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# Craniometric variation and nonmetric skull divergence between populations of the Pine marten, Martes martes

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With 4 tables and 7 figures

**Abstract**

The variation of Pine marten series, *Martes martes* (Linné, 1758), from the Hercynian region and from various landscapes of the Oberlausitz are compared using skull measurements and nonmetrical skull traits. No clear differences in skull size were found between the two studied populations. Nevertheless there exist mosaic size differentiations among the regional subsamples compensated in larger areas.

The nonmetric skull characters manifest with a high measure of divergence that the Oberlausitz and the Hercynian martens belong to significantly different populations. Within the Oberlausitz only the Pine martens of the Eastern Hill Landscape show morphologic differentiations from each others. This seems to be caused by the reduced reproductive exchange between restricted wood isles.

**Zusammenfassung**

**Populationsdifferenzierung beim Baummarder, *Martes martes*, nach kraniometrischen Kriterien und nonmetrischen Schädelmerkmalen.**

Schädelserien des Baummarders aus dem Hercynischen Raum und aus verschiedenen Landschaftseinheiten der Oberlausitz werden kraniometrisch und mittels qualitativer nonmetrischer Merkmale verglichen.

Beide Populationen unterscheiden sich nicht in der Schädelgröße. Starke Abweichungen in den nonmetrischen Schädelmerkmalen weisen die Baummarder der Oberlausitz und des Hercynischen Raums aber als getrennte Populationen aus.

Innerhalb der Oberlausitz bestehen gesicherte Größenunterschiede zwischen den Baummardern einzelner Landschaftseinheiten. Nur einer dieser Naturräume hebt sich jedoch nach qualitativen Schädelmerkmalen von allen anderen ab. Hier ist der Lebensraum des Baummarders auf wenige größere Waldgebiete beschränkt. Ein geringer reproduktiver Austausch mit den Hauptvorkommen in der Oberlausitz dürfte als Ursache für die morphologische Differenzierung in Betracht kommen.

## Introduction

Besides cytogenetical and biochemical techniques the classic morphological skull studies are able to obtain conclusive results in research to the intraspecific structure of a species even on the level of populations. Craniometrical investigations comprise morphological variations determined genetically as well as environmental modifications in broadest sense. The evaluation of nonmetric morphological characters supplies more successful findings for the geographic and genetic differentiation . This qualitative method allowes to define the "epigenetic distance" between populations or the existence of a reproductive unit at all.

Such point in question gets especially importance to species of low abundance and discontinuous distribution like the Pine marten, *Martes martes* (Linné, 1758), in Central Europe. The stenotopic carnivore inhabiting mature forests has become very rare by removal of wooded area or changes to short-lived forests, so that for instance regions without Pine martens can be mapped.

Therefore with exceptions (REIG & RUPRECHT 1989) only poor morphometrical data are available from Central European populations. The aim of the present paper is to improve this fact despite of the accordingly small series. Moreover it describes an effort to determine the differentiation of Pine marten populations.

## Material and sample areas

The study is based on 115 skulls of the Pine marten from the Oberlausitz region and 82 skulls from Middle Germany (Hercynian region)[1]. The main material has been collected between 1981 and 1990 on a territory of about 3000 km² enclosing a large part of the Oberlausitz in the south-east of Eastern Germany. This region consists of different landscapes being manifoldly structured from the "Pondlands" via "Hill Landscapes" to the mountainous "Lausitz Highlands" and the "Zittau Mountains" (fig.1). A detailed description of the study area is given by ANSORGE (1991).

The Pine marten arrived to a generally rare species in the Oberlausitz. The mean yearly game bag amounts to 0.3 specimens per 1,000 hectares woodland only. Because the occurence of the Pine marten is associated with wide forests the wooded area is plotted in fig.1. The Highland, the Zittau Mountains and the Pondlands especially show a high degree of forests covering 30 % to 50 % of the total area whereas the Field Landscapes are nearly woodless (about 5 %). In the Eastern Hill Landscape wide ploughland alternates with isolated larger woodland. Accordingly the Pine marten is distributed in the Oberlausitz (fig. 2) concentrating on the Pondlands, the Western Hill Landscape and the mountainous regions (ANSORGE 1988). The Eastern Hill Landscape show a low density and in the Field Landscapes no continually occurences exist.

The Hercynian material originates from different regions and localities of Middle Germany including a series of skulls from the closed woodland "Fallstein".

## Methods

To consider age related variations all skulls were classified into 0 to 1, 1 to 2 and more than 2 years old specimens. This classification is based on the tooth abrasion, obliteration of sutures, development of the sagittal crest and the general aspect of the skull according to MALŽJUNAITE (1957), RYABOV (1962), STUBBE (1968), PAVLINOV (1976) and REIG & RUPRECHT (1989). More than 2 years old specimens and difficult skulls were aged by the configuration of incremental cementum lines. A paraffined canine was used for longitudinal root section following the method described generally by GRUE & JENSEN (1979) for the Pine marten too. The skulls are grouped in age classes, whereby the age class 2 for example means a marten in its second year of life.

To characterize the skull size 15 linear dimensions corresponding mostly with the measurements defined by VON DEN DRIESCH (1976) and one volume measure were used (fig.3). They were taken with an accuracy of 0.1 mm and 0.25 cc :

1 (*cbl*) condylobasal length: posterior margin of condyli occipitales - prosthion
2 (*mxl*) maxillar length: palatinoorale - posterior margin of I¹-alveole

[1] The Pine marten skulls are deposited in the collections of the State Museum of Natural History Görlitz and of the Zoological Institute of the Martin Luther University Halle.
I am very grateful to Dr.D.Heidecke and Prof.M.Stubbe (Halle/S.) for the generously access to their collections.

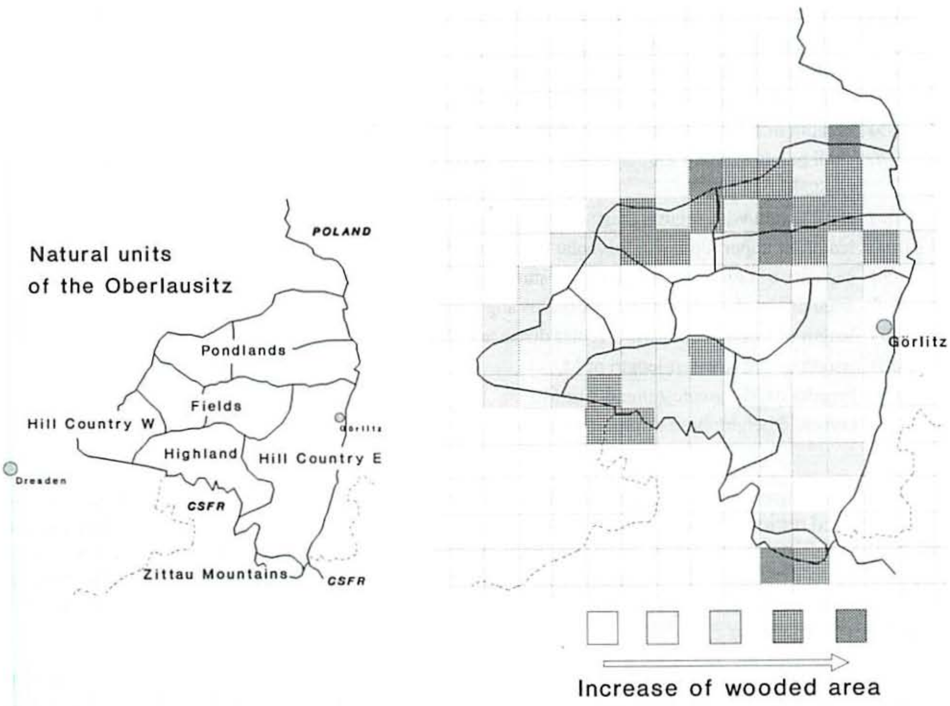


Fig. 1 Wooded area of the Oberlausitz region

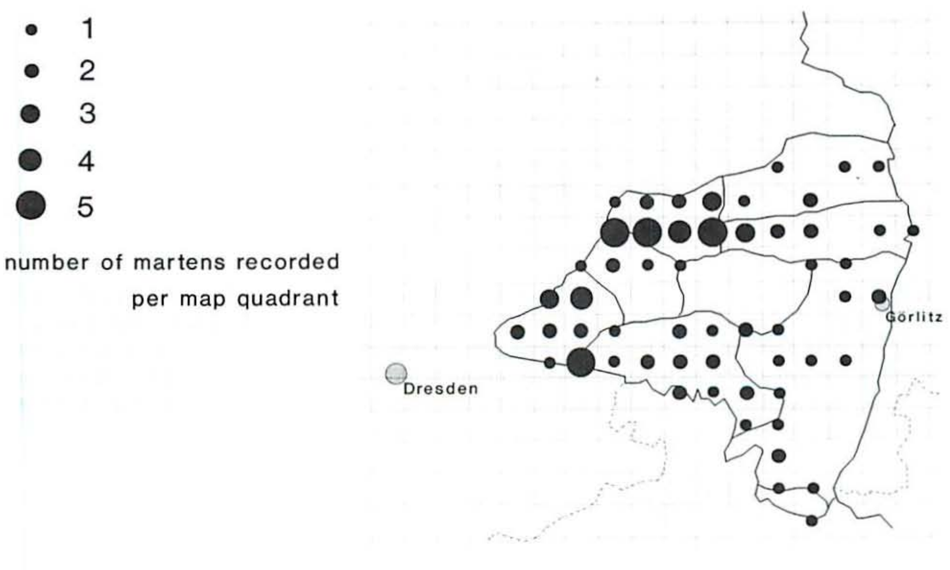


Fig. 2 Distribution of the Pine marten

3 (*blbs*) pharyngeal base length of the brain-stem: basion - suture between pterygoid and palatinum
4 (*zb*) zygomatic breadth: zygion - zygion
5 (*eob*) ectorbital breadth: ectorbitale - ectorbitale
6 (*pob*) postorbital breadth: smallest distance behind the processi supraorbitalia
7 (*bb*) breadth of braincase: euryon - euryon
8 (*sh*) skull height without sagittal crest: base of os occipitale - upper point of braincase beside the crista sagittalis
9 (*shc*) skull height with sagittal crest: base of os occipitale - highest point of crista sagittalis
10 (*utr*) length of upper tooth row: alveolar distance C-$M^1$
11 (*cb*) capacity of braincase: measured by stuffing the neurocranium with glass globules
12 (*al*) angular length: infradentale -processus angularis
13 (*ltr*) length of lower tooth row: alveolar distance C-$M_2$
14 ($M_1l$) length of $M_1$: greatest length of $M_1$
15 ($M_1b$) breadth of $M_1$: greatest breadth of $M_1$
16 (*ch*) coronoid height: base of processus angularis-infradentale

The skull measurements were statistically processed separately for each group considering sexes, age classes and regions. Simple parameters like mean ($\bar{x}$), range ($x_{max}$, $x_{min}$), standard deviation (s) and variability coefficient ($v = 100\ s / \bar{x}$) were calculated for all measurements. Student's t-test was used to secure the significance of mean differences in case it is permitted by the variances and the normal distribution of the measuring data. Significance is postulated by an error probability of $\alpha < 0.05$ if not specified otherwise.

For the evaluation of the morphological differentiation 11 nonmetrical traits have been chosen according to the rare investigations on other carnivores (SJOVOLD 1977, WIIG & LIE 1984, WIIG & ANDERSEN 1988) and own preliminary studies (fig. 4):

1 (*Feth*) foramina ethmoidalia completely separated
2 (*Focc*) upper foramen occipitale present
3 (*Cc*) canalis condylaris open ventrally
4 (*Fsph*) foramen sphenoidale present
5 (*eFov*) emissary foramen beside the foramen ovale present
6(*pFpal*) accessory posterior foramen palatinum present
7 ($P^1$) first upper premolar missing
8 (*Fme*) two foramina mentalia present
9(*aFme*) accessory posterior foramen mentale present
10(*aFmd*) accessory anterior foramen mandibulare present
11 ($P_1$) first lower premolar missing

Bilateral traits were taken from both sides of the skull and separately as well as together calculated. The frequencies of trait expressions were compared by the chi-square test including the analyse of homogeneity in age and sex. Only traits with significantly differences could be used to calculate morphological separation with the formula of "mean measure of divergence" (MMD) proposed and derived by SJOVOLD (1977). The variance and the standard deviation ($S_{MMD}$) of the MMD are necessary to prove statistically significance by MMD > 2 · $S_{MMD}$ (SJOVOLD 1977).

$$MMD = \frac{1}{r}\sum_{i=1}^{r} [(\theta_{1i} - \theta_{2i})^2 - v_i]$$

r = number of traits
n = sample size
p = frequency of traits

$$S_{MMD} = \sqrt{\frac{2\sum_{i=1}^{r} v_i^2}{r^2}}$$

$\theta = \arcsin(1 - 2p)$

$v_i = \frac{1}{n_1} + \frac{1}{n_2}$

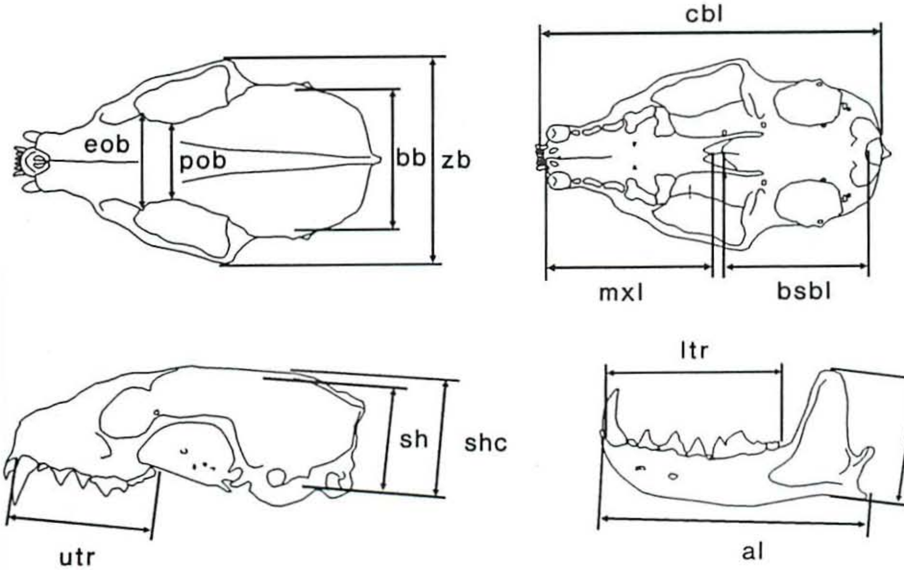


Fig. 3 Skull measurements of the Pine marten

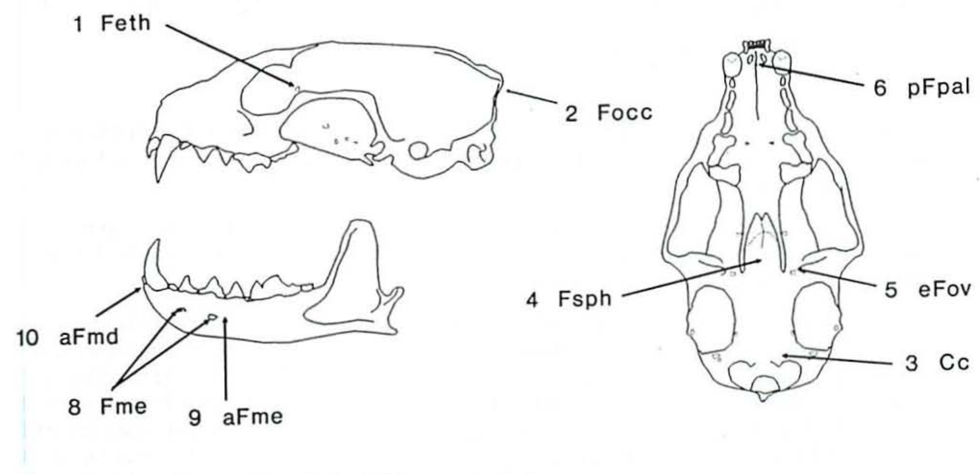


Fig. 4 Positions of nonmetric traits in the Pine marten skull

**Results**

Craniometric variation

The statistical tests adduce significant differences in all skull mesurements between the sexes and for the most dimensions between age classes 1, 2, and 3-11 excepting the measures of the braincase skull part. The sex and age structure of the Pine marten collection from the Oberlausitz region is illustrated in fig.5. In the sample the yearling males predominate and werefore only few specimens represent the higher age classes. Werefore in tab.1 the parameters of skull measurements are listed by separating sexes, age class 1 and age class 2-11 for the Oberlausitz and the Hercynian region. In addition the body measures of 53 specimens are given in tab.2.

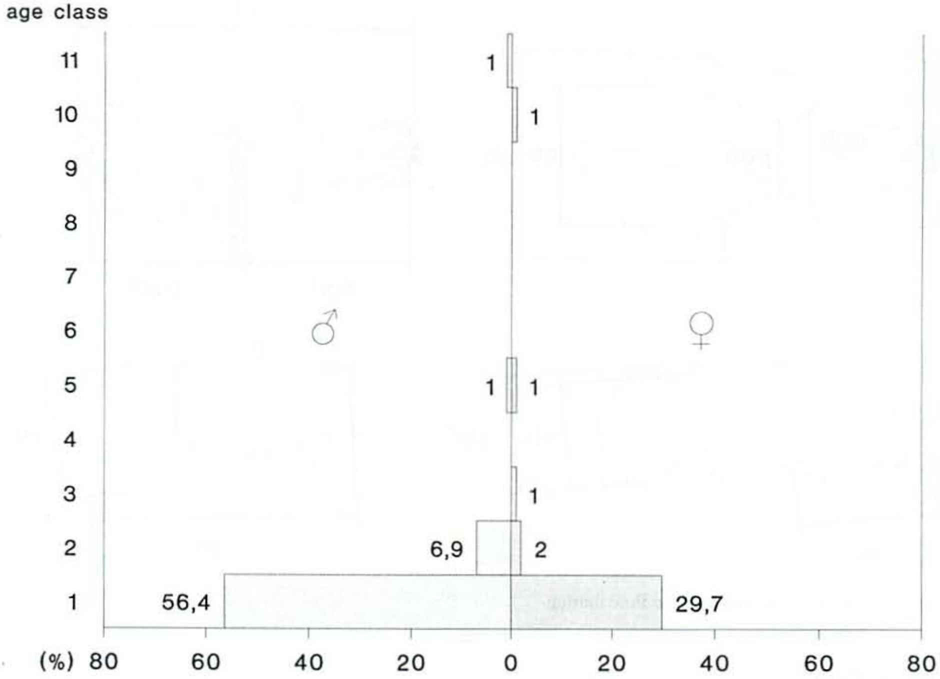


Fig. 5 Sex and age structure of Pine martens recorded in the Oberlausitz region

Caused by the rarity of the Pine marten in the study areas there are sufficient data for reliable results only in the male age class 1 (see fig.5). Thats why this population group will be used as the basis for the following comparisons.

The skull measurements of the yearling males from the Oberlausitz and the Hercynian region show no significant differences. Alternating measure variations exist in the other age classes and in females. This means that the population samples are similar in their skull size.

Within the Oberlausitz there are remarkable differences in skull size between the landscape units although statistically significance is secured only in few measurements due to the small sample range. The size relations in the fig.6 illustrate this fact. The Pine martens of the Pondlands are mostly larger in their skull size. In the Highland and the Hill Landscapes obviously smaller martens live (significant in *cbl, utr* and *blbs*). The few specimens from the Field Landscapes have larger skulls than those of the adjacent Hill Landscape (significant in *utr* and *blbs*). They seem to be nearly equal the great Pondland martens.

The Pine marten sample from the closed woodland "Fallstein" of the Hercynian region has significantly larger skulls than those of the Pondland (secured in *cbl, utr* and *ltr*). They are classified in their size out of all the skulls from Oberlausitz landscapes .

**Nonmetrical skull divergence**

The frequencies of occurence of 8 bilateral and 3 unilateral traits are set out in tab.3 for the population samples from the Oberlausitz and the Hercynian region . No age related changes in the incidence of the variants were obtained by all the nonmetrical traits. Sex dependence was significantly proved for two variants in the considered material: the missing of the first lower premolar ($P_1$) and the presence of an acessory anterior mandibular foramen (aFmd). They are excluded from the further investigation.

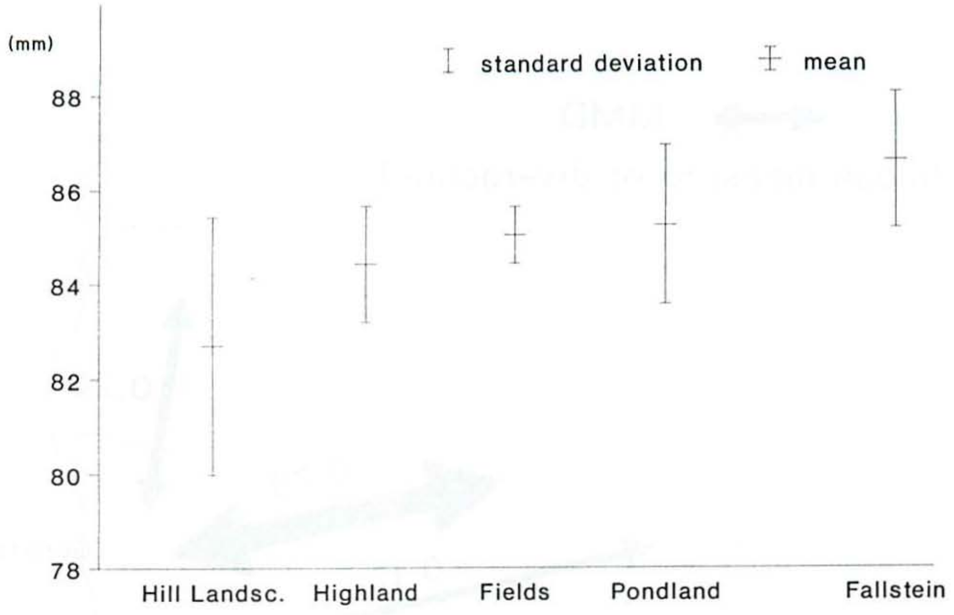


Fig. 6 Condylobasal length of the Pine martens (♂ age class 1) from different landscape units

Only few of the selected qualitative features show sufficient differences between the regional population samples secured by the chi-square test. For the Oberlausitz and the Hercynian region these are the presence of an upper occipital foramen (*Focc*) and the incidence of an accessory posterior palatin foramen (*pFpal*). In bilateral consideration it is the presence of an acessory anterior mental foramen (*aFme l.* and *aFme r.*) and an emissary foramen beside the foramen ovale (*eFov l.* and *eFov r.*). Two traits were added as differentiating features within the Oberlausitz region from different landscape units: the occurence of an completely separated ethmoid foramen remarked for each side separately (*Feth r.* and *Feth l.*).

The "mean measure of divergence" (MMD) was calculated using these nonmetrical characters. The Oberlausitz and the Hercynian population samples show an MMD-value of MMD=0.409 with the respective standard deviation of $S_{MMD}$ = 0.019. The Pine martens of these populations differ significantly in their qualitative skull features. The epigenetic distance in the form of MMD between the martens of different Oberlausitz landscapes appears in tab.4. All the units have very low distances but only the population of the Eastern Hill Landscape contrasts clearly with each of the others. Statistically significance is proved by three sample pairs. Only one MMD-value is slightly beneath the significance level because of the small sample size.

## Discussion

Morphometric studies for solving taxonomical questions of rare species suffer under the main problem of a poor sample size. In addition to the existing sex and age related variations, as it is shown by the Pine marten skull (ROSSOLIMO & PAVLINOV 1974, PAVLINOV 1977, GERASIMOV 1983), the small material basis must be disunited. Therefore in this analysis significant results were obtained only for one population group, the yearling males of age class 1. According to this the alternating values of the Oberlausitz and the Hercynian sample splits (tab.1) mean no size differences between these populations.

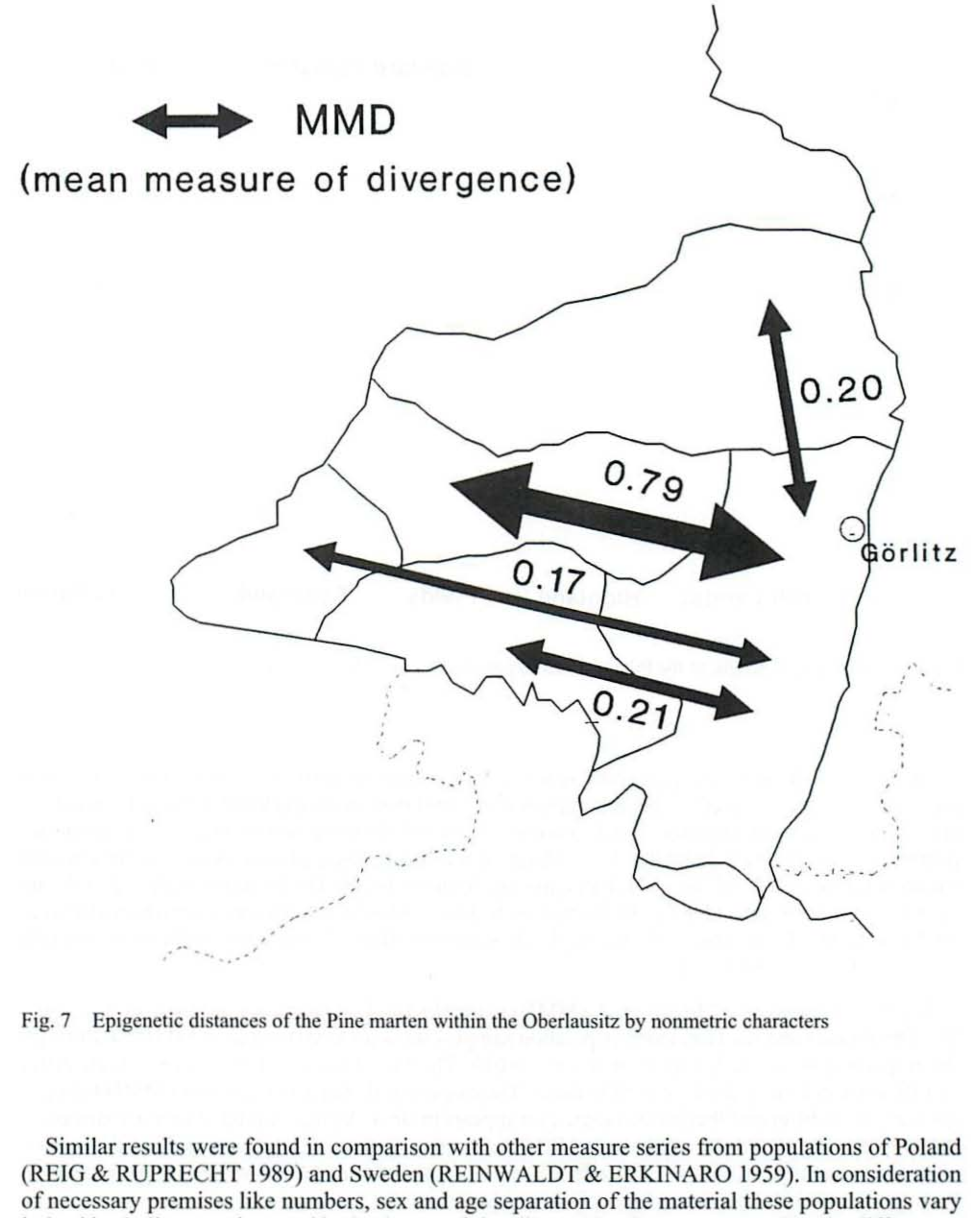


Fig. 7 Epigenetic distances of the Pine marten within the Oberlausitz by nonmetric characters

Similar results were found in comparison with other measure series from populations of Poland (REIG & RUPRECHT 1989) and Sweden (REINWALDT & ERKINARO 1959). In consideration of necessary premises like numbers, sex and age separation of the material these populations vary indeed in skull proportions and in the degree of size dimorphism between sexes. But the differences are seldom of taxonomic relevance. In contrast the Pine martens from Bulgaria (GERASIMOV 1983) or Southern Ural (PAVLINOV 1977) differ clearly from the Central European series. These are typical geographic variations and for example used for subspecific classification by GIANNICO & NAGORSEN (1989) in the Pacific coast marten and by HUMPHREY & SETZER (1989) in the Mink.

On the other hand significant differences in skull characters are not sufficient as taxonomic criterion (MAYR 1975). Local subpopulations of one taxonomic unit can distinctly differ in characters mostly related to environmental factors. For the genus *Martes* MONAKHOV (1989) reports about morphological changes in different populations of Siberian sables introduced only 30 years before from the same origin.

The established variations in skull size within the Oberlausitz should be seen in similar view. The remarkable size differences between Pine martens of the Pondlands and the hilly and mountainous parts of the study area may be related to climatic factors and to a generally better food supply in the Pondlands. A separation effect by the nearly woodless Field Landscapes (see fig.1) can explain this fact too. It is striking that the few specimens of the Fields hardly differ from those of the Pondlands but are clearly distinguished from the Highland's martens. They seem to be migrants from the Pondland well inhabited by the Pine marten (see fig.2).

However, the large Pine martens from the Fallstein are taller than the martens of all Oberlausitz landscapes although no distinct size differences exist between the Hercynian and the Oberlausitz regions. Regional variations are obviously compensated in larger areas. This fact especially stresses the importance of extensive series for the evaluation of clinal directed geographic size variations.

Different biological relevance were established for the nonmetrical characters being slightly influenced by environmental factors. The occurence of the qualitative features does not randomly arise, and it is affected by genetic components. The heritability of the traits are estimated in various manner (HILBORN 1974; BERRY 1975; KOREY 1980; CHEVERUD & BUIKSTRA 1981, 1982; RICHTSMEIER & MCGRATH 1986). However the morphological differentiation of the samples represents a certain measure of the epigenetic populations distance.

The results obtained by this method show a completely different view than the craniometric variation. The Pine marten populations of the Oberlausitz and of the Hercynian regions show a high measure of divergence according to their geographic distance and separation. Although the samples could not be separated by their skull measurements the nonmetric skull characters manifest two significantly differing populations. Unfortunately no comparable data of the Pine marten exist from other regions. Only STEINER & STEINER (1986) tested 11 nonmetric criterions for species discrimination being not useful in the present study. However it seems to be remarkable that WOLSAN (1985, 1989) established sexual dimorphism in the congenital tooth loss of $P_1$ in about the same degree as in the present investigation.

Unexpected results are adduced by the comparison of the morphological skull differentiation between the natural units within the Oberlausitz. It can be concluded that the epigenetic variability in the areas mainly inhabited by the Pine marten is very low. The martens of the Pondland, the Highland and the Western Hill Landscape can be regarded as a reproductive unity. There must be sufficient migration via the Field Landscape to ensure the connection between the well wooded main habitats.

In contrast the martens of the Eastern Hill Landscape occupy a special position within the Oberlausitz differing from each of the others in their nonmetric skull characters (fig.7). In this landscape the wooded area suitable to the Pine marten is generally restricted in the granitic mountainchains and the basaltic hilltops. The poor but permanent occurence of Pine martens is considerably isolated in these places. Both migration and genetic drift to the neighbouring landscapes are diminished so that the described differences could be developed. If the insulating of the Pine marten habitats is advanced so far, the reproductive exchange is widely reduced.

Results like above mentioned may arise from the connection of taxonomical methods and ecological evaluation. They offer a chance to identify potential differentiations between populations and to use it as a signal even in endangered species.

Table 1 Skull measurements of the Pine Marten sample from the Oberlausitz and the Hercynia region

| | **Oberlausitz** | | | | | | **age class 1** | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | males | | | | | | females | | | | | |
| | $\bar{x}$ | s | v | $x_{min}$ | $x_{max}$ | n | $\bar{x}$ | s | v | $x_{min}$ | $x_{max}$ | n |
| 1 (*cbl*) | 84,48 | 1,91 | 2,26 | 79,4 | 87,5 | 38 | 77,71 | 1,97 | 2,54 | 74,7 | 82,2 | 24 |
| 2 (*mxl*) | 41,60 | 1,34 | 3,22 | 38,8 | 44,3 | 52 | 38,14 | 1,19 | 3,11 | 36,6 | 42,0 | 29 |
| 3 (*blbs*) | 33,08 | 1,19 | 3,58 | 31,2 | 37,4 | 33 | 30,83 | 1,12 | 3,64 | 29,1 | 33,3 | 23 |
| 4 (*zb*) | 49,22 | 2,25 | 4,58 | 44,9 | 52,8 | 46 | 44,39 | 1,45 | 3,27 | 42,2 | 47,0 | 26 |
| 5 (*eob*) | 24,74 | 1,19 | 4,83 | 22,3 | 27,6 | 49 | 22,73 | 1,23 | 5,41 | 19,0 | 24,6 | 25 |
| 6 (*pob*) | 19,76 | 1,22 | 6,18 | 17,1 | 22,4 | 47 | 19,09 | 0,84 | 4,39 | 17,1 | 20,5 | 24 |
| 7 (*bb*) | 37,02 | 1,14 | 3,08 | 34,6 | 40,1 | 40 | 35,21 | 1,07 | 3,05 | 33,6 | 37,7 | 24 |
| 8 (*sh*) | 27,52 | 0,61 | 2,22 | 26,4 | 28,9 | 35 | 24,99 | 0,87 | 3,48 | 22,9 | 27,5 | 23 |
| 9 (*shc*) | 28,69 | 0,60 | 2,09 | 27,6 | 29,8 | 35 | 26,25 | 0,80 | 3,04 | 24,6 | 28,4 | 23 |
| 10 (*utr*) | 30,25 | 0,91 | 2,99 | 28,4 | 32,2 | 57 | 27,71 | 0,84 | 3,05 | 26,1 | 29,4 | 29 |
| 11 (*cb*) | 24,14 | 1,49 | 6,19 | 20,8 | 26,8 | 29 | 20,21 | 1,60 | 7,91 | 17,5 | 25,0 | 20 |
| 12 (*al*) | 54,13 | 3,36 | 6,21 | 32,3 | 58,3 | 57 | 49,62 | 1,72 | 3,46 | 44,5 | 54,0 | 30 |
| 13 (*ltr*) | 34,93 | 1,04 | 2,99 | 32,4 | 37,5 | 57 | 31,82 | 1,00 | 3,14 | 28,6 | 33,8 | 30 |
| 14 ($M_1l$) | 10,19 | 0,41 | 3,98 | 9,2 | 11,1 | 57 | 9,31 | 0,46 | 4,93 | 8,2 | 10,4 | 30 |
| 15 ($M_1b$) | 4,08 | 0,21 | 5,04 | 3,7 | 4,6 | 57 | 3,73 | 0,21 | 5,54 | 3,4 | 4,3 | 30 |
| 16 (*ch*) | 24,69 | 1,01 | 4,08 | 22,4 | 26,5 | 56 | 22,01 | 0,96 | 4,35 | 19,5 | 24,2 | 30 |

| | **Oberlausitz** | | | | | | **age classes 2-11** | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | males | | | | | | females | | | | | |
| | $\bar{x}$ | s | v | $x_{min}$ | $x_{max}$ | n | $\bar{x}$ | s | v | $x_{min}$ | $x_{max}$ | n |
| 1 (*cbl*) | 87,14 | 1,33 | 1,53 | 85,4 | 88,9 | 7 | 79,34 | 0,78 | 0,98 | 78,3 | 80,6 | 5 |
| 2 (*mxl*) | 42,87 | 0,97 | 2,26 | 41,3 | 44,1 | 9 | 38,58 | 0,30 | 0,78 | 38,0 | 38,8 | 5 |
| 3 (*blbs*) | 34,87 | 0,76 | 2,18 | 33,3 | 35,8 | 7 | 32,16 | 1,19 | 3,69 | 31,1 | 34,3 | 5 |
| 4 (*zb*) | 52,24 | 1,15 | 2,20 | 49,6 | 53,2 | 7 | 46,44 | 1,08 | 2,33 | 44,5 | 47,7 | 5 |
| 5 (*eob*) | 27,47 | 0,90 | 3,27 | 25,8 | 28,7 | 7 | 24,47 | 0,90 | 3,66 | 23,2 | 25,1 | 3 |
| 6 (*pob*) | 18,74 | 1,12 | 6,00 | 17,3 | 20,5 | 8 | 18,24 | 1,04 | 5,72 | 16,7 | 19,6 | 5 |
| 7 (*bb*) | 36,46 | 1,58 | 4,34 | 34,1 | 39,5 | 7 | 34,72 | 0,74 | 2,13 | 33,9 | 36,1 | 5 |
| 8 (*sh*) | 27,03 | 0,37 | 1,38 | 26,6 | 27,7 | 6 | 25,22 | 0,72 | 2,84 | 24,4 | 26,5 | 5 |
| 9 (*shc*) | 28,78 | 0,53 | 1,84 | 27,8 | 29,6 | 6 | 26,66 | 0,66 | 2,48 | 26,0 | 27,8 | 5 |
| 10 (*utr*) | 31,74 | 0,87 | 2,75 | 30,4 | 33,6 | 9 | 28,32 | 0,39 | 1,38 | 28,0 | 28,8 | 5 |
| 11 (*cb*) | 22,67 | 0,24 | 1,04 | 22,5 | 23,0 | 3 | 20,05 | 1,33 | 6,62 | 18,8 | 22,5 | 5 |
| 12 (*al*) | 57,44 | 1,42 | 2,46 | 55,1 | 59,6 | 9 | 50,70 | 0,64 | 1,26 | 49,8 | 51,6 | 5 |
| 13 (*ltr*) | 36,39 | 0,95 | 2,61 | 34,8 | 37,7 | 9 | 32,68 | 0,62 | 1,89 | 32,2 | 33,8 | 5 |
| 14 ($M_1l$) | 10,39 | 0,20 | 1,90 | 10,1 | 10,8 | 9 | 9,58 | 0,29 | 3,05 | 9,3 | 10,1 | 5 |
| 15 ($M_1b$) | 4,09 | 0,12 | 2,93 | 3,9 | 4,2 | 9 | 3,76 | 0,14 | 3,61 | 3,6 | 4,0 | 5 |
| 16 (*ch*) | 25,61 | 0,47 | 1,83 | 24,8 | 26,4 | 9 | 22,54 | 0,74 | 3,30 | 21,2 | 23,3 | 5 |

Table 1

| | Hercynian region | | | | | | age class 1 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | males | | | | | | females | | | | | |
| | $\bar{x}$ | s | v | $x_{min}$ | $x_{max}$ | n | $\bar{x}$ | s | v | $x_{min}$ | $x_{max}$ | n |
| 1 (*cbl*) | 85,00 | 2,84 | 3,34 | 76,8 | 89,1 | 31 | 78,62 | 2,00 | 2,54 | 74,9 | 82,0 | 24 |
| 3 (*blbs*) | 33,06 | 1,57 | 4,75 | 28,2 | 35,3 | 30 | 31,20 | 1,05 | 3,37 | 29,4 | 32,9 | 24 |
| 4 (*zb*) | 49,05 | 2,10 | 4,28 | 44,2 | 53,2 | 30 | 44,90 | 1,56 | 3,47 | 41,0 | 49,5 | 24 |
| 7 (*bb*) | 36,78 | 1,15 | 3,13 | 34,6 | 39,3 | 30 | 35,58 | 0,87 | 2,45 | 33,1 | 37,5 | 24 |
| 8 (*sh*) | 27,46 | 0,78 | 2,84 | 25,8 | 28,9 | 31 | 25,62 | 0,99 | 3,86 | 23,5 | 27,6 | 24 |
| 10 (*utr*) | 30,19 | 1,43 | 4,73 | 25,8 | 32,8 | 32 | 27,47 | 2,28 | 8,28 | 16,8 | 29,8 | 27 |
| 12 (*al*) | 55,02 | 2,32 | 4,22 | 47,7 | 58,6 | 30 | 50,23 | 1,52 | 3,03 | 46,9 | 54,1 | 27 |
| 13 (*ltr*) | 35,01 | 1,53 | 4,38 | 31,1 | 37,6 | 31 | 32,33 | 1,03 | 3,18 | 30,8 | 35,1 | 27 |
| 14 ($M_1l$) | 10,14 | 0,55 | 5,45 | 8,8 | 11,6 | 31 | 9,41 | 0,35 | 3,75 | 8,7 | 10,1 | 27 |
| 15 ($M_1b$) | 4,07 | 0,22 | 5,33 | 3,7 | 4,6 | 31 | 3,79 | 0,19 | 5,02 | 3,5 | 4,3 | 27 |

| | Hercynian region | | | | | | age classes 2-11 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | males | | | | | | females | | | | | |
| | $\bar{x}$ | s | v | $x_{min}$ | $x_{max}$ | n | $\bar{x}$ | s | v | $x_{min}$ | $x_{max}$ | n |
| 1 (*cbl*) | 85,83 | 2,04 | 2,38 | 82,0 | 88,0 | 6 | 79,10 | 0,98 | 1,15 | 77,4 | 80,6 | 8 |
| 3 (*blbs*) | 33,47 | 1,86 | 5,57 | 30,5 | 35,7 | 6 | 31,64 | 0,86 | 2,72 | 30,3 | 32,5 | 8 |
| 4 (*zb*) | 51,29 | 2,31 | 4,51 | 47,3 | 54,0 | 7 | 45,44 | 1,04 | 2,30 | 43,6 | 47,0 | 7 |
| 7 (*bb*) | 36,79 | 1,27 | 3,45 | 34,3 | 38,2 | 7 | 33,98 | 0,84 | 2,46 | 33,3 | 35,8 | 6 |
| 8 (*sh*) | 28,12 | 0,58 | 2,05 | 27,4 | 29,2 | 6 | 24,63 | 0,47 | 1,90 | 23,9 | 25,5 | 8 |
| 10 (*utr*) | 31,11 | 0,85 | 2,75 | 29,5 | 32,1 | 9 | 28,65 | 1,23 | 4,28 | 27,3 | 31,6 | 8 |
| 12 (*al*) | 55,89 | 1,23 | 2,19 | 53,3 | 57,3 | 9 | 50,59 | 0,75 | 1,48 | 49,5 | 51,5 | 8 |
| 13 (*ltr*) | 35,53 | 0,76 | 2,14 | 33,7 | 36,7 | 9 | 32,40 | 0,81 | 2,49 | 31,1 | 33,7 | 8 |
| 14 ($M_1l$) | 10,36 | 0,35 | 3,38 | 9,7 | 10,8 | 9 | 9,47 | 0,21 | 2,24 | 9,2 | 9,8 | 7 |
| 15 ($M_1b$) | 4,10 | 0,15 | 3,64 | 3,9 | 4,3 | 9 | 3,71 | 0,06 | 1,72 | 3,6 | 3,8 | 7 |

Table 2 Body measures of the Pine Marten sample from the Oberlausitz

*m* mass
*hb* head and body lenght
*t* tail lenght
*hf* hind foot lenght
*e* ear lenght

**age class 1**

| | males | | | | | | females | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | s | v | $x_{min}$ | $x_{max}$ | n | $\bar{x}$ | s | v | $x_{min}$ | $x_{max}$ | n |
| *m* | 1343,5 | 173,02 | 12,88 | 820,0 | 1640,0 | 30 | 985,4 | 139,59 | 14,17 | 750,0 | 1210,0 | 13 |
| *hb* | 464,17 | 17,50 | 3,77 | 416,0 | 495,0 | 30 | 415,85 | 15,75 | 3,79 | 375,0 | 445,0 | 13 |
| *t* | 248,93 | 17,19 | 6,91 | 220,0 | 300,0 | 30 | 220,42 | 18,85 | 8,55 | 182,0 | 260,0 | 12 |
| *hf* | 95,20 | 5,66 | 5,94 | 83,0 | 110,0 | 30 | 84,33 | 6,59 | 7,81 | 74,0 | 95,0 | 12 |
| *e* | 43,34 | 3,69 | 8,51 | 30,0 | 48,0 | 29 | 39,00 | 2,97 | 7,62 | 33,0 | 44,0 | 12 |

**age classes 2-11**

| | males | | | | | | females | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | s | v | $x_{min}$ | $x_{max}$ | n | $\bar{x}$ | s | v | $x_{min}$ | $x_{max}$ | n |
| *m* | 1602,5 | 144,62 | 9,02 | 1450,0 | 1885,0 | 6 | 1037,5 | 89,55 | 8,63 | 960,0 | 1190,0 | 4 |
| *hb* | 487,0 | 18,35 | 3,77 | 460,0 | 522,0 | 6 | 425,75 | 11,37 | 2,67 | 410,0 | 438,0 | 4 |
| *t* | 243,17 | 10,99 | 4,52 | 226,0 | 255,0 | 6 | 243,00 | 26,16 | 10,77 | 215,0 | 280,0 | 4 |
| *hf* | 93,33 | 6,52 | 6,99 | 86,0 | 102,0 | 6 | 84,50 | 2,87 | 3,40 | 80,0 | 88,0 | 4 |
| *e* | 45,33 | 2,56 | 5,65 | 42,0 | 49,0 | 6 | 36,50 | 4,39 | 12,02 | 30,0 | 41,0 | 4 |

Table 3 Frequencies of occurence of nonmetrical traits in the skulls of Pine martens from the Oberlausitz and the Hercynian region

* significant difference

l. left side
r. right side
b. both sides

| | | **Oberlausitz** | | **Hercynian region** | |
|---|---|---|---|---|---|
| | | frequency (%) | n | frequency (%) | n |
| 1 | *Feth l.* | 36,9 | 103 | 37,8 | 74 |
| 1 | *Feth r.* | 23,5 | 102 | 35,6 | 73 |
| 1 | *Feth b.* | 42,2 | 102 | 48,6 | 74 |
| 2 | *Focc* | 74,5 * | 98 | 54,4 * | 79 |
| 3 | *Cc l.* | 4,3 | 93 | 10,4 | 77 |
| 3 | *Cc r.* | 7,6 | 92 | 3,9 | 77 |
| 3 | *Cc b.* | 9,8 | 92 | 11,7 | 77 |
| 4 | *Fsph* | 78,6 | 103 | 68,6 | 70 |
| 5 | *eFov l.* | 95,0 * | 101 | 67,1 * | 73 |
| 5 | *eFov r.* | 96,0 * | 99 | 76,7 * | 73 |
| 5 | *eFov b.* | 98,0 * | 99 | 86,3 * | 73 |
| 6 | *pFpal* | 81,3 * | 112 | 92,4 * | 79 |
| 7 | $P^1$ *l.* | 99,1 | 115 | 95,1 | 82 |
| 7 | $P^1$ *r.* | 99,1 | 115 | 95,1 | 82 |
| 7 | $P^1$ *b.* | 98,3 | 115 | 96,3 | 82 |
| 8 | *Fme l.* | 99,1 | 115 | 93,8 | 80 |
| 8 | *Fme r.* | 99,1 | 114 | 97,5 | 80 |
| 8 | *Fme b.* | 99,1 | 114 | 98,8 | 80 |
| 9 | *aFme l.* | 37,4 * | 115 | 18,5 * | 81 |
| 9 | *aFme r.* | 30,7 * | 114 | 13,6 * | 81 |
| 9 | *aFme b.* | 46,5 * | 114 | 19,8 * | 81 |
| 10 | *aFme l.* | 48,7 | 115 | 35,8 | 81 |
| 10 | *aFme r.* | 50,0 | 114 | 60,0 | 80 |
| 10 | *aFme b.* | 68,4 | 114 | 66,7 | 81 |
| 11 | $P_1$ *l.* | 94,8 | 115 | 92,6 | 81 |
| 11 | $P_1$ *r.* | 93,0 | 114 | 92,6 | 81 |
| 11 | $P_1$ *b.* | 90,4 | 115 | 97,5 | 81 |

Table 4 Mean measures of divergence of the population samples from different landscape units of the Oberlausitz

| | |
|---|---|
| Pondland | Pl |
| Field Landscape | Fl |
| Eastern Hill Landscape | EH |
| Western Hill Landscape | WH |
| Highland | Hl |

* significant difference

| | Fl | EH | WH | Hl |
|---|---|---|---|---|
| Pl | 0.086 | 0.202 * | < 0.001 | < 0.001 |
| Fl | | 0.789 * | < 0.001 | 0.029 |
| EH | | | 0.166 | 0.209 * |
| WH | | | | < 0.001 |

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