and Paule 1989), or Great Britain and Ireland (Lynch et al. 1997; Johnson and Macdonald 2001). Hysing-Dahl (1954) studied the variation of 51 craniological characters of 49 badgers from Norway. According to his data, the skulls of the males (except the teeth) are characterized as being more heavily built than those of the females and as having a relatively greater zygomatic width and wider rostrum. Subsequently, Wiig (1986) re-examined sexual dimorphism in the skull of badgers from Norway using a combination of multiple group principal component and discriminant analyses and obtained the same results. Hell and Paule (1989) performed a craniometric investigation of 210 skulls (only 47 of them were sex determined) of the European badger from the Slovak Carpathians. According to their results, the skulls of males are slightly larger than those of females, but the size and shape of the skull show only a very slight sexual dimorphism, so that it is not possible to determine the sex of individuals on the basis of skull characters. Studies of dental characters show that significant differences between males and females are observed in canine sizes only (Lüps and Roper 1988; Johnson and Macdonald 2001).

All previously published studies have focused on the populations of the European badger only. It should be noted that in the majority of these studies (Wiig 1986; Hell and Paule 1989; Lynch et al. 1997), their own data were combined with those of Hysing-Dahl (1954) on badgers from Norway. However, as has been shown in our previous study (Baryshnikov et al. 2003), badgers inhabiting Norway are morphologically heterogeneous and belong to two different subspecies, namely *M. m. meles* and *M. m. milleri*. These subspecies differ substantially, in particular, in the sizes of their teeth, and it would be biologically more appropriate to study the sexual dimorphism of these forms separately. Sexual dimorphism of the Asian and Japanese badgers has not been studied before.

In this paper, we compare the variation of SSD among different badger populations across Eurasia to clarify the taxonomy of badgers, and we examine the null hypotheses about the absence of distinctions between the sexes in the three species of badgers and in their geographical populations.

2. Material and methods

This study is based on 400 skulls of badgers. The age classes were defined by scoring morphological features of skull structure, such as the development of crests, the obliteration of sutures, tooth wear, etc. Only adults were used in the analysis in order to minimize variations due to age differences. The skulls were classified in geographic samples (Fig. 1): (1) European sample of *Meles meles* (Eastern Europe and European part of Russia; $n = 131$); (2) Transcaucasian sample of *Meles meles* (Transcaucasia, South Turkmenistan, and Pamir; $n = 77$); (3) Siberian sample of *Meles leucurus* (Siberia, Kazakhstan, and Central Asia; $n = 155$); (4) Far-Eastern sample of *Meles leucurus* (Russian Far East and Korea, $n = 22$); (5) *Meles anakuma* (Japan: Honshu and Kyushu, $n = 15$). These samples are representatives of the above-mentioned morphologically distinct forms. We did not determine the subspecific affiliation of these samples because the taxonomic revision of the *Meles* spp. has not yet been completed.

We examined the collections of the Zoological Institute of the Russian Academy of Sciences, ZIN, (Saint-Petersburg, Russia), the Institute of Animal Systematics and Ecology of the Siberian Branch of the Russian Academy of Sciences (Novosibirsk, Russia), the Zoological Museum of Moscow State University (Moscow, Russia), the Russian Research Institute of Game Management and Fur Farming (Kirov, Russia), the Craniological Laboratory of the Central-Forest Nature Reserve (Nelidovo, Russia), the Institute of Zoology of the Uzbekistan Academy of Sciences (Tashkent, Uzbekistan), the Institute of Zoology and Soil (Bishkek, Kirghizstan), the Museum of the Faculty of Agriculture of Hokkaido University (Sapporo, Japan), the National

Science Museum, NSM, (Tokyo, Japan), and the Kitakyushu Museum and Institute of Natural History (Kitakyushu, Japan).

Thirty measurements were taken on each skull using sliding callipers to the nearest 0.1 mm. The scheme of cranial measurements used is shown in Fig. 2, and the measured skull characters are listed in Table 1. Some specimens ($n = 38$) had a few missing values because of skull damage. These values were estimated in each case by stepwise multiple regression of the remaining variables available according to Wiig (1985), Reig and Ruprecht (1989), and Reig (1997).

As the first step, both non-parametric Kruskal–Wallis ANOVA and median test were used separately to identify the variables with sexual dimorphism (Sokal and Rohlf 1981) in all the taxonomic and geographical samples. Subsequently, the stepwise discriminant analysis based on these variables was used to classify 128 individuals with unknown sex.

For the assessment of sexual dimorphism, standard methods of univariate and multivariate analyses were used, but preference was given to non-parametric methods. The testing of variables has shown that, as a rule, the normality of distributions was not observed, but the absolute majority among distributions was not like any canonical distribution, and some of the distributions were multimodal. Therefore, we had to reject parametric multivariate "dimension-reducing" methods and use their non-parametric analogue, i.e., non-metric multidimensional scaling (MDS) for a generalized description of sexual dimorphism (Shepard 1962; Davison and Jones 1983). We have chosen this method because MDS is much more flexible with regard to the types of input data, and is more appropriate for non-linear cases, than the common linear parametric multivariate techniques (James and McCulloch 1990). Initial configuration was calculated according to the classical metric algorithm. Metric solution was used as a starting configuration for the non-metric algorithm.

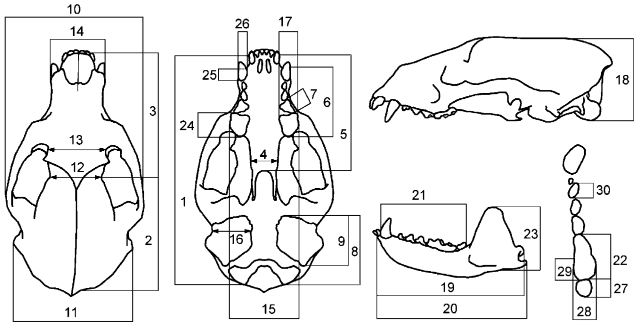

Fig. 2. Measurements taken of the badger skulls: 1: condylobasal length, 2: neurocranium length, 3: viscerocranium length, 4: minimum palatal width, 5: palatal length, 6: maxillary tooth-row length, 7: length of upper carnassial tooth Pm^4, 8: greatest length between oral border of the auditory bulla and aboral border of the occipital condyle, 9: length of the auditory bulla, 10: zygomatic width, 11: mastoid width of skull, 12: postorbital width, 13: interorbital width, 14: width of rostrum, 15: greatest palatal width, 16: width of the auditory bulla, 17: width of upper molar M^1, 18: cranial height, 19: total length of the mandible, 20: length between the angular process and infradentale, 21: mandibular tooth-row length, 22: length of lower carnassial tooth M_1, 23: height of the vertical mandibular ramus, 24: length of upper molar M^1, 25: length of upper canine, 26: width of upper canine, 27: length of lower molar M_2, 28: width of lower molar M_2, 29: talonid length of lower carnassial tooth M_1, 30: length of lower premolar Pm_2.

Variables were standardized to exclude any influence of the "scale" of the different measurements on the results while preserving properties of their distribution. Transformation was used according to the following equation :

$$\underset{i}{\overset{\frown}{x}} = \frac{x_i - x_{\min}}{x_{\max} - x_{\min}},$$

in which $\underset{i}{\overset{\frown}{x}}$ is standardized measurement, x_i, $x_{\min}$, $x_{\max}$ are observed, minimum and maximum values of the ith variable, respectively. The square dissimilarity matrix contained the Euclidean distances matrix, and the matrix of Kendall's τ-b rank-order coefficients among all the pairs of specimens were calculated. The elements of Kendall's matrix (r_{ij}) were transformed in dissimilarity according to the equation $D_{ij} = \sqrt{1 - r_{ij}}$. Those matrices were used in the MDS procedure. Euclidean metric as simple geometric distance in multidimensional space describes the variability of the skull sizes. Kendall's coefficient is the difference between the probability that the observed data are in the same order for the two specimens versus the probability that they are in a different order. Thus, rank Kendall's coefficient generally describes the variability of the "proportions" or "shape".

In this study, the MDS-axes for a model based on Euclidean distances matrix are marked as $D1$, $D2$,... and MDS-axes based on Kendall's rank correlation matrix are marked as $K1$, $K2$,... In the first case, the "best-minimum" dimension for MDS models will be marked as d_D, and in the second one as d_K.

The "best-minimum" dimension in a MDS model was estimated based on "stress formula 1" (so-called Kruskal Stress). We used a modified "scree test" [analogue of a plot of the eigenvalues in descending value factor analysis (Cattell 1966)] of the first 15 stress values for finding the "best-minimum" dimensionality of the data. It is assumed that if the distribution of the dissimilarities in the input matrix is close to random (normal distribution), the value of the stress function must be maximal, and the stress monotonic decreases according to an increase of the number of dimensions (Kupriyanova et al. 2003). This assumption is more realistic when the number of objects is approximately greater than 25–30 (Puzachenko 2001) . Under equal

Table 1. Mean, standard deviation, min–max values of skull measurements (in millimetres), absolute mean difference between sexes (Δ*S*, *S*) and sexual size dimorphism ratios (*S*) in the Eurasian badgers

##	Characters	*Meles meles*								*Meles leucurus*			
		European sample				Transcaucasian sample				Siberian sample			
		Male $n = 72$	Female $n = 59$	Δ*S*,*S*	*p*	Male $n = 48$	Female $n = 29$	Δ*S*,*S*	*p*	Male $n = 111$	Female $n = 44$	Δ*S*,*S*	*p*
1	Condylobasal length	131.5, 4.24 119.3–140.1	129.2, 3.43 119.0–136.0	2.2, 0.8	0.044	122.3, 4.61 112.9–132.1	116.3, 3.20 110.7–122.5	6.0, 2.5	0.012	122.9, 4.56 114.0–133.0	120.3, 3.64 112.9–128.4	2.7, 1.1	0.000
2	Neurocranium length	68.9, 2.33 63.1–73.7	67.3, 2.23 63.0–74.0	1.6, 1.2	0.056	65.1, 2.27 61.2–69.4	62.7, 1.90 59.6–67.0	2.5, 1.9	0.009	67.6, 2.70 61.5–74.0	66.1, 2.21 62.0–71.4	1.5, 1.1	0.023
3	Viscerocranium length	84.4, 3.62 76.8–93.7	82.9, 2.81 76.4–91.0	1.6, 0.9	0.114	74.6, 4.76 65.8–87.4	71.1, 3.46 65.5–78.4	3.6, 2.4	0.188	74.5, 3.97 65.7–84.0	71.8, 3.22 65.0–77.4	2.7, 1.9	0.002
4	Minimum palatal width	15.9, 0.95 13.7–18.2	16.0, 0.92 14.1–17.9	−0.1, −0.3	0.486	15.6, 0.97 13.4–17.8	15.3, 0.67 13.9–16.5	0.4, 1.1	0.392	15.1, 1.01 12.8–18.0	15.1, 1.11 12.3–17.7	0.0, 0.0	0.146
5	Palatal length	73.2, 2.32 67.5–78.8	71.9, 2.36 67.0–78.0	1.3, 0.9	0.043	68.2, 3.03 62.2–74.7	65.3, 2.29 62.3–70.8	3.0, 2.2	0.041	67.2, 2.41 61.2–73.0	66.2, 2.25 61.7–72.2	1.0, 0.7	0.000
6	Maxillary tooth-row length	43.8, 1.54 40.0–47.60	43.1, 1.42 39.8–46.5	0.7, 0.8	0.178	41.0, 1.81 37.4–46.2	38.9, 1.51 36.0–42.0	2.2, 2.7	0.041	39.7, 1.39 36.7–43.4	39.1, 1.71 36.2–42.8	0.6, 0.7	0.102
7	Length of upper carnassial tooth Pm^4	8.6, 0.45 7.6–9.6	8.6, 0.39 7.7–9.3	0.0, 0.0	0.382	7.9, 0.58 7.0–9.5	7.5, 0.56 6.7–9.1	0.5, 2.9	0.024	7.9, 0.50 6.7–9.1	7.9, 0.52 6.7–9.0	0.1, 0.5	0.489
8	Greatest length between oral border of the auditory bulla and aboral border of the occipital condyle	37.4, 1.51 33.6–41.2	37.4, 1.4 34.0–39.7	0.0, 0.0	0.650	34.8, 1.62 32.0–39.1	33.2, 1.20 31.5–37.0	1.6, 2.3	0.001	36.9, 1.88 32.2–40.4	36.3, 1.50 33.7–39.0	0.6, 0.8	0.310
9	Length of the auditory bulla	28.3, 1.24 25.3–30.6	28.0, 1.27 24.4–30.5	0.2, 0.4	0.207	26.3, 1.41 23.7–29.9	25.2, 1.06 23.0–27.6	1.0, 2.0	0.188	27.9, 1.52 23.5–31.0	27.6, 1.31 25.4–30.7	0.3, 0.6	0.180
10	Zygomatic width	80.9, 4.23 71.9–89.4	77.7, 3.77 68.4–86.2	3.3, 2.0	0.044	75.5, 4.29 65.2–84.0	70.8, 3.81 62.9–80.4	4.7, 3.2	0.188	74.6, 4.45 60.4–85.0	71.4, 3.79 62.9–81.2	3.2, 2.2	0.000
11	Mastoid width of skull	62.7, 2.57 56.8–68.9	61.6, 2.34 55.6–66.8	1.1, 0.9	0.090	60.5, 2.33 56.5–65.2	57.1, 2.53 53.5–62.6	3.4, 2.9	0.041	63.1, 3.23 54.8–70.0	61.6, 2.63 57.7–67.3	1.5, 1.2	0.033
12	Postorbital width	23.9, 1.39 20.7–27.3	23.5, 1.30 21.4–26.5	0.4, 0.8	0.073	23.0, 1.35 19.4–25.4	22.7, 1.54 19.1–26.1	0.3, 0.7	0.947	22.7, 1.63 19.2–26.5	22.3, 1.68 19.3–25.8	0.4, 0.8	0.537
13	Interorbital width	31.2, 1.69 27.8–34.2	30.1, 1.65 27.0–34.1	1.1, 1.8	0.004	27.7, 2.48 23.9–34.7	26.3, 1.56 24.1–30.3	1.4, 2.6	0.188	26.9, 1.61 23.0–30.6	26.4, 1.69 23.6–30.7	0.5, 0.9	0.255
14	Width of rostrum	32.2, 1.49 28.5–35.1	30.8, 1.45 27.0–34.4	1.4, 2.2	0.003	29.4, 1.61 26.0–32.6	27.8, 1.36 25.3–30.6	1.7, 2.9	0.188	29.3, 1.52 25.0–32.5	27.6, 1.45 24.9–32.1	1.8, 3.1	0.000
15	Greatest palatal width	42.3, 1.74 37.4–46.2	41.7, 1.52 36.9–45.2	0.5, 0.6	0.814	40.7, 1.88 35.7–44.0	39.4, 1.41 37.2–43.7	1.2, 1.5	0.188	38.9, 1.57 35.7–43.4	38.2, 1.79 34.0–42.2	0.7, 0.9	0.024

Table 1. (*continued*)

##	Characters	*Meles meles*								*Meles leucurus*			
		European sample				Transcaucasian sample				Siberian sample			
		Male $n = 72$	Female $n = 59$	Δ*S*,*S*	*p*	Male $n = 48$	Female $n = 29$	Δ*S*,*S*	*p*	Male $n = 111$	Female $n = 44$	Δ*S*,*S*	*p*
16	Width of the auditory bulla	22.8, 1.31 20.0–25.7	22.2, 1.22 19.5–24.6	0.6, 1.3	0.054	22.1, 1.1 19.8–25.3	21.1, 1.04 19.4–23.1	1.0, 2.3	0.553	22.6, 1.26 19.3–25.2	21.9, 1.01 19.2–23.9	0.7, 1.6	0.044
17	Width of upper molar M^1	11.7, 0.64 9.9–13.3	11.5, 0.55 10.4–13.0	0.2, 0.9	0.968	11.4, 0.59 10.0–12.7	10.8, 0.75 9.6–13.0	0.6, 2.5	0.550	10.8, 1.05 9.0–14.8	11.3, 1.55 9.8–14.7	−0.5, −2.2	0.569
18	Cranial height	53.7, 2.83 47.9–59.8	52.9, 2.51 47.2–59.4	0.8, 0.8	0.428	49.1, 2.99 43.0–55.8	46.3, 2.79 42.6–53.4	2.8, 2.9	0.041	51.3, 2.98 44.6–59.1	49.7, 2.91 44.4–58.9	1.6, 1.6	0.012
19	Total length of the mandible	91.3, 2.78 84.5–97.0	89.4, 2.60 84.2–94.3	1.9, 1.1	0.014	83.9, 3.77 77.1–91.1	79.9, 3.07 75.8–88.2	4.0, 2.4	0.081	82.7, 3.22 76.0–90.8	80.9, 2.35 75.7–86.3	1.9, 1.2	0.000
20	Length between the angular process and infradentale	92.2, 2.91 85.0–97.7	90.4, 2.69 84.3–95.8	1.8, 1.0	0.014	83.9, 4.08 77.2–93.7	80.1, 3.30 75.7–89.0	3.8, 2.3	0.081	83.4, 3.10 76.5–91.2	81.5, 2.26 78.2–86.8	1.9, 1.1	0.000
21	Mandibular tooth-row length	51.4, 1.58 47.7–54.5	50.4, 1.23 47.6–53.0	1.0, 1.0	0.070	48.5, 1.92 45.0–53.2	45.7, 1.70 43.0–49.5	2.8, 3.0	0.013	47.4, 1.56 44.5–51.6	46.7, 1.58 43.5–49.9	0.7, 0.8	0.208
22	Length of lower carnassial tooth M_1	13.9, 0.80 12.4–16.0	13.7, 0.72 11.9–15.30	0.3, 1.2	0.263	14.5, 0.81 12.2–16.1	13.7, 0.88 12.0–15.9	0.8, 2.8	0.041	13.6, 0.86 11.8–15.6	12.9, 0.73 11.7–14.4	0.6, 2.3	0.013
23	Height of the vertical mandibular ramus	38.9, 1.83 33.3–43.1	38.1, 1.7 33.4–42.30	0.8, 1.0	0.044	35.8, 2.54 29.1–41.7	33.6, 1.87 29.8–37.5	2.3, 3.3	0.081	33.9, 2.24 28.3–39.7	32.3, 1.66 29.7–35.9	1.7, 2.6	0.000
24	Length of upper molar M^1	16.3, 0.72 14.8–17.7	15.9, 0.66 14.5–17.6	0.4, 1.1	0.114	15.7, 0.88 14.0–17.3	15.1, 0.80 13.7–16.6	0.5, 1.8	0.138	15.8, 0.92 13.7–17.7	15.6, 0.94 14.0–17.4	0.2, 0.5	0.657
25	Length of upper canine	8.6, 0.49 7.6–9.8	7.9, 0.41 6.7–8.8	0.7, 4.4	0.000	7.6, 0.54 6.5–9.2	6.8, 0.45 6.0–8.0	0.8, 5.8	0.012	7.7, 0.55 6.7–9.0	7.1, 0.53 6.1–8.1	0.6, 4.2	0.001
26	Width of upper canine	6.3, 0.44 5.40–7.30	5.9, 0.39 4.9–7.2	0.5, 3.7	0.000	5.8, 0.40 5.1–6.7	5.2, 0.31 4.5–6.3	0.6, 5.7	0.001	5.8, 0.42 5.0–6.8	5.2, 0.29 4.7–6.0	0.6, 5.9	0.000
27	Length of lower molar M_2	5.48, 0.44 4.5–6.5	5.4, 0.42 4.4–6.8	0.1, 0.6	0.523	5.8, 0.60 4.8–6.9	5.6, 0.57 4.7–7.0	0.2, 2.1	0.980	5.4, 0.51 4.2–6.6	5.1, 0.49 4.0–6.2	0.4, 3.3	0.145
28	Width of lower molar M_2	7.4, 0.36 6.4–8.2	7.2, 0.44 6.2–8.2	0.2, 1.4	0.760	7.3, 0.42 6.0–8.0	7.1, 0.36 6.4–8.1	0.2, 1.3	0.332	6.9, 0.41 5.9–7.9	6.6, 0.43 6.0–7.4	0.3, 1.9	0.406
29	Talonid length of lower carnassial tooth M_1	7.3, 0.52 6.0–8.9	7.1, 0.49 6.1–8.4	0.2, 1.3	0.642	7.5, 0.53 6.3–8.9	7.3, 0.42 6.6–8.0	0.2, 1.3	0.135	6.9, 0.59 5.7–8.2	6.6, 0.55 5.6–7.7	0.3, 2.3	0.388
30	Length of lower premolar Pm_2	4.6, 0.30 3.9–5.3	4.6, 0.32 3.8–5.1	0.1, 0.8	0.502	4.2, 0.36 3.4–5.0	3.9, 0.39 3.2–4.9	0.2, 2.8	0.081	3.3, 0.38 2.5–4.1	3.09, 0.34 2.4–3.6	0.2, 2.7	0.627

##	Characters	*Meles leucurus*				*Meles anakuma*			
		Far-Eastern sample							
		Male $n = 15$	Female $n = 7$	ΔS, S	p	Male $n = 8$	Female $n = 7$	ΔS, S	p
1	Condylobasal length	109.6, 4.61 103.0–117.1	107.2, 2.11 104.0–110.0	2.4, 1.1	0.169	105.1, 3.94 101.3–112.2	104.0, 3.50 100.8–110.7	1.1, 0.5	0.659
2	Neurocranium length	62.8, 2.38 58.4–66.7	61.7, 2.11 60.0–66.0	1.1, 0.9	0.169	61.1, 1.84 57.7–62.4	60.4, 2.50 58.3–64.0	0.6, 0.5	0.270
3	Viscerocranium length	65.8, 4.18 60.2–72.7	61.4, 2.44 57.2–65.0	4.5, 3.5	0.022	63.8, 4.44 57.1–70.4	61.6, 3.99 54.5–67.0	2.2, 1.8	0.782
4	Minimum palatal width	13.9, 0.99 11.9–15.1	13.4, 0.79 12.3–14.3	0.5, 1.8	0.647	14.8, 0.91 13.8–16.0	14.7, 1.34 13.2–17.1	0.1, 0.4	0.593
5	Palatal length	60.8, 2.20 57.1–65.0	58.4, 0.94 57.3–59.9	2.4, 2.0	0.169	56.1, 1.56 54.2–59.2	54.9, 1.87 53.2–58.6	1.2, 1.1	0.188
6	Maxillary tooth-row length	36.1, 1.68 32.5–39.0	34.9, 0.67 34.0–35.7	1.2, 1.7	0.044	33.1, 0.90 32.1–34.5	32.3, 1.13 30.2–34.0	0.9, 1.3	0.188
7	Length of upper carnassial tooth Pm^4	7.6, 0.55 6.5–8.5	7.3, 0.37 6.7–7.8	0.3, 2.1	0.277	7.2, 0.26 6.7–7.6	6.9, 0.26 6.7–7.3	0.2, 1.6	0.465
8	Greatest length between oral border of the auditory bulla and aboral border of the occipital condyle	32.7, 1.69 30.4–35.3	32.2, 1.01 31.0–33.6	0.4, 0.7	0.867	31.1, 1.51 29.3–33.2	30.7, 1.33 29.8–33.3	0.3, 0.5	0.280
9	Length of the auditory bulla	25.5, 1.45 23.4–28.2	25.4, 1.26 23.5–26.8	0.1, 0.3	0.867	23.1, 0.93 21.8–24.3	22.9, 1.08 21.8–25.0	0.1, 0.2	0.780
10	Zygomatic width	68.8, 4.25 60.7–75.0	64.8, 1.93 62.6–67.2	4.0, 3.0	0.022	64.5, 6.05 56.3–72.4	62.1, 4.68 55.1–69.3	2.3, 1.8	0.270
11	Mastoid width of skull	57.9, 3.14 52.7–63.4	55.9, 1.78 53.4–58.2	2.0, 1.7	0.647	56.2, 3.07 51.7–62.1	54.4, 3.09 50.6–59.0	1.8, 1.6	0.270
12	Postorbital width	20.7, 1.62 17.5–23.1	20.6, 1.66 18.1–22.2	0.1, 0.3	0.647	22.5, 1.09 21.3–24.3	22.8, 0.56 21.7–23.4	−0.3, −0.6	0.460
13	Interorbital width	24.1, 1.71 21.7–26.6	23.5, 1.28 22.4–25.4	0.6, 1.2	0.277	23.56, 1.91 21.7–27.4	23.9, 0.97 22.7–25.3	−0.3, −0.7	0.782
14	Width of rostrum	27.2, 1.28 25.0–29.7	25.0, 0.74 24.1–26.4	2.2, 4.2	0.022	24.6, 1.36 23.2–27.0	23.7, 1.29 22.4–25.9	0.9, 1.8	0.188
15	Greatest palatal width	36.6, 1.78 33.4–40.1	34.8, 1.32 33.4–37.6	1.8, 2.5	0.022	34.4, 0.68 33.5–35.1	33.5, 1.20 31.7–35.4	0.9, 1.3	0.460
16	Width of the auditory bulla	20.6, 1.58 17.7–23.8	19.7, 0.72 18.8–20.7	0.9, 2.1	0.277	19.4, 1.74 17.3–22.0	18.8, 1.38 16.8–20.7	0.6, 1.6	0.782

Table 1. (*continued*)

##	Characters	*Meles leucurus*				*Meles anakuma*			
		Far-Eastern sample							
		Male $n = 15$	Female $n = 7$	ΔS, S	p	Male $n = 8$	Female $n = 7$	ΔS, S	p
17	Width of upper molar M^1	10.6, 0.54 9.9–11.6	9.8, 0.53 9.1–10.7	0.8, 4.0	0.031	9.5, 0.41 8.9–10.0	8.9, 0.48 8.3–9.6	0.6, 3.2	0.157
18	Cranial height	46.6, 2.38 43.4–50.3	44.7, 1.32 43.1–46.7	1.9, 2.1	0.022	42.9, 2.32 39.9–46.7	41.9, 2.20 38.7–44.9	0.9, 1.1	0.270
19	Total length of the mandible	75.5, 3.19 70.7–81.2	72.2, 0.68 71.3–73.2	3.3, 2.3	0.002	72.1, 2.51 69.8–76.9	69.5, 3.56 66.7–76.3	2.6, 1.8	0.157
20	Length between the angular process and infradentale	75.8, 3.30 70.1–81.4	72.7, 0.99 71.4–74.0	3.1, 2.1	0.002	72.7, 1.71 70.7–75.9	69.9, 3.02 66.9–75.4	2.7, 1.9	0.157
21	Mandibular tooth-row length	43.6, 1.56 41.2–46.3	41.1, 0.49 40.4–41.7	2.5, 2.9	0.002	39.9, 0.87 38.2–41.0	38.7, 1.67 37.0–41.3	1.3, 1.6	0.650
22	Length of lower carnassial tooth M_1	15.3, 0.88 14.0–16.8	14.3, 0.66 13.4–15.5	1.0, 3.5	0.030	12.7, 0.46 11.9–13.2	12.7, 0.40 12.1–13.3	0.0, 0.0	0.465
23	Height of the vertical mandibular ramus	30.9, 1.91 28.1–33.8	28.8, 0.75 27.5–29.8	2.2, 3.6	0.005	30.3, 1.54 28.3–32.2	28.5, 1.30 26.7–30.7	1.8, 3.0	0.248
24	Length of upper molar M^1	13.3, 1.12 11.7–15.1	11.9, 0.44 11.3–12.5	1.4, 5.4	0.002	11.1, 0.67 10.1–12.0	10.4, 0.75 9.5–11.3	0.7, 3.4	0.188
25	Length of upper canine	7.1, 0.45 6.7–8.2	6.1, 0.20 5.8–6.4	1.0, 7.8	0.001	6.5, 0.27 6.2–7.0	5.7, 0.38 5.1–6.2	0.8, 6.3	0.028
26	Width of upper canine	5.3, 0.35 4.6–6.0	4.5, 0.28 4.2–5.0	0.7, 7.6	0.003	4.9, 0.23 4.6–5.2	4.2, 0.26 3.7–4.5	0.7, 8.0	0.005
27	Length of lower molar M_2	5.5, 0.74 4.5–6.7	5.0, 0.37 4.7–5.7	0.5, 4.3	0.216	4.8, 0.43 4.3–5.3	4.7, 0.26 4.4–4.9	0.1, 0.6	0.659
28	Width of lower molar M_2	6.6, 0.44 5.6–7.3	6.1, 0.33 5.7–6.7	0.5, 3.9	0.031	5.4, 0.18 5.2–5.7	5.4, 0.23 5.0–5.7	0.0, 0.0	1.000
29	Talonid length of lower carnassial tooth M_1	6.9, 0.58 5.8–8.0	6.4, 0.85 5.6–8.0	0.5, 3.5	0.216	6.3, 0.16 6.1–6.5	6.3, 0.31 5.8–6.7	0.0, 0.0	0.465
30	Length of lower premolar Pm_2	2.8, 0.53 2.1–3.6	2.7, 0.48 2.0–3.3	0.0, 0.0	0.530	2.5, 0.33 2.0–3.0	2.3, 0.17 1.9–2.3	0.4, 8.8	0.047

Significant differences ($p < 0.05$) according to median test underlined.

circumstances for real non-random data, the best MDS solution must be associated with a minimum stress value that (accurate to a scaling constant) deviates relatively maximally from the model value. In general, we assumed the following linear regression model:

$$\mathrm{Stress}_i = B\,\mathrm{Stress}_{i,\mathrm{mod}} - A + \varepsilon_i,$$

in which Stress_i is the value of stress function for real data, i is the number of dimensions in MDS solution, $\mathrm{Stress}_{i,\mathrm{mod}}$ is the value of stress function for model random data set (normal distribution), A and B are "scaling" constants, and ε_i are the errors with the normal distribution. Furthermore, at the plot of standardized residuals from this regression model, the minimum value and corresponding dimensionality can be easily found. In the first case, the "best-minimum" dimension will be marked as d_D, and in the second one as d_K.

Using axes of multivariate scaling, Mahalanobis' D^2 distances between males and females were assessed. A UPGMA cluster was constructed using the matrix of Mahalanobis' D^2 distances to summarize the pattern of morphological similarity depicted by the MDS-axes.

As a measure of sexual dimorphism by a single variable, we chose both the absolute mean difference between the sexes (ΔS) and the ratio of male size to female size because they are intuitively simple and easily interpretable. SSD ratios were calculated as $S = (\mathrm{mean}_{\mathrm{male}} - \mathrm{mean}_{\mathrm{female}}/\mathrm{mean}_{\mathrm{male+meanfemale}}) \times 100$.

The quantitative index of morphological diversity, i.e., Shannon's measure of indefiniteness (entropy) was computed for each MDS-axis, the number of gradations being $k = \log_2(n)$ (n equals sample size). By virtue of the orthogonal character (i.e., independence) of MDS-axes, the final value of the diversity was computed as a sum of diversity by all axes. Sizes of groups obtained as a result of classification of sample were essentially different. ($k_i - k_j > 1$). Therefore evenness (E) was used:

$$E = \left[\sum_1^m H_m\right] \Big/ m \log_2 k,$$

in which H_m is Shannon's indefiniteness (entropy), m is the number of MDS-axes (i.e., dimension). The maximum value of E is achieved in the case of the uniform distribution of data. From the biological point of view, maximum evenness ($E = 1$) correlates with the extremely non-equilibrium state of character when (within limits) any value from the range occurs with equal probability. The high value of evenness is evidence for a high variation ability of the character, and a lower value indicates a low variation.

We assessed the morphological diversity of the sexes, geographic samples, and species separately. Moreover, the assessment of diversity was obtained for other (independent) samples of Eurasian badgers (including West European and South European populations) that had been used by us for the analysis of morphotypical and size variation of teeth (Baryshnikov et al. 2003). In the case of morphotypes, the square dissimilarity matrix for MDS procedure contained the "percentage of disagreement" measures among all pairs of specimens was calculated. This distance between specimens x and y is computed as

$$d(x, y) = \left(\sum x_i \neq y_i\right) \Big/ i,$$

in which i is the number of the categorical variables.

3. Results

Descriptive statistics are given in Table 1. All craniological measurements have shown overlapping values within the observed range of variation between sexes. In all samples, the males are on average larger than females, but in the majority of cases, these differences are statistically non-significant as revealed by the Kruskal–Wallis test and median test.

Of the total 30 skull measurements, 25 are subject to sexual dimorphism to a certain extent. The set and number of characters with sexual dimorphism vary in the various samples (see Table 1). SSD is displayed mostly in the general size of the skull (i.e., condylobasal length, zygomatic width, width of rostrum, and cranial height) and mandible (i.e., height of the vertical mandibular ramus, total length of the mandible, and length between the angular process and infradentale), and in some dental characters (i.e., length of upper molar M^1). Sexual dimorphism is not observable in the length of the auditory bulla, the postorbital width, the minimum palatal width, the length of the lower molar M_2, and the talonid length of the lower carnassial tooth M_1. The most stable dimorphism is manifested in the size of the canines, which is pronounced in all studied samples. Within the limits of a particular form, sexual dimorphism of the size of the upper canine varies in different populations. For instance, in different populations of the European *M. meles*, the level of dimorphism (ΔS, calculated by medians) changes from 1.01 mm ($S = 6.1$) in Tula Province (Russia) and 0.85 mm ($S = 5.0$) in Moscow Province (Russia) to 0.61 mm ($S = 4.0$) in Wytham Woods (Great Britain) (Fig. 3).

Values of d_D and d_K for the entire sample, including all taxonomic and geographical samples, are 2. Proportions of variance are 0.97 and 0.69, respectively. Fig. 4a illustrates the position of male and female values of different samples of badgers in relation to the $D1$ and $D2$ MDS-axes. Squared Mahalanobis' distances D^2 between male and female samples summarize the morphological differentiation based on both D- and K-axes (Table 2, Fig. 4b). According to this analysis, sexual dimorphism is more pronounced in the Transcaucasian sample of *M. meles* and Far-Eastern sample of *M. leucurus* than in the other samples. The European sample of *M. meles* shows a minimal level of sexual dimorphism. A separation of the sexes by the shape of the skull based on *K*1 and *K*2 is less clear than by the size of the skull (Fig. 5).

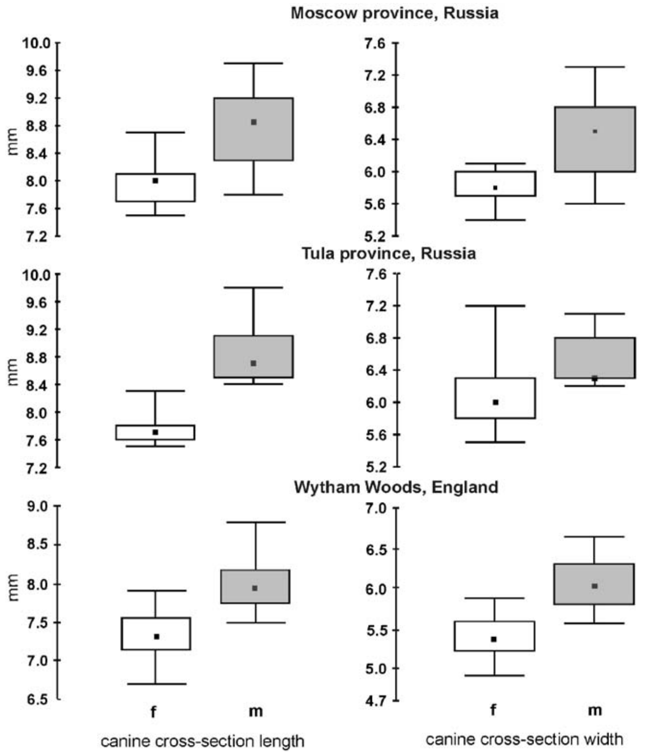

Fig. 3. Sexual dimorphism in upper canine cross-section length and width in three *Meles meles* populations – Wytham Woods, England (after Johnson and Macdonald 2001), Moscow, and Tula provinces, Central Russia. Box = interquartile range; point = median; whiskers = min–max interval; m = males, f = females.

The assessment of SSD by ΔS and S confirmed the above differences in the manifestation of dimorphism in different species and geographical samples of badgers (Fig. 6). Moreover, it was found that in *M. anakuma*, as well as in the European *M. meles*, SSD is very weakly expressed, except for the size of the canines. A comparison of different intraspecific geographical samples shows that the value ΔS depends on the size of females rather than on that of males for the majority of measurements. For example, the difference in the condylobasal length of the skull between males of the relatively large European and the small Transcaucasian *M. meles* is on average 9.4 mm and that between females is 12.8 mm. Correspondingly, ΔS for the European sample of *M. meles* is 2.2 mm ($S = 0.8$) and for the Transcaucasian sample of *M. meles* is 6.0 mm ($S = 2.5$). Differences in size between females of both large and small geographical forms are on average greater than those between males. In the European badger, this pattern is more pronounced than in the Asian badger. In *M. leucurus*, exceptions from this rule are found for the greatest length between the auditory bulla and occipital condyle, postorbital width, neurocranium length, length of the auditory bulla, and length of the lower molar M_2.

The morphological diversity of males in the European sample of *M. meles* is higher than that of females (Table 3, Fig. 7). At the same time an opposite tendency is observed in the other samples of badgers. No correlation has been found between the level of sexual dimorphism and the degree of morphological diversity within each sex. Morphotypical diversity of teeth of males of the European *M. meles*, as in the case of the diversity of cranial characters, is higher than in females (Table 4). In the Siberian sample of *M. leucurus*, an

Table 2. Squared Mahalanobis' distances D^2 between males (m) and females (f) calculated on *D*1-, *D*2-, *K*1- and *K*2-axes (above diagonal) and corresponding *F*-values (under diagonal). Females of *Meles anakuma* were not included in the calculation because of insufficient data

Sample	*Meles meles*				*Meles leucurus*				*Meles anakuma*
	European sample		Transcaucasian sample		Siberian sample		Far-Eastern sample		
	m 1	f 2	m 3	f 4	m 5	f 6	m 7	f 8	m 9
1		1.2	9.6	20.1	16.0	23.8	36.3	63.2	84.8
2	8.8		5.4	13.1	9.9	15.9	24.9	48.1	68.2
3	61.5	32.1		3.6	10.4	14.8	16.6	37.5	50.9
4	90.1	55.3	14.0		10.6	10.9	7.2	21.6	31.3
5	150.9	83.1	75.6	51.4		1.2	10.0	22.1	31.4
6	100.2	63.6	55.0	32.4	5.4		6.1	14.0	21.5
7	91.1	60.6	38.5	14.4	26.2	11.9		4.3	13.6
8	86.0	64.3	48.9	25.9	30.8	16.5	4.2		6.3
9	40.7	32.6	24.1	14.4	15.2	9.8	5.8	2.3	

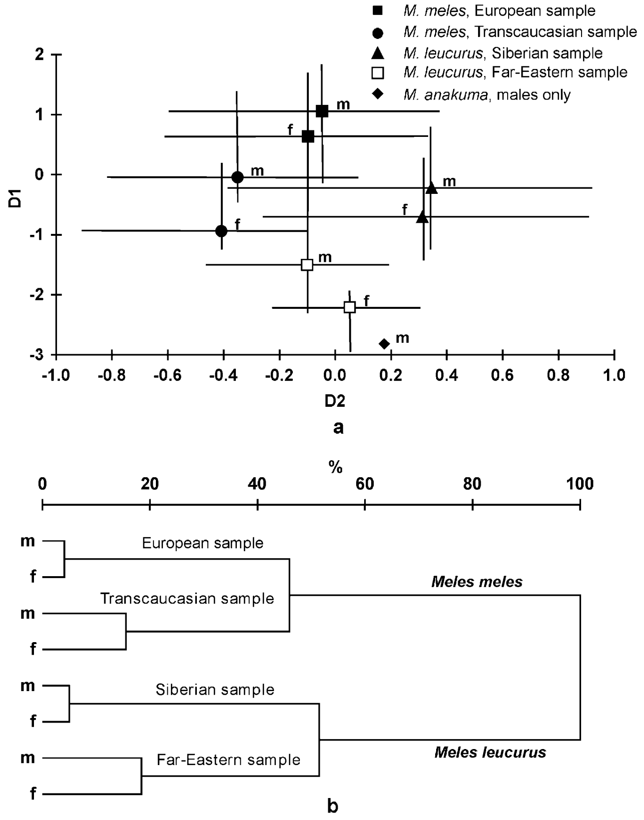

Fig. 4. Separation of males (m) and females (f) of badgers on the basis of *D*1 and *D*2 MDS-axes: (a) min–max interval for sample medians; (b) UPGMA dendrogram constructed using both *D* and *K* MDS-axes.

opposite pattern is observed in that females display a greater variability. Size diversity of teeth E_D (Table 4) in the European sample of *M. meles* and Siberian sample of *M. leucurus* is greater in females (Fig. 8).

The degree of morphological diversity of the entire skull correlates positively with the level of sexual dimorphism, expressed by the indices ΔS and S (Table 3, Fig. 9). Maximum values of morphological diversity are observed in the Transcaucasian *M. meles* and Far-Eastern *M. leucurus*. Diversity of the structure, expressed in the number of independent factors of skull variation and reflected in the value "best-minimum" dimension in the MDS model (d_D, d_K), is greatest in the Transcaucasian *M. meles*. At the species level, the value E_D (Table 3), reflecting mostly the diversity of sizes of the skull, and morphotypical diversity E (Table 4) are greater in *M. meles* than in *M. leucurus*. At the same time, the diversity of the proportions and size of skulls are greater in *M. leucurus* (Table 4).

There is no direct relationship between the number of characters exhibiting sexual dimorphism and the degree of sexual dimorphism. Thus, at comparable levels of sexual dimorphism assessed by ΔS and S, the number of characters with sexual dimorphism is only 9 in the

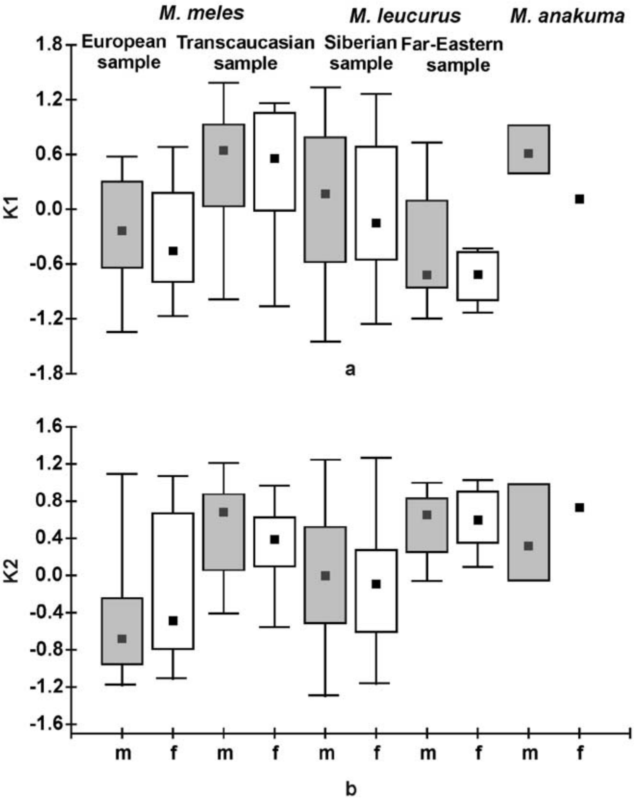

Fig. 5. Separation of males (m) and females (f) of badgers in *K*1 (a) and *K*2 (b) MDS-axes. Box = inter-quartile range; point = median; whiskers = min–max interval.

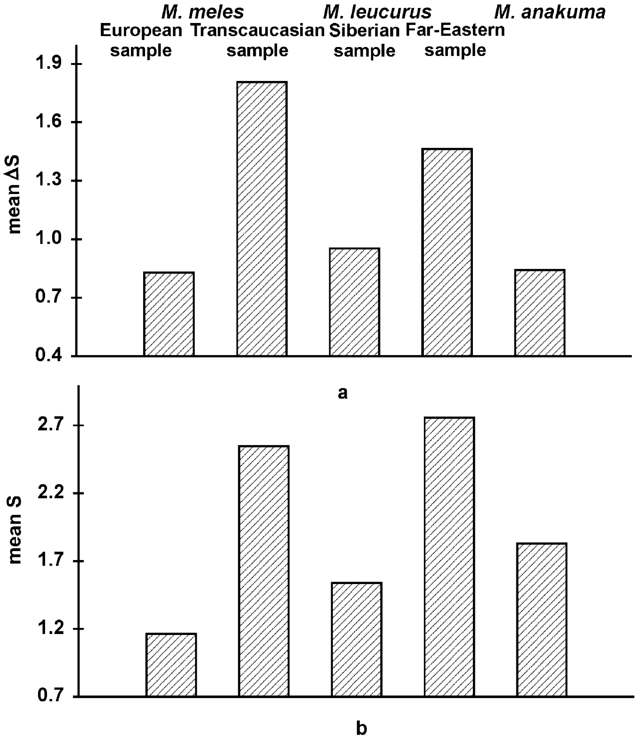

Fig. 6. Means of ΔS (a) and the sexual size dimorphism ratios S (b) in the Eurasian badgers.

Table 3. Feature of the morphological diversity of the skull in the Eurasian badgers. *Meles anakuma* was not included in the calculation of morphological diversity because of insufficient data for this analysis

	Sex	d_D	d_K	k	E_D	E_K
Meles meles		2	4	8	0.845	0.842
European sample		3	3	7	0.789	0.891
Transcaucasian sample		4	4	6	0.810	0.895
Meles leucurus		2	4	7	0.828	0.853
Siberian sample		2	4	7	0.793	0.873
Far-Eastern sample		3	3	4	0.853	0.945
European sample of *Meles meles*	Male	3	3	6	0.823	0.922
	Female	3	4	6	0.769	0.892
Transcaucasian sample of *Meles meles*	Male	2	4	5	0.842	0.883
	Female	4	3	5	0.871	0.891
Siberian sample of *Meles leucurus*	Male	2	6	6	0.842	0.836
	Female	3	3	5	0.854	0.923

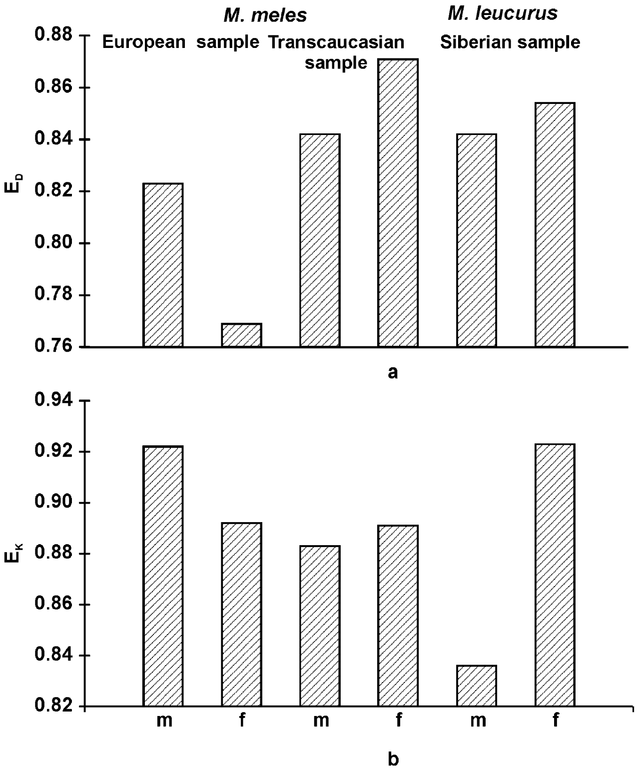

Fig. 7. Morphological diversity E_D (a) and E_K (b) of the male (m) and female (f) in the Eurasian badgers. *Meles anakuma* and Far-Eastern *Meles leucurus* were not included in the calculation of morphological diversity because of insufficient data for this analysis.

European *M. meles* versus 15 in the Siberian *M. leucurus*. On the whole, SSD was revealed by a larger number of characters in *M. leucurus* than in *M. meles.* In *M. anakuma*, sexual dimorphism is displayed in only a few cranial characters, such as canine size.

4. Discussion

Sexual dimorphism of cranial characters are generally correlated with variations in skull size, but exceptions can be expected on theoretical grounds: (1) the dimorphism ratio (S) may be constant and not vary with body size, (i.e., isometry); (2) the mean difference between the sexes (ΔS) may be approximately constant, but SSD ratios (S) may vary with skull size (i.e., simple allometry); and (3) both ΔS and S may change (i.e., complex allometry). Our research shows that sexual dimorphism of the skull in badgers is displayed mostly in the form of complex allometry (variant 3), whereas isometric variation (variant 1) is nearly absent.

Based on our results, we can reject the statistical null hypotheses of sexual dimorphism being absent in the various species and geographical samples of the Eurasian badger. However, only some skull characters exhibit sexual dimorphism in the three species of Eurasian badgers. Sexual dimorphism is most clearly expressed in the overall size of the skull and mandible and in the length of the upper molar M^1 (see Fig. 10), but was not detectable in the length of the auditory bulla, the interorbital width, the length of lower molar M_2, and the length of the lower carnassial tooth M_1. In all studied samples of badgers, there is a pronounced dimorphism in the size of the upper canines, which is typical of many mammalian taxa that possess these teeth, including all carnivores (see Gittleman and Van Valkenburgh 1997).

In both the European and Asian badgers, two forms that differ in the degree of SSD have been identified. In the larger badgers (i.e., the European *M. meles* and Siberian *M. leucurus*), sexual dimorphism is weaker in both absolute and relative terms than in the smaller badgers (i.e., the Transcaucasian *M. meles* and

Table 4. Feature of the morphological diversity of the teeth in the Eurasian badgers. *Meles anakuma* and Far-Eastern *Meles leucurus* were not included in the calculation of morphological diversity because of insufficient data for this analysis

	Sex	Morphotypical diversity			Size diversity				
		D	k	E	d_D	d_K	k	E_D	E_K
Meles meles		2	9	0.766	2	3	8	0.689	0.843
European sample		2	8	0.734	1	3	8	0.649	0.841
Transcaucasian sample		2	6	0.792	2	4	6	0.799	0.867
Meles leucurus		2	7	0.656	2	3	7	0.737	0.841
Siberian sample		2	7	0.635	2	1	7	0.747	0.826
European sample of *Meles meles*	Male	2	6	0.896	2	2	6	0.702	0.932
	Female	2	7	0.755	1	1	6	0.748	0.868
Siberian sample of *Meles leucurus*	Male	2	5	0.652	2	2	5	0.770	0.877
	Female	2	5	0.748	2	2	5	0.786	0.906

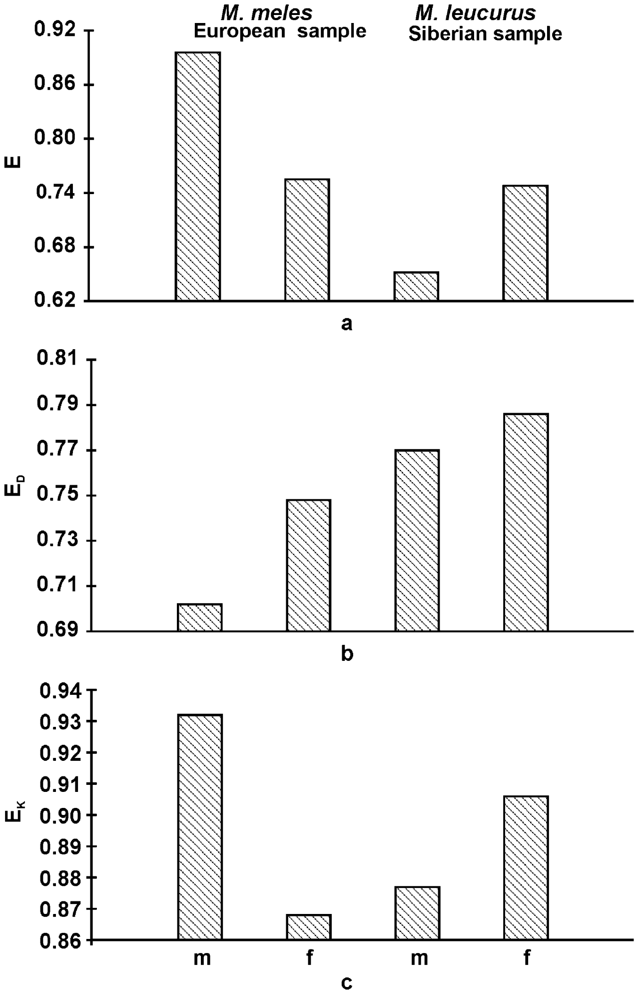

Fig. 8. Morphotypical (E, a), size (E_D, b) and shape diversity (E_K, c) of the teeth in males (m) and females (f) of the Eurasian badgers.

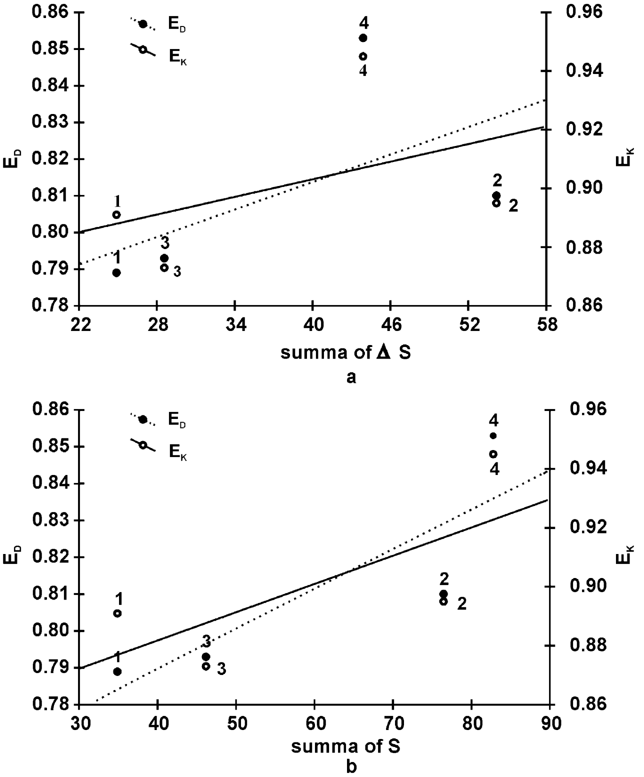

Fig. 9. Relationships between absolute (ΔS, a) and relative (S, b) sexual size dimorphism with morphological diversity (E_D, E_K) in the Eurasian badgers: 1: *Meles meles*, European sample, 2: *Meles meles*, Transcaucasian sample, 3: *Meles leucurus*, Siberian sample, 4: *Meles leucurus*, Far-Eastern sample. Dotted lines mark linear regression ΔS or S with the size diversity (E_D) and full lines mark regression with the shape diversity (E_K).

Far-Eastern *M. leucurus*). The degree of sexual dimorphism in Eurasian badgers is related mainly to a variation of the females. For the majority of characters, including those for which SSD is statistically non-significant, the absolute difference between females of the large and small forms is greater than the analogous difference between males. This pattern is particularly pronounced in the two forms of *M. meles*.

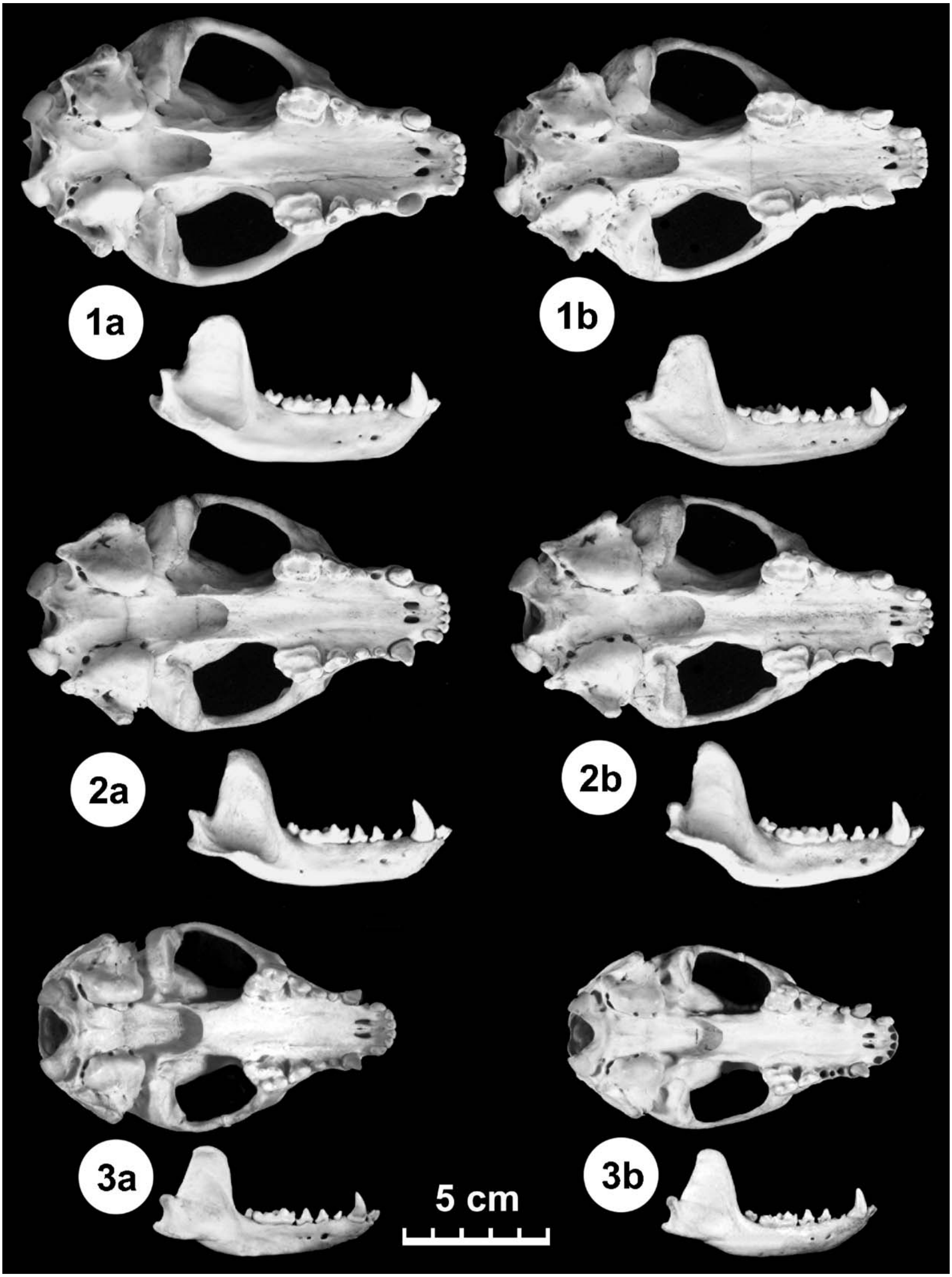

Fig. 10. Skulls of a male (a) and a female (b) of the three species of Eurasian badgers: 1. *Meles meles*, European form (1a: ZIN 35056, 1b: ZIN 16909, specimens from Leningrad Province, Russia), 2. *Meles leucurus*, Siberian form (2a: ZIN 1148, 2b: ZIN 1139, specimens from Eastern Kazakhstan), 3. *Meles anakuma* (3a: NSM 1071, 3b: NSM 27353, specimens from Honshu, Japan).

In the Far-Eastern *M. leucurus,* an increase of an absolute mean difference between the sexes (ΔS), and particularly of SSD ratios (S), of some characters (e.g., viscerocranium length, zygomatic breadth, breadth of rostrum, length and width of upper canine, etc.) is accompanied by a general decline in the values of these characters in both sexes relative to the Siberian *M. leucurus*. In the Japanese badger *M. anakuma* (the smallest representative of *Meles*), a decline of skull size relative to that of the continental *M. leucurus* is accompanied by a decline of sexual dimorphism in absolute terms (except canine size). Isometry, however, is complicated by virtue of a more basic decline of skull size in both sexes. As a consequence, the relative index of sexual dimorphism (S) is greater in the Japanese badger than in the larger European *M. meles* and Siberian *M. leucurus*. The Transcaucasian *M. meles* and the Far-Eastern *M. leucurus* are characterized by a complex allometry related to a change in both relative and absolute differences in skull size between males and females. But for all that, sexual dimorphism is maximal in the Transcaucasian *M. meles* in absolute terms, but it is maximal in the Far-Eastern *M. leucurus* in relative terms.

The morphological diversity of the skull, as defined in this study, is generally greater in female badgers than in males, except in the European *M. meles*, in which it is greater in males than in females. The degree of size diversity of teeth appears to be greater in females in all forms of the three badger species. On the whole, the degree of morphotypical diversity is apparently correlated with the degree of diversity of tooth shape and does not depend on the size of teeth. A comparison of the morphotypical diversity of teeth of the European and Asian badgers shows that dental variation is relatively independent of skull variation.

The degree of morphological diversity of the skull on the whole is positively correlated with the degree of sexual dimorphism expressed by the indices of the absolute mean difference between the sexes (ΔS) and SSD ratios (S). At the species level, the diversity of skull size is greater between the two forms of *M. meles* than between the two forms of *M. leucurus*, but the diversity of skull proportions is greater in *M. leucurus*. Therefore, *M. meles* has more a stable shape of the skull across the studied forms than *M. leucurus*.

The characteristics of sexual dimorphism in badgers do not quite conform to the data known for other representatives of the family Mustelidae (Shubin and Shubin 1975; Zyll de Jong 1992; Abramov and Baryshnikov 2000; Abramov and Tumanov 2003), in which sexual dimorphism is more pronounced in large forms than in smaller ones. In the Eurasian badgers, in contrast, the smaller intraspecific forms display a greater degree of sexual dimorphism than the larger forms. Only the Japanese badger, the smallest representative of the genus *Meles*, conforms to the pattern observed in other Mustelidae.

Even though numerous investigations of sexual dimorphism of Mustelidae have been published, the reasons for sexual dimorphism in the sizes of the skull and body, and for the variation in the degree of sexual dimorphism within a species, have remained unclear. The resource partitioning model attributes differences in sizes to differences in the diet of males and females (Brown and Lasiewski 1972; Shubin and Shubin 1975; Dayan et al. 1989; Dayan and Simberloff 1994; Gittleman and Van Valkenburgh 1997). According to this rule, the sexes achieve optimal sizes, and differences in body size correlate with the size of the food items ingested. It is believed that differences in the feeding apparatus and, in particular, in canine size, indicate some level of selection for niche separation between the sexes (Dayan and Simberloff 1996). Johnson and Macdonald (2001) discussed the applicability of this hypothesis to badgers and suggested that feeding competition between the sexes is not negligible in *M. meles*. Other researchers, however, pointed to the absence of actual resource partitioning in badgers and assumed that this sexual dimorphism may rather be related to interspecific or intergroup aggression (Lynch et al. 1997; McDonald 2002).

Given the omnivorous nature of the Eurasian badgers, dietary specialization is not likely to be a factor for the existence of sexual dimorphism. Eurasian badgers inhabit various biotopes, which determine the composition and breadth of their diet (Roper 1994; Roper and Mickevicius 1995). In the forest zone of the temperate region, earthworms and insects comprise a major portion of the diet of the European badger (Heptner et al. 1967; Danilov and Tumanov 1976; Neal and Cheeseman 1996), but in Mediterranean areas, earthworms represent only secondary prey, and the proportion of vertebrates and plants in the diet is greater (Rodríguez and Delibes 1992; Martín et al. 1995; Revilla and Palomares 2002a). In Transcaucasia as well as in Eastern Europe (i.e., Ukraine, Moldavia), plant food comprises a large portion of a European badger's diet (Ognev 1931; Heptner et al. 1967). In the forest zone of Kazakhstan and Siberia, earthworms also play a significant role in the diet of the Asian badger *M. leucurus*, whereas in the steppes of northern Kazakhstan and the forest–steppe and steppe regions of southern Siberia, there is an increase in the proportion of mammals and insects in a badger's diet (Smirnov and Noskov 1977; Sludsky et al. 1982; Shibanov 1989). A considerable part of the diet of the Asian badger in the foothills and mountain regions of Middle Asia and Siberia consists of fruits and berries (Heptner et al. 1967). The diet of the Far-Eastern *M. leucurus* does not differ from that of Asian badgers from the forest zone of Western Siberia (Stroganov 1962; Yudin 1984). In

Tatarstan, *M. meles* and *M. leucurus* live in similar biotopes on the right and left banks of the Volga River and do not display any differences in their diets (Gorshkov 1997). Data on the diet of the Japanese badger *M. anakuma* also do not differ significantly from those of the European and Asian badgers. A study of the Japanese badger on Honshu Island shows that its diet consists for the most part of earthworms and insects, and only to a small extent of mammals (Yamamoto 1991, 1994).

Thus, the currently available data do not indicate that there are significant differences in the diet between the European and Asian badgers and, in particular, between the diets of different geographic forms of the species *Meles*. Furthermore, no significant differences have been found between the diets of European badgers from England and Central Russia (Ognev 1931; Roper and Mickevicius 1995; Neal and Cheeseman 1996), even though a preliminary analysis of different populations of the European *M. meles* indicates the existence of interpopulational differences in SSD (Fig. 3). It is highly improbable, therefore, that dietary differences alone can explain the observed intraspecific differences in sexual dimorphism, although changes in the diet may have an indirect influence on sexual dimorphism through different ontogeny reactions of males and females (Yom-Tov et al. 2003).

The occurrence of sexual dimorphism in Mustelidae has also been explained by taking into account the polygynous mating system that is typical in mustelids and by assuming differing sex-specific selective pressures (Ralls 1977; Erlinge 1979; Moors 1980). According to this model, larger males are favoured by the sexual selection that takes place during competition with other males for achieving the highest reproductive success by mating with the greatest possible number of females. In this case, the larger canines in males may be selected for by intrasexual display or fighting, as Lüps and Roper (1988) suggested for the European badger. However, the competitive advantages of sexual dimorphism are predicted to be small for males in multi-male badger social groups (Johnson and Macdonald 2001). These authors attributed the relatively low level of sexual dimorphism of English badgers to their social mode of life. Similarly, other social mustelid species (e.g., the giant otter *Pteronura brasiliensis*, the sea otter *Enhydra lutris*) are known to display a relatively low degree of SSD (Johnson et al. 2000; Johnson and Macdonald 2001). In this context, it is noteworthy that the European otter *Lutra lutra* in Shetland is particularly social and also displays a lesser degree of sexual dimorphism in its skull than otters from other parts of Europe (Lynch et al. 1996). In European badgers, however, the degree of sociality varies geographically (Johnson et al. 2002). In the UK, for example, badgers commonly form large multi-male, multi-female groups of up to 30 individuals that share a single territory (Neal and Cheeseman 1996), but in continental Europe, badgers seem to be non-social, with a mean group size of only one to three (Ognev 1931; Rodríguez et al. 1996; Brøseth et al. 1997; Revilla et al. 1999; Revilla and Palomares 2002b). Our data on the sexual dimorphism of the upper canine, however, did not support the expectation of major differences between the more social English badgers in Wytham Woods (Johnson and Macdonald 2001) and the badgers from Tula Province in the European part of Russia, which do not form large groups (Ognev 1931). The difference in the SSD ratio (S) between the Wytham Woods population and the population from Tula Province is approximately equal to the difference between the latter population and the population from Moscow Province, which are also not very social. The Far-Eastern and Siberian *M. leucurus* exhibit a different degree of SSD and, therefore, might have different social structures. However, Asian badgers normally do not form large social groups in the Far East, Siberia, and Middle Asia (Stroganov 1962; Heptner et al. 1967; Shibanov 1989; Gorshkov 1997). The Japanese badgers, which are characterized by a relatively low degree of sexual dimorphism, also have a non-social organization (Tanaka et al. 2002). Therefore, the relatively low degree of SSD found in the Siberian *M. leucurus* and in *M. anakuma* cannot be explained by their particular social organization.

Our observations support Dayan and Simberloff (1994, 1996), who proposed that sexual selection for an increase of the size of canines is unlikely to be significant for badgers and mustelids in general, because threat displays are relatively rarely observed in the Mustelidae. We also agree with LeBlanc et al. (2001) and Badyaev (2002) who suggested that it is necessary to take into account the frequency of display of sexually dimorphic dental characters and the possible variation through time when local populations of badgers are compared.

From the above reasoning, we suggest that the differences in the degree of sexual dimorphism among the three species of badgers and the intraspecific forms (i.e., the European–Transcaucasian forms and the Siberian–Far-Eastern forms) may have been caused not by differences in their diet or social structure, but may be explained rather by the history of speciation events and the formation of intraspecific distribution ranges. In other words, differences in sexual dimorphism may be simply a reflection of phylogenetic and paleobiogeographical relationships. Several investigators have found large (Cheverud et al. 1985; Ely and Kurland 1989) or small, but nevertheless significant (Björklund 1990), effects of phylogeny on SSD in some other groups of vertebrates, such as some primates and birds.

The differences in the manifestation of SSD in the Eurasian badgers support an earlier hypothesis that *M. meles*, *M. leucurus*, and *M. anakuma* are separate species (Abramov 2001, 2002, 2003). The analysis of craniological characters of the Eurasian badgers shows different levels of SSD and geographic variation of SSD in the three species that were studied. The ancestral form of badgers might have displayed a relatively pronounced SSD, which on the whole is typical of Mustelidae. This size dimorphism may subsequently have levelled off to a certain degree, because badgers, which are food generalists, inhabit various biotopes, and do not exhibit biotope specialization, have a tendency for a social mode of life, and are characterized by low aggressiveness. In this context, the degree of SSD in badgers may at least partly be correlated with the evolutionary age of their populations. According to an earlier hypothesis (Baryshnikov et al. 2003), the Late Pliocene *M. thorali*, which had a Palaearctic distribution, was the ancestor of the Eurasian badgers. In the Early Pleistocene, divergence of its peripheral populations had probably begun as a result of a separation of the western (European) and eastern (Asian) populations. Such a separation could have been the result of mountain glaciation, extensions of the Caspian Sea, landscape changes in the glacial epochs, and other palaeoclimatic factors. It presumably led to the formation of allopatric species: In the Middle Pleistocene, *M. meles* emerged as a species in Western Europe and the Mediterranean and *M. leucurus* in Central and Eastern Asia. On the whole, European populations are morphologically, particularly in skull shape, very similar, but differ notably from badgers in Asia Minor, the Middle East, and Transcaucasia. The Transcaucasian badgers were apparently isolated from European badgers periodically by the Greater Caucasus ridge and by the Bosporus and Dardanelles straits, which prevented an exchange of genetic information. The degree of genetic variability in the mitochondrial DNA control region within the European populations of badgers is very low, but significant nucleotide differences have been revealed between badgers of continental Europe and Asia Minor, including those on Crete Island (Marmi et al. in press). In subsequent periods of the Pleistocene cooling, the ranges of *M. meles* and *M. leucurus* retreated southward, southwestward, and south-eastward. Our study has demonstrated that the maximum degree of sexual dimorphism was discovered in the Transcaucasian *M. meles* and Far-Eastern *M. leucurus*. These forms occupy the range of Pleistocene refugia, where they occurred in the periods of the lowest temperatures during the Pleistocene. Recent extensive distribution ranges of continental forms with low sexual dimorphism (i.e., European *M. meles* and Siberian *M. leucurus*), the presumably younger forms, were formed in the last 15,000 years (Baryshnikov et al. 2003). The Japanese badger probably diverged from *M. leucurus* during the Middle or Late Pleistocene. The low level of genetic variation within the Japanese populations suggests that *M. anakuma* could have occupied the present habitats in Japanese islands in the relatively short period after the last glacial age (Kurose et al. 2001; Sato et al. 2003). A subsequent continuous insular isolation led to separation of *M. anakuma* from the Eurasian badgers at the species level.

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