

Dental and cranial anomalies in Austrian and Polish brown hare *Lepus europaeus* populations

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A total of 598 Austrian and 1117 Polish skulls of brown hares *Lepus europaeus* Pallas, 1778 was examined for dental anomalies, occurrence of Wormian bones and formation of a fenestra in the *fossa mandibularis ossis temporalis*. In addition, the degree of ossification of skull sutures and frequencies of traceable interparietal sutures were analysed in Austrian hares. Frequencies of missing M^3 were 1.95% for Austrian and 2.1% for Polish hares from 1986 – 1990. No significant differences as to age or sex were found for incidences of missing M^3 ; the left side of the tooth row was significantly more often affected by missing M^3 , which indicates directional asymmetry. Rotation of the I^2 (mainly of low magnitude) was noticed in 27.9% of subadult and adult Austrian hares. Occurrences of all other dental anomalies such as abnormal shape of M^3 , missing I^2 , missing M_3 , supernumerary I^2 , additional upper molar and various cases of malformation or irregular position of teeth were very low, respectively. Ossification of skull sutures was presently reduced as compared to the material investigated by Caboń-Raczyńska (1964) and regional differences in the degree of sutural obliteration were found. Temporal fenestration was encountered in 24.6% of subadult and adult Austrian hares and in 11.6% in Polish hares sampled during 1986 – 1990 ($p < 0.001$). Frequency of temporal fenestration increased with age: 2.9% in fetuses/neonates, 16.5% in subadult and 28.1% in adult hares from Austria ($p < 0.01$, d.f. = 2); 8.7% in subadult and 23.8% in adult Polish specimens. Average frequency of Wormian bones in Austrian hares was 4.8% and 4.4% in the Polish material. Within subadults 3.7% of males and 16.3% of females ($p < 0.01$) exhibited a traceable outline of the *os interparietale*.

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Introduction

Recent population genetic studies in the brown hare *Lepus europaeus* Pallas, 1778 did not reveal essential biochemical genetic differences among samples collected from four countries in Central Europe although several alleles appeared

to be restricted to certain geographical areas (Hartl *et al.* 1989, 1990; Hartl 1991, Suchentrunk *et al.* in press). However, it is not yet clear to what extent biochemical-genetic diversity is indicative for the endogenic component of variation in morphological characters at the population level (Schnell and Selander 1981, Palmer and Strobeck 1986). Therefore, in addition to biochemical-genetic studies, the geographical analysis of genetically based abnormalities of the dentition and skull bones (Nachtsheim 1936, Torgersen 1951, Grüneberg 1965, Lindsey and Fox 1974, Wiesner and Willer 1974, Meyer 1975, Wolsan 1984) can be of population genetic value (Vigal and Machordom 1987 for Spanish mountain goats). The fact that a reduction or agenesis of the third upper molar obviously occurs more frequently in brown hares from New Zealand than in European populations – a phenomenon probably indicating a genetic bottleneck in hares from New Zealand (Flux 1980) – is a good hint for the utility of surveying morphological anomalies in connection with genetic studies.

Due to the rather scarce or accidental information about teeth and skull anomalies in European brown hares (Pucek 1962, Szabo 1965, Herzog 1967, Hochstrasser 1969a, b, Oldenburg 1986, Kratochvíl 1987), no comprehensive conclusions as to regional differences in occurrence and meaning for population studies could have been drawn so far.

In this paper we present the frequencies of abnormal dentition, wormian bones and temporal fenestration based on a large sample of central European brown hares and discuss the data in relation to the geographical distribution, the structure and the biochemical genetic differentiation of populations. Furthermore, observations on the ossification of skull sutures and the occurrence of rotation of the second upper incisors in Austrian specimens are presented.

Material and methods

A total of 598 Austrian and 1117 Polish skulls of the brown hare *Lepus europeus* Pallas, 1778 were studied. Five hundred twenty eight subadult and adult Austrian hares were obtained during the autumnal hunting period of 1988. Another sample of 37 individuals was used from the breed at the Forschungsinstitut für Wildtierkunde und Ökologie (Veterinary University of Vienna). The geographical distribution of the sampling sites is displayed in Fig. 1. For the geographical analyses of prevalences of the respective anomalies sample sites were treated both as separate units and as combined regional samples.

The Polish material was collected during the hunting seasons within the period of 1986 – 1990. In addition, skulls and mandibles from the years 1959 – 1963 ($n = 682$) and 1970 – 1975 ($n = 125$) were made available by the Mammal Research Institute of the Polish Academy of Sciences at Białowieża. For the geographical distribution of the Polish sample locations see Fig. 2.

Sex determination of the hares was performed by inspection of the internal reproductive organs. Animals were classified as adults (AD; at least one year old) whenever their average dry eye lens weights exceeded 270 mg. All others were considered as subadults (SA) – i.e. young of the year (Suchentrunk *et al.* 1991).

The ossification of skull sutures was assessed according to the scheme provided by Caboń-Raczyńska (1964) and additionally to a slightly modified scale (Suchentrunk *et al.* 1991).

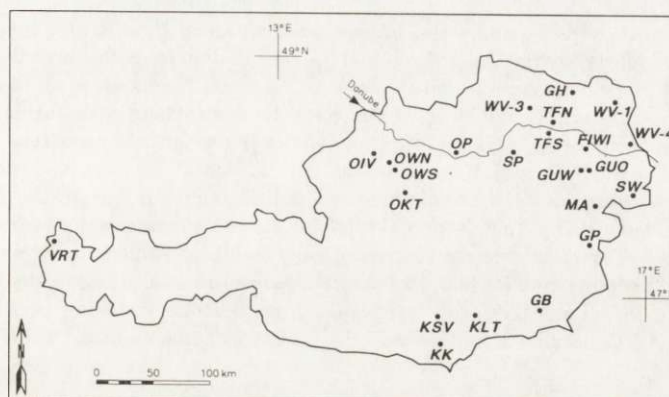


Fig. 1. Geographical distribution of Austrian brown hare samples.

FIWI = Forschungsinstitut f. Wildtierkunde u. Ökologie (Vet. Med. Univ. Vienna), GB = Gralla (Leibnitz), GH = Großharras (Mistelbach), GP = Großpetersdorf (Oberwart), GUV and GUO = Guntramsdorf (Mödling), KK = Grafenstein/Poggersdorf (Klagenfurt-Umgeb.), KSV = St. Georgen/L. (St. Veit/Gl.), KLT = St. Margarethen/L. (Wolfsberg), MA = Mattersburg, OIV = Wendling (Grieskirchen), OP = Naarn (Perg), OVN = Edt/Lambach/Steinkirchen (Wels-Umg.), OWS = Ried/Trk. (Kirchdorf/Kr.), Nußbach (Kirchdorf/Kr.), SP = Markersdorf/Haindorf (St. Pölten), SW = Illmitz (Neusiedl/S.), TFN = Frauendorf/Bierbaum (Tulln), TFS = Rust (Tulln), VRT = Fussach/Höchst/Gaißau (Bregenz), WV-1 = Bullendorf (Mistelbach), WV-3 = Hohenwarth (Hollabrunn), WV-4 = Zwerndorf (Gänserndorf).

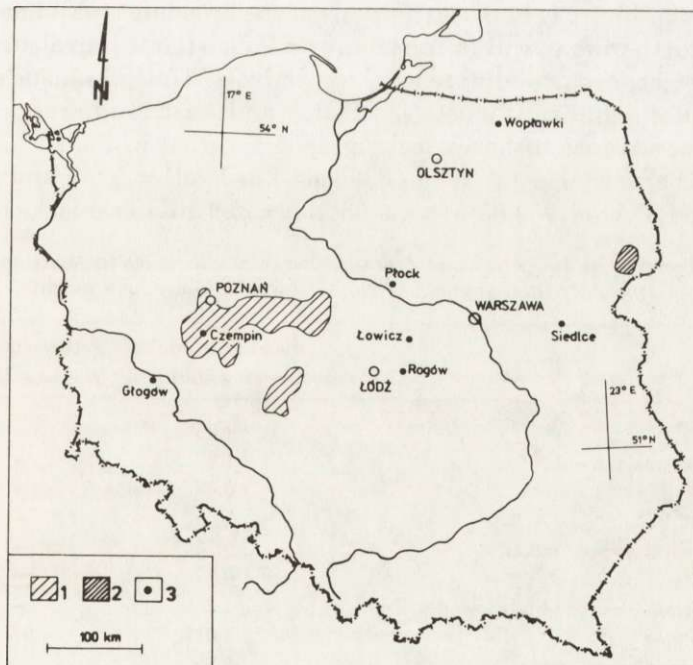


Fig. 2. Geographical and temporal distribution of Polish brown hare samples. 1 = 1959 – 1963, 2 = 1970 – 1975, 3 = 1986 – 1990.

Skulls of 33 brown hare neonates and fetuses were obtained from a wild living population in Austria (district of Mattersburg, (MA) Burgenland; Fig. 1) and from the breeding station of the Forschungsinstitut für Wildtierkunde und Ökologie in Vienna. Neonates were maximally two days old and fetuses presently examined had come almost to the end of their intrauterine development (as indicated by the respective body weights in comparison to the weights of neonates).

Skulls were controlled for deviations from the normal dental formula, incidences of abnormal dental development, occurrence of Wormian bones as well as temporal fenestration (*fenestra in fossa mandibularis ossis temporalis*). In Austrian skulls and mandibles abnormal placement of teeth (e.g. rotation), incidence of *os interparietale*, degree of ossification of skull sutures and frequencies of extrinsic dental and bone anomalies (e.g. periodontal disease) were also registered.

Concerning the Polish material only specimens from the last sampling period were used for regional comparisons. Generally, significance of χ^2 -tests was accepted on a level of $p < 0.05$.

Results

Dental anomalies

The frequencies of dental anomalies encountered in Austrian and Polish specimens are listed in Table 1 and Table 2.

Missing of M^3 was recognized irrespective of absence or occurrence of a considerably reduced tooth socket (*alveolus dentis*). No sex or age (SA vs. AD) specific differences in occurrence of this anomaly were found. In SA and AD Austrian hares the frequencies of missing M^3 (uni- and bilateral cases combined) did not differ significantly between animals of the breeding station and wild living individuals. Furthermore, within Austrian and Polish hares prevalences of missing M^3 showed no geographical differences, respectively. Thus, frequencies of missing M^3 did not differ significantly between Polish and Austrian hares.

However, occurrence of hares lacking an M^3 varied in Polish hares between the sampling periods: 1970 – 1975 (Podlasie Lowland) = 5.6% and 1959 – 1963 (Wielkopolska Lowland) = 2.05% ($p < 0.05$, d.f. = 2). Unilateral lack of M^3 occurred

Table 1. Frequencies (in percent) of dental and cranial anomalies in Austrian brown hares. * in hares older than approx. six months (accord. to eye lens weights).

	Subadults/adults (n = 565)	Fetuses/neonates (n = 33)
Missing M^3	1.95	–
Reduced expression of M^3	1.0	–
Missing I^2	0.53	–
Rotation of I^2	27.9	–
Supernumerary upper molar	0.17	–
Missing M_3	0.17	–
Miscellaneous tooth anomalies (comp. Table 4)	1.2	–
Wormian bone	4.6	9.7
Traces of <i>os interparietale</i> *	3.2	–
Missing <i>os interparietale</i>	–	3.2
<i>Fenestra ossis temporalis</i>	24.6	2.9

Table 2. Teeth and skull anomalies in the brown hare from Poland in three different series. Number of cases and frequency of occurrence (in parenthesis) are given. L - left side, R - right side.

	Wielkopolska Lowland		Podlasie Lowland		Mazovian Lowland		Mazurian Lakes		Low-Silesian Lowland		Total
	Czempin 1959 - 63 n = 682	1986 - 90 n = 54	Siedlce 1970 - 75 n = 125	1986 - 90 n = 79	Rogów 1986 - 90 n = 66	Łowicz 1986 - 90 n = 10	Płock 1986 - 90 n = 15	Wopławki 1986 - 90 n = 44	Głogów 1986 - 90 n = 42		
Teeth and skull anomalies											
Absent Incisivi							1 L				1 (0.09)
Supernumerary Incisivi							1 L				1 (0.09)
Missing M ³	L	9	5								14 (1.25)
	R	2	2				2				4 (0.36)
	L + R	3	1								5 (0.45)
Total		14 (2.05)	7 (5.60)	1 (1.27)	1 (1.52)	1 (10.0)	1 (6.66)				25 (2.24)
Wormian bones		7 (1.03)	2 (2.53)	3 (4.5)	5 (7.58)	1 (10.0)	1 (1.52)	1 (2.27)			17 (1.52)
<i>Fossa temporalis fenestra</i>		13 (1.91)	3 (2.4)	6 (7.59)	3 (4.5)	2 (20.0)	2 (13.3)	5 (11.36)	9 (21.43)		50 (4.48)

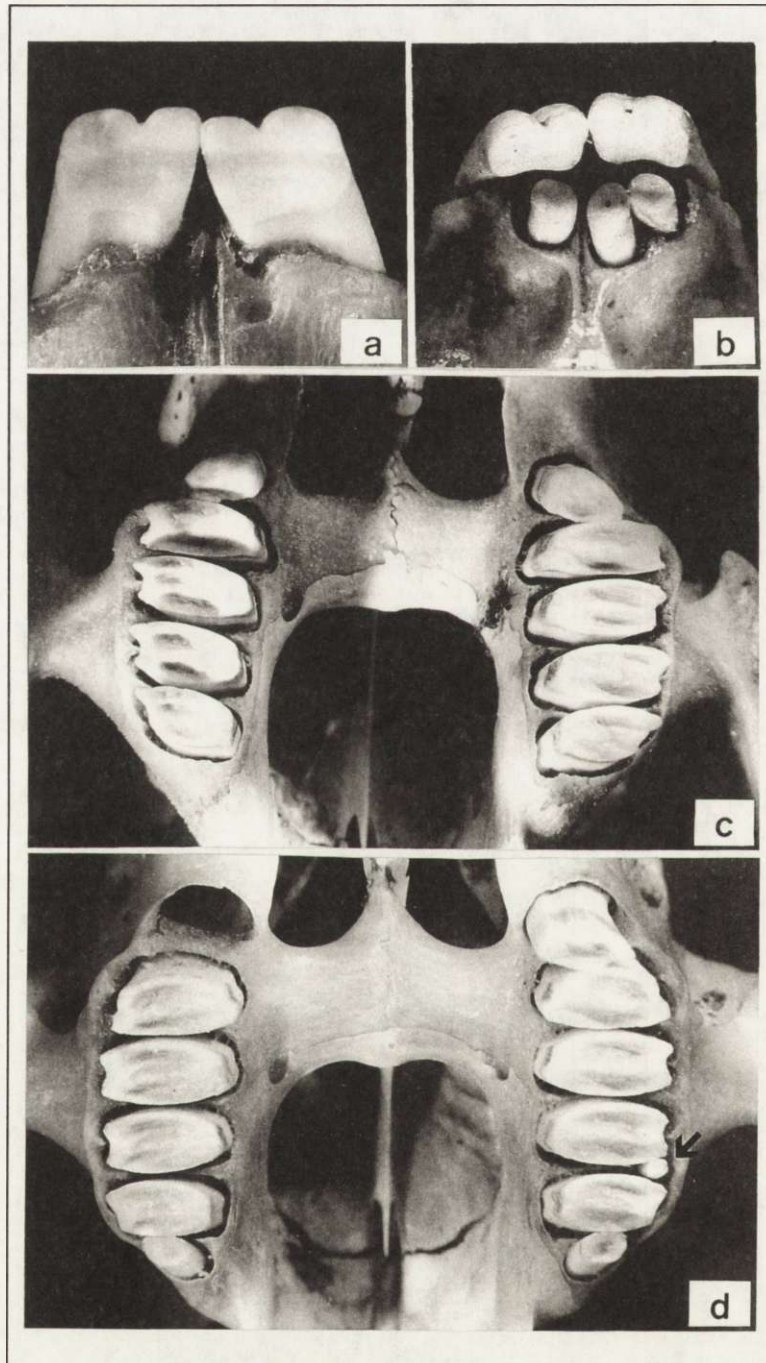


Fig. 3. Dental anomalies in the brown hare: a - Bilateral missing of I^2 , b - unilateral supernumerary I^2 , c - bilateral missing of M^3 , d - unilateral supernumerary upper molar (arrow).

in 76% of all specimens with missing M^3 ($n = 34$). Within all concerned cases of unilateral lack of M^3 ($n = 26$) the left molar was missing more often (79%) than was the right one: the approximation of a hypothetical binomial distribution by a standard normal distribution yielded a z -value of 2.6; $p = 0.9953$ for the registered difference.

A b n o r m a l d e v e l o p m e n t o f M^3 was characterized by a significant reduction of its buccolingual diameter (< 1.4 mm) as compared to the normal range of regularly developed M^3 (1.4 – 3.0 mm, in 424 SA and AD Austrian hares). However, the crown height of abnormal M^3 was reduced only in one case. The tooth socket of an M^3 exhibiting abnormal shape was either developed normally or affected by reduction too. Only specimens with unilateral reduction of M^3 were observed.

M i s s i n g o f I^2 : Two Austrian hares displayed an unilateral and one individual a bilateral lack of the I^2 (Fig. 3). In the cases of unilateral lack the respective present I^2 was normally developed. In each affected hare a tiny pit in the praemaxillary bone was noticed instead of the absent I^2 .

M i s s i n g o f M : This type of oligodonty occurred in one Austrian hare; the right posterior lower molar was absent and the respective tooth socket showed a slight reduction in connection with an uneven rim.

S u p e r n u m e r a r y t e e t h: one Polish hare exhibited an extra incisor in addition to the regularly developed pair of I^2 (see Fig. 3). Further on, one supernumerary upper cheek tooth was found in an Austrian hare. It was located between the first and second left molars in buccal position. It had a cylindrical shape, a diameter of approx. 0.8 mm and reached the same crown height as the regular molars (see Fig. 3d).

R o t a t i o n o f I^2 : In Austrian hares (SA + AD, $n = 516$) 27.9% exhibited rotation of at least one I^2 , whereby no sex specific difference was found. In 45.6% of all rotated I^2 ($n = 226$) the angle of rotation amounted to approx. $10^\circ - 25^\circ$, in 48.7% to approx. $26^\circ - 45^\circ$, in 2.2% to approx. $46^\circ - 70^\circ$ and in 3.5% to approx. $71^\circ - 90^\circ$. There was a positive association of rotation of the right and the left I^2 for each dental row as indicated by the "Cole's association - coefficient" (Mühlenberg 1976): $C = + 0.71 \pm 0.05$ ($n = 481$ SA + AD hares), $C = + 0.69 \pm 0.07$ ($n = 173$ SA hares), $C = + 0.50 \pm 0.09$ ($n = 91$ AD hares). The incidence of rotated I^2 (uni- or bilateral rotation) was significantly higher in SA hares than in AD specimens (Table 3). Because of the higher prevalence of I^2 -rotation in SA hares and in order to make samples comparable only this age group was considered for geographical analyses: no regional differences were found in prevalences of I^2 -rotation. However, within the region "Eastern Austria" (comp. Fig. 4) occurrence of I^2 -rotation was significantly ($p < 0.025$) higher in the area north of the river Danube (39.5%) than in the part south of it (20.0%). Also, within the region of "Northern Austria" (Fig. 4) I^2 -rotation occurred in SA hares from north of the river Traun (56.3%) more often than south of it (0%) ($p < 0.01$, Fisher-test).

Table 3. Age dependency of rotation of I² in Austrian brown hares; all degrees of rotation (0 – 90°) concerned. Age determination according to eye lens weights.

Item	Subadults (n = 173)	Adults (n = 91)
Unilateral rotation	11.8%	11.0%
Bilateral rotation	23.1%	9.9%
No rotation	65.1%	79.1%

Table 4. A list of miscellaneous tooth anomalies found in Austrian and Polish brown hares: each type occurred once.

- crown of right M³ slightly S-shaped, but normal height
- malocclusion of left cheek teeth due to reduced appearance of P₃, P₄ and M₁; corresponding upper cheek teeth normally developed
- crown of left I¹ broken transversally, specimen found as carcass
- rotation of both I¹, tops of both crowns pointing mesiad, uneven rims of alveoli, reorganisation of bony parts around the alveoli of lower incisors probably caused by inflammatory process
- crowns of both I² pointing mesiad
- probably paradontitis in the dentale
- probably periostitis in the dentale

Miscellaneous tooth anomalies: in further 7 individuals various other tooth anomalies were registered, which are listed in Table 4.

Ossification of skull sutures

The vanishing of skull sutures due to their ossification with increasing age has been outlined in detail by Caboń-Raczyńska (1964) for Polish brown hares. When applying her definitions of skull age categories (4 age classes; class 4 represents adult individuals at least one year old) to the presently investigated Austrian hares, only 21.7% of all adults (dry lens weight > 270 mg, n = 115) reached age class 4. Especially ossification of the parietotemporal sutures was hardly observed. Therefore, for the following analyses specimens exhibiting (almost) complete ossification of *sutura sagittalis* and *sut. frontalis* but not necessarily ossification of *sut. coronaria* and *sut. parietotemporalis* were grouped into age class 4. In wild living AD hares from Austria the age distribution was as follows: 24.3% in age class 2, 30.6% in age class 3 and 45.0% in age class 4. Regional differences in the distribution of skull age classes of AD hares (Fig. 5) were statistically significant ($p < 0.025$, d.f. = 8, *G*-test) although average lens weights of AD hares did not vary significantly (Kruskal-Wallis-test) between the particular regions. The distribution of age classes of AD (> 365 days) individuals from the breeding station (32.0% in class 2, 36.0% in class 3 and 32.0% in class 4, n = 25) did not differ from that of wild living hares.

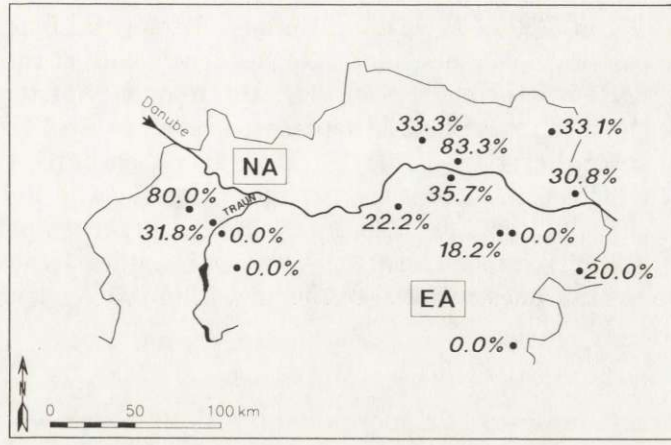


Fig. 4. Relative frequencies of rotated I² (all degrees of rotation concerned) within the regions "Northern Austria" (NA) and "Eastern Austria" (EA).

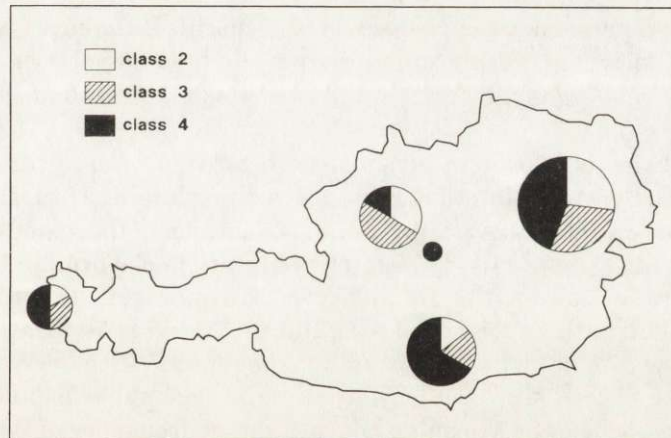


Fig. 5. Regional differences in the degree of ossification of skull sutures in AD Austrian brown hares. Class 2 = low, class 3 = moderate and class 4 = most advanced step of sutural obliteration (refer to the Results section).

Formation of a fenestra in the *fossa temporalis*

Fenestrae in the *fossa mandibularis ossis temporalis* were noted in 24.6% of SA and AD hares in Austria. In Polish hares sampled during 1986 – 1990 a temporal fenestration was observed only in 11.6% ($p < 0.001$). The frequency of a temporal fenestration increased significantly ($p < 0.001$, d.f. = 2) within the last 30 years (1959 – 1963: 1.9%, 1970 – 1975: 2.4%, 1986 – 1990: 11.6%) in Polish hares (Table 2).

Within Austrian hares (AD + SA) showing a temporal fenestration bilateral formation of a fenestra was encountered in 27.4% and in Polish individuals (AD

+ SA, 1986 – 1990) in 33.3%. In cases of unilateral temporal fenestration both sides were affected with the same chance. No sex-dependence of the formation of a *fenestra temporalis* was detected. However, the frequency of temporal fenestration increased with age: in 2.9% of fetuses/neonates, in 16.5% of SA and in 28.1% of AD Austrian hares ($p < 0.01$, d.f. = 2). In Polish hares the respective values were 8.7% for SA and 23.8% for AD specimens. In wild living AD hares from the Austrian populations ossification of skull sutures was not retarded in specimens that exhibited a temporal fenestration. Neither local nor regional differences in temporal fenestration were found within AD Austrian and Polish hares.

Occurrence of Wormian bones

For the present analyses of supernumerary skull bones we followed the terminological concept as given by Pucek (1962) and acknowledged both sutural (*ossa suturarum*) and fontanelle (bregmatic) bones as *ossicula wormiana*. Total prevalence of Wormian bones in SA and AD Austrian hares (including the specimens from the breeding station) was 4.6% and 4.8% when wild living specimens were concerned solely. No sex or age specific differences were found in Austrian hares. However, within animals from the breeding station frequency of Wormian bones was higher in fetuses and neonates (17.6%) than in SA and AD hares (0.0%) ($p < 0.025$).

In 63.6% sutures of Wormian bones showed no sign of ossification, in 22.7% sutures were partly vanishing and in 13.6% a considerable sutural obliteration was noted. However, there was no hint for an association of the general ossification of skull sutures (age classes 1 – 4) with the obliteration of Wormian bone sutures: there was no reduction in the frequency of Wormian bones with increasing ossification of skull sutures (classes 1 – 4). But in AD hares ossification of regular skull sutures was somewhat reduced in specimens with a Wormian bone (Mann-Whitney *U*-test, $p = 0.049$). There were no regional or population-specific differences in frequencies of Wormian bones. Average frequency of Wormian bones in Austria was 4.8% and in Poland it was 4.4%.

Os interparietale

Generally, in fetuses and neonates the formation of *os interparietale* was registered. However, in one neonate individual (3.2%) the *os interparietale* was completely missing. In 96.8% of all hares older than approx. 6 months (dry lens weight about 200 mg; comp. Suchentrunk *et al.* 1991) the sutures of the *os interparietale* had been already ossified. Nevertheless, the outline of the *os interparietale* could be traced in some SA individuals: in 3.7% of males and in 16.3% of females ($p < 0.01$, $n = 168$). General ossification of skull sutures in SA hares was not retarded in specimens with a traceable outline of an *os interparietale* (age class 1 not considered).

Discussion

Types and prevalences of tooth anomalies

The low number of various tooth anomalies (disregarding occurrence of I²-rotation) presently found in Austrian and Polish brown hare populations complies with the respective data reported already for one central European sample (Kratochvíl 1987). It is suggested, that the encountered dental abnormalities hardly impair the mastication of the affected individuals; only in 4 specimens (0.24% of all SA and AD hares; Table 4) essential problems in chewing were considered. Accordingly, abnormal dental development, caused either by hereditary or extrinsic factors, appears to be of no importance for the dynamics of population abundances of the brown hare in the investigated areas (i.e. influencing body condition or mortality rates). However, nothing is known about dental abnormalities in very young wild living leverets.

Among the presently found dental abnormalities on the one hand numerical alterations of the regular dentition (oligo- and polyodonty) and on the other hand irregular position (e.g. rotation) and shape of teeth have to be distinguished. Missing of the M³ was the most frequent type of oligodonty encountered in this study. According to the literature available to us information about the incidences of missing M³ in *Lepus europaeus* appears to be scarce (e.g. Szabo 1965 for a survey of the literature). Corbet (1983) in his review of classification in the family *Leporidae* only pointed out the occasional lack of M³ in the genus *Pentalagus* (see also Diersing 1984, Thenius 1989). Angermann (1966) having studied more than 2000 skulls of the genus *Lepus* from the Palaearctic and the aethiopic regions did not mention any case of missing M³ (however, Flux, 1980 cited a pers. comm. of R. Angermann about very rare cases of an abnormal situation concerning the M³ in *Lepus*). Flux (1980) found 2 (0.6%) of 347 specimens of *Lepus capensis* from Kenya with missing M³. In *Lepus crawshayi* collected in Rwanda 1 of 8 skulls with the M³ missing on both sides was noted (Van Der Loo and Hamers 1981). In *Lepus europaeus* from New Zealand 7.9% of the specimens showed either a missing or a reduced development of the M³ (Flux 1980). For the areas of Bohemia and Moravia in Central Europe Kratochvíl (1987) reported the lack of M³ in 1.4% of brown hares. The frequencies of missing M³ in hares from Central Europe (1.3%, n = 1115; calculation is based on the present material from 1986 – 1990 combined with Kratochvíl's data) and from New Zealand (5.7%, n = 105; calculated from data given by Flux 1980 for sexed specimens only) differed significantly ($p < 0.001$).

The size reduction of the M³ occurred already in the Oligocene (*Desmatolagus gobiensis*, *Palaeolagus haydeni*) leporids (Sych 1965, Thenius 1989). But this has not led to its obligatory loss in any recent species of this family. In contrast, within the *Ochotonidae*, which are assumed to have diverged from the *Leporidae* in the Oligocene (Diersing 1984), the fossil species *Amphilagus antiquus* from the upper Oligocene of Europe is reported to possess still a rudimentary M³, whereas the

phylogenetically younger species have already lost it (Thenius 1989). This indicates a much more faster phylogenetic reduction of the M^3 in the morphologically more generalized *Ochotonidae* than in the *Leporidae*. Because of its reduced size and the most distal position in the tooth row we conceive the M^3 in the genus *Lepus* not to be of particular importance for the mastication. However, in view of the slow evolutionary trend to reduce the M^3 in *Leporidae*, a possible selective pressure acting against the expression of the M^3 (saving energy instead of its ontogenetic development) appears to be rather weak.

In the present material we could not distinguish occurrence of pseudooligodonty (i.e. a loss *intra vitam* and subsequent closure of the respective tooth socket or a retention of the molar within the *substantia compacta* of the maxillary bone) from primary oligodonty caused by a genetically based lack of the tooth germ or its involution during embryogenesis (Meyer 1975).

The genetic background of M^3 agenesis in brown hares is not known so far. However, according to Grüneberg (1965) in inbred mice *Mus musculus* individuals are usually lacking the third molars whenever a metric reduction of lower incisors and other molars is apparent. This comprehensive alteration of the whole dentition is caused by a single semi-dominant gene (Grüneberg 1965). Likewise, Le Bot and Salmon (1976) found that the agenesis of a particular tooth within the dental row of humans was associated with reduction or agenesis of other teeth of the respective dentition: percentages of missing third molars were higher in persons exhibiting a reduction or lack of lateral upper incisors (see Garn *et al.* 1963 for occurrence of linked tooth anomalies in humans). In the present material no hint for tooth anomalies associated with the lack of the M^3 was detected. However, that kind of analysis should be carried out on much more individuals displaying M^3 agenesis.

Generally, no significant local differences in occurrence of M^3 agenesis were found between the populations investigated in central Europe. However, during 1970 – 1975 the frequency of missing M^3 in hares from Podlasie Lowland (see Table 2) amounted to 5.6% which is almost identical with the respective value given for hares from New Zealand. This local (and temporal) increase within a Polish population could be interpreted as the result of a random fluctuation of the genetic variants responsible for agenesis of the M^3 (genetic drift). The occurrence of genetic drift within a hare population being not completely separated from its neighbours might be the result of considerable fluctuations in its density.

Regarding unilateral M^3 agenesis, the left side of the tooth row was significantly more often affected than the right one; this indicates directional asymmetry for that quasi-continuous trait (Van Valen 1962 and Leamy 1984). Apart from the obviously adaptive significance of directional asymmetry in particular organs such as the mammalian heart it appears that both occurrence and extent of directional asymmetry (e.g. Leamy 1984 for metric characters in *Mus musculus* and Petznek 1990 for non-metric traits in *Lepus europaeus*) as well as its heritability (Leamy 1984) are low. However, the genetic influence on directional asymmetry could be

somewhat higher in characters with minor functional significance and underlying phylogenetical reduction. In order to elucidate the exogenic component of directional asymmetry of M^3 agenesis in the brown hare it would be of particular value to study the masticatory movements.

Four skulls exhibited either uni- or bilateral agenesis of the I^2 . This type of oligodonty appears to be rather scarce in the genus *Lepus*: Flux (1980) mentioned one case in *Lepus capensis*. In rabbits *Oryctolagus cuniculus* it occurs both in wild specimens and in various races reaching a prevalence of up to 10% (Nachtsheim 1936, Geiger 1976). According to Nachtsheim (1936), agenesis of I^2 is caused by an (incompletely) dominant gene (Lindsey and Fox 1974). In rabbits agenesis has not been noticed in deciduous I^2 which are changed into permanent peg teeth approximately within the third and fourth week after birth (Nachtsheim 1936). All brown hare fetuses and neonates checked up in this study for tooth anomalies exhibited deciduous I^2 ; however, at the present state of investigations we can not decide whether I^2 agenesis in the brown hare is due to a failure to develop permanent peg teeth after having lost their deciduous incisors (cf Fraguglione 1957). The occurrence of a tiny pit in the praemaxillary bone right in the position of the missing I^2 renders support for this hypothesis.

Polyodonty of incisors was encountered in one Polish hare (Fig. 3). As to our knowledge this is the first case of an additional peg tooth reported for *Lepus europaeus*. It occurs occasionally in rabbits between the two regular permanent I^2 resulting from a single recessive gene (Nachtsheim 1935, Lindsey and Fox 1974). Nachtsheim (1936) considered it to be caused by a duplication of the tooth germ of the permanent I^2 (for a general overview of causes of polyodonty in mammals see Wolsan 1984).

In contrast to the rare numerical variations of permanent incisors, rotation of the I^2 was noticed rather often; but, most cases were of low magnitude and no one exceeded an angle of 90° . Rotation of teeth has been reported for various mammals (e.g. Esaka 1982 for domestic dogs, Kierdorf and Kierdorf 1988 for cervils). In dolichocephalic dogs rotation of premolars appears already in the bud or cap stage during odontogenesis when there is enough space for regular development, but is reduced or even disappears during further growth (Esaka 1982). Nevertheless, tooth rotation may persist in some dogs although there is enough space for the teeth. This suggests an additional regulatory factor to be responsible for the reduction of tooth rotation (Esaka 1982). In the dentition of the brown hare there is no space limit for the growth of I^2 . A higher frequency of rotated I^2 in subadult hares as compared to adult ones is fostering the hypothesis of reduction of rotation during the juvenile development. Different frequencies of rotated I^2 in hares from geomorphologically separated areas in northern and eastern Austria (see Fig. 4) suggest a genetic background of this tooth anomaly. However, in both regions biochemical genetic differentiation of hare samples was rather low and gene flow between locations was hardly influenced by geographical boundaries (Hartl *et al.* 1989, G. B. Hartl, in prep.).

A remarkable type of polyodonty detected in the present study concerned an additional upper molar in buccal position between M^1 and M^2 (see Fig. 3). Supernumerary premolars in the rabbit and in the brown hare have been interpreted as atavistic traits (Hochstrasser 1969a, b). Such an interpretation of the presently found additional molar would mean that it represented the phylogenetically reduced M^1 . This would be in contradiction with the theory of the posteroanterior process of successive phylogenetical reduction of molars within therian mammals (Ziegler 1971). Therefore, we consider this supernumerary cheek tooth rather as caused by a split tooth germ of a neighbouring molar. Splitting of tooth germs may have a genetic basis or originate from exogenic factors as for instance an infection (Wolsan 1984).

Ossification of sutures and skull bone anomalies

Within the present Austrian hare skulls obliteration of skull sutures was clearly retarded as compared to the Polish material sampled during 1958 – 1960 in the Poznań area (Caboń-Raczyńska 1964). Even if all specimens exhibiting visible parietotemporal and coronar sutures are appointed to the class 4, only approx. one fourth of adult hares reach this class. Especially in one particular agricultural region ("Northern Austria", see Fig. 5) the degree of ossification of skull sutures was rather low. But we do not suppose a simple relation between intensive agricultural landuse and retarded sutural ossification, because in other regions (EA) with extended arable acreages skull ossification was more advanced. Eventually, the unfavourable climatic conditions (high annual precipitation) within the region "Northern Austria" are contributing to reduced ossification.

The occurrence of fontanelles (i.e. areas of connective tissue between skull bones) is widely known in adult animals of various species. Pucek (1962) has noticed fontanelles in the brown hare, both at locations where Wormian bones usually developed and additionally beside them. The presently reported phenomenon of fenestration in the temporal fossa might be caused by an impact of the masticatory apparatus on the formation of bone tissue. Higher percentages of temporal fenestra in adult specimens suggest an increasing thinning of the bone through mastication in the course of ontogenetic development. Regional differences of frequencies appear to be the result of varying age compositions of samples. The recent increase of incidences of a fenestra in the Polish material is due to changes in the age structure of the hunting bag (presently a high percentage of adults has been noticed, J. Markowski *et al.*, in prep.). Furthermore, a high percentage of temporal fenestration in hares from the Głogów region (copper mills) suggests an influence of environmental factors on thinning of the temporal bone. Heavy metals, such as cadmium and fluor may lead to disturbances in the metabolism of mineral compounds and result in the malformation of bones (Markiewicz 1990).

Both frequencies, shapes, dimensions and localisations of Wormian bones found in this study in the brown hare are in good accordance with the data reported by Pucek (1962). This author has analysed brown hare skulls from the Wielkopolska

Lowland and detected at least one Wormian bone in 0.85% of all individuals. The present results concerning skulls from this region are almost identical with those of Pucek (1962) because they largely include the same material. Geographical differences in frequencies of Wormian bones occur in various therian mammals: especially in forest dormice *Dryomys nitedula* prevalences of Wormian bones were found to gradually decrease from north to south (Pucek 1962). In the brown hare such a geographical trend is not evident.

In humans formation of supernumerary skull bones is conceived to be caused by genetic factors that produce secondary ossification centres (Torgersen 1951, Finkel 1976, El-Najjer and Dawson 1977). In the brown hare ossification of sutures of Wormian bones is likely to occur during postembryonic ontogenesis; however, there is no clear age-specific difference in frequency of Wormian bones. The sutural ossification of these additional bone elements is largely independent from the general degree of ossification of regular skull sutures. However, obliteration of normal skull sutures appears to be somewhat retarded in specimens which possess a Wormian bone.

The *os interparietale* is an obligatory element of the cranial vault of *Lepus europaeus* and is formed from two bilateral symmetric bony plates that are already fused in neonates (Caboń-Raczyńska 1964). Presently, a one day old neonate was found to lack any sign of an *os interparietale*. In order to evaluate a possible genetic basis for this anomaly further neonates and fetuses have to be controlled for missing *os interparietale*. Generally, in the genus *Lepus* the interparietal suture obliterates within the first months of life (Caboń-Raczyńska 1964, Angermann 1966, Corbet 1983). However, Angermann (1966) noticed 22.3% of adult brown hares with persisting or partly ossified interparietal sutures. In the present study only 3.2% of specimens older than six months exhibited a traceable outline of interparietal sutures. Thereby, sutures were more often detectable in females than in males. However, in both sexes the general progress of ossification of skull sutures was likely to be not influenced by a reduced ability to ossify interparietal sutures.

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