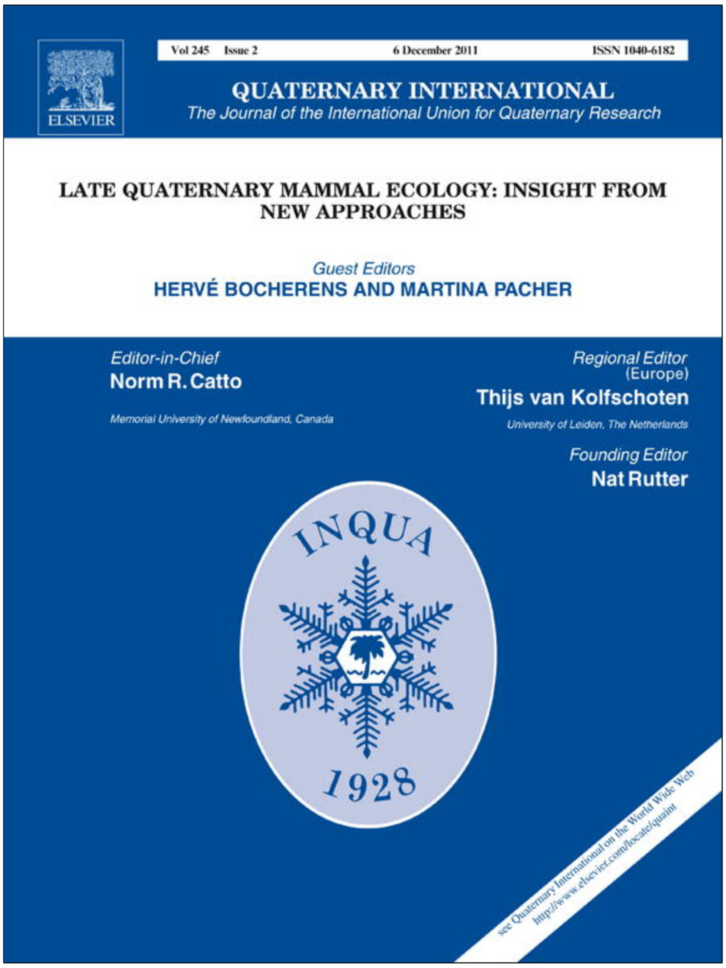

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LATE QUATERNARY MAMMAL ECOLOGY: INSIGHT FROM NEW APPROACHES

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Craniometrical variability in the cave bears (Carnivora, Ursidae): Multivariate comparative analysis

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ABSTRACT

Morphological and molecular data suggest the existence of several taxa of cave bears, which were found to belong to three major mitochondrial haplogroups: kudarensis (*kudarensis*), spelaeus (*ladinicus, eremus, spelaeus*), and ingressus (*uralensis, ingressus, kanivetz*). An analysis of craniometrical variability was carried out based on 20 measurements of 279 skulls from 40 European, Ural, and Caucasian localities, in order to investigate morphological similarity/dissimilarity of these taxa in a multivariate approach. The craniometrical analysis divides cave bears into two groups: small cave bears and large cave bears. The group of small bears consists of *rossicus*/*uralensis* and *ladinicus*. In some skull proportions, these taxa display intermediate position between brown and cave bears, i.e. presumably possessing archaic characters of their common ancestor. The group of large bears includes taxa with more specialized skulls. An early radiation within this group is demonstrated by *kudarensis* which probably ranged across Asia, and *deningeri* which occupied Europe east to the Ural Mountains. In its craniometrical characters, *kanivetz* from the Late Pleistocene of the Urals resembles *deningeri*. Other taxa of large cave bears (*spelaeus, ingressus* and *eremus*) reveal further evolution of cranial characters, being similar in the skull proportions. The level of difference between *spelaeus* and *ingressus* does not exceed that between subspecies of the recent brown bear, such as *Ursus arctos beringianus* and *U. a. piscator*. The examined isolated population of large cave bears from Volga River region (Zhiguli Hills) is similar to *ingressus*. Thus, based on the craniometrical data, the following species of cave bear are recognized: *Ursus kudarensis* (with the subspecies *U. k. praekudarensis* and *U. k. kudarensis*), *U. deningeri* (several subspecies), *U. rossicus* (with subspecies *U. r. rossicus* and *U. r. uralensis*), *U. ladinicus*, *U. spelaeus* (with subspecies *U. s. spelaeus, U. s. eremus, U. s. ingressus,* and, provisionally, *U. s. kanivetz,*).

1. Introduction

Cave bears are one of the most well-known representatives of the Quaternary mammal fauna of Northern Eurasia. Morphological peculiarities of the skeleton and teeth provide evidence for regarding cave bears as a separate subgenus *Spelearctos* E. Geoffroy, 1833 within the genus *Ursus* (Baryshnikov, 2007). Specialization of the dentition indicates that cave bears predominantly consumed plants (Kurtén, 1968; Garsia, 2003), a conclusion which is ascertained by the results of isotopic analysis of ancient bones (Bocherens et al., 1997, 2006). However, at least in some populations, cave bears might have become omnivorous before overwintering (Peigné et al., 2009).

For a long time it was accepted that the distribution of cave bears is confined to Europe eastwards to the Urals and Caucasus, with their geographical origin being regarded as European (Kurtén, 1968; Musil, 1980, 1981). Two chronospecies were recognized: *Ursus deningeri* von Reichenau, 1904 and *U. spelaeus* Rosenmüller, 1794 for the Middle and Late Pleistocene, respectively.

Until recently, the taxonomic diversity of Late Pleistocene cave bears remained unstudied. European researchers suggested an absence of geographical differentiation in *U. spelaeus*, with the exception of a smaller size of animals from high altitude locations in the Alps (Fischer, 1991; Rabeder et al., 2000). In contrast, Vereshchagin (1973) has distinguished a large cave bear from the Ural Mountains into as a distinct subspecies, *U. s. kanivetz*.

Baryshnikov (1998) showed that large cave bears from the Southern Caucasus preserved an archaic dentition until the Late

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Pleistocene, referring them to *U. deningeri* and distinguishing two subspecies: *U. d. praekudarensis* (Middle Pleistocene) and *U. d. kudarensis* (Late Pleistocene). Deningeri-like bears have also been found in Israel, in Northern and Southern Siberia, Central Asia, and the Korean Peninsula (Tchernov and Tsukala, 1997; Baryshnikov and Kalmykov, 2005; Knapp et al., 2009).

In the Late Pleistocene, in addition to the widely distributed large cave bears, a small cave bear was found to occur. It was described from the Northern Caucasus (Krasnodar) by Borissiak (1930) as *U. spelaeus rossicus*. Later it started to be regarded as a separate species *U. rossicus*, including as the subspecies *U. uralensis* based on the remains of a small cave bear from Kizel Cave in the Urals (Vereshchagin, 1973). It was also revealed that *U. rossicus* possessed a wide distributional range during the Middle and Late Pleistocene, occupying the steppe zone from the Ukraine to Transbaikalia (Vereshchagin and Baryshnikov, 2000; Baryshnikov and Foronova, 2001).

The analysis of ancient mitochondrial DNA revealed genetic heterogeneity in the cave bears from the Late Pleistocene of Europe. It was shown that they belong to two major mitochondrial haplogroups, potentially corresponding to species rank: *U. spelaeus* and *U. ingressus* (Rabeder and Hofreiter, 2004). In addition, within the spelaeus-haplogroup two subclades of subspecies rank were established: *U. spelaeus eremus* and *U. s. ladinicus* (Rabeder et al., 2004; Hofreiter, 2005). These subspecies are confined to the highlands of the Alps.

The results of latest molecular genetic studies grouped cave bears from Europe, Caucasus, and Siberia into three major haplogroups: *spelaeus* (Western Europe and the Altai Mountains in Western Siberia), *ingressus* (Central and Eastern Europe, including the Urals) and *kudarensis* (Southern Caucasus and North-Eastern Siberia) (Knapp et al., 2009). Each of them is regarded now as a distinct species (Rabeder et al., 2010).

The small cave bear *U. rossicus uralensis* from the Urals is most closely related to the *ingressus*-bears but is still genetically distinct (Pacher et al., 2009). Therefore, ingressus-haplotype was established in the cave bears treated earlier as taxa of species group: *uralensis* and *kanivetz* (Vereshchagin, 1973) and *ingressus* (Rabeder et al., 2004).

DNA-analyses of cave bears from the locality of Nerubai near Odessa in the Ukraine have referred them to the ingressus-haplotype (Nagel et al., 2005; Knapp et al. 2009). However, the cave bear from Nerubai was examined by von Nordmann (1858), who denoted it in the title of his publication as *U. spelaeus* (*odessanus*). The name *odessanus* has been included into synonymy of *U. spelaeus* (e.g. de Torres Perezhidalgo, 1992: 637), providing grounds for Baryshnikov (2003: 336) to use it as a subspecies name for the cave bear of Eastern Europe and to regard *U. ingressus* as a junior synonym of *U. spelaeus odessanus*. Rabeder et al. (2008: 61) pointed out that "*odessanus*" is not a valid taxonomic name, since, in their opinion, it was proposed by von Nordmann for geographical but not taxonomic notation of the cave bear from Odessa, not being accompanied by designation of the separate subspecies. Earlier, Erdbrink (1953: 479) supposed that von Nordmann supplemented the affix *odessanus* to the species name *U. spelaeus*, probably implying a separate race of the cave bear in Odessa. Erdbrink used the combination *U. spelaeus odessanus*, which, however, does not make this name available (International Code of Zoological Nomenclature, 1999; Article 11.5.2).

Based on morphological characters, Baryshnikov (2007) recognized three species of cave bear: *U. deningeri* (including *U. d. kudarensis*), *U. spelaeus* (including *U. ingressus*), and *U. savini* (including *U. rossicus*). However the genetic data question this revision of the taxonomic structure of the group as well as the comparison of the morphological and genetic results.

The ancestor of the cave and brown bears is usually regarded to be *U. etruscus* Cuvier (Kurtén, 1968; de Torres Perezhidalgo, 1992; Baryshnikov, 2007; Rabeder et al., 2010), although Mazza and Rustioni (1992) treated this species to be highly specialized and to have no descendents. Sher et al. (2010) mistakenly referred to the publication by Mazza and Rustioni (1992) as to a source of information on the morphological similarity between *U. etruscus* and cave bear *U. savini* Andrews.

The current hypotheses on evolutionary-morphological modifications in cave bears are predominantly based on the analysis of dental morphology (Baryshnikov, 2006; Rabeder et al., 2010) or on the proportions of metacarpal and metatarsal bones (Withalm, 2001). To date, the important system of craniometrical variability, which is widely used in the taxonomy of recent mammals, was not used for the classification of cave bears. Methods of multivariate analysis provide a possibility to include a large set of characters in order to adequately compare samples differing by geographical location, geological position or belonging to different genetic groups. In addition, this analysis can include samples without genetic data. This approach has already been successfully applied in craniometrical studies of modern populations of the brown bear (*Ursus arctos* L.) from the region of the Sea of Okhotsk (Baryshnikov et al., 2005; Baryshnikov and Puzachenko, 2010).

The aim of the present study is an attempt to interpret the taxonomic structure of the subgenus *Spelearctos* based on the evaluation of stratigraphical and geographical variability of cave bear skulls as well as on the development of sexual dimorphism in their size. This study aims to clarify the relationships within cave bear taxa, reconstruct pathways of their evolution and dispersion, elucidate the level of craniometrical differences or similarity between brown and cave bears, and develop hypotheses with regard to the causes for the extinction of the latter connected to their morphological diversity.

2. Material and methods

The examined material on fossil bears comprises 279 skulls from 40 localities of Europe, Urals, and Caucasus (Table 1, Fig. 1).

The authors have examined the collections of the Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia), Paleontological Institute of the Russian Academy of Sciences (Moscow, Russia), Zoological Museum of Moscow State University (Moscow, Russia), Museum of Mines (Saint Petersburg, Russia),

Table 1
Cave bear (according to *a priori* taxonomy) and brown bear samples.

Species	Subspecies	Sample size		
		n	Males	Females
U. spelaeus	*U. s. spelaeus*	93	47	46
	U. s. eremus	21	12	9
	U. s. ladinicus	3	3	–
U. ingressus		101	69	32
U. kanivetz		28	16	12
U. kudarensis	*U. k. praekudarensis*	1	–	1
	U. k .kudarensis	7	7	–
U. rossicus	*U. r. rossicus*	2	2	–
	U. r. uralensis	12	5	7
U. deningeri		11	6	5
Total		279	167	112
U. arctos	*U. a. piscator*	77	53	24
	U. a. yesoensis	77	46	31
	U. a. arctos	75	75	–
	U. a. collaris	27	27	–
	U. a. beringianus	32	32	–
Total		288	233	55
All groups	567			

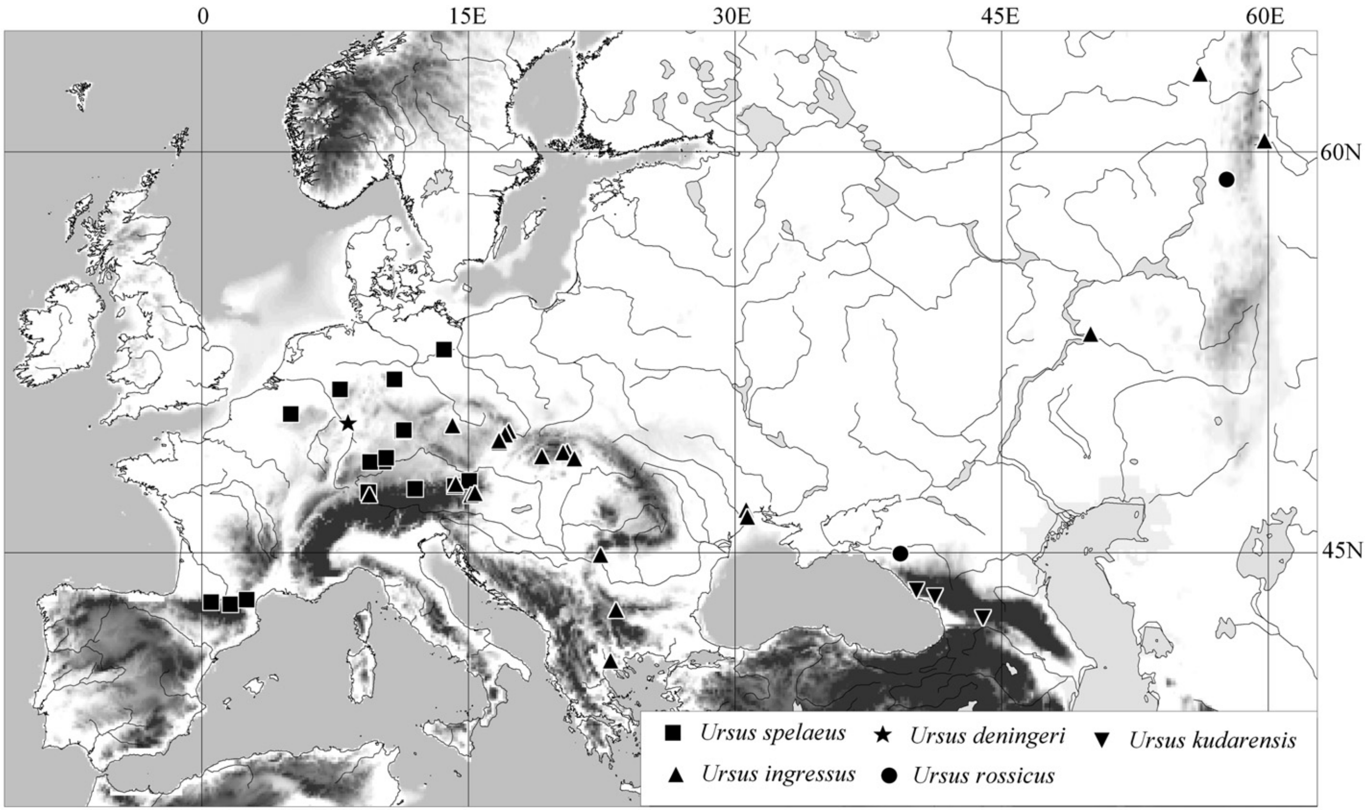

Fig. 1. Map of the cave bear's subsamples which were in used (according to *a priori* taxonomy).

Geological and Mineralogical Museum of Kazan State University (Kazan, Russia), Natural History Museum (Kiev, Ukraine), Finnish Museum of Natural History (Helsinki, Finland), Natural History Museum (London, UK), Institut Royal des Sciences Naturelles de Belgique (Brussels, Belgium), Museum für Naturkunde, Humbold-Universität (Berlin, Germany), Institut für Paläontologie (Erlangen, Germany), Staatliches Museum für Naturkunde (Stuttgart, Germany), Naturhistorisches Museum (Mainz, Germany), Naturwissenschafliche Sammlung, Museum Wiesbaden (Wiesbaden, Germany), Landesamt für Denkmalpflege Hessen (Wiesbaden, Germany), Niedersächsischen Landesmuseum (Hannover, Germany), Muséum National d'Histoire Naturelle (Paris, France), Naturmuseum (St. Gallen, Switzerland), Museum Appenzell (Appenzell, Switzerland), Institut für Paläontologie (Vienna, Austria), National Museum (Prague, Czech Republic), Moravské Museum (Brno, Czech Republic), Slovak National Museum (Bratislava, Slovakia), Museum of Spiš (Spišská Nová Ves, Slolovakia), Aristotle University of Thessaloniki (Thessaloniki, Greece).

The examined material is represented by the following taxa: *U. spelaeus*, with subspecies: *U. spelaeus spelaeus* Rosenmüller, 1794 (including type locality Zoolithen Cave and 10 other localities from Germany, Belgium and France, Late Pleistocene), *U. s. eremus* Rabeder et al., 2004 (type locality Ramesch Cave and 2 others localities from Austria and Switzerland, Late Pleistocene), *U. s. ladinicus* Rabeder et al., 2004 (type locality Conturines Cave in Italy, Late Pleistocene); *U. ingressus* Rabeder et al., 2004 (type locality Gamssulzen and 16 others localities from Ukraine, Czech Republic, Slovakia, Switzerland, Austria and Greece, Late Pleistocene); *U. kanivetz* Vereshchagin, 1973 (type locality Medvezhiya Cave and 2 others localities in East European Russia, Late Pleistocene); *U. rossicus*, with subspecies: *U. rossicus rossicus* Borissiak, 1930 (type locality Krasnodar in Northern Caucasus, Russia, Late Pleistocene), *U. r. uralensis* Vereshchagin, 1973 (type locality Kizel Cave and also Mokhnevskaya Cave, Middle Ural, Russia, Late Pleistocene); *U. kudarensis*, with subspecies: *U. kudarensis kudarensis* Baryshnikov, 1985 (type locality Kudaro 3 Cave, layers 3–4, Southern Caucasus, Late Pleistocene), *U. k. praekudarensis* Baryshnikov, 1998 (type locality Kudaro 1 Cave, layer 5, Southern Caucasus, Middle Pleistocene); *U. deningeri* von Reichenau, 1904 (type locality Mosbach, Middle Pleistocene). The taxon *U. savini* Andrews, 1922 from Middle Pleistocene Bacton Forest Bed in England was not analyzed in our study, since we had no cranial material; recently cave bear with similar dental morphology was find in Arctic Siberia (Sher et al., 2010). This list of cave bears is regarded as *a priory* taxonomy.

For comparison, samples of the recent brown bear from various geographical regions were used, including 288 skulls (Table 1) (subspecies *U. a. arctos* L., *U. a. piscator* Pucheran, *U. a. collaris* G. St-Hillaire et Cuvier, *U. a. beringianus* von Middendorff, and *U. a. yesoensis* Lydekker).

A scheme of the measurements taken is shown in Fig. 2. Twenty measurements were taken from each skull. Generally, only skull crania of adult individuals were measured, but because of their importance several probably subadult specimens were also included in the analysis. Age classes were defined by the characters of skull structure (development of crests, obliteration of sutures, tooth wear, etc.). The gender of fossil skulls was determined by the size of the upper canines and occasionally by the skull dimensions (Baryshnikov, 2006).

For the fossil skulls with incomplete sets of measurements, the EM (expectation maximization) estimation method was used (Dempster et al., 1977) for the missing values, separately for subsamples of males and females. EM estimates the means, the covariance matrix, and the correlation of variables with missing values, using an iterative process. Grubbs two-sided test (Stefansky, 1972) for revealing outliers in new variables was used. Extreme values were changed to their estimations received by the EM

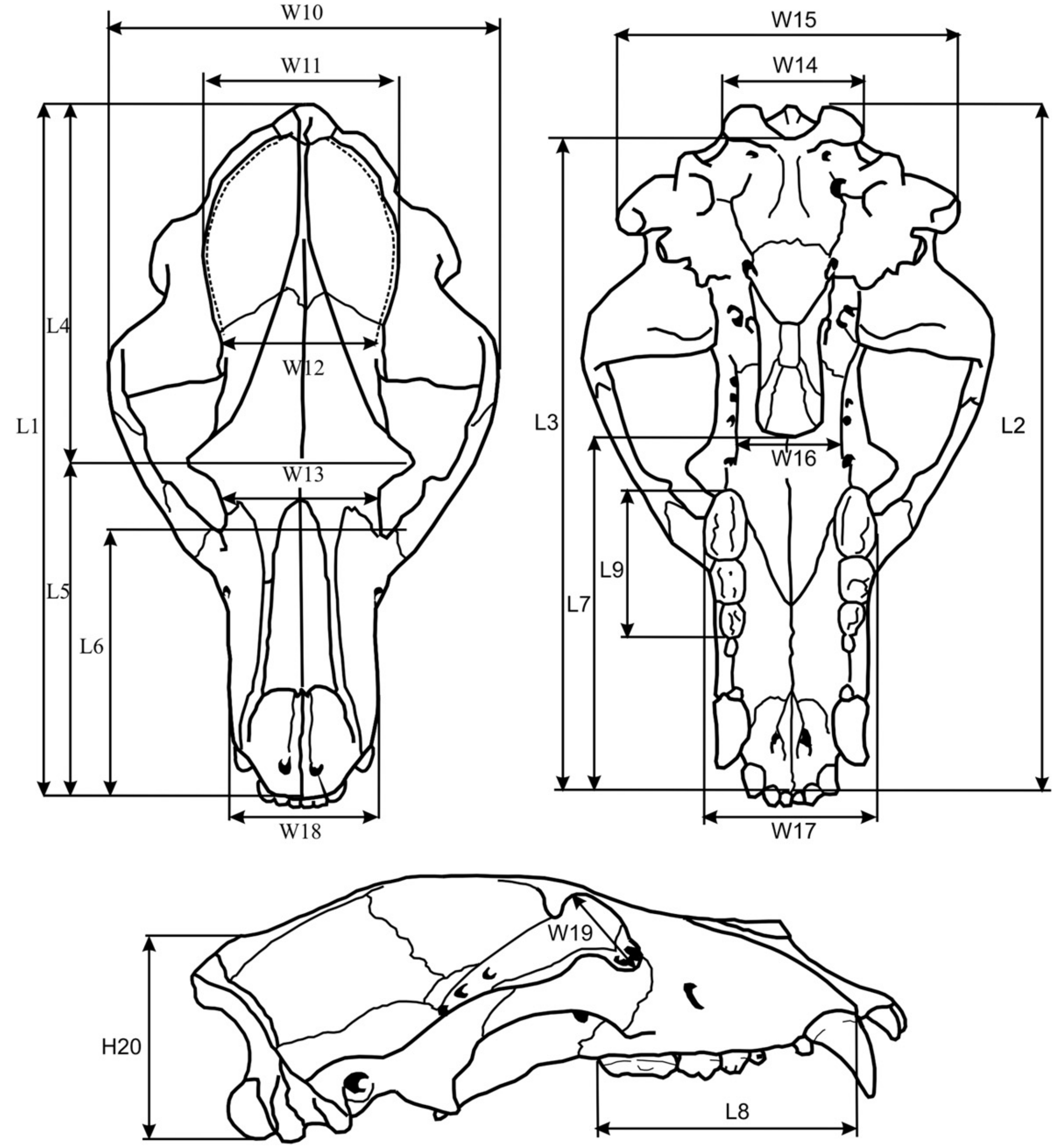

Fig. 2. Scheme of skull measurements in *U. arctos*. Abbreviations: L1 – total length; L2 – condylobasal length; L3 –basal length; L4 – neurocranium length; L5 – viscerocranium length; L6 – length of rostrum; L7– palatal length; L8 – tooth-row length C1 – M2; L9 – tooth-row length P4 – M2; W10 – zygomatic width; W11– neurocranium width; W12 – minimal skull width (postorbital width); W13 – interorbital width; W14 – condylar width; W15 – mastoid width; W16 – minimal palatal width; W17 – greatest palatal width; W18 – width of rostrum (at canines); W19 – greatest diameter of orbit; H20 – cranial height.

method. Statistical differences (average, variance, type of distribution) between the variables were tested by comparing the data set including the missing values filled in by the EM method compared to the initial data set. No statistical differences could be detected between the two data sets. Subsequently, the variables with the filled missing values for estimating morphological distances between any pairs of the specimens were used exclusively.

Statistical methods were used which were based on minimal number of prior statistical hypotheses about the objects of investigation. Furthermore, the principle of “minimal number of prior hypotheses” was used as the basis for the research as a whole and, wherever possible, the simplest assumptions were used and tested. At the beginning of this research, samples were considered “homogeneous” and were not divided by their *a priori* taxonomic division and sex. Also, following the above reasoning, restrictions were not imposed on the sample distributions of raw data and relationships between variables (linear or nonlinear). For this latter reason, the application of parametric statistical methods that assumed normal distribution, homogeneity of variances/covariance within the samples or groups, and linear correlation between variables were minimized. Also, from the above reasoning, no restrictions were imposed on the sample distributions of raw data and relationships between variables (linear or nonlinear).

Variables were standardized to exclude any influence of the scale of the different measurements on the results. Transformation was done according to the following equation:

$\widehat{x}_i = (x_i - x_{\min})/(x_{\max - \min})$, where $\widehat{x}_i$ is the standardized measurement, x_i, $x_{\min}$, $x_{\max}$ are observed, minimum and maximum value of *i-th* variable, respectively. Thus, the scale of the transformed values ranges from 0 to 1.0. This transformation is sensitive to outliers, but during the preliminary data preparation we excluded any clear outliers (extremes) from the data set and replaced with their estimations received by the EM method. Transformation generally preserves the individual variables' variances better than standardization using sample mean and standard deviation. Furthermore, transformation is suitable for variables with any type of distribution.

The square dissimilarity matrix contained the Euclidean distances and the matrix of Kendall's tau-b rank order coefficients (Kendall, 1970) among all the pairs of specimens were calculated based on all variables. The Kendall's tau-b coefficients (τ_b) were transformed to dissimilarity (d) according to the equation: $d = \sqrt{1-\tau_b}$.

The Euclidean metric, as the simple geometric distance in the multidimensional space, describes most of the variability of the skull sizes. Kendall's coefficient is the difference between the probabilities that the observed data are in the same order (accordance) for the two specimens vs. the probability that they are in a different order (discordance). For any individual, the measurements may be ranked by their values (e.g., $V_1 > V_3 > V_5 > \ldots V_k$) (Kendall, 1970). If any two specimens have equal sequences of measurements it impels high similarity of their "proportions" or "shape". Thus, Kendall's tau-b between any pair of specimens can be interpreted as an integrated metric that describes the variation of skull "shape".

The matrix of Euclidean distances and the matrix of Kendall's coefficients were used in a non-metric multidimensional scaling (MDS) procedure that visualizes proximity relations of objects by distances between points in a low dimensional Euclidean space (Shepard, 1962; Davison and Jones, 1983). Initial configuration was calculated according to the metric MDS algorithm (Torgerson, 1952). Metric solution was used as a starting configuration for the non-metric algorithm (Kruskal, 1964). In contrast the different methods of factor analysis, MDS takes into account a nonlinear part of variability (James and McCulloch, 1990). Thus, MDS is the nonparametric analog of the well-know PCA and other similar parametric techniques.

MDS is one of the most unprejudiced and robust multivariate methods in cases when no assumptions about the type of multivariate sample distribution or about clear linear relationships between variables exists. In this sense, MDS has methodological advantages compared to standard PCA and other parametric linear methods of multivariate exploratory data analysis (for details, see James and McCulloch, 1990). MDS also offers an opportunity to use any kind of distance or similarity matrix (e.g., Euclidian, nonparametric correlations, and so on) in contrast to traditional PCA and factor analysis which are based on correlation/covariation matrixes. Practice shows that in most cases, MDS results are close to PCA results, but in cases when there is a significant non-linear component of variation, the MDS axes reproduce observed variables (through multiple regression from MDS axes) better than PCA. In the framework of multivariate analysis (James and McCulloch, 1990), an attempt was made to analyze the pattern of relationships among the individuals by reduction of their dissimilarity/similarity matrix to few uncorrelated dimensions, as MDS produces underlying uncorrelated MDS axes which are carrying the main information about the variation among the specimens (analogous to the factor scores in PCA).

The "best-minimum" dimension (number of MDS axes) in the MDS model was estimated based on "stress formula 1" (Kruskal Stress). Kruskal Stress is the standard deviation of the reproduced distances from the observed ones. It is assumed that if the distribution of the dissimilarities in the input matrix is close to random, the value of the Kruskal Stress ($Stress_{\text{mod}}$) must be maximal, and the stress decreases monotonically according to increasing numbers of dimensions. For the values of stress received from observations it is possible to write down the linear regression model: $Stress_i = \mathrm{B} \cdot Stress_{i,\,\text{mod}} - \mathrm{A} + e_i$, where $Stress_i$ is the observed Kruskal Stress for *i-th* dimension (i from 1 to 15, in our case), A and B are constants, e_i represents a residual. Required values of i correspond to the dimension ("best-minimum" dimension) of MDS model which have maximum negative residual e_i (Puzachenko, 2001). According to the initial assumption, in the last case, locations of the individuals in multidimensional space are mainly deviate from stochastic model of variability.

In this study the MDS axes for a model based on Euclidean distances matrix are marked as E1, E2… and MDS axes based on Kendall's rank correlation matrix are marked as K1, K2… All were interpreted as the main components of the morphological variation observed.

Spearman rank order correlation coefficients were used as a nonparametric analogue of factor loadings in PCA and the coefficients of determination between the MDS axes and measurements as value of explained variance, in order to interpret their biological content. Modules of Spearman coefficients that are equal or higher than 0.5 are considered as important, which correspond to Pearson correlation of approximately about 0.6 or higher. The measurements with low values of explained variance ($r^2 < 0.5$) had more "disordered or stochastic variability" compared to other measurements. At this stage of analysis, MDS axes were interpreted in a "biological" sense.

Effects of sex and *a priori* taxonomy factors in MDS axes variation were estimated using variance components analysis (Searle et al., 1992). Nonparametric Kruskal–Wallis Tests and Mann–Whitney *U* Tests were used for testing for the effects of taxonomy and sex. At these stages of analysis, the hypothesis of homogeneity of the sample was tested in all cases. It was assumed that variance of MDS axes can include geographical depending component in two relatively independent variants. The first variant is conditional on geographical position of the site, and the second with its height above sea level. For a check of this hypothesis in linear regression models, the parts of variance (as r^2) explained by latitude, longitude and height above sea level (altitude) were measured separately and for all three factors (as a linear combination).

Based on the MDS axes, different methods of clustering were used: hierarchic classification (Unweighted Pair Group Method using Arithmetic Mean – UPGMA, metric - Euclidian distance) and dichotomous classification. Dichotomous classification used the algorithm designed by Puzachenko et al. (2004), and Fracdim ver. 1.9 software. When the results of different classifications were similar, the following formal selection criterion was used: the best classification was based on a level of the morphological differentiation between clusters based on *F*-criteria in one-way ANOVA. In general, the best classification should have of the largest *F*-value in this test. Cross-tabulation was used to examine match/mismatch of the *a priori* taxonomy and formal morphometrical classifications.

At first, the complete sample including cave and brown bears (males and females) was investigated (Section 3.1 and 3.5). Then, samples of males and females of cave bears were investigated independently from each other (Sections 3.2 and 3.3). The basic results are illustrated using cave bear males, because the results for males and females were very similar.

A high degree of sexual dimorphism was observed for the cave bear (Kurtén, 1955; Grandal-d'Anglade, 2001; Baryshnikov, 2007). For the assessment of size sexual dimorphism (SSD), standard methods of univariate analyses were used, with preference given to non-parametric methods. The methods and mathematical approach of SSD analysis were expanded in Abramov and

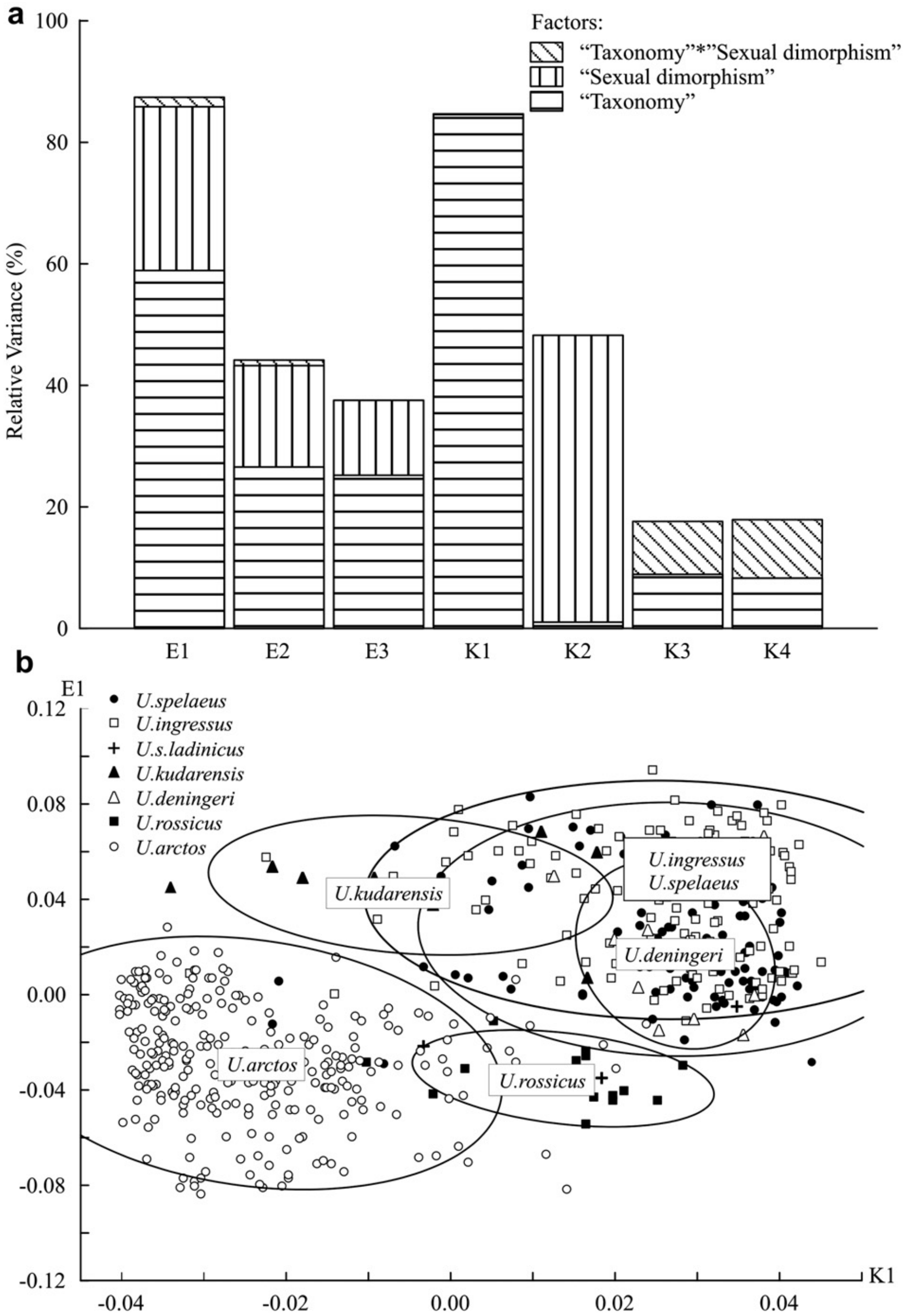

Fig. 3. a- Relative variance components (%) in MDS axes which are explained by cave and brown bear samples partition: *a priori* taxonomy and sexual dimorphism. Columns denote cumulative sums of components. b- Scatter plot of the most important MDS axes (E1, K1) for cave and brown bears (males and females together).

Puzachenko (2005, 2006, 2009). For a measure of SSD by a single variable, the index of male to female size was selected, as intuitively simple and easily interpretable. SSD indices were calculated as $S = (\text{mean}_{\text{male}} - \text{mean}_{\text{female}}/\text{mean}_{\text{male}} + \text{mean}_{\text{female}}) \times 100$.

3. Results: morphological differentiation

3.1. Testing and explanation of the method

The multivariate analysis of cranial variability in the cave and brown bears (jointly) shows that the main patterns of size/shape variability include at least three/four virtual factors (MDS axes) (Appendix, St.1). Overall, a linear combination of the MDS axes accounts for 71–99% (mean: 92%) of the variation for each character.

The first 'size' MDS axis E1 reflects the variability of 18 characters with Spearman correlations higher than 0.5. All these characters correlate with the "general size" of skull. The axis E2 mainly reflects the part of variability in the minimum palatal width (W16) and the maximal orbital diameter (W19). Axis E3 also correlates with maximal orbital diameter.

Allometry (nonlinearity in the general case) was confirmed for many characters: palatal length (L7), neurocranium length and width (L4, W11), postorbital width (W12), tooth-row length C1 – M2 and P4 – M2 (L8, L9), width between occipital condyles (W14), mastoid width of skull (W15), minimum palatal width (W16),

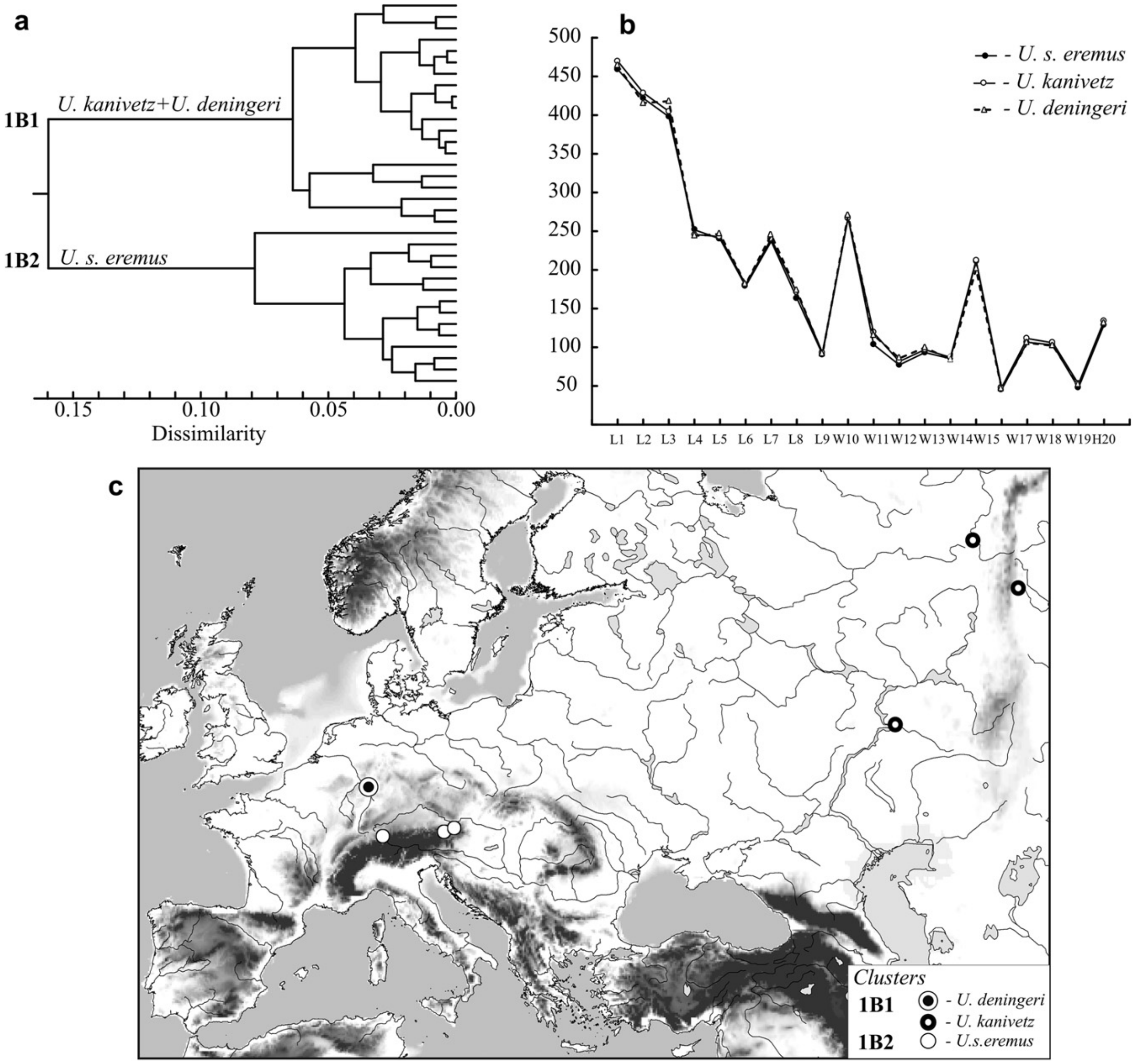

Fig. 4. a-UPGMA cave bear' (males) classification based on the MDS axes (cophenetic Correlation –0.83). b- Profiles of the characters (means, mm) for two morphological clusters 1B1 and 1B2 (see St. 5), *U. kanivetz* and *U. deningeri*.

maximal orbital diameter (W19). Isometry (relative to a change in the general length of skull) was confirmed for total length of skull (L1), basal length (L3), length of rostrum (L6), viscerocranium length (L5), zygomatic width (W10), interorbital width (W13) and cranial height (H20). Allometry (nonlinearity) is symptom of quantitative and/or qualitative changes in skull proportions (shape) as the skull increases in dimensional.

The results of hypothesis tests are shown in Appendix, St 2. The Kruskal–Wallis Tests reject the hypothesis of sample homogeneity for all MDS axis. The variance components which were associated with taxonomy and SSD are presented in Fig. 3a. Axes E1 – E3 reflect both interspecific variability and SSD. Axes K1 and K2, on the contrary, are connected with only one of the two types of variability. Axes K3 and K4 reflect variability of species-specific peculiarities of SSD.

The location of taxa within the space of the first principal MDS axes E1 and K1 is shown in Fig. 3b. Brown bear are relatively clearly isolated from the group of cave bears. The difference is due to the proportions of the skull rather than its sizes.

The variability of recent brown bear skulls in Northern Eurasia is comparable to that of cave bear skulls. It should be noted that these results have to be treated with caution as the analysis includes several species and both sexes. More importantly, this test confirms the potential of using MDS axes and the approach in general, for further investigations of cave bear skulls.

3.2. Cave bears: males

For males from the cave bear group the estimated "best-minimum" dimensions for the MDS models are 3 ("size variability") and 4 ("shape variability"). On average, linear combination of the MDS axes explains 84% (53–95%) of the characters' variance. The first MDS axis E1 reflects the variability of 17 characters (L1-W10, W12-W15, W17, W18 and H20). The second (E2) axis is strongly

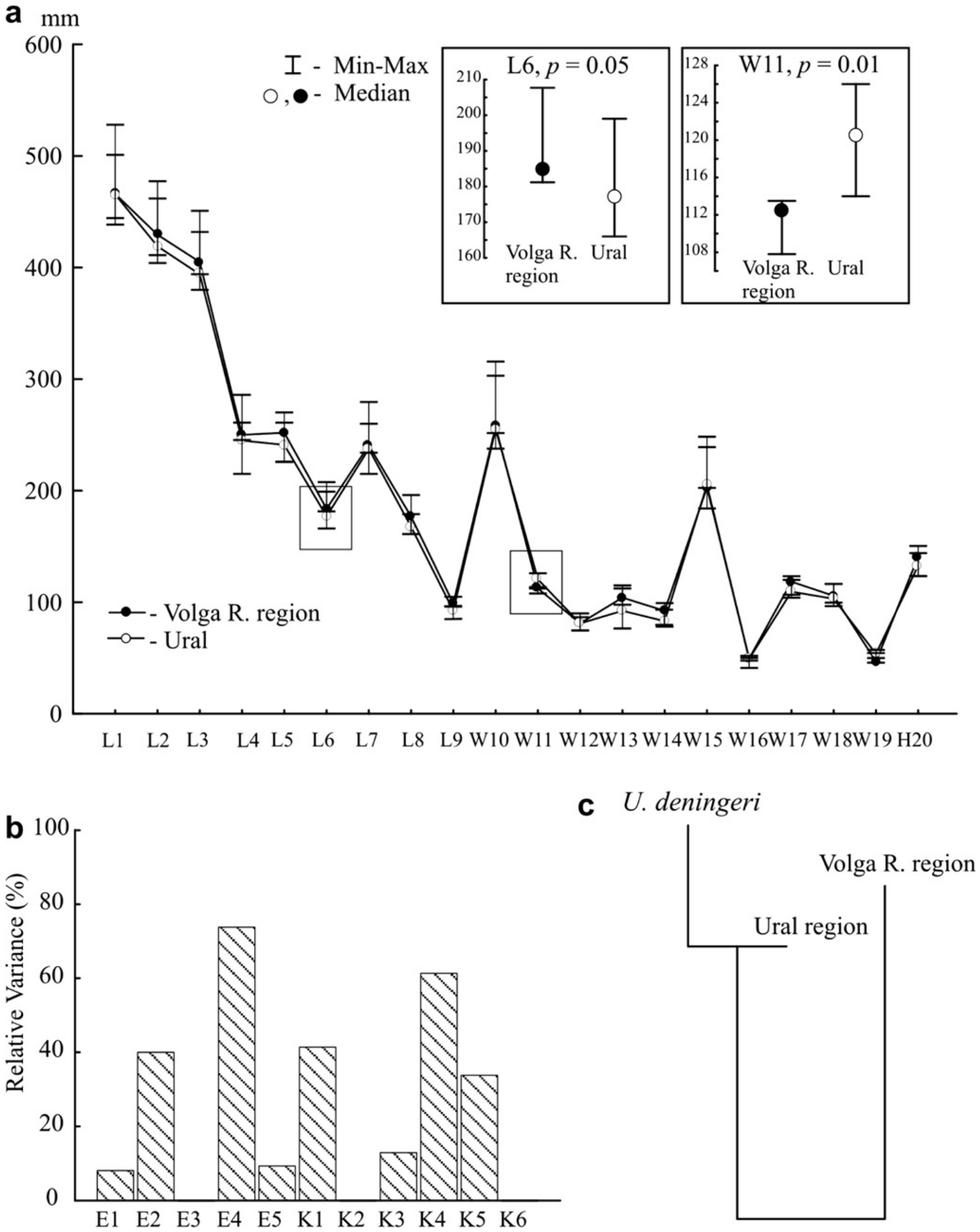

Fig. 5. a- Profiles of the characters (medians, min-max, mm) for *U. kanivetz* from the two regions and the whiskers plots (median, min-max) of the length of rostrum (L6) and neurocranium width (W11); statistical significance (*p*) according to Kruskal–Wallis Test. b - Relative variance components (%) in MDS axes which are explained by geographical differentiation in the *U. kanivetz* sample. c- Additive tree (based on the E2, E4, K1, K4 and K5 MDS axes (see also Fig. 11b)) of the two geographical variants of *U. kanivetz* (Ural and Volga River regions) and *U. deningeri*.

correlated with the greatest diameter of orbit, and partly with neurocranium width. Axis E3 partly describes postorbital width variability. Variability of 11 characters (L1, L3-L6, L8, W10, W13, W17, W18, H20) conforms to isometry. The other characters show allometric variation.

The main effect of *a priori* taxonomy was observed in the size components of variability (axes E1-E3). K1 and K2 axes also contribute to morphological differentiation, especially on the species level.

On the first level of classification (dichotomy and hierarchy) the sample of cave bears is divided into two groups (Appendix, St. 3, Sf. 1). The first group is mostly formed by larger cave bears *U. s. spelaeus, U. kudarensis, U. ingressus, U. s. eremus*, while the second group (cluster 2) includes smaller cave bears *U. rossicus* and *U. s. ladinicus*. Regarding some variables (L1, L2, L4, W10, and the other) *U. kanivetz* and *U. deningeri* occupy an intermediate location between them. However, overall the last two taxa are much closer to cluster 1.

Two groups of cave bears were later analyzed separately. MDS model for large cave bears (cluster 1) included 3 axes of E-type and 6 axes of K-type. On average, linear combination of the MDS axes explained 81% (68–94%) of the cranial variability. Relative variance components explained by *a priori* taxonomy were comparatively low (<50%: from 0 up to 48.6). Cluster 1 was divided into two clusters. The core of cluster 1A is represented by *U. s. spelaeus* and *U. ingressus* (Appendix, St. 4). The second cluster (1B) is formed by *U. s. eremus*, *U. kanivetz*, and *U. deningeri*. *U. kudarensis* takes up an intermediate position. Based on this intermediate result the bears from the clusters 1A and 1B were investigated separately. The presence of a unique combination of characters in *U. kudarensis* motivated us to deal with this taxon as a separate morphological cluster.

The MDS model for *U. s. eremus*, *U. kanivetz* and *U. deningeri* (cluster 1B) includes 4 components of size variability and 5 components of skull proportion variability. Their combination mirrors 68%–99% (average – 89%) of the variability of the individual measurements. It is necessary to emphasize that only two of these components (E2 and K1) mirror the variability which probably connected with the taxonomy of the group. Dichotomy and hierarchical classification of the samples, based on axes E2, K1, give the same result (Fig. 4, Appendix, St. 5). On the one hand, the classification confirms essential difference of *U. s. eremus* to the other taxa. On the other hand, there is morphological similarity between *U. kanivetz* and *U. deningeri*. Components E2 and K1 correlate significantly with the height of the locality above sea level (Spearman correlation coefficients are −0.67 and 0.56, respectively). The cave bear localities from morphological clusters 1B1 and 1B2 are shown in Fig. 4c. The range of *U. s. eremus* is bordered by highland Alps. For *U. kanivetz*, the samples from the Urals and Volga River (Zhiguli Hills) are included, i.e. the bears of this region originated from lowlands. This explains the correlation between the components of morphological variability and the altitude of the localities.

In the framework of the research on bears from cluster 1B1, the hypothesis of absence of the difference between the samples *U. kanivetz* from the Urals and Zhiguli Hills was tested (Fig. 5). The effect of geographical variability of *U. kanivetz* was discovered for several measurements, where the difference for the length of rostrum (L6) and neurocranium width (W11) were statistically significant between the two locations (Fig. 5a). Geographical variability contributes essentially to the variance of some MDS axes (Fig. 6b). *U. deningeri* shows morphological similarity with *U. kanivetz* from the Urals (Fig. 5c).

The morphological cluster 1A that includes *U. s. spelaeus* and *U. ingressus* was considered. Three components of size variability and 6 axes revealing the variability of skull proportions, replicate on average 79% of variation of the variables (from 46% for minimal palatal width up to 94% for total length of the skull). Statistical assessment of the effects of *a priori* taxonomy and geographical factors on the variability of cave bear skulls in cluster 1A is shown in Table 2. Table follows that ecological-geographical factors (longitude, latitude and altitude) are reflected in morphological variability, reproduced by the axes E2, K1 and K4. In summary, the hypothesis of morphological homogeneity of cluster 1A was rejected.

The level of morphological differentiation between subclusters 1A1 and 1A2 appeared to be higher on average than between the *a priori* forms - *U. ingressus* and *U. s. spelaeus* (Fig. 6, St. 6), but the distribution of the specimens included in them does not show a legible pattern in geographical space (Fig. 6c). When interpreting the results of classification it is necessary to bear in mind that in the distribution of the bears from clusters 1A1 and 1A2 as well as in the distribution of *a priori* classified *U. ingressus* and *U. s. spelaeus*, there are statistically significant ($p = 0.006$) differences in the altitude of their localities (Appendix, Sf. 2). *U. ingressus* and the representatives of the cluster 1A1 are mostly from medium height mountains and highlands, while *U. s. spelaeus* originates from lowlands and medium height mountains but not from highlands. Thus, the detected morphological forms of bears can be "ecological forms", adapted to different environmental conditions (in general to more or less severe climate). This could be the cause of their "mosaic" spatial pattern, although genetic isolation cannot be excluded. The majority, if not the whole of cluster 1A1 (at minimum more than 70% of individuals) is connected to *U. ingressus,* while *U. s. spelaeus* comprises all of cluster 1A2.

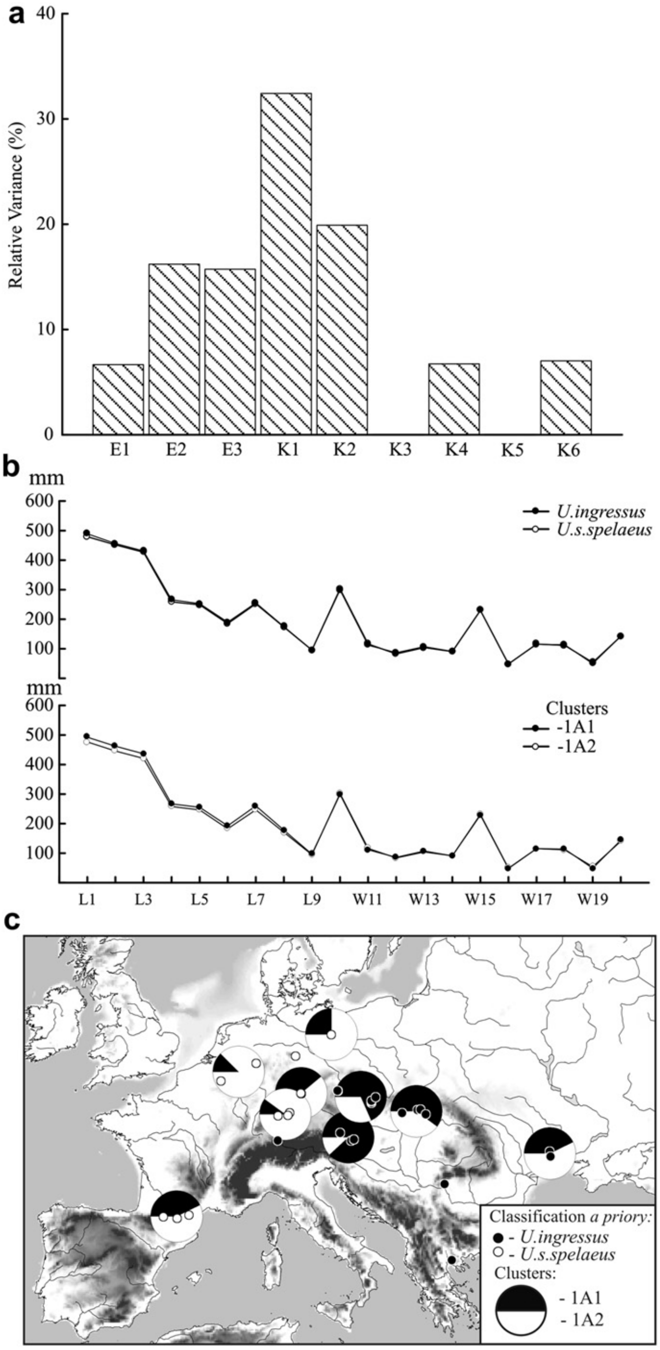

Fig. 6. a- Relative variance components (%) in MDS axes which are explained by differentiation between *U. ingressus* and *U. s. spelaeus*. b- Profiles of the characters (mean, mm) for cave bears which classified *a priori* as *U . ingressus* or *U. s. spelaus* and the analogous profiles for two morphological clusters 1A1, 1A2 (see St. 6). c- Sketch map of spatial distribution of the *U. ingressus - U. s. spelaus* group and cave bears from the clusters 1A1, 1A2.

Variability in cluster of small cave bears (cluster 2) (Appendix, St. 3) is revealed satisfactory by 2 components of size variability and by three components of proportional variability. The effect of *a priori* classification mostly shows in components E2, K1 and K3 (Fig. 7a). The MDS axis E2 mostly correlates ($r_s \geq |0.7|$) with neurocranium length (L4), zygomatic width (W10), mastoid width (W15), and greatest palatal width (W17). Axis K1 describes the variability of neurocranium length, tooth-row length P4–M2 (L9), zygomatic width, neurocranium width (W11), condylar width (W14), greatest

Table 2
Statistical tests of the hypothesis about homogeneity for the morphological cluster 1A.

MDS axis	Taxonomy (*a priory*): *U. s. spelaeus* – *U. ingressus*, N = 115, df = 1		"Complex Geographical factor": linear combination of altitude, longitude and latitude		Single "Geographical factor" (Spearman Rank Order correlation)					
	Kruskal–Wallis Test Statistic	p	r^2	p	Altitude	p	Longitude	p	Latitude	p
E1	6.2	0.01	0.0	n.s.		n.s.		n.s.		n.s.
E2	12.4	<0.001	0.24	<0.001	0.44	<0.001		n.s.		n.s.
E3	10.9	<0.001	0.08	0.03		n.s.		n.s.		n.s.
K1	21.7	<0.001	0.13	0.002		n.s.	−0.32	<0.001	0.25	0.009
K2	12.8	<0.001	0.16	<0.001	0.30	0.001		n.s.		n.s.
K3	0.29	n.s.	0.07	0.02		n.s.		n.s.		n.s.
K4	5.6	0.02	0.17	<0.001		n.s.		n.s.	0.32	<0.001
K5	0.0	n.s.	0.0	n.s.		n.s.		n.s.		n.s.
K6	4.2	0.04	0.0	n.s.		n.s.		n.s.		n.s.

palatal width and greatest diameter of orbit (W19). The component K3 generally correlates with the measurement mastoid width. Fig. 7b shows that *U. s. ladinicus* is separated well from *U. rossicus.* Within *U. rossicus,* no difference is seen between the North Caucasian (*U. r. rossicus*) and Ural (*U. r. uralensis*) individuals.

The schemes on Fig. 8 show the results of the analyses of morphological differentiation among cave bear males, with the following results: 1) morphological isolation of *U. s. ladinicus/U. rossicus* from all other cave bears, 2) similarity of *U. deningeri* and Urals *U. kanivetz*, and, probably, similarity of *U. s. eremus* and *U. kanivetz* from Volga Region, 3) isolation of *U. kudarensis* with not clear relation with *U. deningeri*, 4) strong morphological similarity between *U. ingressus* and *U. s. spelaeus*. Within different clusters, distinct sets of characters contribute to the differentiation of the groups. Therefore, the variability cannot be described appropriately in the framework of a single hierarchical model. Therefore, tree-like depictions presented on Fig. 8 are insufficient for reflecting morphological differentiation.

3.3. *Cave bears: females*

The sample of females differed from that of males because of the absence of *U. s. ladinicus, U. r. rossicus* and *U. kanivetz* from the Volga Region. The research of cave bear males showed that their morphological differentiation in general corresponds to the division of males into morphological groups. This section briefly describes the main independent results of the analysis of females and comparison to the data obtained from the analysis of males.

Dimensions of the MDS models of the morphological space in the female sample were equal to 2 for the size and 6 for the shape cranial variability. On average, linear combination of the MDS axes explains 57–94% (mean- 83%) of the variables' variations. Thus, the quality of description of separate characters of females corresponds to that of males.

The parameters of variability of both female and male skulls of cave bear are shown in Table 3. The principal pattern of morphological variability in females is similar to that in males. In comparison with the variability of male skulls, variability of female ones are characterized by less correlation of rostrum part with cerebral part of skull and less importance of allometry in whole.

Fig. 9 shows the schemes of differentiation of female cave bear skulls. Comparison of them with the same schemes independently obtained for males allows inferences about stability and validity of the division of cave bears into two groups according to cranial characters (clusters 1 and 2). The division of cluster 1 into groups 1A and 1B can also be discussed. As with the data obtained for males tree-like depictions of morphological differentiation are not completely adequate. For example, according to the analysis, females of *U. kanivetz* (Ural Region) are consistently closer to females of *U. deningeri*, while on dendrograms (Fig. 9b, c) they fall between *U. s. eremus* and *U. ingressus*. As well as for males, females of the largest and most specialized bears *U. ingressus* and *U. s. spelaeus* appear to be morphologically more similar.

3.4. *Pairwise comparisons of the species and subspecies within cave bears*

The results when cave bear male skulls of different taxa are compared for separate measurements (Mann–Whitney *U* Test) are presented in Appendix, St. 7. The main role in the variability of the skull is played by the following measurements: neurocranium width (the forms differ in 68% of cases), width of rostrum (at canines) (62%), greatest palatal width (59%), tooth-row length C1–M2 (57%), neurocranium length (57%), condylobasal length (54%), interorbital width (54%), cranial height (54%). In addition minimal palatal width (the forms differ in 32% of cases), greatest diameter of orbit (32%), condylar width (32%) and tooth-row length P4–M2 (35%) represent measurements that change consistently, but only slightly.

The most isolated position is occupied by *U. rossicus*, which corresponds to the result from the multivariate analysis and classification, while *U. s. eremus* is separated both from *U. s. spelaeus* and *U. ingressus.* The differentiation between *U. s. spelaeus* and *U. ingressus* corresponds to the level of differentiation between them and *U. deningeri*.

The differentiation of *U. s. ladinicus* also corresponds with the results of the multivariate analysis. This taxon is separated from *U. s. spelaeus* and *U. ingressus* and is much closer to *U. rossicus*.

U. kanivetz from Zhiguli Hills (Volga River region) is very close to *U. s. spelaeus*, *U. s. eremus,* and *U. ingressus*. Between Volga and Ural samples of *U. kanivetz* there is statistically significant difference in neurocranium width (W11). *U. kanivetz* from the Urals in turn differs clearly from *U. s. spelaeus, U. ingressus*, and is closest to *U. deningeri*.

In general, the result of pairwise comparisons corresponds to the scheme of differentiation in the group of cave bears described above. The samples of *U. s. ladinicus*, *U. kanivetz* (Zhiguli Hills), *U. kudarensis* and *U. rossicus* and some other forms were quite small, which can decrease the reliability of the result of comparing samples in pairs.

3.5. *General model for cave and brown bears*

To estimate the scale of morphological divergence in the group of cave bears it is reasonable to base classification on analyses that include modern subspecies of the brown bear (*U. arctos*). Males

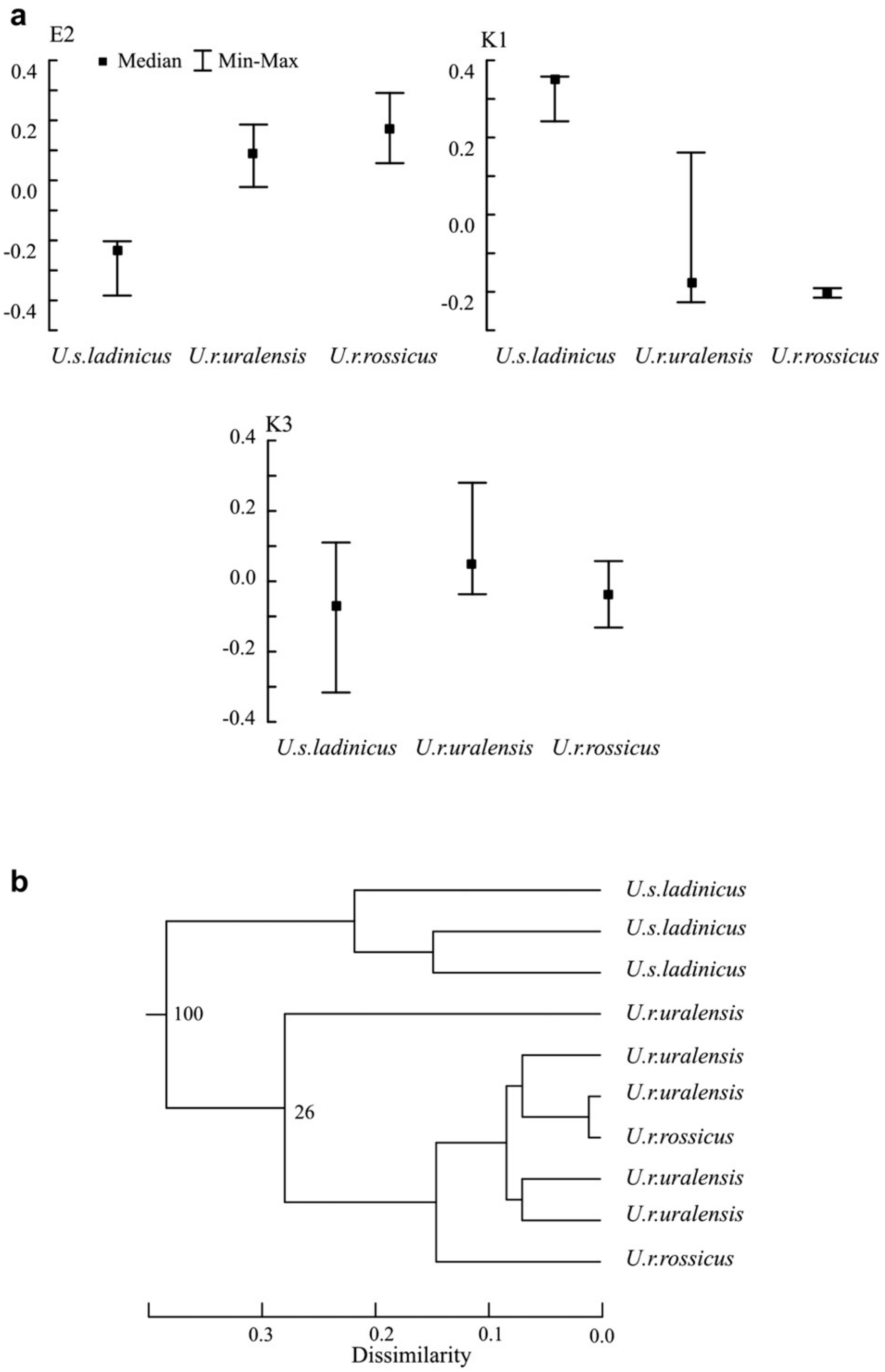

Fig. 7. a- Whiskers plots of the MDS axes E2, K1, and K3 in the *U. s. ladinicus* and the *U. rossicus* taxa. b- UPGMA classification based on the selected MDS axes (E2, K1, K3) of the morphological cluster 2 members (see St. 3); numbers near the nodes – bootstrap supports in %.

were used to show morphological differentiation and used the MDS model of brown and cave bear,. The result is shown in Fig. 10 as both the additive tree and consensus tree.

3.6. Sexual size dimorphism in cave and brown bears

The importance of SSD was shown above (Fig. 3 and Appendix, St. 2). This section presents quantitative estimations of SSD in different representatives of brown and cave bears. For cave bears, the classification according to the results described above is used.

The average SSD of cave bear skulls (ASSD = [SUM(SSD)]/n, where n – number of the variables) varied from 3.4 (*U. rossicus*) to 6.7 (*U. s. spelaeus*). Table 4 shows comparable data for some taxa of carnivorous mammals. ASSD in cave bears varies from average (*U rossicus, U. s. eremus*), to high (the largest forms). SSD can differ considerably not only among different species but also among subspecies and even different populations of the same species (Table 4).

SSD was larger in the group of large cave bears (Fig. 11a, Appendix, St. 8). Generally, the size of female skulls correlates more with ASSD than that of male skulls. Spearman rank coefficient for

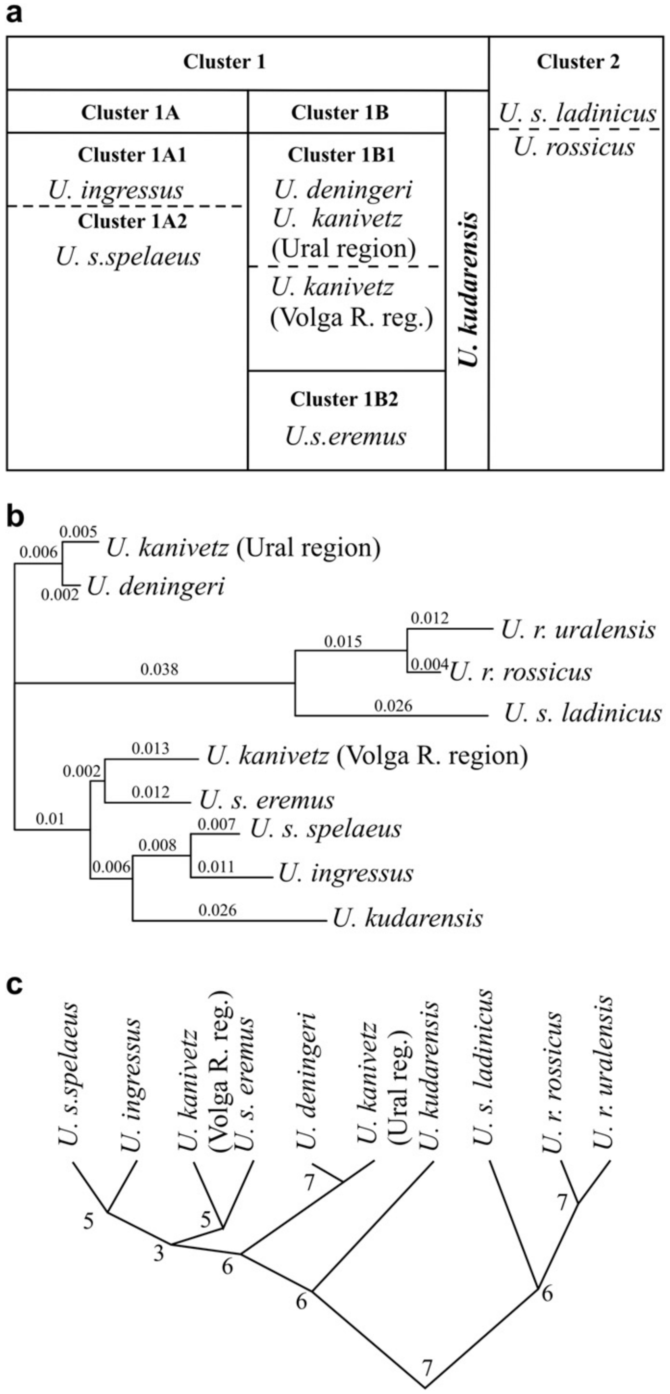

Fig. 8. Three variants for the presentation of the results of cave bears' craniometry (males): a- morphological differentiation based on successive "dichotomy"; b- additive tree based on the group median values of the MDS axes (see also Fig. 6), branches lengths are present; c- cladogram based on the group median values of the 7 MDS axes; number for each (interior) node show how many of the generated trees (Jackknife resampling method used) had an equivalent interior node.

the total length of skull and ASSD is 0.71 for females and 0.60 for males. Females are rather smaller in largest forms of cave bears in comparison with smaller forms of cave bears. This is not a strict law, but only a tendency. There seems to be no such rule for brown bears. The greatest SSD is found in relatively small island subspecies *U. a. yesoensis* (Hokkaido, Japan), and SSD for one of the largest subspecies of brown bear *U. a. piscator* (Kamchatka Peninsula) is lower.

The main difference of SSD patterns between large and small cave bears lies in different relative participation of the main lengthwise measurements of the skull (Fig. 11b). The greatest SSD values are found in *U. s. spelaeus*, *U. ingressus* and *U. deningeri* (large forms) for the following characters: zygomatic width (W10), mastoid width (W15), width of rostrum (at canines) (W18), and in *U. deningeri*, additionally, for minimal skull width (postorbital width) (W12) and cranial height (H20). Small cave bears have the greatest SSD values for neurocranium length (L4), viscerocranium length (L5), mastoid width (W15), width of rostrum (at canines) (W18) and zygomatic width (W10). *U. s. spelaeus* and *U. ingressus* show the most similar SSD. Some characters of infantilism of female skulls can be seen in *U. s. eremus.* Postorbital wide shows infantilism which is expressed by disproportionally high values of this character (W12) and minimal palatal width (W16). These measurements are on average bigger in females than in males. SSD in brown bear forms is quite different, but the difference between small and large brown bears is connected to lengthwise measurements of the skull, as it is in cave bears.

4. Discussion

The dendrogram of similarity built as a result of the study of morphological differentiation of the skull in cave bears shows the reliability of the taxa accepted *a priori*, but does not always coincide with their taxonomical ranks as well as with relationships based on the molecular data. On the basis of craniometrical characters, cave bears were revealed to be clearly divided into two groups, which may be designated as "small" and "large" cave bears. The group of "small" cave bears comprises *U. rossicus* (and, presumably, *U. savini*) and *U. ladinicus*. The group of "large" cave bears incorporates the rest of examined taxa.

The differentiation between two groups seems to be quite reliable. Presumably, these groups diverged quite early, shortly after the splitting of lineages of brown bears and cave bears. Both groups evolved independently, evolving with different rates towards the development of speleoid characters of the skull. A lag in the progress of specialization is revealed in "small" cave bears by the persistence of several ancestral craniometrical features shared with the brown bear.

Following this interpretation, *U. ladinicus* may be regarded as a highly specialized relic taxon of small cave bears, which were shifted to the high zone of Alps by representatives of the group of large cave bears. The more archaic *U. rossicus* possessed a wider distribution range in the Pleistocene, not competing, however, in the larger portion of its areal with "large" cave bears, since it was confined to steppe regions. As a relict, *U. rossicus* survived in the Urals until the Late Pleistocene (Pacher et al., 2009). The morphometry of the cheek teeth of *U. rossicus* is similar to that of *U. deningeri* (Baryshnikov, 2006).

According to the results of the mtDNA analysis, *U. ladinicus* (within the spelaeus-haplogroup) and *U. rossicus* (within the ingressus-haplogroup) split earlier than large cave bears correspondingly belonging to these groups (Rabeder et al., 2004; Pacher et al., 2009). This also testifies a basal position of small cave bears. Another result of these analyses, both small and large cave bears are not monophyletic groups. However, at the moment this is based only on a single genetic locus, mtDNA.

The present study examined only morphological similarity/dissimilarity of cave bear groups. As a result, the classification and dendrograms and cladograms illustrating it (Figs. 10, 11 and 12) does not contain directly phylogenetical signals. With the same aim of comparative morphometric research, brown bear was included in this study. However, this species *de facto* was an outer group for cave bears in a restricted sense. Very cautiously, the results do not

Table 3
Parameters of the morphological skull variability patterns in cave bear males and females.

Parameter	Males	Females
Number of the MDS axes:		
Type E (size variability)	3	2
Type K (shape variability)	4	6
Spearman rank correlations (absolute values) for the loading of the first MDS axes of the males and the females:		
Type E (size variability)	0.89	
Type K (shape variability)	0.91	
Portion of the variance of the characters which explained by linear combination of the MDS axes (coefficient of determination), %:		
Average	84	83
Min-max	53–94	57–94
Percentage of the characters with the allometry, ($N = 19$):		
%	42	32
Spearman rank correlations (absolute values) for the loading of the first MDS type E and K in the males and the females:		
	0.76	0.67
Average relative variance per MDS axis explained by *a priory* taxonomy (subspecies level):		
%	35.7	21.8
Number of the characters with the more then one independent component of the variability:		
Size variability	1 (W12)	3 (L5-L7)
Shape variability	2 (L5, W19)	4 (L1, L4, W10, W13)
Number of the characters which are independent (in full or in part) from the general size of the skull:		
	3 (W11, W12, W19)	4 (L5-L7, W19)

contradict the polyphyletic hypothesis for cave bear group. At the same time, morphometrical similarity between brown bear and the smallest cave bears (Fig. 12) can be interpreted as the result of parallel evolution of these different clades, evolutional heritage from the common ancestor.

As for the large cave bears, the common ancestor was a deningeri-like bear widely distributed in Eurasia in the Middle Pleistocene. The ancestral lineage diverged into a western branch (*U. deningeri*) and eastern branch (*U. kudarensis*). The distribution range of *U. deningeri* covered Europe, Urals, and, probably, Western Siberia. The rest of North-Eurasian territory was presumably occupied by *U. kudarensis,* since its presence in the northern part of Eastern Siberia (Yana River) was ascertained by the molecular evidence (Knapp et al., 2009). The present study provides grounds

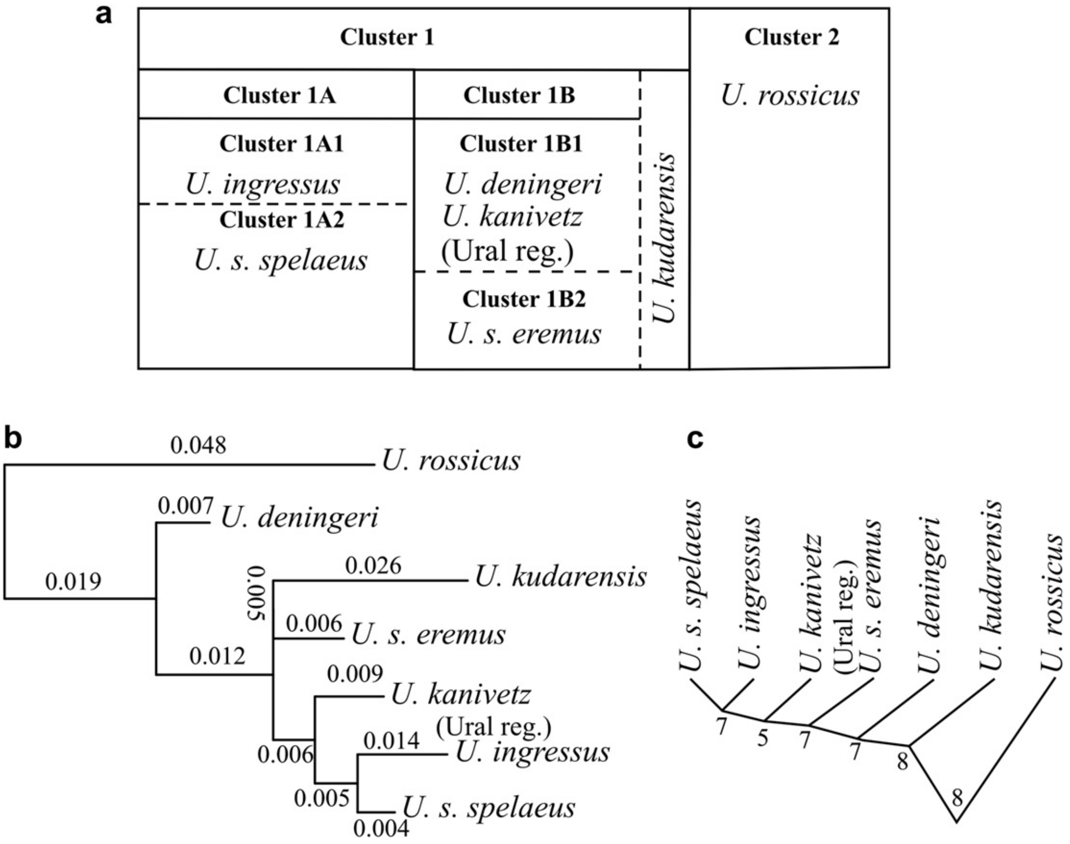

Fig. 9. Three variants of the presentation of the results of cave bears' craniometry (females): a- morphological structure based on successive "dichotomy"; b- additive tree based on the group median values of the MDS axes, branch lengths are present; c- rooted cladogram based on the group median values of the 8 MDS axes; number for each (interior) node show how many of the generated trees (Jackknife resampling method used) had an equivalent interior node.

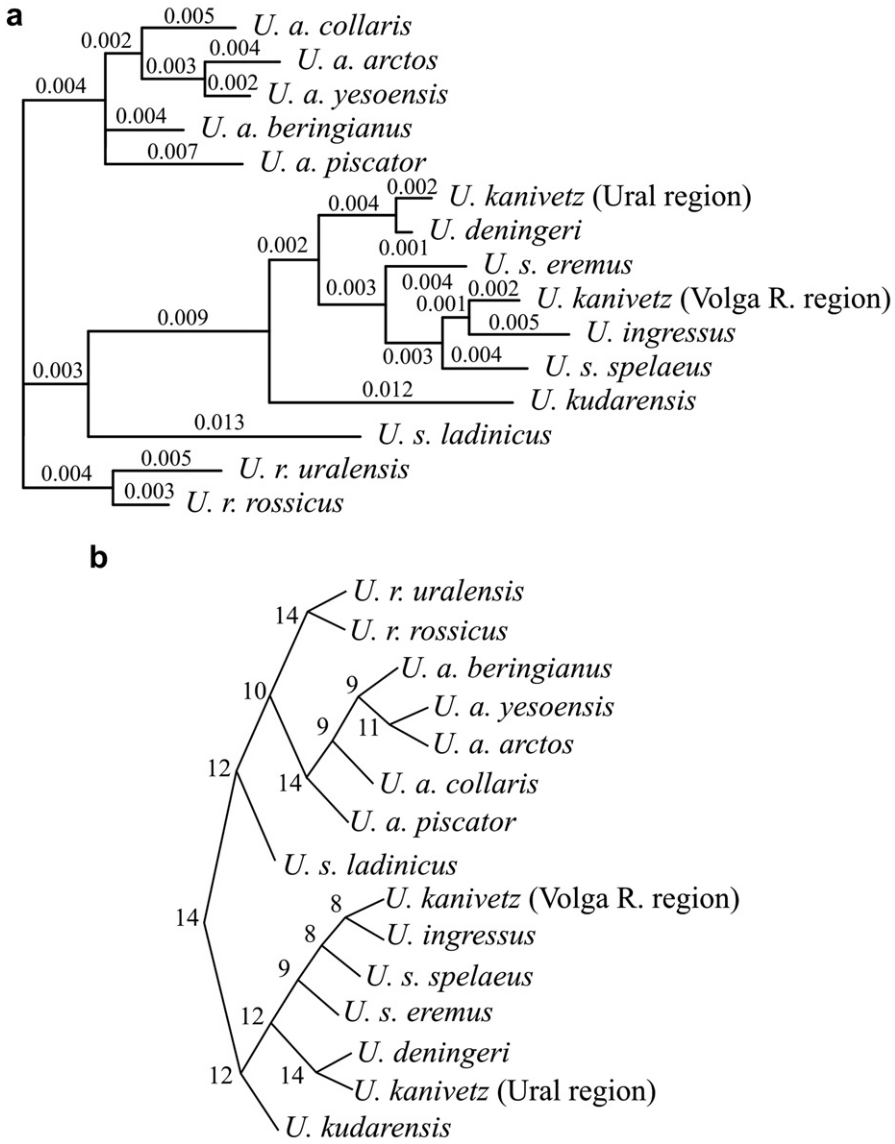

Fig. 10. a- Additive tree of the cave and brown bears (males) based on the median values of the MDS axes (MDS model presented in Table 2); branches lengths are present. b- Rooted consensus tree for the same samples of bears based on the 14 trees which were built on the means (7 trees) and medians (7 trees) of 7 MDS axes used by Jackknife resampling method: numbers near forks indicate the number of times the group consisting of the present taxa occurred among the 14 trees.

for regarding *U. kudarensis* as a distinct species. This taxonomic hypothesis has been earlier suggested in the analysis of DNA sequences of Asian cave bears (Knapp et al., 2009). Dental characteristics reveal the similarity between *U. kudarensis* and *U. deningeri* (Baryshnikov, 1998, 2006).

Consequently, several populations of *U. deningeri* were modified towards development of morphological characters leading to appearance of *U. spelaeus.* The most ancestral population survived as a relict in the Urals till the Late Pleistocene (*U. kanivetz*), where it might coexist with *U. rossicus*, occupying different biotopes. In the skull proportions, *U. kanivetz* corresponds to *U. deningeri,* its tooth morphology being, however, more modified and resembling that of *U. spelaeus* (Baryshnikov, 2006).

The next stage of the evolution of speleoid bears is represented by the medium-size cave bears *U. spelaeus eremus*, which already correspond to typical *U. spelaeus* with regard to the level of craniometrical divergence and may be regarded as a separate subspecies. Most probably, *U. s. eremus* was widely distributed throughout central and eastern Europe but later, under the pressure of larger cave bears, disappeared from the greater part of its range, surviving only in the Alp Mountains.

Finally, in the Late Pleistocene, the largest cave bears, *U. s. spelaeus* and *U. ingressus*, appeared. The original distribution range of *U. s. spelaeus* presumably occupied the greater part of Europe and south of Western Siberia. Later, its eastern populations became partially extinct, since, according to molecular data, the territory of the distribution of this taxon underwent disjunction, and the taxon survived in Western Europe and Altai (Knapp et al., 2009).

According to the taxonomy accepted *a priori*, cave bears from the Volga River region (Zhiguli Hills) were referred to as *U. kanivetz* (Baryshnikov, 2007). However, this study demonstrates a substantial similarity of this population with *U. ingressus.* Craniometrical resemblance of Zhiguli cave bears with *U. ingressus* provides a possibility to suggest an East-European origin of this taxon. *U. ingressus* probably has been ecologically better adapted to continental environments and, therefore, might prevail over *U. s. spelaeus* during cold and arid climates resulting in changes of forage reserves and in prolongation of hibernation. Within these

Table 4
Average of the SSD (ASSD) of the skull in several carnivores.

Taxa		ASSD	Reference
Ursus	*U. s. spelaeus*	6.7	This work
	U. ingressus	6.0	This work
	U. s. eremus	4.8	This work
	U. kanivetz	4.7	This work
	U. deningeri	6.4	This work
	U. rossicus	3.4	This work
	U. a. piscator	4.7	This work
	U. a. yesoensis	7.7	This work
Meles	*M. canescens*	2.7	Abramov and Puzachenko, 2005
	M. leucurus amurensis	2.9	Abramov and Puzachenko, 2005
	M. l. leucurus	1.8	Abramov and Puzachenko, 2005
	M. meles europaeus	1.2	Abramov and Puzachenko, 2005
	M. m. meles	1.8	Abramov and Puzachenko, 2005
	M. m. milleri	1.5	Abramov and Puzachenko this work
Mustela	*M. sibirica* (subspecies and populations)	5.9–9.3	Abramov and Puzachenko 2009
	M. putorius	8.4	Abramov and Puzachenko this work
	M. eversmanii	5.1	Abramov and Puzachenko this work
	M. lutreola	5.1	Abramov and Puzachenko this work
	M. erminea	7.3	Abramov and Puzachenko this work
Martes	*M. martes*	4.5	Pavlinov and Puzachenko, this work
Canis	*C. upus albus*	1.9	Lavrov and Puzachenko, this work
	C. lupus albus	2.8	Lavrov and Puzachenko this work

periods, the westward expansion of *U. ingressus* led to replacing *U. s. spelaeus* not only in Eastern Europe, but also in eastern regions of Central Europe.

The level of morphological differentiation between *U. s. spelaeus* and *U. ingressus* does not exceed subspecies rank, therefore both taxa may be referred to a single species, *U. spelaeus*. In the case of the brown bear, a similar level of differentiation was observed for the subspecies *U. arctos piscator* and *U. a. beringianus* (Baryshnikov and Puzachenko, 2010; Fig. 12).

The new conception of morphological segregation of cave bears based on craniometrical characters reveals the following taxonomic structure of the subgenus *Spelearctos*, which comprises 5 morphologically distinct species: *U. kudarensis* (*U. k. praekudarensis* and *U. k. kudarensis*), *U. deningeri* (several subspecies not discussed here), *U. rossicus* (*U. r. rossicus* and *U. r. uralensis*), *U. ladinicus*, and *U. spelaeus* (*U. s. eremus, U. s. ingressus, U. s. spelaeus* and, presumably, *U. s. kanivetz,* which corresponds more closely to *U. deningeri* in its craniometrical characters). *U. savini*, which was not included in the analysis, should be also recognized as another separate species.

Thus, analysis has established successive modifications of the skull in cave bears from the primitive state in the smallest *U. rossicus/ladinicus* to an advanced state in the largest *U. spelaeus/ ingressus*. Different taxa evolved at different rates, which resulted in the coexistence of geographical populations of cave bears during the Late Pleistocene that were different in their level of craniometrical modification. A wide distribution is revealed for *U. rossicus* and several subspecies of *U. spelaeus* (*U. s. spelaeus*, *U. s. ingressus*), whereas other taxa survived only as relicts in mountainous regions of the Alps (*U. ladinicus, U. spelaeus eremus*), the Urals (*U. spelaeus kanivetz*), and the Caucasus (*U. kudarensis*). The comparison of the phylogenetic relationships based on our study with the phylogeny based on the molecular analysis (Rabeder et al., 2004; Hofreiter, 2005; Knapp et al., 2009) showed both schemes to only partially coincide.

Molecular and morphological data retain the view that small cave bears are predecessors of large cave bears. It was suggested that small size may have been an ancestral trait in cave bears (Hofreiter et al., 2002). Large size evolved independently within each genetic lineage; within the spelaeus-lineage: *ladinicus – eremus – spelaeus*; within the *ingressus*-lineage: *rossicus – kanivetz - ingressus*; within *kudarensis*-lineage: *praekudarensis – kudarensis*. The last lineage is regarded to be provisional, since the taxon *praekudarensis* was not genetically examined; however, the taxa *praekudarensis* and *kudarensis* are found to be in the status “ancestor-descendant” (Baryshnikov, 1998).

Both analyses agree in the recognition of *U. deningeri* as the ancestor only for the cave bears of the Late Pleistocene of Europe and Western Siberia (*U. kanivetz/eremus/spelaeus/ingressus*). Large cave bears from the remaining part of Asia are, presumably, closely related to *U. kudarensis*, which survived in Southern Caucasus till the second half of the Late Pleistocene (Baryshnikov, 1998).

A discrepancy between the results of morphological and molecular analyses becomes obvious in the interpretation of the taxonomic position of *U. spelaeus* and *U. ingressus*. The level of morphological difference between these taxa does not exceed subspecies level. However, molecular data distribute them into different haplogroups, regarding these taxa as separate species (Rabeder and Hofreiter, 2004; Rabeder et al., 2010). Moreover, it was suggested that in a zone of geographical contact of *U. spelaeus* and *U. ingressus* no gene flow was presented (Hofreiter et al., 2004).

In summary, cave bears are characterized by pronounced craniometrical variability. The diversity of this group is determined by local adaptations of phytophagous cave bears to the environments in different geographical regions as well as by their poor capability for migrations. The classification of the cave bears elaborated as a result of our study is similar to that accepted *a priori*, excepting the status of *U. ingressus*, which remains controversial. The evolution of cave bears occurred on the greater part of Northern Eurasia, so that it seems that cave bears had Asian rather than European origins.

SSD in skulls of cave bears was studied in detail enough for separate “populations” or regions in Europe (Cordy, 1972; Grandal-d’Anglade, 2001). In this work, for the first time variability of SSD in different taxonomical lineages was studied. Cave bears demonstrate noticeable sexual dimorphism in the skull size, with the intensity of dimorphism increasing in the group of large cave bears. SSD indices of cave bears correspond to medium to high measures of this index in other carnivorous mammals.

Concerning SSD: 1) SSD does not depend on a size variation of the skull; 2) the absolute size difference between sexes is rather constan; 3) and both absolute and relative measures of SSD are changed include allometry (see also Grandal-d’Anglade and Lopez-Gonzalez, 2005). This study’s results testify that SSD of cave bears

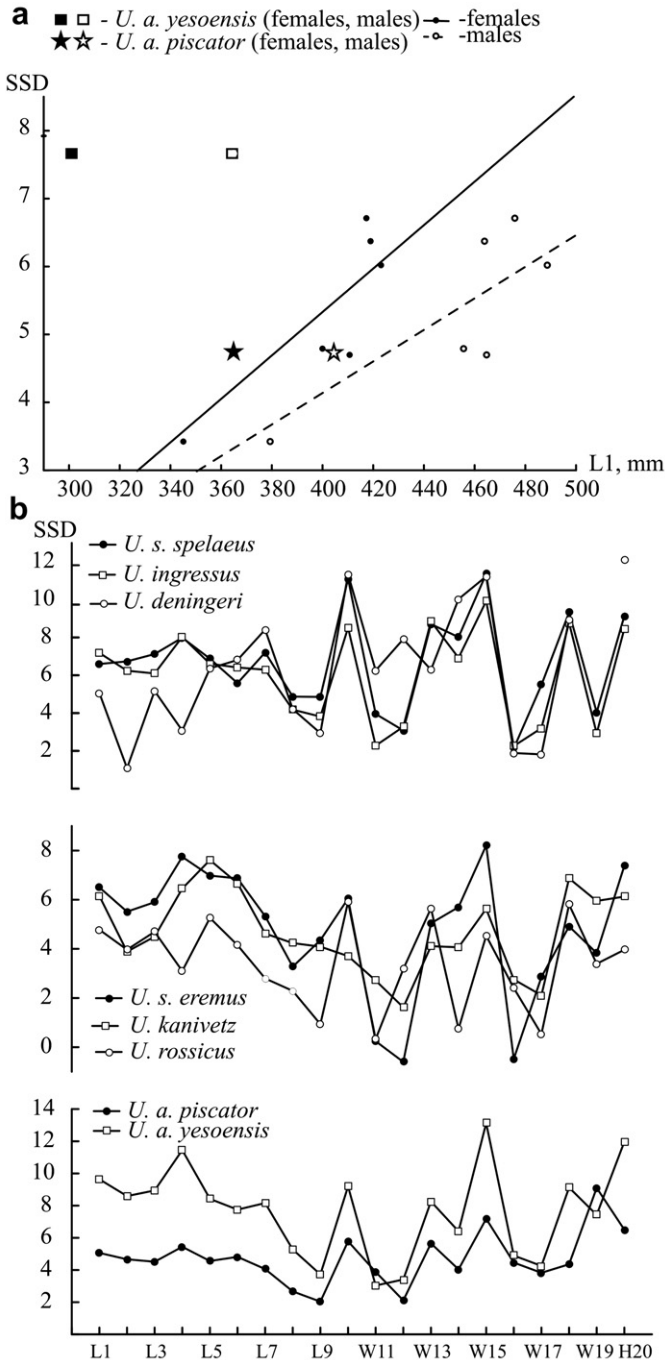

Fig. 11. a- Correlation average SSD and general size of skull in the cave bears (L1- total length of skull). b- SSD in the different cave bears forms and two brown bear subspecies.

resulted according to the third version. Several investigations of SSD in brown bear and American black bear (*U. americanus*) indicate geographical variability of SSD (Miller et al., 2009; Farkaš et al., 2009). Such variability can specify adaptable significance of SSD or group variation in ontogeny within the different species populations (Badyaev, 2002). SSD in mammals is not a constant parameter, but can vary in time and in geographical space, including connection with population dynamics (LeBlanc et al., 2001). Explanations of SSD in a mammalian skull include several hypotheses: 1) dimorphism avoids intraspecific competition, and thus animals of different sex consume various eatable resources (Frafjord, 1992; Dayan and Simberloff, 1994, 1996); 2) females are smaller because consumed energy basically is directed towards reproduction (Wiig, 1986); 3) SSD in canines and skulls of carnivorous animals directly connects with the mating strategy: species having one male-leader and harem animals have higher SSD than species without the male-leader and monogamous carnivores; 4) dimorphism is directly concerned with food specialization – in carnivores it is more expressed than in omnivores (Ralls, 1977; Gittleman and Van Valkenburgh, 1997). For the cave bears, there are no forcible arguments to reject hypotheses 1–3. The fourth hypothesis is more doubtful because these animals were basically herbivorous or omnivorous (Grandal-d'Anglade, 2010; Richards et al., 2008; Peigné et al., 2009).

The contributions from sexes in to SSD are not identical in different taxa of cave bears. In large forms (*U. spelaeus*) females were rather less than males, than in small cave bears (*U. rossicus*). This phenomenon demands further research. Various SSD in males and females were observed in different subspecies of European (*Meles meles*) and Asian (*M. leucurus*) badgers (Abramov and Puzachenko, 2005; Abramov et al., 2009) and in the subspecies of polar fox (*Alopex lagopus* L.) (Zagrebelny and Puzachenko, 2006).

The analysis of morphological differentiation and structure of variability in subspecies of the brown bear (*U. arctos*) has established several groups of measurements determining principal patterns of skull changes (Baryshnikov and Puzachenko, 2010). In cave bears, the morphological differentiation is most strikingly developed in the metric characteristics of the neurocranium and palatal width.

In spite of the cave bear variability revealed during the course of this work, the scale of skull variability in cave bears is comparable with the scale of skull variability in the recent brown bears from Northern Eurasia (Fig. 3b). Indeed, morphological variability in recent brown bear is more impressive. Suffice it to mention that only on relatively small terrain of the Caucasian mountains there were three well differentiated morphological forms ("ecomorphs") (Chestin and Mikeshina, 1998). A high morphological diversity of brown bear probably corresponds with its rather high recent and past (Late Pleistocene) genetic diversity (Calvignac et al., 2008; Stiller et al., 2009, 2010) and with well-known ecological plasticity. Therefore, when comparing the variability of brown and cave bears, the following facts must be taken into consideration: 1) brown bears all belong to one species, while cave bears are a group of species; 2) skull variability of brown bears reflects a time period of not more than one or two hundred years (the main period of collecting), while in cave bears variability is examined formed over a time period of probably several hundred thousands years. Thus, skull variability in the cave bear group was relatively lower than in recent brown bears, if it is "standardized" to the same time period, which implies a rather low potential of morphological modifications in cave bears.

A comparison of coefficients of variation of individual skull characters in cave and brown bears demonstrates similarity of the coefficients of variation for skull length (including the length of rostrum and neurocranium), width of palate and rostrum, orbital diameter, skull height, and several other metric characters (Fig. 12). Variation of palatal length, tooth-row length, and condylar width are found to be more pronounced in cave bears. At the same time, zygomatic width and mastoid width of the cranium is more variable in brown bears.

A comparatively low potential for cranial variability in cave bears could have contributed to their extinction under the climatic and landscape changes that happened in Northern Eurasia during the Late Pleistocene. Cave bears were non-specialized herbivores, a diet probably making them vulnerable to sharp environmental changes.

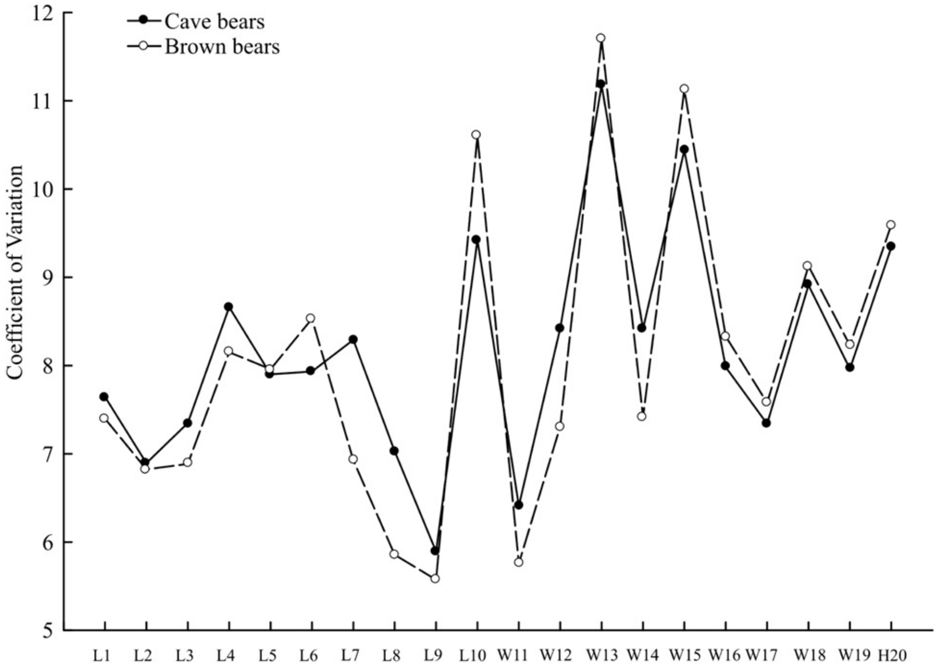

Fig. 12. Coefficients of variation of the cranial characters (L1-H20) in the cave and brown bears (males).

In addition, an increase of competition with large omnivores (brown bear, hominids) and specialized phytopages (ungulates) might have taken place. Under these conditions, the adaptation of dentition to processing predominantly vegetable food and comparatively low potential for cranial modifications prevented cave bears from rapid changes in their life strategy. As a result, the reduction of cave bears numbers, partition of distributional ranges, isolation of local populations, and displacement of cave bears to marginal habitats may have occurred.

These processes were increased by cave bear interrelationships with Pleistocene hominids, including competition for food sources and rock shelters. Especially negative consequences came from the dispersal of modern humans (*Homo sapiens* L.) throughout Northern Eurasia beginning 45–40 thousand years B.P. (Middle Pleniglacial) and subsequently replacing Neanderthalsin this region. Both species of hominids differed in their diet, way of foraging (Hoffecker, 2009) and, presumably, migration capacities. Modern humans were more dangerous enemies and competitors for cave bears. They considerably reinforced the factor of disturbance, pressing bears from cave habitats, which ceased to be available for animals as safe winter dens.

As the comparative study of ancient DNA from cave bears and brown bears shows, a decline in population size of cave bears started 25,000 years before their extinction, while brown bear population size remained constant (Stiller et al., 2010). This dynamic might have been a result of a complex of reasons designated above. Their mutual influence led to their unstable position in ecosystems of the Late Pleistocene and, finally, to their final extinction, which occurred in central Europe near 24,000 BP (Pacher and Stuart, 2009).

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Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.quaint.2011.02.035.

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