# Variability and differences in the skulls of the common hamster (Cricetus cricetus) from several areas in Central Europe and from different time periods

Author: Stefen, Clara

Source: Folia Zoologica, 62(2) : 155-164

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/fozo.v62.i2.a11.2013

Folia Zool. – 62 (2): 155–164 (2013)

# Variability and differences in the skulls of the common hamster (*Cricetus cricetus*) from several areas in Central Europe and from different time periods

**Clara STEFEN**

*Senckenberg Naturhistorische Sammlungen Dresden, Museum für Tierkunde, Königsbrücker Landstraße 159, 01109 Dresden; e-mail: Clara.stefen@senckenberg.de*

Received 22 October 2012; Accepted 14 January 2013

**Abstract.** The craniometric variability of skulls of the common hamster (*Cricetus cricetus*) from different countries (Belgium, the Netherlands, Austria, Germany) and different regions within Germany was studied. The aim was to study the variability in different regions and to see if differences between populations exist now and might have existed in former times also. The discriminant analyses were performed for females and males separately. The material was assigned to three different age classes and tests were attempted with all age classes. For the largest sample from Saxony-Anhalt, differences could also be observed between the three selected time periods (1900-1930, 1931-1960 and 1961-1990). Discriminant analyses were performed by keeping the sexes, age classes, and time periods separate wherever the material allowed for it. Regional samples differed to some degree (depending on the set of samples used). Particularly the samples from Austria, Belgium, and the Netherlands were more offset from the German samples; nevertheless, some overlap existed for the males of the third time period. The position of the small sample from the Rhineland was ambiguous in the different discriminant analyses but seemed rather to fall within the range of other German samples and not clearly in-between the German and the Dutch/Belgian samples. Overall variability, changes with time, and possible yearly fluctuations, as described in the literature, influenced the results and overlaid existing regional differences. The existence of a western subspecies could not be supported. The lack of substantial numbers of specimens illustrated the importance of collecting even the common species at all times for future research.

**Key words:** subspecies *C. c. canescens*, Thuringia, Saxony-Anhalt, Austria, Belgium, the Netherlands, discriminant analyses

## Introduction

The common hamster, *Cricetus cricetus* (Linnaeus, 1758), which had been very common and considered a pest for a long time, is now regarded susceptible to critically endangered in eight of the European countries. Particularly in the last four to five decades the common hamster populations have decreased markedly, mainly in the westernmost distribution range of Belgium, the Netherlands, France, and Germany (Weinhold 2011). In Germany, at least in some regions such as Saxony, the decline started unnoticed in the 1950s (Meyer 2009); the major decline occurred between 1960 and 1970 and, today, only scattered populations remain in Germany (Stubbe et al. 1998, Weinhold & Kayser 2006). In the past, many publications dealt with pest control and some of the related ecological aspects of *C. cricetus*. More recently, conservation issues of the common hamster, still in decline in several countries, have come into the focus of studies and publications (e.g. Nechay 2000, Weinhold & Kayser 2006, La Haye et al. 2011). Common hamsters are rather sedentary (Weinhold 1996), and dispersal over larger distances is rare (Karaseva 1962). Some barriers to their dispersal are mountainous regions (Vohralík & Anděra 1976, Berdyugin & Bolshakov 1998, Tkadlec et al. 2012), large wooded areas, and sandy soil (Banaszek et al. 2012).

Several recent papers addressed the genetic structure and variability of the species in Europe (Smulders et al. 2003, Neumann et al. 2004, Banaszek & Ziomek 2012, La Haye et al. 2012). Different phylogenetic lineages for common hamsters with distinct distributions have been distinguished: the northern phylo-group is found in Western Europe, the Pannonian phylo-group inhabits the South, and two other groups occur in Poland (Banaszek et al. 2009). The genetic variability in the western common hamster has decreased markedly comparing historic museum specimens with more recent ones (Smulders et al. 2003).

The lack of taxonomical data was pointed out by Grulich (1987). He presented the first detailed work on the variability of physical and cranial measurements based on a study of more than 1800 common hamsters from the Carpathian region over a three-year-period and compared them to other data from the literature.

A western subspecies, the *C. s. canescens* from Belgium, was named by Nehring (1899a). This subspecies was based on two stuffed skins from Fexh-Slings, only. These specimens were supposed to differ on the basis of their colouration, larger ears, and smaller size. The condylobasal lengths of two specimens with moderately worn teeth from Tirlemont, Liège were given as 44.0 and 45.2 mm (Miller 1912). This subspecies was assumed to occur at the western edge of the distribution area of common hamsters in France, Belgium, Luxemburg, the Netherlands, and the Rhine Valley. According to some authors, it also occurred around Braunschweig, Lower Saxony (Grulich 1987). A number of them discussed the validity of this subspecies: Wepner (1936) and Husson (1959) supported the subspecies, but, e.g., Novikov (1935), Frechkop (1936), Niethammer (1982), Grulich (1987), and Neumann et al. (2004) rejected it. Miller (1912) noted that common hamsters from the western edge were smaller than those from the centre of the distribution range; Niethammer (1982) indicated a possible cline in size. Husson (1959) found that the length of the foramen incisivum was fairly large in the western common hamster and used an incisive-palatal index (length of foramen incisivum: length from posterior end of foramen incisivum to posterior median border of the palatinum) to differentiate the western subspecies *C. c. canescens* from the *C. c. cricetus*. However, he indicated that more material would be needed "to decide 1) the exact range of distribution of the western" subspecies and 2) whether the values gradually pass to the typical values further east (Husson 1959). Data from mitochondrial DNA did not support separate subspecies (Smulders et al. 2003).

In the discussion of the western subspecies *C. c. canescens*, the aspects of colouration are also important and were discussed by Husson (1959). Generally, the colouration of common hamsters is not uniform: for example, melanistic common hamsters are particularly known from Thuringia (Petzsch 1940, Petzsch & Petzsch 1956) but also occur in other areas in different abundances (Niethammer 1982). However, based on his coat colour analyses, Husson (1959) assumed that the white marking of the chest, which Wepner (1936) used to characterize the *C. c. canescens*, had since expanded to the East whereas the melanistic form had expanded into Germany from the East. This would need to be discussed on the basis of historic literature and skins but is beyond the scope of the current study.

This study addresses the question whether, even prior to today's strong isolation of *C. cricetus* populations, cranial morphometric differences existed between the populations of different regions. Therefore, the variations found in the different regions must be compared and determined. Wepner (1936) indicated changes in the coat colouration patterns over time. Therefore, comparisons of regional samples will be attempted separately for different time periods. Of course, the specimens' sex and age must be considered, too. Understanding the morphometric structure of the populations in the past and comparing it to the genetic structure may prove helpful in developing conservation strategies in cases where local populations differ markedly and should be considered as different evolutionary units, thus deserving special consideration in conservation. Also, the question of the existence of a smaller western subspecies will be addressed.

## Material and Methods

To explore the craniometric variability within, and the geographic differences between populations of *C. cricetus*, specimens from different regions within Germany and some of its adjacent countries were studied:

Rhineland-Palatinate: 20 males (m), 54 undetermined sex (uns) from 1980/81, mainly from Alsheim, Eimsheim, Wintersheim, and Dorn-Dürkheim, all about 15-20 km from Alzey; Rhineland: 10 females (f), 12 m, 6 uns, from the 1920s-1990s, stemming from around Bonn and Cologne and up to Hürth; Saxony: 9 f, 10 m, 7 uns, from 1871-1950 from around Dresden, Mobschatz, and Leipzig; Saxony-Anhalt: 34 f, 96 m, 29 uns, from 1929-1997, mainly from the Magdeburger Börde from around Halberstadt, Erxleben, Haldensleben; Thuringia: 8 f, 43 m, 15 uns, from 1920 to 1965, more wide spread but mainly from Gräfentonna, around Weimar and Groß-Wusterlitz; Belgium: 5 f, 10 m, 2 uns, from 1929-1950 mainly from Brabant and a few from Naumur; Lower Saxony, from around Braunschweig: 4 f, 4 m, 1 uns, from 1949/50 and unknown dates; Netherlands: 19 f, 31 m, 1 uns, from 1920 to 1971, mainly from Houthem and

Oude Valkenburgh; Austria: 16 f, 15 m, 31 uns, 1981-1990 mainly from Groß-Enzersdorf, Lower Austria. The material from the following collections was studied: Heineanum Halberstadt, Institut für Biologie (now Zentralmagazin) der Martin-Luther-Universität Halle-Wittenberg, Germany; Institute royal des Sciences naturelles de Belgique in Brussels, Belgium; Museum der Natur Gotha, Germany; Naturhistorisches Museum Wien, Austria; Nederlands Centrum voor Biodiversiteit Naturalis Leiden, the Netherlands; Senckenberg Museum und Forschungsinstitut, Frankfurt/M, Germany; Senckenberg Naturhistorische Sammlungen Dresden, Germany; Museum für Tierkunde, Zoologische Staatssammlung München, Germany, and Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

The skulls were grouped into three age classes (AGs): 0 – juvenile with M3/m3 not at occlusal height yet, 1 – just adult with all the molars at occlusal height and none to only little wear, and 2 – old adult with the molars showing marked to heavy wear. Specimens from the age group 0 were not considered further as in early postnatal development the body measurements and most skull measurements increase nearly linearly. The material was also assigned to three time periods: 1 – 1900-1930, 2 – 1931-1960, and 3 – 1961-1990. Most of the studied material came from these periods. There existed few specimens that were older, and these were only considered in the analyses in which all the time periods were grouped together.

Eighteen linear variables were measured on the skulls in partial accordance with Husson (1959) and Vohralík (1975) (Fig. 1): bull – length of the bulla tympanica, cbl – condylobasal length, corh – height of coronoid, diast – diastema at maxillary, gsl – total length of skull, hsb – width of cranium at squamosum just caudal to the zygomatic arch, infl – length of incisive foramen, iob – interorbital breadth, mand – length of the mandible, mandh – height of the mandible, nasb – width across nasals, nasl – length of the nasals, ocb – width of the cranium at occipital, ozr – length of maxillary tooth row, rostb – width of rostrum, skh – height of skull above bulla, uzr – length of mandibular tooth row, zw – width of zygomatic arch.

All the measurements were taken with digital callipers to the nearest 0.01 mm. The descriptive statistics were calculated separately for the sexes, but for AG 1 and AG 2 individuals as well as the time periods, they were combined. The attempt was made to test for statistically relevant differences between the sexes in all the studied samples, but due to the sample sizes this was only plausible for Saxony-Anhalt and Austria.

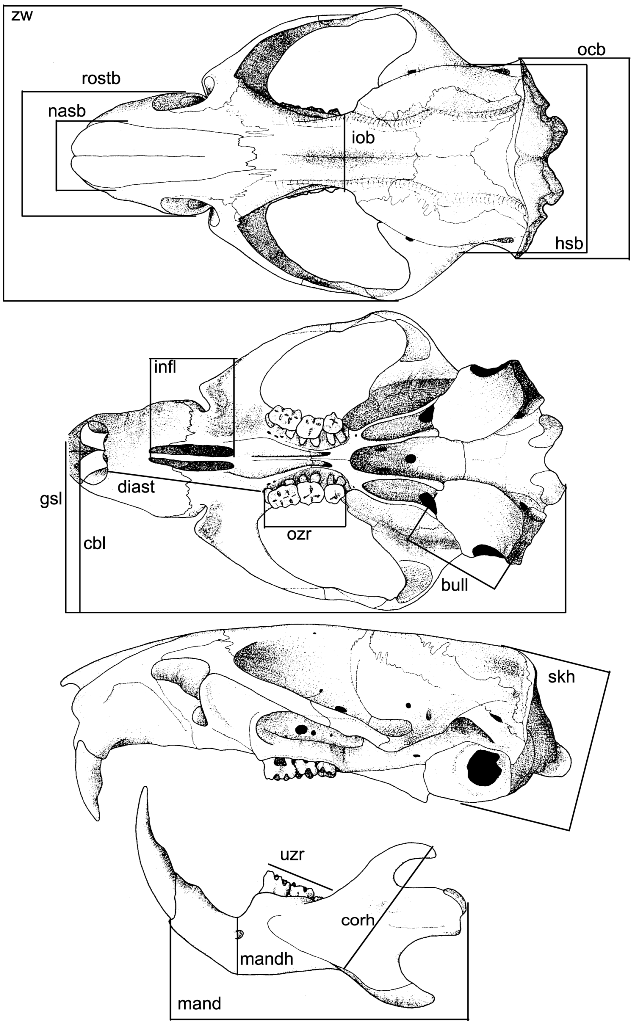

**Fig. 1.** Schematic illustration of the measurements taken on the skulls. Abbreviations are explained in the text.

The student's T-test on the 95 % significance level was used to test for sexual dimorphism. Samples with several variables of unequal variances were tested with the nonparametric Man-Whitney-U test, 2-sided significances are given. Sexual dimorphism is well-known for common hamsters (Husson 1953, Vohralík 1975, Niethammer 1982, Grulich 1987), and it has been suggested that taxonomic studies should consider age and sex. Therefore, the attempt was made to carry out as many tests as possible with the material separated according to sex and age class and even to time period. Pearson correlations were used to test for significant correlations between the variables and the age group or the time period. The results are given in the following way: $r^2 = -0.694$**, (* indicates significance on the 0.05 significance level and ** on the level of 0.02, p = probability, n = quantity).

Discriminant analyses were used, including all the variables or a random sample of the variables, to see to which degree a separation of the geographic groups was possible. Discriminant analyses were performed using Wilk's lambda statistics, entering all the variables at once, not stepwise, with equal prior probabilities for the groups and covariance within the groups. Most analyses were carried out using one sex and one age group, only. All statistical analyses were performed using SPSS 16.

## Results

Descriptive statistics for the regional samples of the studied *C. cricetus* separated according to sex are in Appendix. The basic statistical characteristics of the measurements studied are shown in Table 1. Considering the individuals as a whole, the variables of the largest sample (from Saxony-Anhalt) show the largest size range. The samples from Saxony, Austria, Belgium, and the Netherlands fall within the lower range with smaller values, and the sample from Rhineland-Palatinate is found in the upper size range and the larger values of this large sample.

In the largest sample (from Saxony-Anhalt) with a sufficient number of males and females, a statistically significant sexual dimorphism was shown for several variables in AG 1 individuals of all time periods: bull (p = 0.015), zw (p = 0.027), diast (p = 0.042), ozr (p = 0.001), ocb (p = 0.000). For more specific results, tests were performed for different time periods, but the sample sizes were rather low.

For AG 1 individuals of time period 3 (1961-1990) alone more variables show different variances and therefore were tested with the Man-Whitney-U test. Significant sexual dimorphism was found in cbl (0.032), nasb (0.027), rosb (0.030), infl (0.011), ocb (0.044), skh (0.040), corh (p = 0.034) for at least 17 females and 24 males. Samples from other time periods are considered too small for a reasonable test. Pearson correlations show statistically significant correlations to the time period in AG 1 individuals only in few variables: for females in nasb ($r^2$ = –0.694**, p = 0.000, n = 21), infl ($r^2$ = –0.456*, p = 0.038, n = 21) and for males in bull ($r^2$ = –0.457*, p = 0.011, n = 30) and Uzr ($r^2$ = 0.391*, p = 0.044, n = 27).

*Differentiation of regional samples and time periods*

Discriminant analyses of AG 1 and 2 individuals for all the time periods showed some separation of the groups, more so for females than for males (Fig. 2). The regional samples of the females were well separated, and 96.0 % were grouped correctly. Particularly the samples from the Netherlands and Belgium, but also those from Austria, were separated from the samples from Saxony-Anhalt and Thuringia along function 1. This was mainly influenced by hsb, nasb, uzr and infl. The sample from the Rhineland was in-between but with few individuals. The Dutch/Belgian sample and the Austrian one as well as the ones from Saxony-Anhalt and Thuringia, were separated along function 2. This was mainly based on ozr, mand, nasb and infl.

The regional samples of males, particularly from Germany, overlapped much more even though 93.9 % of the cases were grouped correctly. Again, the Belgian and the Dutch samples were separated from the German and the Austrian ones. The Austrian sample was closer to the German ones than in the discriminant analysis with female samples.

To reduce the influence of the individual age, the age classes were considered separately, but with

**Table 1.** The means of condylobasal length (cbl), zygomatic width (zw) and incisive foramen length (infl) of samples of *Cricetus cricetus* of different age class (AG) from different geographic regions from this study (see Supplementary online materials). Data for females and males are combined. N – number of specimens in sample, SD – standard deviation.

| Locality | N | cbl | SD | N | zw | SD | N | infl | SD |
|---|---|---|---|---|---|---|---|---|---|
| AG 1 | | | | | | | | | |
| Saxony | 11 | 43.24 | 2.99 | 9 | 26.61 | 2.27 | 12 | 8.60 | 0.42 |
| Saxony-Anhalt | 68 | 45.94 | 3.56 | 62 | 28.42 | 2.66 | 70 | 9.1 | 0.72 |
| Thuringia | 48 | 45.30 | 2.55 | 37 | 28.62 | 1.79 | 47 | 9.11 | 0.65 |
| Rhineland-Palatinate | 59 | 47.12 | 2.44 | 55 | 39.06 | 2.06 | 59 | 9.39 | 0.54 |
| Belgium | 7 | 45.63 | 2.07 | 10 | 26.73 | 1.73 | 10 | 9.38 | 0.51 |
| Netherlands | 20 | 44.53 | 2.46 | 22 | 26.44 | 1.80 | 25 | 9.28 | 0.57 |
| Austria | 22 | 44.23 | 2.10 | 23 | 25.92 | 1.68 | 23 | 8.54 | 0.42 |
| AG 2 | | | | | | | | | |
| Saxony-Anhalt | 22 | 50.4 | 3.50 | 22 | 30.10 | 2.53 | 22 | 9.47 | 0.73 |
| Rhineland-Palatinate | 15 | 48.85 | 1.81 | 15 | 30.20 | 1.33 | 15 | 9.67 | 0.39 |
| Belgium | 3 | 48.37 | 1.37 | 5 | 28.45 | 1.09 | 6 | 10.23 | 0.28 |
| Netherlands | 19 | 48.16 | 2.03 | 15 | 29.03 | 0.34 | 21 | 10.04 | 0.48 |
| Austria | 8 | 46.56 | 1.25 | 8 | 27.17 | 1.10 | 8 | 8.72 | 0.50 |

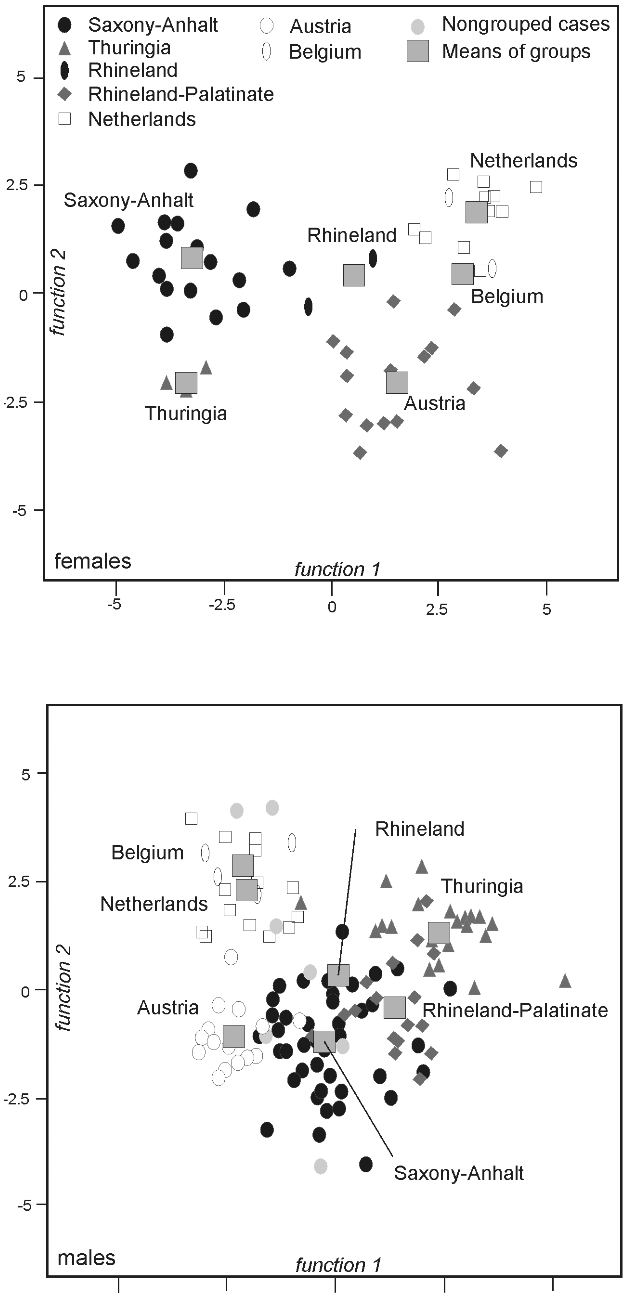

**Fig. 2.** Result of the discriminant analysis calculated with all the variables of the studied regional samples including AG 1 and 2 individuals of all time periods. Females only (upper). The discriminant analyses yielded four functions, the first and second with an Eigen value of 9.102 and 2.814 respectively. The first function is mainly influenced by hsb, nasb, uzr and bull, the second by ozr, infl, uzr and mand. 96 % of cases are grouped correctly. Males only (lower). The discriminant analyses resulted in five functions, the first and second with Eigen values of 3.000 and 2.117 respectively. The first function is mainly influenced by hsb, bull, ocb and mand, the second by infl, hsb and corh. 93.9 % of cases are grouped correctly.

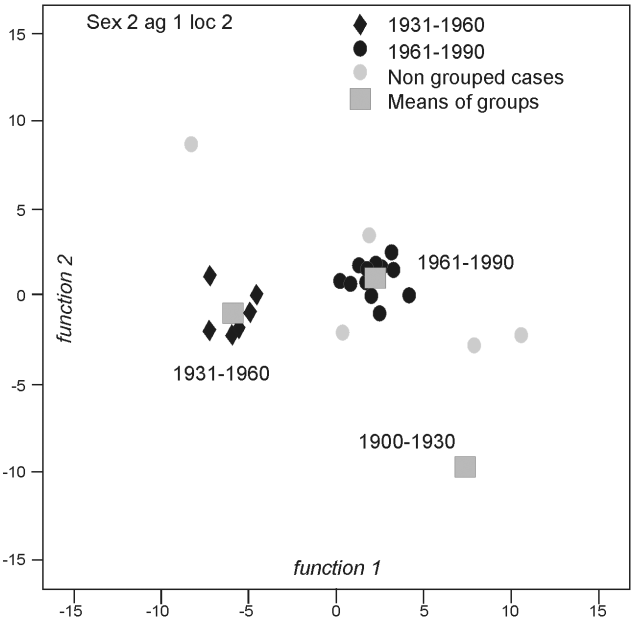

**Fig. 3.** Discriminant analyses with all variables and males of AG 2 from Saxony-Anhalt differentiated according to time period. The discriminant analyses resulted in two functions with an Eigen value of 18.450 and 5.780 respectively. Function one is mainly influenced by bull, mand and ocb, function two mainly by ozr, bull, uzr, infl, mand and hsb. 100 % of cases were grouped correctly.

the material from all the time periods together. AG 1 females from different localities clearly separated; 100 % of cases were grouped correctly.

For AG 1 males again, particularly the German regional samples overlapped more, and 94.4 % of groups were grouped correctly. Here, the Austrian, Belgian and Dutch samples were closer together.

For AG 2 of all the time periods, only the discriminant analysis with the females was calculated, but with only 11 valid cases. All the means of the samples were close together; only 57.9 % of cases were grouped correctly.

For the largest sample from Saxony-Anhalt, a discriminant analysis with AG 1 males indicated a clear separation of the three time periods so that morphometric changes over time (Fig. 3) were indicated.

With this in mind, discriminant analyses with specimens separated according to sex and time period were performed (Fig. 4). A discriminant analysis of AG 1 females (27 valid cases) of time period 3 (1961-1990) resulted in a separation of groups, but regions were represented with few or even no individuals; 100 % were grouped correctly. The discriminant analysis with AG 1 males of the same time period (63 valid cases) also resulted in a good separation of the regional samples; 96.8 % of cases were grouped correctly. The German samples were separated from the Austrian and the Dutch one as well as the samples from Saxony-Anhalt and Rhineland-Palatinate or Thuringia, mainly along function 1. This was influenced in the main part by hsb, bull, nasl, mand, zw and diast.

Other discriminant analyses including AG 1 individuals of time period 1 or AG 2 individuals of the three time periods separated according to sex were

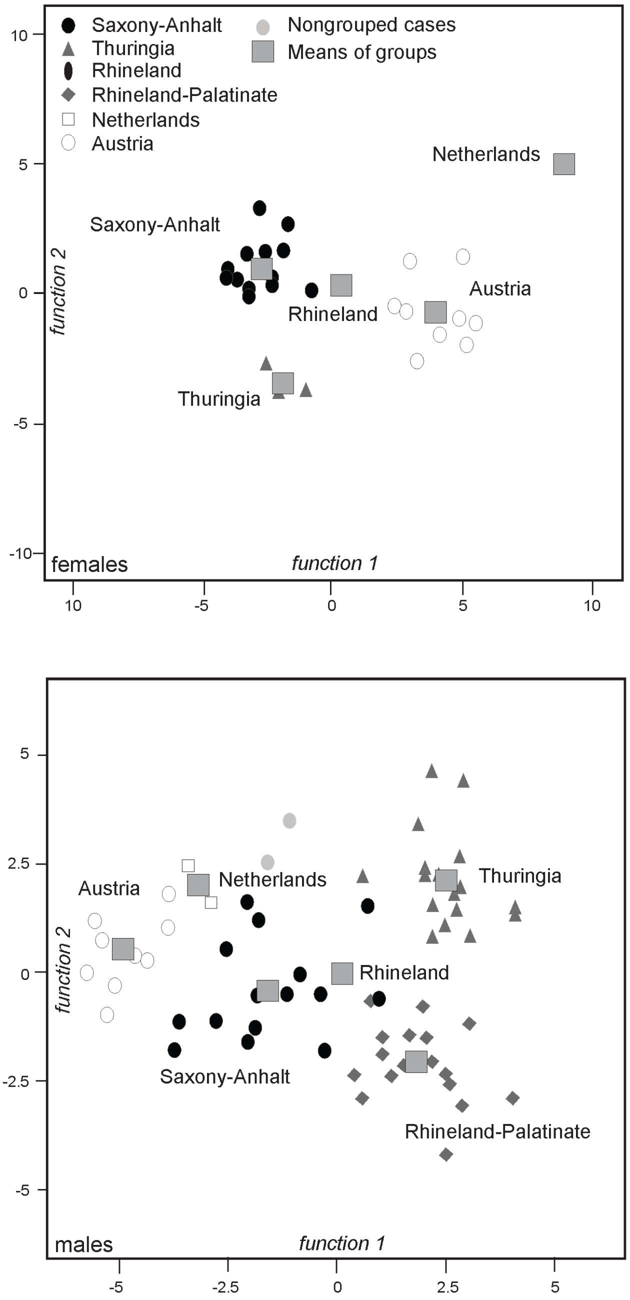

**Fig. 4.** Discriminant analyses calculated with all variables including AG 1 individuals from the time period from 1961-1990 only. Females (upper). The discriminant analyses resulted in three functions, the first with an Eigen value of 14.935 mainly influenced by mand, ocb, bull and skh, and the second with an Eigen Value of 3.364 and influenced by uzr, ozr and ocb. 100 % of cases are grouped correctly. Males (lower). The discriminant analyses resulted in four functions, the first two with Eigen values of 8.082 and 2.947 respectively. Function one is mainly influenced by mand, gsl, zw, corh, and mand, function two by zw, corh, ocb, and cbl. 100 % of cases are grouped correctly.

attempted, but for a reasonable calculation, too few cases remained.

## Discussion

Niethammer (1982) indicated that common hamsters from Thuringia and Saxony-Anhalt were larger than those from Rhineland-Palatinate. The data were not sorted according to age classes. AG 2 individuals from Saxony-Anhalt also were the largest individuals in the present study. The large average values in cbl given for the common hamsters (irrespective of age class) from Alzey, Rhineland-Palatinate, and Saxony-Anhalt (Badersleben and Merseburg) by Husson (1959) were not reached, here. On average, common hamsters from these regions were found to be slightly smaller (Table 2). The few studied and mainly unsexed

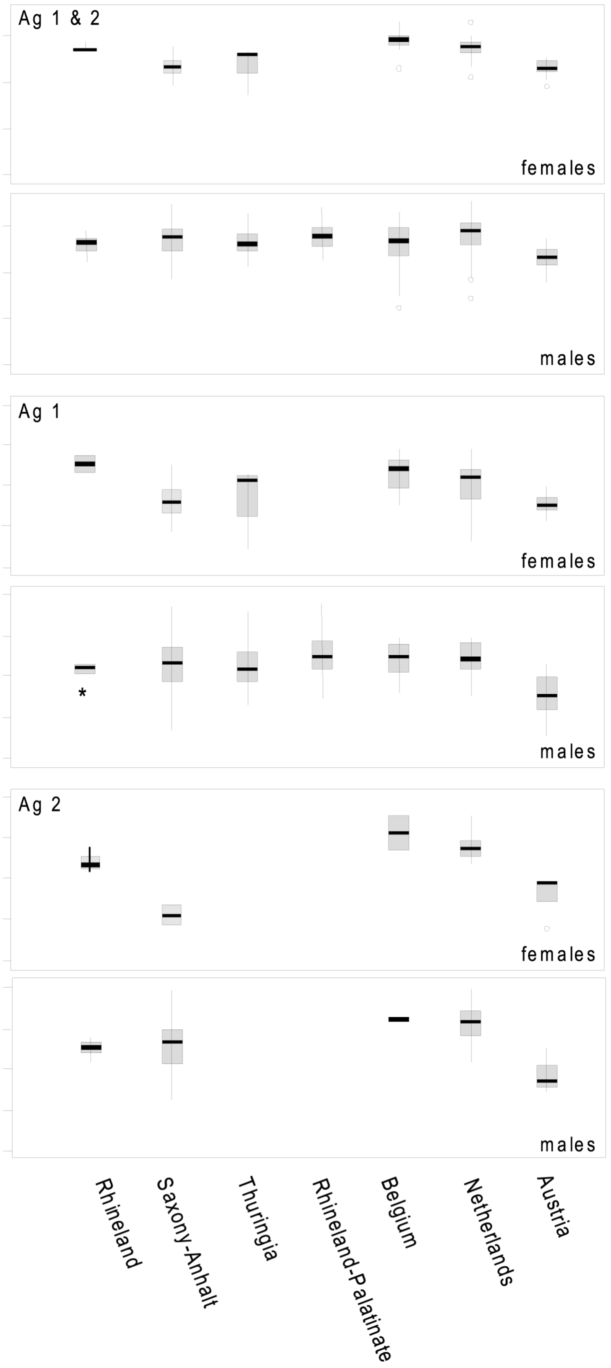

**Fig. 5.** Box plots of incf for common hamsters of the different localities separated according to sex and age groups (Ag).

**Table 2.** Comparative overview of the length of the incisive foramen of common hamsters from different regions compiled from this study and the literature. N – sample size, min – minimum, max – maximum.

| | sex | N | min | max | mean | source |
|---|---|---|---|---|---|---|
| Alzey | f | 13 | 8.9 | 10.1 | 9.4 | Husson 1959 |
| Belgium | f | 5 | 8.55 | 10.56 | 9.6260 | this study |
| Netherlands | f | 18 | 7.77 | 10.54 | 9.3039 | this study |
| Belgium & Netherlands | | 18 | 8.2 | 11 | 9.54 | Husson 1959 |
| Saxony-Anhalt | f | 25 | 7.86 | 9.50 | 8.6216 | this study |
| South Slovakia | f | 599 | 6.2 | 10.6 | 8.49 | Grulich 1987 |
| Thuringia | f | 4 | 7.50 | 9.30 | 8.7750 | this study |
| Alzey | m | 25 | 8.4 | 10.6 | 9.67 | Husson 1959 |
| Austria | m | 15 | 7.55 | 9.48 | 8.5947 | this study |
| Belgium | m | 9 | 8.66 | 10.28 | 9.5933 | this study |
| Netherlands | m | 27 | 8.54 | 10.99 | 9.8270 | this study |
| Belgium & Netherlands | m | 26 | 8.9 | 11.3 | 10.10 | Husson 1959 |
| Rhineland-Palatinate | m | 20 | 8.50 | 10.80 | 9.5100 | this study |
| Saxony-Anhalt | m | 56 | 7.70 | 10.92 | 9.4029 | this study |
| South Slovakia | m | 760 | 6.4 | 11.2 | 8.92 | Grulich 1987 |
| Thuringia | m | 34 | 8.30 | 10.60 | 9.2500 | this study |

specimens from Saxony were generally smaller than those from the other studied regions within Germany (Stefen in press).

In all the age classes, common hamsters from Austria turned out to be the smallest. Also those from Belgium and the Netherlands were generally smaller than those from Saxony-Anhalt. The small sample from around Braunschweig (Lower Saxony) was similar in cbl size to the Belgian and the Dutch sample. The ranges observed here e.g. for cbl generally fell into the range of a large sample from Eastern Slovakia (Grulich 1987).

Sexual dimorphism of the common hamster was reported, for example, by Husson (1953, 1959), Hell & Herz (1969), Vohralík (1975), and Grulich (1987) and was supported by this study in the larger samples for several parameters. The sample size and the age composition may have played a role in giving different results.

The larger incisive foramina in western common hamsters recorded by Husson (1959) were supported, here (Table 2, Fig. 5). However, the incisive foramen of the samples from Rhineland-Palatinate and Saxony-Anhalt were of a similar size on average, and Husson (1959), himself, found them to be comparable in length in his samples from Saxony-Anhalt. It was actually very difficult to assess the size difference in incf (or other variables) between the regional populations due to the small sample sizes. Comparing AG 1 and 2 individuals together but separated by sex, Austria shows the smallest values and females from the Netherlands and Belgium the largest. Considering AG 1 and AG 2 individuals separately, the small values of incf from Austria and the large size of those from the western distribution range were supported. It even seems that the size differences in AG 2 individuals are more pronounced than in younger individuals. Thus, probably only very old individuals show typical geographic differences.

### *Differences between regions and time periods*

The studied material was assigned to three time periods in an attempt to see if there were any differences in the separation of the regional groups into different time periods. In the first and second period (1900-1960), common hamsters were abundant, and it can be assumed that at least the populations from Thuringia and Saxony-Anhalt still occupied a continuous distribution area. A distribution map from the end of the 19th century (Nehring 1894) indicated a patchy distribution in Germany with a continuous large distribution area in eastern Germany and few apparently isolated patches in South-Western and Western Germany. However, Husson (1949) indicated a continuous distribution range for the common hamster in the Netherlands, Belgium, and Western Germany. Therefore, it may be speculated that also for Rhineland-Palatinate there might have been other connections between populations. The gross picture supplied by Nehring (1894) was supported by sources from the 1960s and from the 1970s as summarized by Niethammer (1982).

Even though the analyses indicate some separation of the Dutch and Belgian common hamsters from the

German ones (degree depends on samples used in discriminant analyses, Figs. 2, 3), there is not enough information to support a clear separation of a western subspecies *C. c. canescens*. There are rather subtle regional differences which are superimposed by sexual dimorphism, overall variability, age structure, changes over time as indicated here in Saxony-Anhalt (Fig. 3), and perhaps even year to year fluctuations (see Grulich 1987). Depending on the sample set used, the common hamsters from Austria, the Netherlands, and Belgium are separated similarly from the German ones. The slight separation of the westernmost common hamsters and the Austrian ones may also be influenced by their position at the edge of the distribution range. Both have an edge position, but the Austrian population is or, at least, has been in continuity compared to other populations (Niethammer 1982) whereas the ones in the Netherlands and Belgium have probably been separated much longer. Genetically, the historic common hamsters from the Netherlands show alleles that are also present in samples from the Czech Republic. At present, hamsters from the Netherlands and France show only one of these alleles (Smulders et al. 2003). This indicates that, formerly, common hamsters from the western distribution edge at least genetically did not differ from others and that there must have been connections between the populations which are separate now as well as already in Nehring's map (1894). Whether currently these western common hamsters also differ morphometrically cannot be tested.

With respect to the occurrence of *C. cricetus* in the Netherlands and Belgium, the possibility exists that they only expanded their range to these western regions in the 1870s-1880s. Husson (1959) discussed the literature on the occurrence of common hamsters in these regions and stated that the question referring to when they may have begun occupying these regions cannot be resolved. Several authors assumed that common hamsters may have always been present in low numbers and that changes in the abundance occurred, but that migrations did not (e.g. Nehring 1894, Remy 1928, Werth 1934). On the basis of studies from Saxony, Germany, and Belgium, others believed that a marked range expansion took place (e.g. Zimmermann 1923, Dupond 1932). Dens of common hamsters in the region of Zuid-Limburg were recorded in 1879 for the first time (van Bemmelen 1881). The scenario with a marked range expansion of common hamsters at the end of the 19th century would be in accordance with the assumption of a founder effect stated by Neumann et al. (2004) based on genetic data and would also explain the similarity of the alleles in hamsters from the western regions and those from the Czech Republic in the past. It also explains the relatively weak separation of western hamsters (depending on the tested samples) found in the craniometric data presented here. Both would indicate that there were connections between the westernmost populations and others, thus allowing for gene flow.

The sample from Rhineland-Palatinate appears differently separated from the samples from Eastern Germany, depending on the individuals included in the analyses. Thus, a clear statement on their status is difficult. According to the old distribution map of common hamsters by Nehring (1894), this population must have had a long history of isolation from other populations.

The discriminant analyses were only possible with reasonably sized samples for the last time period, thus leaving the question whether possible craniometric differentiations of regional samples date back to the first part of the 20th century unresolved. The specimens from the 1961-1990 time period show a separation of the regional samples in a discriminant analyses for females but less so for males. Even though over 90 % of the cases are grouped correctly in the discriminant analyses, there is an overlap between the German and the Austrian sample. Only the Belgian and the Dutch sample are more separated, yet, subtle regional differences can at least be assumed for the other regions as well. A molecular study indicated separate clusters of common hamsters from Alsace, Saxony-Anhalt, and parts of North Rhine-Westphalia adjacent to the Netherlands (La Haye et al. 2012). It can be speculated that with the currently increasing isolation of the populations and their reduced population size, the regional differences will also increase. Genetically, in the BNN region, a strong drift effect has been shown as "populations have shifted to the edges of their original genetic distribution" (La Haye et al. 2012). Neumann et al. (2004) suggested that the current low diversity in the western populations is "partially caused by a joint historic founder event and not only by recent population breakdowns."

In the discriminant analyses the sample from the Rhineland sometimes appears between the German and the Austrian ones, within the German one (males), or in-between the German and the Dutch/Belgian and the Austrian ones, which is probably due to the small sample size. This, as well as the fact that reasonable discriminant analyses were not possible for comparing the degree of separation over time for the different time periods, indicates that the *C. cricetus* material available is hardly enough to tackle such questions using craniometric tools. Principal component analyses of genetic distances (La Haye et al. 2012) indicated that the specimens from the western parts of Germany adjacent to the Netherlands could be grouped in-between the historic Dutch/Belgian specimens and those from Saxony-Anhalt.

Grulich (1987) studied common hamsters over a three-year-period in large samples and found statistically significant differences in several parameters over the years. To consider the yearly differences in the available material is hardly possible. In this study material, several years had to be grouped together to achieve at least sufficient sample size. Unnoticed yearly differences might influence the result of the discriminant analyses, and regional and yearly differences might be difficult to tell apart.

This study shows that even though relatively abundant material of the *C. cricetus* from several regions is available in collections, not all specimens are sexed, and age classes as well as geographic regions are unevenly represented and the time periods even more so. This makes it difficult to actually address the question whether the separation of the regional populations based on craniometric features has changed over time. As regional samples from the time period 1961 to 1990 had been separated to some degree, it may be assumed that, at least, subtle differences existed even prior to that time. The overall variability of the common hamster as well as annual fluctuations probably render regional differences irrelevant for a subspecies differentiation. With separated populations and hardly any possibility for gene flux between them now, it can be expected that regional populations will differ more in future. The study also points toward the importance of collecting large series of specimens – even such common ones as the common hamster.

## Acknowledgements

*I would like to sincerely thank the following individuals for enabling the study of the material under their care: Prof. Dr. F. Mayer, Berlin, Dr. C. Schmidt, Halle, Dr. B. Nicolai, Halberstadt, Dr. R. Kraft, Munich, Dr. Samitz, Dr. Bellstädt, Gotha, Prof. Dr. A. Gamauf, Vienna, Dr. G. Lengfeldt, Brussels, Dr. S. van der Mije, Leiden, Dr. R. Hutterer, Bonn, and Mrs. K. Krohmann, Frankfurt. Mrs. Orriosn, Dresden checked the English.*

## Literature

Banaszek A., Jadwiszczak K.A., Ratkiewicz M. & Ziomek J. 2009: Low genetic diversity and significant structuring of the common hamster populations *Cricetus cricetus* in Poland revealed by the mtDNA control region sequence variation. *Acta Theriol 54: 289–295.*

Banaszek A. & Ziomek J. 2012: Genetic variation and effective population size in an isolated population of the common hamster, *Cricetus cricetus*. *Folia Zool. 61: 34–43.*

Banaszek A., Ziomek J., Jadwiszczak K.A., Kaczyńska E. & Mirski P. 2012: Identification of the barrier to gene flow between phylogeographic lineages of the common hamster *Cricetus cricetus*. *Acta Theriol 57: 195–204.*

Berdyugin K.I. & Bolshakov V.N. 1998: The common hamster (*Cricetus cricetus* L.) in the eastern part of the area. In: Stubbe M. & Stubbe A. (eds.), Ecology and protection of the common hamster. *Wissenschaftliche Beiträge Martin-Luther-Universität Halle-Wittenberg, Halle, Germany: 43–79.*

Dupond Ch. 1932: La propagation du Hamster en Belgique. *Bull. Mus. Hist. Nat. Belg. 8: 1–43.*

Frechkop S. 1936: Remarque au suject du Hamster belge. *Ann. Soc. Zool. Belg. 66: 123–126.*

Grulich I. 1987: Variability of *Cricetus cricetus* in Europe. *Acta Sc. Nat. Brno 21: 1–53.*

Hell P. & Herz J. 1969: Beitrag zur Taxonomie und Verbreitung des Eurasischen gemeinen Hamsters (*Cricetus cricetus* L., 1758) in der Slowakei. *Biológia, Bratislava 24: 839–851.*

Husson A.M. 1949: On the distribution of the common hamster, *Cricetus cricetus* (L.), in the Netherlands. *Publicaties Natuurh. Gen. Limburg, Reeks 2: 14–54. (in Dutch)*

Husson A.M. 1953: On the foramen magnum occipitale and some other skull-measurements of *Cricetus cricetus canescens* Nehring with respect to sexual dimorphism. *Proc. Kon. Ned. Akad. Wetensch., Amsterdam Ser. C 56: 609–630.*

Husson A.M. 1959: On the systematic position of the western hamster, *Cricetus cricetus canescens* Nehring (Mammalia: Rodentia). *Bijdragen Dierkunde (Amsterdam) 29: 187–201.*

Karaseva E.V. 1962: A study of the peculiarities of territory utilization by the hamster in the Altai territory carried out with the use of labelling. *Zool. Zh. 41: 275–284. (in Russian)*

La Haye M.J.J., Müskens G.J.D.M. & Van Kats R.J.M. 2011: European-wide conservation of the common hamster (*Cricetus cricetus*): what do we know? *Säugetierkd. Inf. 8: 25–29.*

La Haye M.J.J., Neumann K. & Koelewijn H.P. 2012: Strong decline of gene diversity in local populations of the highly endangered common hamster (*Cricetus cricetus*) in the western part of its European range. *Conserv. Genet. 13: 311–322.*

Meyer M. 2009: Feldhamster *Cricetus cricetus* (Linnaeus, 1758). In: Hauer S., Ansorge H. & Zöphel U. (eds.), Säugetieratlas der Säugetiere Sachsens. *Sächsisches Landesamt für Umwelt, Landwirtschaft und Geologie, Dresden, Germany: 216–219.*

Miller G.S. 1912: Catalogue of the mammals of western Europe. *British Museum London, England.*

Nechay G. 2000: Status of hamsters: *Cricetus cricetus*, *Cricetus migratorius*, *Mesocricetus newtoni* and other hamster species in Europe. *Nature and Environment Series 106, Council of Europe Publishing.*

Nehring A. 1894: Die Verbreitung des Hamsters (*Cricetus vulgaris*) in Deutschland. *Archiv für Naturgeschichte 1894: 15–32.*

Nehring A. 1899a: Einige Varietäten des gemeinen Hamsters (*Cricetus vulgaris* Desm.). *Sitz.-Ber. Gesellsch. Naturforsch Freunde Berlin 1899: 1–3.*

Neumann K., Jansman H., Kayser A., Maak S. & Gattermann R. 2004: Multiple bottlenecks in threatened western European populations of the common hamster *Cricetus cricetus*. *Conserv. Genet. 5: 181–193.*

Niethammer J. 1982: *Cricetus cricetus* (Linnaeus, 1758) – Hamster (Feldhamster). In: Niethammer J. & Krapp F. (eds.), Handbuch der Säugetiere Europas, Bd 2/I, Rodentia II. *Aula Verlag, Wiesbaden, Germany: 7–28.*

Novikov K.L. 1935: Systematic peculiarities of the hamster (*Cricetus cricetus* L.). *Bull. Soc. Nat. Moscow, sect. Biol. N. Sn. 44: 302–313. (in Russian with English summary)*

Petzsch H. 1940: Vererbungsuntersuchungen (I) an Farbspielen des Hamsters (*Cricetus cricetus* L.). *Z. Tierzüchtung Züchtungsbiol. 48: 67–83.*

Petzsch U. & Petzsch H. 1956: Zum Problem des Vererbungsmodus für Melanismus bei dem gemeinen Hamster (*Cricetus cricetus* L.) in Hinsicht auf die Evolution. *Zool. Garten (N.F.) 22: 119–154.*

Remy P. 1928: Le Hamster (*Critus cricetus* L.) est-il fixé en Champagne? *Compte rendu somm. Séances Soc. Biogegr. (Paris) 5: 40–43.*

Smulders M.J.M., Snoek L.B., Booy G. & Vosman B. 2003: Complete loss of MHS genetic diversity in the common hamster (*Cricetus cricetus*) population in the Netherlands. Consequences for conservation strategies. *Conserv. Genet. 4: 441–451.*

Stefen C. in press: Zur Craniometrie sächsischer Feldhamster (*Cricetus cricetus*). *Veröffentlichungen Naturkundemuseum Leipzig.*

Stubbe M., Seluga K. & Weidling A. 1998: Bestandssituation und Ökologie des Feldhamsters *Cricetus cricetus* (L., 1758). Ökologie und Schutz des Feldhamsters. *Martin Luther Universität Halle-Wittenberg Wissenschaftliche Beiträge Halle 1998: 137–181.*

Tkadlec E., Heroldová M., Víšková V., Bednář M. & Zejda J. 2012: Distribution of the common hamster in the Czech Republic after 2000: retreating to optimum lowland habitats. *Folia Zool. 61: 246–253.*

van Bemmelen A.A. 1881: Mededeelingen over den Hamster (*Cricetus frumentarius*). Verslag van de gewone huishoudelijke vergadering der Nederlandsche Dierkundige Vereniging van 15. Nov 1879 en 3 Juli 1880. *Tijdschr. Ned. Dierk. Ver. 5: 37–38.*

Vohralík V. 1975: Postnatal development of the common hamster *Cricetus cricetus* (L.) in captivity. *Rozpravy Československé Akdademie Věd 85: 3–48.*

Vohralík V. & Anděra M. 1976: Distribution of the common hamster, *Cricetus cricetus* (L.) in Czechoslovakia. *Lynx 18: 85–97.*

Weinhold U. 1996: Radiotelemetrische Untersuchungen zum Raum-Zeitverhalten des Feldhamsters (*Cricetus cricetus* L., 1758) auf landwirtschaftlich genutzten Flächen im Raum Mannheim-Heidelberg. *Säugetierkd. Inf. 20: 129–134.*

Weinhold U. 2011: Auszüge aus dem europäischen Aktionsplan zum Schutz des Feldhamsters (*Cricetus cricetus*). *Säugetierkd. Inf. 8: 9–23.*

Weinhold U. & Kayser A. 2006: Der Feldhamster. Neue Brehmbücherei 625. *Westarp Wissenschaften, Hohenwarsleben, Germany.*

Wepner A. 1936: Zur Frage der subspezifischen Abtrennung des Westhamsters. *Z. Säugetierkd. 11: 254–256.*

Werth E. 1934: Der Gegenwärtige Stand der Hamsterfrage in Deutschland. *Arb. Biol. Reichsanst Land- u Fortsw. 21: 201–253.*

Zimmermann R. 1923: Ueber das Vorkommen des Hamsters, *Cricetus cricetus* (L.) uns eine Erweiterung seines Verbreitungsgebietes in Sachsen. *Zool. Palaearkt. 1: 9–23.*

**Supplementary online materials**

**Appendix.** Descriptive statistics for the different samples of hamsters differentiated for AG 1 and 2 individuals together, for both sexes together and separated for females (f) and males (m). Abbreviations of the measurements as explained in Fig. 1 and the text. N – sample size, min – minimum, max – maximum, SE – standard error of mean, SD – standard deviation, Au – Austria, Bel – Belgium, Nl – The Netherlands, RhP – Rhineland-Palatinate, SaAnh – Saxony-Anhalt, Thu – Thuringia (Excel file; URL: http://www.ivb.cz/folia/download/stefen_c_appendix_supp.pdf).