Fluctuating asymmetry as an indicator for differentiation among roe deer *Capreolus capreolus* populations

Janusz MARKOWSKI

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Fluctuating asymmetry in 30 bilateral cranial non-metric traits was investigated in three roe deer *Capreolus capreolus* (Linnaeus, 1758) populations living in different habitats in Poland. For each sample, the mean proportion of asymmetric traits per individual (FA_{NM}) was calculated and used for comparisons among populations. The highest value of FA_{NM} (0.18) was displayed by roe deer belonging to the 'field ecotype', a lower one by roe deer belonging to the 'forest ecotype' (0.14), and the lowest (0.12) in a 'transient' population. In contrast to the 'forest' roe deer and the 'transient' population, a gradual and statistically significant decrease of FA_{NM}-values over the last 30 years was recorded in the 'field ecotype'. There the proportion of asymmetric traits was also significantly higher in juveniles than in other age classes. Fluctuating asymmetry in roe deer is discussed with regard to the environmental stress hypothesis and the gradual development of a coadapted gene pool in the 'field ecotype'.

Department of Ecology and Vertebrate Zoology, University of Łódź, 90-237 Łódź, Banach Str. 12/16, Poland

Introduction

The roe deer *Capreolus capreolus* (Linnaeus, 1758) is an opportunistic species with low migration distances, but with high ecological adaptability and colonizing ability (Pielowski 1970, Stubbe and Passarage 1979, Lehman and Sägesser 1986). It is also one of the genetically most variable deer species yet studied (Hartl *et al*. 1991, Lorenzini *et al*. 1993). In Central Europe, roe deer is found also in large agricultural areas since the twenties and a new, ecologically, morphologically, and even biochemically well defined 'field ecotype' has been postulated (Pielowski 1970, 1977, Fruziński and Łabudzki 1982, Majewska *et al*. 1982, Pielowski and Bresiński 1982). However, an analysis of differentiation in cranial non-metric traits performed by Markowski and Markowska (1988) did not support the existence of different ecotypes in the roe deer.

Numerous studies showed a significant increase of fluctuating asymmetry (FA) in bilateral morphological characters as a result of environmental stress (e.g. Siegel and Smookler 1973, Valentine *et al*. 1973, Palmer and Strobeck 1986,

Zakharov 1987, Livshits and Kobyliansky 1991). Based on these results many authors stated that the magnitude of FA could be useful for assessing the suitability of habitats for the development of thriving populations of various animals (Perzigian 1977, Pankakoski 1985, Zakharov 1987).

The major hypothesis to be tested in the present paper is that developmental stability, measured by FA in non-metric characters, decreases during the first years of colonizing a new habitat and later increases again. Due to the colonization of a new habitat within the last 70 years, the roe deer provides an excellent example for testing these predictions. FA in the 'field' roe deer should have been high in the early phase of colonization of open field habitats and, given a certain stability of those populations, should have gradually decreased over time. Furthermore, if the magnitude of FA is indicative for favourable or suboptimal habitat conditions, a negative correlation between FA and the size or the variance of size of morphological characters could be expected.

Study area

Skulls of roe deer were collected from three experimental hunting units in the lowlands of Central Poland (Fig. 1):

(1) Czempiń – An experimental area of the Research Station of the Polish Hunting Association, situated about 30 km south of Poznań and covering about 15,000 ha. This area is a typical field habitat with only a small proportion of tree stands (7%) and extensive stretches of cultivated fields maintained at a high level of cultivation. Large fields occupy about 70% of the whole area (Kałuziński 1982), which are inhabited by roe deer belonging to the 'field ecotype' (see Pielowski 1988).

(2) Rogów – An experimental hunting area of the Academy of Agriculture in Warsaw, situated in Central Poland and covering 13,000 ha. Forest and shelterbelts are found in about 21% of the whole area. Small fields are predominating, whereby average field size is about 1 ha. This transient area between field and forest is inhabited by roe deer called the 'transient' type throughout the paper.
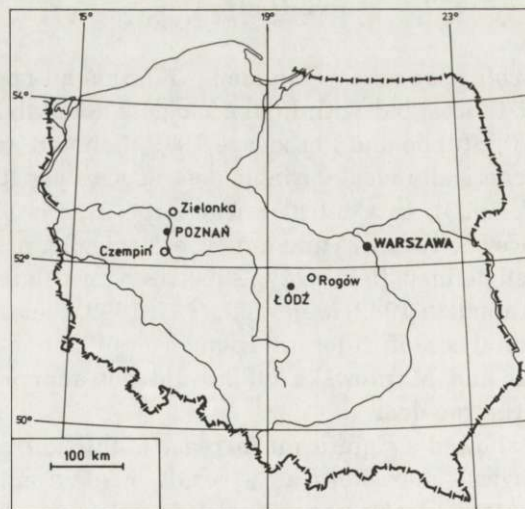

Fig. 1. The localities of the experimental hunting areas, marked with open circle.

(3) Zielonka – An experimental hunting area of the Academy of Agriculture in Poznań, covering about 8,000 ha. The whole area consists of woodland in which pine forests and mixed stands of pine and oak are predominating. The area is situated 30 km north of Poznań and is inhabited by the 'forest ecotype' (Fruziński and Łabudzki 1982).

Material and methods

A total of 399 skulls from the three sampling sites described above were investigated. Two hundred and fourteen skulls were obtained during the hunting seasons 1980 – 1984, a further 185 skulls were made accessible for examination from collections by the Research Station of the Polish Hunting Association in Czempiń and the Department of Wildlife Management of the Academy of Agriculture in Poznań, (skulls collected from 1967 to 1979). Some 30 skulls obtained from the Słonin forest in the Czempiń hunting area were used only for a restricted comparison of roe deer inhabitating this forest with roe deer dwelling in cultivated fields. The hunted deer were dissected and various morphological measurements were taken. Age of each deer was estimated from mandibular tooth wear (Pielowski 1970). The material from Czempiń contained also skulls of roe deer born in captivity or marked in the field and the age of these individuals was exactly known. For the purpose of the present study the roe deer were divided into 6 age classes: I(= up to 1 year old), II(= 1-2), III(= 3-4), IV(= 5-6), V(= 7-8), VI(over 8 years old), respectively, in order to examine the relationship FA in non-metric traits and age. According to known dates of the hunts and backageing of specimens the whole material was also subdivided into distinct samples, separated by intervals of five years.

A set of 30 bilateral traits was selected from a total of 79 cranial non-metric traits previously used for examining inter-individual morphological variation by Markowski and Markowska (1988) (see Appendix). Rejection of various traits was due to the occurrence of directional asymmetry or anti-symmetry (detected by means of the paired t-test and the χ^2-test (Soulé 1967). Each trait was scored on the left and on the right side of the skull as present or absent. Asymmetry was given, when the character expression differed between body sides. As an overall asymmetry index, the proportion of traits asymmetric per individual was used. FA of populations was characterized by the mean proportion of traits asymmetric per individual (FA_{NM}).

Following Trinkaus (1978) two tests were used to provide a reasonable indication of the prevalence of bilateral asymmetry in each population: (1) The frequency of FA per trait is less than or equal to 5%, (2) the unilateral frequency of a trait is less than or equal to half of the bilateral frequency (Table 1).

In each of the study areas, relationship between the proportion of traits asymmetric per individual and body size (as indicated by mandible length) was examined using the Pearson correlation co-efficient. Relationship between individual asymmetry and age was examined by means of Spearman rank correlations.

Statistical significance of differences in the incidence of each trait between populations was calculated using arcsin transformation: $(\Theta_1 - \Theta_2)^2$, where Θ = arcsin $(1-2p)$ and p is the frequency of variants. The differences are statistically significant at $p = 0.05$ if $(\Theta_1 - \Theta_2)^2$ is three times bigger than $(1/n_1 + 1/n_2)$, where n_1 and n_2 are the sample sizes. The mean measure of divergence (MMD) between populations was calculated using the formula of C. A. B. Smith (Sjøvold 1977).

Results

In the 30 bilateral non-metric traits remaining in the analysis, no directional asymmetry or antisymmetry was detected. There was also no sex or age depend-ence of FA in any of the three populations studied ($F_{sex} = 1.51$, $F_{age} = 0.43$,

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Table 1. Asymmetry indices of cranial non-metric traits (listed in Appendix) in the roe deer populations studied. * and ** mean that the unilateral frequency is significantly higher than 5% at $p < 0.05$ and $p < 0.01$, respectively. † and ‡ mean that the unilateral frequency is significantly higher than half of the bilateral frequency at $p < 0.05$ and $p < 0.01$, respectively. + and ++ results of paired t-test significant at $p < 0.05$ and $p < 0.01$, respectively.

Trait no.	Population			Results of tests		
	Czempiń [1] $n = 116$	Rogów [2] $n = 128$	Zielonka [3] $n = 125$	[1]-[2]	[1]-[3]	[2]-[3]
1	.39 ** ‡	.18 **	.30 ** †	++		+
2	.35 ** ‡	.23 **	.30 ** ‡	+		
3	.24 **	.13 *	.17 **	+		
4	.35 **	.23 **	.30 **	+		
8	.16 **	.08	.16 **	+		
12	.06	.06	.06			
14	.16 ** ‡	.03	.15 ** ‡	++		++
21	.09	.03	.08	+		
23	.09 †	.05	.06			
25	.09	.05	.02		++	
26	.15 * †	.13 *	.15 ** †			
29	.09 ‡	.05	.07			
31	.29 ** ‡	.30 ** ‡	.22 ** ‡			
34	.30 ** ‡	.21 ** †	.24 ** ‡			
38	.12 *	.10	.06			
39	.32 ** ‡	.24 ** ‡	.30 ** ‡			
41	.08 †	.06	.06			
44	.37 ** ‡	.27 ** ‡	.30 ** †			
47	.24 ** ‡	.17 ** ‡	.23 ** ‡			
51	.16 **	.19 ** ‡	.06		++	++
52	.29 ** ‡	.21 **	.23 **			
65	.09 ‡	.02	.09 ‡	++		++
66	.24 ** ‡	.23 **	.22 ** ‡			
67	.03	.00	.01			
68	.02	.02	.02			
69	.01	.07 †	.01	++		++
70	.11 * ‡	.05	.03	+	++	
71	.09	.11 *				
72	.03	.13 *	.01	++		++
FA_{NM}	.18	.12	.14			
SD	.11	.08	.09			

$F_{interaction} = 0.40$). In the samples from Czempiń (1) and Zielonka (3), about 50% of the traits showed a statistically significant occurrence of FA whereas in the sample from Rogów (2) this proportion was lower (Table 1). In the material from Czempiń, there was no statistically significant difference in the mean proportion

Table 2. Mean measure of divergence (MMD) and standard deviation (in parentheses), based on: (a) all non-metric traits, (b) non-metric traits not significantly differing in FA among study areas. * – significant at $p < 0.05$, ns – not significant.

	(a)	Rogów	Zielonka	(b)	Rogów	Zielonka
Czempiń		0.0345 * (0.0087)	0.0075 ns (0.0041)		0.0130 * (0.0061)	0.0113 ns (0.0057)
Rogów		– (0.0069)	0.0227 *		–	0.0127 * (0.0059)
Zielonka			–			–

of asymmetric traits between specimens killed during hunts (FA_{NM} = 0.16, SD = 0.11, n = 89) and specimens that died for other reasons (FA_{NM} = 0.18, SD = 0.12, n = 30).

The highest value of FA_{NM} was recorded in the 'field ecotype' (0.18), a lower one in the 'forest ecotype' (0.14), and the lowest one in the population from Rogów (0.12) (Table 1). However, the differences between FA_{NM} were not statistically significant (F = 1.97, one-way ANOVA). The same was the case as to differences between the 'field ecotype' and specimens from the Słonin forest (Czempiń hunting area), where FA_{NM} was 0.16.

Differences in the occurrence of FA in single non-metric traits were more pronounced among the geographically more separated populations (FA significantly different in 11 traits between Rogów and Czempiń and in 6 traits between Rogów and Zielonka) than between 'ecotypes' (FA significantly different in only 3 traits between Czempiń and Zielonka; Table 1).

Based on all traits, the mean measure of divergence (MMD) was significant between Rogów – Czempiń and Rogów – Zielonka (Table 2a). There the MMD--values were in the same range (Table 2b), when traits showing significant differences in FA among study areas were excluded from the comparisons (traits 1, 8, 14, 65, 69 – Table 1).

When FA_{NM} (measured at intervals of five years) in each population was analyzed for changes within a time span of 30 years, a gradual decrease was recorded in the 'field ecotype', while in the other populations the respective indices showed only slight and nondirectional fluctuations. In the material from Czempiń there was a decrease of FA_{NM} with time, both when specimens were assigned to groups according to culling dates and to birth dates (r_s = 0.80, p = 0.07; Fig. 2). In the 'field' roe deer, there was a significant negative relationship between FA_{NM} and age ($r_s = -0.26$, n = 116, p = 0.04), and the FA_{NM}-value for the youngest age class was statistically different from the corresponding values from the other populations (F = 2.89, $p < 0.05$).

The proportion of asymmetric traits per individual and mandible length were significantly correlated only in bucks from Rogów (r = 0.241, $p < 0.05$, n = 74),
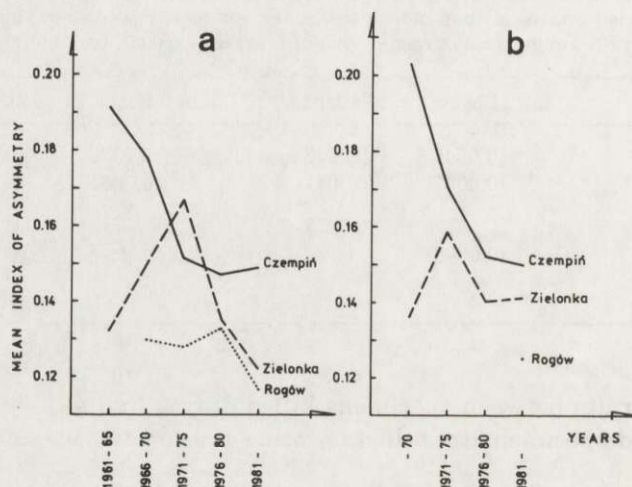
Fig. 2. Changes of the mean index of asymmetry in roe deer populations from Poland: (a) calculated at intervals of five years of birth, (b) calculated at intervals of five years of culling.

but not in bucks from the other areas and in does. In the 'forest ecotype' and the 'transient' type, negative correlations between FA_{NM} and the variance of the mandible length were observed in both sexes (Zielonka – males: $r_p = -0.42$, ns, females: $r_p = -0.25$, ns; Rogów – males: $r_p = -0.87$, $p < 0.01$, females: $r_p = -0.75$, ns).

In the 'field ecotype', however, this correlation was positive (Czempiń – males: $r_p = 0.62$, ns, females: $r_p = 0.66$, ns).

Discussion

Many authors have argued that skeletal non-metric traits are more useful than metric traits for the purpose of various population studies in mammals (Berry 1963, 1968, Berry and Berry 1967, Berry and Jakobson 1975, Hartman 1980, Andersen and Wiig 1982, Bauchau 1988, see Markowski and Sikorski 1987, for review). The main arguments are that non-metric traits show little variation with sex and age, are hardly correlated with one another, and are readily scored so that large samples of both characters and individuals can be examined (Berry 1963, 1968, Finnegan 1978).

Both genetic and environmental factors might be important in the control of non-metric traits (Berry 1963, Corruccini 1974). Some authors demonstrated a very low heritability of those traits in mammal species (e.g. Self and Leamy 1978, Thorpe 1981, Cheverud and Buikstra 1982, Leamy 1984). However, the genetic component for regulating their bilateral expression is often significantly heritable (Revee 1960, Bailit *et al.* 1970, Jackson 1973, Valentine *et al.* 1973, see Zakharov

1987, for review). Several studies on various animal species revealed a strong negative correlation between fluctuating asymmetry and heterozygosity at protein loci (Kat 1982, Leary et al. 1984, Zouros and Foltz 1987). Based on a hypothesis proposed by Lerner (1954), these findings have been interpreted to reflect the better buffering of heterozygous individuals against environmental insult.

Fluctuating asymmetry has been used for measuring developmental instability both at the individual and population level (e.g. Mather 1953, Thoday 1958, Beardmore 1960, Van Valen 1962, Soulé 1979, 1982, Leamy 1984, Zakharov 1987). The possible causal background of a relationship between FA and developmental homeostasis has been outlined in at least three different models. The first model emphasizes the role of environmental influences in affecting the expression of non-metric traits. Some traits may be changed in response to mechanical forces acting upon the skeleton during remodelling processes (Trinkaus 1978). Others, such as various foramina and processus, may be affected by environmentally induced changes in soft tissues like an increased vascularization in response to climatic stress or muscular hypertrophy. The second model has been proposed by Berry (1968). He claims that there are different thresholds for the continuous genetic basis of unilateral and bilateral expression of a trait. Genetic stress, such as inbreeding, can increase the distance between thresholds and thus result in higher levels of asymmetry. The third hypothesis is based on competition between body sides as to the quantity of gene products produced by different alleles at structural genes. If too much of the needed product is available, both sides of an organism would receive sufficient amounts for adequate development. If the product is present in limited quantities, the competing sides would probably receive slightly different amounts (Livshits and Kobyliansky 1991).

In the present study the highest FA_{NM}-value occurred in the 'field ecotype', where population density is lowest, whereas the lowest FA_{NM}-value was found in the Rogów population, where density is highest (Pielowski 1988). Thus, the increased FA in the roe deer from Czempiń could be the result of a higher degree of inbreeding occurring in this population. Also the gradual decrease of FA_{NM} observed in the 'field ecotype' could be explained by an increase in outbreeding due to an increasing number of roe der settling in the open field habitat (Pielowski 1988). However, this interpretation is not in accordance with inbreeding co-efficients (F_{IS}), as assessed for each population using frequencies of character expressions and the occurrence of asymmetry in non-metric traits in the way suggested by Piontek (1979). The lowest F_{IS}-value (0.0007) occurred in the 'field ecotype' and highest one was found in the Rogów population ($F_{IS} = 0.021$). This result is supported by analyses of spatial and social organization of field and forest populations of roe deer. The 'field' roe deer forms bigger herds during autumn and winter and recently the small herds have been noted even during the summer time (Bresiński 1982), whereas in forest populations individuals live solitarily or form small family clans (Kurt 1968, Pielowski 1988). In the 'forest' roe deer bucks maintain territories and several females exclusively copulate with one and the

same buck. Depending on population density, merely about 20% of all males
contribute to the gene pool of the next generation, which should result in a certain
degree of inbreeding. In contrast, in field populations territories are largely lacking
and the mating system is considered promiscuous (Kurt *et al.* 1993).

The statistically higher level of asymmetry in the young specimens of the field
population suggested considering the environmental stress hypothesis. Due to the
long gestation period in the roe deer (Prell 1937), a considerable part of embryonic
development takes place under severe climatic conditions (i.e. during the winter
and early spring). In field habitats, pregnant females are much more exposed to
unfavourable environmental conditions than in forest habitats. Generally, mater-
nal effects, such as the physiological status and the diet of females are known to
have an influence on skeletal epigenetic traits of offspring in mice and rats (Searle
1954, Howe and Parsons 1967, Dahinten and Pucciarelli 1981, 1983). Livshits and
Kobyliansky (1991) demonstrated a significant midparent-child correlation for
mean fluctuating asymmetry but not for each specific anthropometric trait and
they concluded that: (1) there is a genetic mechanism predisposing a developing
organism to high or low stability in relation to the environment, (2) FA averaged
over many bilateral traits should more precisely reflect the level of developmental
stability than FA in single traits.

In the roe deer, the higher number of significantly asymmetric traits bserved
in the 'field ecotype' could be explained as a result of disturbancies in the syn-
chronization of bilateral expression of traits (Siegel and Doyle 1975a, b, Soulé
1979, 1982) as well as by a possible genetic mechanism predisposing a developing
organism to reduced homeostasis in a particular environment (Livshits and
Kobyliansky 1991).

Age and sex of the roe deer were not significantly related to the magnitude of
fluctuating asymmetry in the whole material studied. A slightly higher level of
FA was found in females, but since this result was the same in all age classes,
this phenomenon cannot be explained by differential hunting pressure with respect
to sex. Reports on differences in FA between sexes in other mammalian species
are rare and fragmentary (Bailit *et al.* 1970, Jackson 1973, Perzigian 1977, Leamy
1984).

If differences in FA_{NM} among populations are due to environmental factors,
and resources available to pregnant females as well as to the offspring during
post-natal ontogenesis induce the development of bones and of skeletal non-metric
traits (Searle 1954, Howe and Parsons 1967, Dahinten and Pucciarelli 1983,
Perzigian 1977), a negative correlation between overall FA and body growth could
be expected. This was supported by data of Perzigian (1977), who showed that the
tallest and the best nourished individuals in prehistoric human populations
displayed the least dental asymmetry. A negative association of asymmetry at the
population level with body growth was observed also in a muskrat from Finland
(Pankakoski 1985). In the present study the expected relationship was found in
the Rogów area. However, in populations of western Poland 'field' roe deer have

larger skull and body sizes (Fruziński and Łabudzki 1982, J. Markowski, in prep.), but also a higher asymmetry level than the 'forest' roe deer.

In conclusion, when roe deer colonized the open field habitat, environmental factors and changes in breeding strategy probably induced perturbations of developmental homeostasis and led to a distortion of a formerly well coadapted gene pool. The decrease of FA_{NM} over time may thus reflect the gradual adaptation of the 'field' roe deer gene pool to the new habitat.

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APPENDIX

The location of non-metric traits of the roe deer skull: (a) ventrolateral view, (b) dorsolateral view, (c) mandible. Numbers refer to non-metric traits listed in the Table, p. 31.
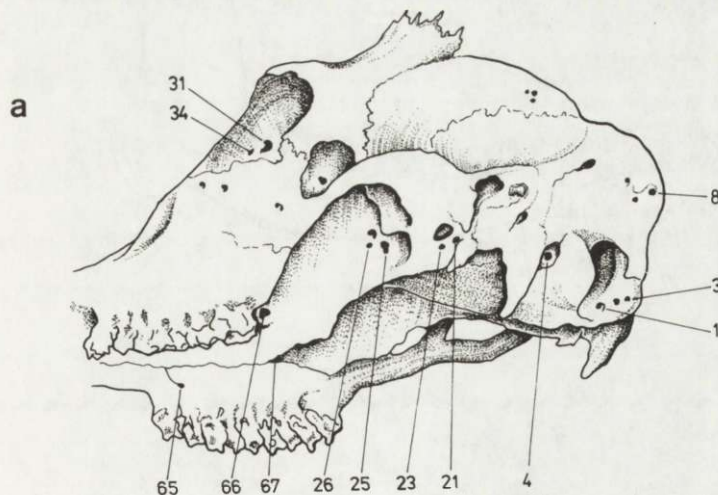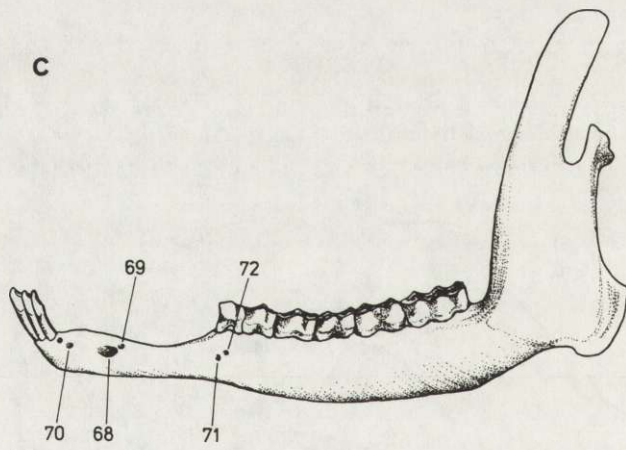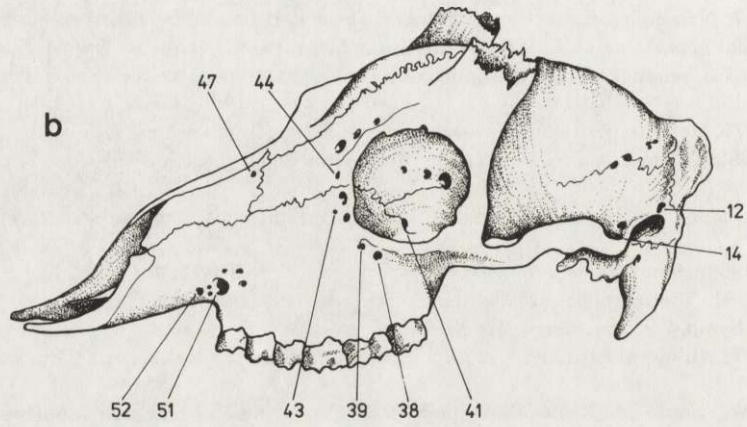
Cranial non-metric traits studied in roe deer (after Markowski and Markowska 1988).

No.	Trait and its morphological expression
1.	Internal hypoglossi foramen double
2.	Accessory internal hypoglossi foramen present
3.	Internal condylar foramen present
4.	External condylar foramen (opens into a mutual canal with external hypoglossi foramen)
8.	External supraoccipital foramen present
12.	*Meatus temporale* double
14.	Accessory *meatus temporale* foramen double
21.	Lateralo-basilar foramen present
23.	Posterior accessory foramen by *foramen ovale*
25.	Accessory foramen II by *foramen orbito-rotundum* present
26.	Accessory foramen I by *foramen opticum* present
29.	Ethmoidale foramen double
31.	*Foramen supraorbitale inferior* double
34.	Accessory foramen III by *foramen supraorbitale inferior* present
38.	Zygomaticum anterior foramen present
39.	Accessory *foramen zygomaticum anterior* present
41.	Intersutura fontanele between lacrimal and zygomatic bones present
43.	Infralacrimale foramen present
44.	Supralacrimale foramen present
47.	Foramina penetrating nasal bone present
51.	Infraorbitale foramen double
52.	Accessory infraorbitale present
65.	Posterior palatal foramen double
66.	Accessory foramen by posterior palatal foramen present
67.	Palatal notch cross the palatal edge
68.	Mental foramen double
69.	Superior accessory mental foramen present
70.	Inferior accessory mental foramen present
71.	Posterior mental foramen present
72.	Posterior accessory mental foramen present