Morphological traits of wild boar in Germany and Russia: comparison of autochthonous and artificial populations

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Introduction

The problem of variation of morphological traits in the process of adaptation to the new conditions is a classical problem for ecology and evolutionary biology. Gradual change of the morphological traits provides the integrity of the biological species. On the other hand, new environment can cause evolution of the traits which are quite distinct from the ancestral ones which in turn can result in speciation. In this study we address this problem on the example of the craniometrical characters of wild boar (*Sus scrofa* L., 1758).

Morphological traits of different populations and subspecies of wild boar are well studied. (for example Kozlo 1975; Briedermann 1986; Gallo Orsi et al. 1995; Kohalmy 1996; Stubbe 1986), including comparative analysis of animals from different parts of the species’ geographical range (Adlerberg 1930; Tikhonov & Knyazev 1985; Philipchenko 1933; Genov et al. 1999; Randi et al. 1989). Discussing the existing intraspecies taxonomy of *Sus scrofa* Briedermann (1986) reported the following main trends in geographical variation of morphological parameters:

- increase of size in northern and eastern direction;
- increase of absolute and relative length of the skull in northern and north-eastern direction, and increase of the length of lacrimal bone and increase of the size of *squama occipitalis*;
- increase of the length and density of hair, darker color, less light spot between the cheeks;
- in the western part of geographical range size decrease, island forms are relatively small.

Concerning craniological parameters Philipchenko (1933) studied changes in the shape of lacrimal bone and basing on these suggested treating Mongolian and Far Eastern wild boars as a separate species. On the other hand Adlerberg (1930) reported transgressive type of variation of craniological parameters and, consequently, lack of reason for such differentiation. Since these studies the question of possibility of identification of subspecies and geographical populations of wild boar basing on cranial traits remains open (Genov 1999; Doichev et al. 2012).
In this study we compare morphological traits of wild boars inhabiting the Urals region with those from the other parts of geographical range. The specific of Urals population is that it has been formed in a very short time (about 30 years) mainly as a result of releases of representatives of four different subspecies of *Sus scrofa* (Markov & Bolshakov 1996). We compare metrics of the skulls of Ural wild boars with those of animals from the western (Germany, subspecies *Sus scrofa scrofa*) and eastern (Russian Far East, Primorje, subspecies *Sus scrofa ussuricus*) parts of the species’ historical distribution range. European and Far Eastern wild boars comprised about 49% of all wild boars released in 1978–1984 in Sverdlovsk oblast’, Middle Urals. We also compare craniometrical parameters of Urals wild boars with those for the other population living close to the species’ northern limit in the North-West of Russia (Leningrad oblast’). The wild boar inhabited North-Western areas of Russia as a result of natural expansion of animals mainly from a historical range in Eastern Europe (Rusakov & Timofeeva 1984). Last population included in analysis were wild boars inhabiting Central Russia (Tverskaya, Ryazanskaya and Smolenskaya oblast’) which like Urals wild boars have “mixed” origin, since population of species in Central Russia also was formed after a series of releases of animals from different parts of Soviet Union, including Middle Asia, Caucasus, Eastern Europe and Russian Far East (Lavrov et al. 1974).

**Methods**

**Material**

We analyzed samples (Table 1) from the collections of Zoological Research Museum Alexander Koenig (Germany, Bonn), Museum of the Zoological Institute of Russian Academy of Sciences (Russia, Sankt-Petersburg), Central Forest Nature reserve (Russia) and skulls of wild boars killed by hunters in Sverdlovskaya

<table>
<thead>
<tr>
<th>Geographical region</th>
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<th>Female</th>
<th>Sex unknown</th>
<th>Total</th>
<th>Source</th>
</tr>
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<tbody>
<tr>
<td>Leningradskya oblast, North-West of Russia (L)</td>
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<td>5</td>
<td>4</td>
<td>14</td>
<td>Museum of the Zoological Institute of Russian Academy of Sciences (Russia, Sankt-Petersburg)</td>
</tr>
<tr>
<td>Primorje, Russian Far East (P)</td>
<td>4</td>
<td>4</td>
<td>0</td>
<td>8</td>
<td>Museum of the Zoological Institute of Russian Academy of Sciences (Russia, Sankt-Petersburg)</td>
</tr>
<tr>
<td>Sverdlovskaya and Kurganskaya oblast’, Urals region (U)</td>
<td>14</td>
<td>5</td>
<td>0</td>
<td>19</td>
<td>Authors’ collections</td>
</tr>
<tr>
<td>Tverskaya, Ryazanskaya and Smolenskaya oblast’, Central Russia (CR)</td>
<td>15</td>
<td>14</td>
<td>0</td>
<td>29</td>
<td>Authors’ collections</td>
</tr>
<tr>
<td>Germany (E)</td>
<td>39</td>
<td>19</td>
<td>0</td>
<td>65</td>
<td>Zoological Research Museum Alexander Koenig (Germany, Bonn)</td>
</tr>
</tbody>
</table>
and Kurganskaya oblast’ (Russia, Urals region) in 1993–1998. All data and measurements were collected in 1993–2000.

**Measurements**

Measurement of skulls were made following the scheme in Kozlo (1975) (Fig. 1). Measurements of symmetrical bones are supposed to be taken from the one and the same (normally left) side of the skull to avoid the effect of fluctuating asymmetry (Kozlo 1975; Le Boulenge et al. 1996). In our case fulfilling this condition was not always possible because in some cases skull were partly damaged by hunters. We compared measurements of bones from the left and the right sides of the undamaged skulls and concluded that differences are negligible. Thus we used measurements from left or undamaged side of the skull. Measurements were taken with caliper and measuring band with accuracy 0.1 mm and 0.5 mm respectively.

Identification of animals’ sex and age was based on the teeth number and eruption following guidelines in Kozlo (1973), Briedermann (1986), Stubbe (1994).

Fig. 1 Scheme of measurements (after Kozlo 1975). Number, description and abbreviation (in parenthesis): 1. Maximum skull length (MSL); 2. Basal skull length (BSL); 3. Condylar skull length (CSL); 4. Palate length (PL); 5. Occipital height (measured from the lower ridge of the foramen magnum to the upper side of the occiput) (OH); 6. bizygomatic width (ZW); 7. Length of lacrimal bone (upper) (ULB); 8. Length of lacrimal bone (lower) (LLB); 9. Height of lacrimal bone (rear) (HLB); 10. Length of mandible (LM); 11. Height of mandible (HM); 12. Width of mandible (WM); 13. Length of mandibular symphysis (LMS).
**Analysis of data**

Only animals in the age 2+ were included in analysis. Stubbe et. al. (1984) have shown that absolute values of most craniometric parameters increase until the age of 4+, however we found possible to put together samples of all animals older than 2 years because the according to the data of the cited authors beginning from 18 months rate of growth decrease and changes in the craniological parameters of wild boars older than 2 years are very small. Besides, using the multivariate methods of statistical analysis allows addressing more shape that size of skull and thus compensates differences in morphological traits between ages 2+, 3+ and 4+.

Since the sizes of samples were small on the first stages of analysis we tried to define the parameters that would allow combining males and females. We used t-criteria to compare different parameters for males and females and found that in the total sample (not accounting for inter-regional differences) differences between males and females were statistically significant for the following traits – basal skull length, palate length, occipital height, bizygomatic width, length of lacrimal bone (lower), length of mandible. These traits were excluded from further analysis.

Thus, comparison of geographical regions was performed using the combined samples of males and females. Main method of analysis was forward stepwise Discriminant Analysis. Interpretation of the differences between samples was performed using canonical analysis (Rayment et al. 1984).

Discriminant analysis allowed discovering the traits which most effectively discriminate samples under consideration. On the next step we compared absolute means of these craniological parameters using Tukey’s range test for samples of unequal size (Tukey 1977). Final interpretation was performed using Discriminant Analysis classification matrix and results of post-hoc comparisons.

**Results**

Generally differences between samples estimated as squared Mahalanobis distances are statistically significant except “mixed” populations (Urals and Central Russia), and populations living close to range margins (Urals and North-Western Russia) (Table 2). The differences between animals from Germany and Far East are highly significant, they also differ significantly from “mixed” populations.

Results of Discriminant analysis (forward stepwise model) (Table 3) show that the traits that plays most important role in discrimination of samples are maximum skull length, condylar skull length and the height of lacrimal bone. Factor structure of the canonical roots (Table 4) shows that Root1 could be interpreted as variation in the height of lacrimal bone. Root2 shows the variation in the general size of the skull.

Position of samples (means of canonical variables) in the space of first two canonical roots (Root 1 vs Root 2) is shown on the Figure 2.

Along the x-axis (Root1) (HLB) wild boars from the western part of geographical range (Germany, North-Western and Central Russia, Urals) are markedly different from the Far Eastern animals.

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**Table 2** Morphological distances between samples of wild boar skulls. Above the diagonal – squared Mahalanobis distances, below the diagonal – p (differences were treated as statistically significant at p<0.05). Abbreviations as in Table 1

<table>
<thead>
<tr>
<th>Region</th>
<th>L</th>
<th>P</th>
<th>U</th>
<th>E</th>
<th>CR</th>
</tr>
</thead>
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<td>0,000000</td>
<td>6,74344</td>
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<td>0,000000</td>
<td>0,000009</td>
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</tr>
<tr>
<td>CR</td>
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<td>0,000000</td>
<td>0,506750</td>
<td>0,000000</td>
<td></td>
</tr>
</tbody>
</table>
Table 3  Contribution (Wilk’s lambda) of craniometrical parameters to discrimination of samples (forward step-wise model, statistically significant values are put in bold)

<table>
<thead>
<tr>
<th>Trait</th>
<th>Wilks’ lambda</th>
<th>Partial lambda</th>
<th>p-level</th>
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<tr>
<td>MSL</td>
<td>0,205455</td>
<td>0,525567</td>
<td>0,000000</td>
</tr>
<tr>
<td>CSL</td>
<td>0,173694</td>
<td>0,621670</td>
<td>0,000006</td>
</tr>
<tr>
<td>HLB</td>
<td>0,134069</td>
<td>0,805407</td>
<td>0,009430</td>
</tr>
<tr>
<td>ULB</td>
<td>0,120659</td>
<td>0,894920</td>
<td>0,142293</td>
</tr>
<tr>
<td>LM</td>
<td>0,125638</td>
<td>0,859455</td>
<td>0,052117</td>
</tr>
<tr>
<td>HM</td>
<td>0,127554</td>
<td>0,846544</td>
<td>0,035293</td>
</tr>
<tr>
<td>LMS</td>
<td>0,121088</td>
<td>0,891751</td>
<td>0,130633</td>
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</table>

Table 4  Results of Tukey’s HSD test (p-values and means) for the height of os lacrimalis. Pairs with statistically significant differences are put in bold

<table>
<thead>
<tr>
<th>Region</th>
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<th>E</th>
<th>CR</th>
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<td>0,0004</td>
<td>0,654</td>
<td>0,567</td>
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<td>0,0001</td>
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<tr>
<td>U</td>
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<td>0,0003</td>
<td>0,387</td>
<td>0,199</td>
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</tbody>
</table>

Mean (mm)  
23,4  
29,7  
24,9  
21,7  
23,3

Fig. 2  Plot of Means of Canonical Variables in the space of first two canonical roots (Root1 vs Root2). Position of samples does not reflect the absolute values of the parameters (sizes of bones) but show how far the given sample is distanced from others.
Along the Y-axis (Root2, general size of skull) wild boars from Germany are separated from other groups, while other are situated close to each other.

Comparison of the samples by mean values of the parameters generally confirms the results of Discriminant Analysis. Height of lacrimal bone is highest for wild boars from Far East, differences between this sample and all others are statistically significant (Table 4).

Differences in HLB between wild boars from Germany, North-Western Russia and Central Russia are statistically insignificant. In wild boars from Urals HLB is significantly higher than in German wild boars, but less than in Far Eastern wild boars. Differences between Urals, Central and North-Western Russia are statistically insignificant.

As concerns the traits characterizing the general size of skull (MSL and CKL), wild boars from Germany are smaller than those from the eastern parts of the range. This trend is most well performed for the condylobasal length of skull (Table 5).

Differences between samples from the territory of Russia are not statistically significant. Shape and size of the mandible (MD, MW) are different for animals from Germany and samples from Far East and Central Russia – wild boars from the eastern areas are bigger than western ones (data not shown).

Classification matrix (Table 6), calculated as a part of Discriminant analysis, shows that the highest percentage of correct classification was observed for the samples from Far East and Germany, thus from the territories inhabited by “pure subspecies” *S. s. ussuricus* and *S. s. scrofa*, and also percentage of correct classification was high for the sample from Central Russia. For animals from the northwestern regions of Russia and Urals percentage of correct classification was less than 50 %.

**Table 5** Results of Tukey’s HSD test (p-values and means) for the condylobasal length of skull. Pairs with statistically significant differences are put in bold

<table>
<thead>
<tr>
<th>Region</th>
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<th>P</th>
<th>U</th>
<th>E</th>
<th>CR</th>
</tr>
</thead>
<tbody>
<tr>
<td>L</td>
<td></td>
<td></td>
<td>0,361</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P</td>
<td>0,370</td>
<td></td>
<td>0,931</td>
<td>0,009</td>
<td>0,966</td>
</tr>
<tr>
<td>U</td>
<td>0,691</td>
<td>0,931</td>
<td></td>
<td>0,0003</td>
<td>0,685</td>
</tr>
<tr>
<td>E</td>
<td>0,009</td>
<td>0,0003</td>
<td>0,0001</td>
<td></td>
<td>0,944</td>
</tr>
<tr>
<td>CR</td>
<td>0,966</td>
<td>0,685</td>
<td>0,944</td>
<td>0,0001</td>
<td></td>
</tr>
<tr>
<td>Mean (mm)</td>
<td>352,17</td>
<td>373,89</td>
<td>364,36</td>
<td>320,47</td>
<td>358,23</td>
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</table>

**Table 6** Classification matrix of the wild boar skulls basing on craniometrical parameters. Abbreviations as in Table 1

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<tr>
<th>Region</th>
<th>Percentage of correct classifications</th>
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<th>P</th>
<th>U</th>
<th>E</th>
<th>CR</th>
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<tbody>
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<tr>
<td>P</td>
<td>83,33</td>
<td>1</td>
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<td>0</td>
</tr>
<tr>
<td>U</td>
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<td>5</td>
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<td>4</td>
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<tr>
<td>E</td>
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<td>2</td>
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<td>0</td>
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<td>2</td>
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<td>CR</td>
<td>76,47</td>
<td>1</td>
<td>0</td>
<td>2</td>
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<td>13</td>
</tr>
<tr>
<td>Total</td>
<td>71,23</td>
<td>9</td>
<td>5</td>
<td>9</td>
<td>30</td>
<td>20</td>
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Discussion

The results obtained in this study should be treated with caution taking into account small sample sizes. This concerns particularly samples from Primorje, Russian Far East and northwestern part of Russia, where N<20. Small sample sizes also determined the necessity of combining samples of males and females and animals from different age classes, which also could affect the reliability of our results (STUBBE et al. 1984). Still, the observed differences in craniometrical parameters allow making some conclusions and compare our results with the literature data on the geographic variability of the skull of Sus scrofa.

First of all our results confirm the conclusion of FILIPCHENKO (1933) and TIKHONOV & KNAYE (1985) about the importance of the shape of os lacrimalis for identification of geographic populations and subspecies. Particularly they confirm specific square shape of lacrimal bone in S. s. ussuricus and elongated shape of this bone in wild boars inhabiting Western, Eastern Europe and Urals region. The fact that “mixed” populations have lacrimal bone similar to that of European animals allows suggesting that representatives of subspecies Sus scrofa ussuricus did significantly affect modern phenotypic type of wild boar in Central Russia and in Urals.

On the other hand, animals from “mixed” populations are noticeably bigger than western European wild boars. This could be explained by both ecological (increase of size in northern direction), and genetic (crossbreeding of representatives of different subspecies) factors. Last suggestion is supported by the proximity of the northern population of wild boars from North-West of Russia to German wild boars, rather than to mixed populations from Central Russia and Urals. Big volume of morphological data presented by DANILKIN (2002) also does not support the suggestion about the increase of size in northern direction – he reports the biggest skulls from Carpathian Mountains, north of Belorus’, Volga delta and Far East. These data concerns the historical range of the species and does not include the territory settled by wild boar in the second half of the 20th century.

Comparison of our data with the literature data presented in DANILKIN (2002) shows that wild boar from Urals are close to the biggest animals from Belorussia, Caucasus (mean value of maximum skull length for males and females older than 3 years is 408,2 ± 6 mm), but they are smaller than animals from Southern Europe (Carpathians, Bulgaria) (DANILKIN 2002; DOIČEV et al. 2012).

Generally our data show that wild boars from “mixed” population are closer in their craniometrical parameters to the European population than to Far Eastern wild boars. Sizes of skulls vary significantly but in general wild boars from “mixed” populations are slightly bigger than German wild boars.

Acknowledgements

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Literature


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