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Genetic analysis of nasal region polymorphism in European moose (*Alces alces* Linnaeus)

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A genetic analysis of four nasal bone structures found in European moose (*Alces alces* L.) was performed. The study was based on a hypothesis of an active role of the temporary ossification centres of developing sutural area during the suturation process. Results suggest that the bone polymorphism is controlled by two gene loci showing dominance but no epistasis. Since nasal region morphs seem to be more stable in males than in females biomechanical strain due to massive antlers with a horizontal pedicle structure may be casual.

1. Introduction

As a widespread, highly mobile and adaptable large ruminant, with a breeding strategy based on female-controlled polygamy (Bubenik 1987), moose populations are often assumed to be genetically fairly stable (Selander & Kaufmann 1973). Observations on body dimensions, coat colour and antler type show remarkably limited variation (Voipio 1948, Nygrén 1986, Geist 1987), as do some early studies on serology (Nadler et al. 1967, Ryman et al. 1977). In later studies of isoenzyme variation based on more detailed and comprehensive sampling, considerably greater genetic non-homogeneity was observed (Ryman et al. 1980). Geburek (1988) compared this non-homogeneity with the data analyzed by several authors in other cervid species, concluding that the moose is among the least genetically varied species of deer.

In the course of craniological studies on material including both sexes and all age groups of Finnish moose collected by the Ahvenjärvi Game Research station at Ilomantsi in eastern Finland, variation was observed in the nasal bone region. Comparable polymorphism of this part of the skull has so far not been reported in any other mammalian species.

Later, similar bone polymorphism was observed in hunting trophy exhibitions displaying male moose antlers and calvarial and nasal bones collected in Poland, Estonia, Lithuania, Latvia, Sweden and Norway (Nygrén 1986). Studies on the ontogeny of the nasal region showed that the variation was congenital and not of pathological or traumatic origin. Twins may have different

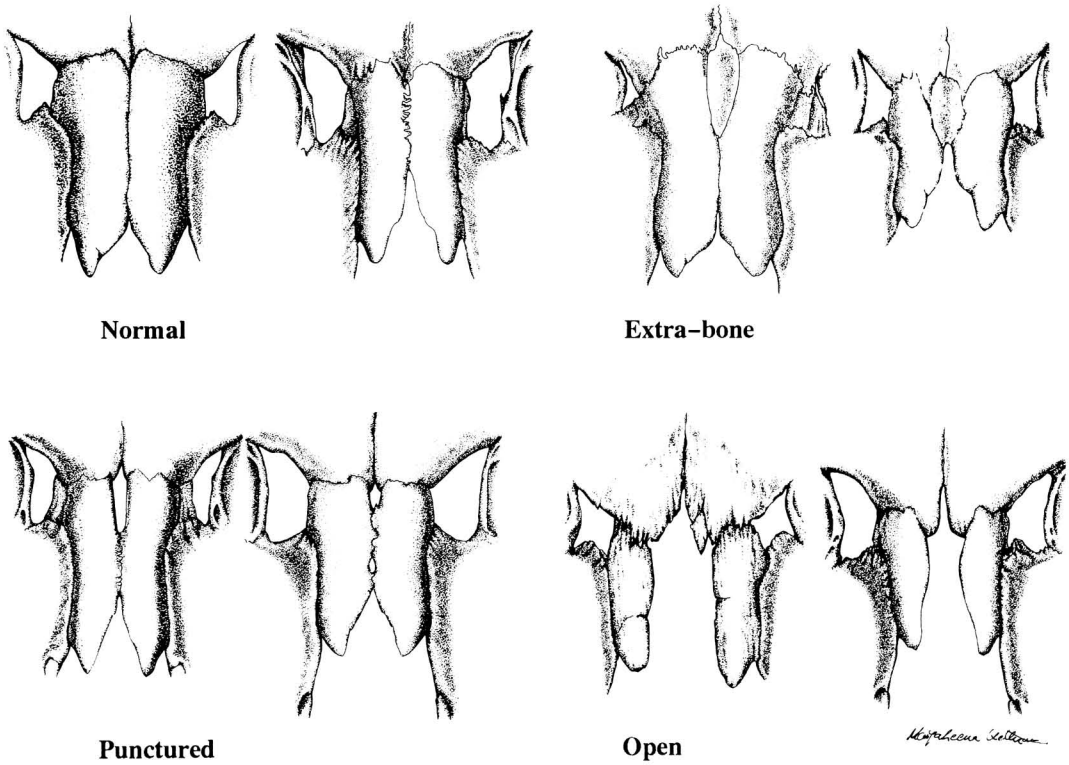

Fig. 1. Nasal region morphs and some inter-type variants in European moose, *Alces alces*.

nasal bone types (Nygrén et al. 1990). Describing a fossil cervid, *Cervalces americanus* (*C. scotti)*, Scott (1885) noted the presence of extra bonelets partially covering the *fissura nasolacrimale*. He also noted that similar structures had been found in recent Canadian moose.

Due to the dysostotic appearance of some of the types, a genetic failure of the normal nasal region suturation was assumed. The purpose of this study is to describe the possible genetic control of four skull phenotypes found in several European moose populations.

2. Material and methods

The nasal bone classification was performed by visual inspection of cleaned, bleached and dry skulls or parts of skulls including the nasofrontal region of adult (≥ 2 years old) moose. In accordance with Nygrén (1986), nasal region morphs were classified into four types (Fig. 1).

Normal: an ossified suture without openings between the nasal bones up to the nasion.

Punctured: an opening or cavity filled with soft tissue, broader than 1 mm, through the internasal suture or in the nasion.

Extra-bone: all of the extra bones situated in the internasal suture or nasion, whether the nasal bones were completely separated or not.

Open: no ossified contact between the nasal bones in the area of the internasal suture.

In total, 1343 nasofrontal regions of male moose, selected by moose hunters for their large antlers, were inspected. In addition, 346 randomly collected Finnish male moose and 169 Finnish and 4 Swedish female moose skulls were included. The age of the animals, determined in 336 Finnish animals by means of the incisor cementum annuli counting method (Sergeant & Pimlott 1959), varied from 2 to 23 years. Most of the animals (86%) checked for age were less than 10 years old; two females were over 20 years old.

The genetic basis of the nasal bone polymorphism was ascertained as follows:

Two gene loci (*A* and *B*) were assumed to determine internasal suture development. Gene locus *A* regulates the establishment of a temporary ossification centre situated near the nasion, while gene locus *B* controls the subsequent distribution of this material along the fusing suture. Both gene loci are biallelic. Genotypes carrying at least one dominant allele (*A*) control the ossification of the fusiform ossification centre. The recessive homozygote (*aa*) is characterized by the absence of this ossification. Genotypes *BB* and *Bb* have a less diffuse distribution of the sutural bone tissue than the recessive homozygote *bb*. The genotypes of the different morphs are suggested to be:

normal	*A*– B–	punctured	*aa B*–
extra bone	*A*– bb	open	*aa bb*

The hypothesis was tested by comparing the observed distribution of the morphs with the expected Hardy-Weinberg distribution. The gene frequencies were calculated as follows:

$$q_a^2 = (punctured + open) / S,$$
$$q_b^2 = (extra\text{-}bone + open) / S,$$

where q_a is the frequency of the *a* allele, q_b the frequency of the *b* allele and *S* the total number of individuals in a given population. The expected frequencies of the different morphs were calculated as follows:

normal	$(1 - q_a^2)(1 - q_b^2) S$
extra bone	$(1 - q_a^2) q_b^2 S$
punctured	$q_a^2 (1 - q_b^2) S$
open	$q_a^2 q_b^2 S$

Observed and expected frequencies were compared by χ^2 -analysis ($df = 1$).

4. Results

The observed and expected frequencies of nasal region morphs are presented in Table 1. With the exception of one sample (combined Finnish and Swedish female moose), none of the populations deviated significantly from the Hardy-Weinberg proportions.

5. Discussion

The results of this population-genetic approach suggest that the nasal bone polymorphism in European moose has a sex-dependent genetic basis, the polymorphism being regulated by two gene pairs.

Table 1. Observed and expected Hardy-Weinberg frequencies of nasal region morphs in European moose populations (** = deviations significant at 1% level, $df = 1$).

Sample		Normal	Extra bone	Punctured	Open	χ^2
Big-antlered Finnish bulls	obs.	395	224	111	73	
	exp.	390.05	228.95	115.95	68.05	0.740
Non-selected Finnish bulls	obs.	164	88	68	26	
	exp.	168.97	83.03	63.03	30.97	1.634
Big-antlered Scandinavian bulls	obs.	82	18	84	23	
	exp.	80.19	19.81	85.81	21.89	0.398
Big-antlered bulls from Estonia, Latvia and Lithuania	obs.	212	35	55	6	
	exp.	214.12	32.88	52.88	8.12	0.796
Big-antlered Polish bulls	obs.	22	2	0	1	
	exp.	21.12	2.88	0.88	0.12	1.421[1]
Non-selected Finnish ($n = 169$) and Swedish (n = 4) females	obs.	77	37	51	8	
	exp.	84.35	29.65	43.65	15.35	7.214**

[1] With Yates's correction.

Several cases of two genes influencing the same character have been observed in vertebrates. Bateson et al. (1908) studied comb morphology in fowls, observing inter- and intra-allelic interactions of the independent gene pairs producing different comb forms. The colour and its distribution in the coat of domestic cattle was also shown to be regulated by two biallelic loci (Lauprecht 1926). The authors did not suggest any causal explanation of the polymorphism. In a genetically similar case producing plumage colour polymorphism in Arctic Stern chicks, Lemmetyinen et al. (1974) found a correlation between the polymorphism of the prey and the predation pressure.

On the basis of the fact that the genetic system underlying the polymorphism is stable in males but unstable in females, we suggest that the polymorphism is connected with the wearing of antlers and thus with the biomechanical stress caused by the antler-transmitted forces affecting the osseous structure of the skull. The distribution and magnitude of such forces have been demonstrated experimentally by Nygrén et al. (1992) and Silvennoinen et al. (1992).

The site of this structural polymorphism is a transitional zone between the neurocranial bone structures, with high growth priority, and the rostral part of the skull, characterized by lower growth priority (de Beer 1937). Furthermore, the calvarial bone structures of the moose are massive, rigid and interdigitally sutured, while those lying rostrally from the naso-frontal junction are typically thin and elastic, articulated in most cases by false or squamous sutures. In the ontogeny of the moose, these differences may produce biomechanical stress in and around the nasofrontal junction, observed to cause bone remodelling (Goodship et al. 1979).

The mammalian nasal bone is an endochondrally ossified structure capable of both appositional and interstitial growth (Persson & Thilander 1985). In an experimental study of the growth of the nasomaxillary bones of isohistogenic rats, Hirabayashi et al. (1988) concluded that the facial bones do in fact regulate their own growth, possibly by means of factors found in the osteogenic cells. The role of the sutures in the growth of skull bones has been a controversial matter, earlier authors suggesting that they are passive formations, but more recent authors claiming that the sutures have a more active role as sites of growth (Persson 1977) These conclusions suggest that the growth and suturation of the mammalian skull bones have a genetic regulation mechanism, as has also been concluded in the present study.

In enzyme histological studies of the growth of both human and rabbit skulls, Persson (1977) and Persson & Thilander (1977) concluded that the closure of sutures is determined by functional forces affecting the specific suture area, following cessation of sutural growth. This supports our conclusion that the nasal bone polymorphism in the European moose may be affected by functional physical forces caused by the almost horizontal wearing of massive antlers.

In his histological studies of human and rat skulls, Markens (1975) observed blastemic spindle-shaped ossification centres, suggested to take part in the formation of the coronal suture. Although Johansen & Hall (1982) and Furtwängler et al. (1985) disputed the significance of these blastemas, considering them to be merely secondary structures, it seems possible that if the sutures of the mammalian skull are in fact active sites of bone growth, and if the bones regulate their own growth, something like such blastemas may exist as the organizational centre of suture formation.

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