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On pileus anomalies in the common lizard *Lacerta vivipara* in Finland — a morphogenetic problem revisited

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The anterior and posterior pileus in 367 specimens of the common lizard *Lacerta vivipara*, collected mainly in southern Finland, show different types of variation: geographical in the anterior and largely stochastic in the posterior. This variation was studied in terms of phenodeviants indicatory of disturbances caused by environmental or genetic stresses during ontogeny, with the following results: 1) the differences in the anterior pileus pattern are probably hereditary, 2) the viabilities of the pileus types vary in different environmental conditions, 3) the postfrontal anomalies are much more common among individuals with a particular pattern called "rectangular" than among the other types, the former thus possibly being connected with some specific system of disturbance particularly susceptible to anomalies, and 4) it seems evident that there are genetically determined interrelations between the anterior and posterior part of the pileus through the mediatory role of the rectangular pattern. The problem is treated in terms of phenodeviants indicating disturbances caused by environmental or genetic stresses during ontogeny.

1. Introduction

The object of this paper is to consider some aspects of anomalous variation revealed by my studies (Voipio 1968b, 1969) on the pileus structure in the common lizard *Lacerta vivipara* Jacquin. My aim is to collate and synthesize the results from studies on two different (though apparently interrelated) phenomena: first, the ordinary pileus polymorphism of the anterior part of the pileus, and, second, the variation of the posterior pileus, the so-called postfrontal pileus. While, in the former, a rather regular variation in the mutual position of the two shields of praefrontalia is concerned, in the latter the variation is not only considerably greater, but also characterized by a high degree of irregularity.

Irregular variation is of interest if it displays considerable local changes or can be shown to be correlated with extreme or abnormal environmental conditions or with certain types of polymorphic variation. I will attempt to treat the problem of irregular variation occurring in the posterior part of the pileus (Voipio 1969) in terms of phenodeviants considered indicators of environmental or genetic stresses acting upon the ontogenies of individuals. It was thus appropriate to recollect the principal types of this irregular variation and their frequencies and to ascertain their possible correlations to the ordinary pileus polymorphism in the species. The main interest is, first, to tentatively assess the contribution of the pertinent agents, genetic and/or environmental factors, disturbing the developmental pathway leading to the normal pattern of the pileus, and, second, to ascertain whether the mutual interrelations between the separate parts of the pileus provide a theoretical framework generating testable predictions of probable morphogenetic outcomes under certain conditions.

2. Material and methods

The material is the same as was used in my previous studies on *Lacerta vivipara* (Voipio 1968b, 1969). It consists of 367 specimens (216 adults and 151 fetuses) collected, with the exception of 48 adults obtained from elsewhere in Finland, mainly in two neighbouring communes (Sumiainen and Suolahti) in the middle of southern Finland (Fig. 1). Collecting took place in July in 1964–1967, mainly during the advanced stage of pregnancy of the females in order to obtain progeny from mothers of known pileus pattern. The fetuses of the 20 pregnant females were removed from the mothers, liberated from their embryonal membranes and examined with a magnifying glass. The collection is located at the Zoological Museum, University of Turku, Finland.

The progress of gestation somewhat varies according to the temperature determining the onset of reproduction, as well as the rate of embryonal growth. Due to this and because the females exhibit individual variation in starting reproduction, a certain number of fetuses may have been missed as too young to show their head-shield pattern. It should be remembered, however, that embryos are still valuable objects for examination because of their suitability for cytological and/or histological inspection for elucidating the rudimentary stages through which their type will be ultimately fixed. This potential, however, awaits study.

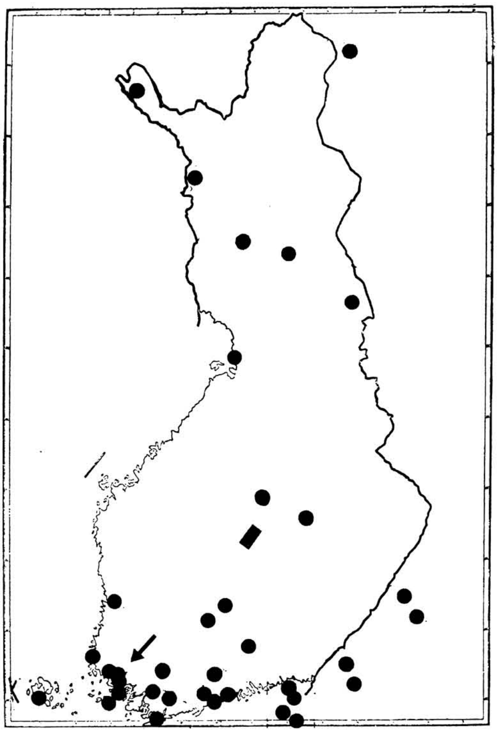

Fig. 1. Sampling localities of the material studied. The Sumiainen-Suolahti area is indicated by the rectangle. Arrow: provenance of the peat-bog sample.

3. Basic facts

3.1. The prefrontal pileus

The ordinary pileus polymorphism of the common lizard applies to the anterior part of the pileus containing six reasonably large shields of which four, viz. the frontonasale (also called internasale), the two praefrontalia, and the frontale vary in regard to their mutual position. Three different constellations, called median, cross and transversal patterns, then emerge (Fig. 2).

The prefrontal pileus patterns, in contrast to the postfrontal pileus, display a marked geographical polymorphism, as has been shown by Wermuth (1955) for continental Europe and by Voipio (1961) for part of Fennoscandia. In populations in which the pileus is polymorphic, all three main head-shield patterns varying in their relative frequencies are regularly present

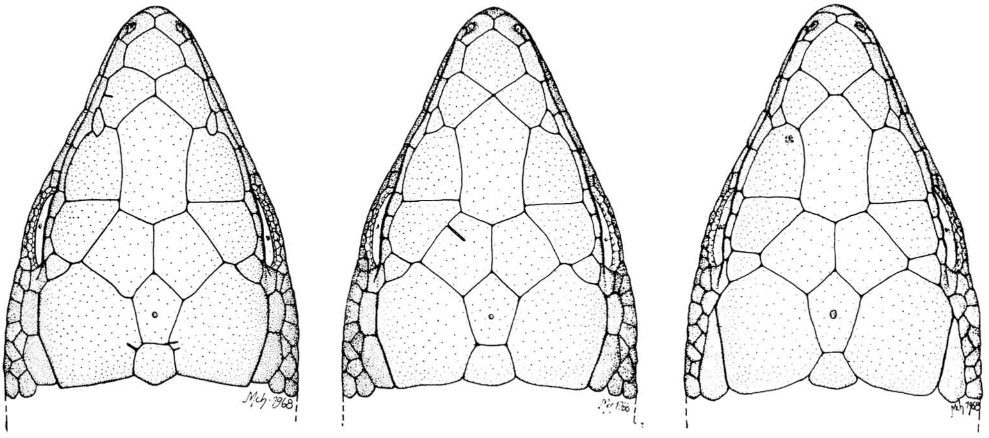

Fig. 2. The three main patterns of pileus in *Lacerta vivipara* median (left), cross (middle) and transversal (right). From Voipio 1968.

and the number of shields is practically constant. One exception exists, however. In this case an extra small rectangular shield lies between the frontonasale and the frontale, separating these two shields and also the two praefrontalia from each other (Fig. 3). In the Finnish population this pattern, which I have called the rectangular pattern, is less than half as frequent as the rarest of the three main types (Voipio 1968b). The overall picture of the Finnish population ($n = 367$) is as follows (%):

Median	64.6	Transversal	12.8
Cross	16.6	Rectangular	6.0

As can be seen from the tabulation, the median type strongly predominates, and this is the case throughout the European area. Its frequency decreases, however, from west to east and southeast, the other morphs correspondingly increasing in their frequency. The Finnish population belongs to the eastern type, thus representing a northern extension of the East European pattern (for the aspects of distribution history, see Voipio 1961 and 1963).

A remark may be appropriate in this context. As it appears from the data presented by Dely & Böhme (1984:364), the number of shields of the prefrontal pileus, in the southern parts of Europe, is not as constant as in the Finnish population. Beside the rectangular pattern, several types of deviations are known. Their relative frequencies vary between 3 and 6 % within the individual populations. This difference may accord with the circumstances that, as has been pointed out by Dely & Böhme (1984), the common lizard tends to be more stenotopic and ecologically bounded by higher altitudes in the mountainous areas of southern Europe.

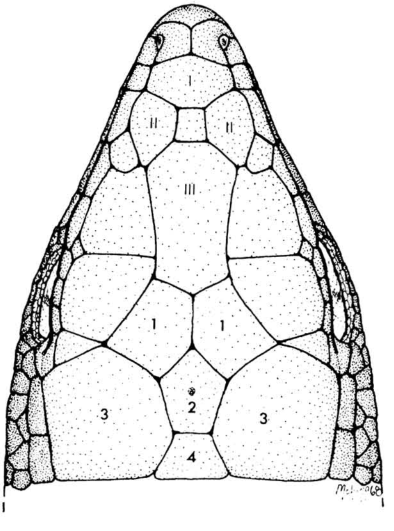

Fig. 3. Pileus with the so-called rectangular pattern and normal postfrontal shields. — I–III: shields involved in the ordinary polymorphism; 1–4: postfrontal shields. I frontonasale, II praefrontalia, III frontale, 1. frontoparietalia, 2. interparietale, 3. parietalia and 4. occipitale. From Voipio 1969.

3.2. The postfrontal pileus

The postfrontal part of the pileus consists of comparatively large shields, of which the scuta frontoparietalia and scuta parietalia are paired, the medially lying unpaired shields, the scutum interparietale and scutum occipitale, being considerably smaller (Fig. 3). In contrast to the anterior or prefrontal pileus, this part of the pileus is rather unstable. The number of shields varies considerably because extra cleavages occur in the individual shields. Small extra shields are also formed between the regular ones, which are partly, or sometimes completely, separated from each other. Occasionally, there is full division of the shields themselves into two almost equal parts. As the cleavages are formed quite irregularly, the variation as a whole consists of anomalies too accidental by nature to allow any distinct classification of the varieties.

3.2.1. Frequency and location of the anomalies

The frequency of anomalous individuals in different age classes in the Finnish population is:

	%	*n*
Adults	16.7	168
Juveniles	14.6	48
Embryos	13.2	151
Total	15.0	367

The frequency of anomalies is of the same class of magnitude as that of the ordinary polymorphic cross and transversal phases of the prefrontal pileus. There is no difference between the age classes. The anomalies can be shorter or longer cleavages directed from the edge of the shield towards its inner part, but sometimes they can extend through the entire shield from one edge to the other. In the frontoparietalia, the commonest anomaly consists of an extra cleavage running across the shield from the interparietale and bisecting the frontoparietale. There may also be an extra shield between these paired shields. In the parietalia, an extra shield of varying size at their medioposterior edges is the commonest anomaly. The commonest anomaly of the interparietale consists of a small shield formed at its anterior tip. A longitudinal bisection of the interparietale is another anomaly of this shield. Finally, in the occipitale the anomaly appears as a transverse division of the shield into two parts, the caudal one being larger (Fig. 4).

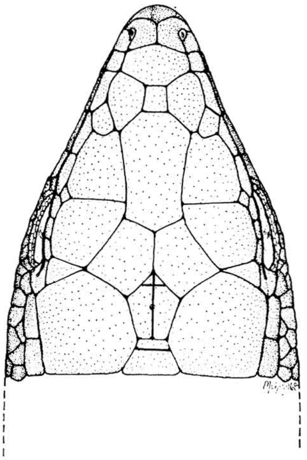

Fig. 4. Positions of the extra cleavages in the interparietale and occipitale. From Voipio 1968 with addenda.

The frequencies with which the individual postfrontal shields are affected vary considerably, as can be seen from the following tabulation based on 55 anomalous specimens:

Frontoparietalia	30
Parietalia	23
Interparietalia	8
Occipitale	6

It also appears from the figures that more than one kind of shield is affected simultaneously in some of the 55 anomalous individuals. The simultaneous anomalies may well be considered a sign of more serious disturbances than those appearing in one kind of shield only. Their frequencies were as follows:

frontoparietalia and parietalia	7
frontoparietalia and interparietale	2
parietalia and interparietale	2
occipitale and frontopar.+ parietalia + interpar.	1

The paired shields (frontoparietalia and parietalia) are affected considerably more often than the unpaired ones (see the tabulation above). Though they are the largest of the shields displaying anomalies, size cannot be a decisive factor as the smaller frontoparietalia are more frequently affected. This may be due to the fact that the frontoparietalia meet in the midline of the head (pileus), i.e. topographically within the most unstable area of the head of which the extra cleavages in the middle area of the postfrontal pileus (Fig. 4) and the prefrontal pileus (variable position of the praefrontalia and the presence or absence of the rectangulare) are also an indicator.

As regards the paired shields in particular, a considerable proportion of the anomalies affects only one of a pair of shields as, e.g. is to be seen in a specimen (depicted in Fig. 2, middle) unintentionally selected for illustration by the author. The asymmetry is thus essentially associated with the formation of anomalies in paired structures.

4. The behaviour of the rectangular pattern, a special case

The rectangular pileus pattern was first recorded in Finnish material in 3 specimens in a museum sample of 89 individuals (Voipio 1961). The problem then arose of whether it is a regular characteristic or an anomaly only. Wermuth (1955) did not specify it from the material from continental Europe, and it seems that specimens of this type were included by him in the category of anomalies in the prefrontal area, "in consequence of which the constellations of the *prefrontal* shields could not be determined" (Wermuth 1955:233; translation and italics mine). However, the same pattern has been recorded as common, except in a Caucasian species *Lacerta praticola* Eversmann according to Schreiber (1912), as well as in several other lacertid species, such as *Podarcis muralis*, *Lacerta rudis*, *L. taurica* and some other species of the genus *Eremias* (Dely 1981a, 1982, Dely & Stohl 1982). As far as *Lacerta vivipara* is concerned, this pattern seems to occur rather commonly in Roumania (Stugren & Vancea 1961). Interestingly, the incidence of the rectangular pattern in Finland appears to be the same as that of the Eastern European populations, on the basis of the data by Wermuth (1955; see Voipio 1961:119) and according to the information given by Dely & Böhme (1984:365). The relative frequency of this pattern there belongs to the class of deviations occurring with a frequency of about 6 per cent at most (see above p. 85). It must be remembered that the Finnish population can be considered a derivative of the eastern and/or southeastern one.

There are indications that the rectangular pattern represents some kind of special case of morphogenetic outcome among the praefrontalia constellations. This becomes evident when the proportions of the anomalous individuals among the ordinary praefrontalia types are compared (Table 1). While the frequencies of anomalous individuals, within the prefrontal morphs, did not significantly differ statistically, and the frequencies in the pooled adult and juvenile data did not differ among the transversal, cross and median one, the relative frequency of the anomalous individuals was significantly higher among the rectangular pattern than among the other types (36.4 vs 13.6 %, Fisher's exact test, $P = 0.0009$, Table 1). Through this, the uniqueness of the rectangular type is emphasized. It appears that the rectangular type is possibly connected with some specific system of disturbance particularly susceptible to various anomalous conditions.

I am obliged to add, in this context, that Dely (pers. comm.), basing his opinion on the experience gained from the species *Podarcis muralis*, expresses some doubt regarding this possibility. I think however, that comparisons between separate species, even those belonging to different genera, do not necessarily produce commensurate results because of the different genetic constitution of the species. This has been shown e.g. by Zakharov (1989:44) in his studies on two sympatric species of *Lacerta* (*agilis* and *strigata*).

Table 1. Frequency (%) of anomalous individuals in different morphs.

Morph	Anomalous		*n*
Median	14.3	13.6	237
Cross	14.7		61
Transversal	8.5		47
Rectangular	36.4		22
Total	15.0		367

They differed considerably in their developmental stability due to "certain general differences between two species" (Zakharov 1987), i.e. due to their different genetic constitution. The developmental stability is a species specific characteristic. For the same reason, even separate geographical populations of the same species may, in this sense, be incommensurable entities.

4.1. Viability relations

The general sensitivity of the shield pattern both in the prefrontal and the postfrontal pileus becomes evident in connection with the case, so far observed only once, of an individual population living in conditions presumably suboptimal to the species. In this case the relative frequencies of the pileus patterns appeared to be strictly different from the average normal distribution (Table 2). Within the peat-bog population the proportion of the median phase is the lowest known, whereas that of the transversal phase is the highest encountered among the adults. This must be considered if not simply purely stochastic variation due to genetic drift (for the heritability of this variation, see later), at the very least a hint of the changed viability relations between the pileus morphs under changed environmental conditions (for arguments as to the improbability of this polymorphic variation being caused by a mere disturbance in ontogeny due to changed environmental factors, see below).

As to the postfrontal pileus, a considerable increase in the anomalies were detected. The frequency of the anomalous individuals (17/30 = 56 %) was much higher there than in the populations of the other habitats (38/337 = 15 %). The difference is statistically highly significant ($\chi^2 = 41.00$, *df* = 1, *P* = 0.0000, Yate's correction). Further, the relative frequency, among the anomalous individuals, of the seriously affected individuals (possessing more than one kind of anomalous shield simultaneously) was also comparatively high, viz. 8 out of 17 specimens = 47 %, instead of 4 out of 38 individuals = 10.5 %, of the populations from the other habitats ($\chi^2 = 7.17$, *df* = 1, *P* = 0.0074, Yates' correction).

Table 2. Comparison of frequencies (%) of different morphs in a peat-bog and other populations.

Morph	Peat-bog (n=30)	Other (n=337)
Median	43.3	66.5
Cross	20.0	16.3
Transversal	26.7	11.6
Rectangular	10.0	5.6

Log-likelyhood ratio G_W for 2×2 contingency tables with William's correction:
Median vs. other morphs, $G_W = 6.02$, *df* = 1, *P* = 0.02
Transv. vs other morphs, $G_W = 4.40$, *df* = 1, *P* = 0.05

4.2. On hereditary relations of the pileus types

On purely morphological grounds the prefrontal patterns could be easily explained as mere phenotypic variation as a result of the varying relative growth rate, say, of the praefrontalia in comparison with that of the frontale and frontonasale. This is the easiest explanation, of course, as long as the information upon the heritability of the variation is insufficient. But when the circumstances in Fennoscandia are taken into consideration, some questions arise as to the nature of the rather regular variation of the prefrontal pileus. How can it be explained, for instance, that, while the pileus of the common lizard is clearly polymorphic within the Finnish area, it is monomorphically median in the south-central parts of Sweden and within the western European continent nearly so (see Voipio 1961)? Further, if the prefrontal varieties were to be considered anomalies or phenodeviants only, as suggested by Dely (1978:12, but see later), why, then, does no such variation exist at all in the prefrontal pileus of the southern Swedish population? There are only two possible explanations to this problem. Either it is a genetic structure which allows or does not allow the cross and transversal morphs to appear as phenodeviants in separate areas differently, or there are differences in the presence or absence of the key alleles themselves on which the three constellations, median, cross and transversal, are based. However it might be, we cannot get away from the inference that the polymorphic variation of the prefrontal pileus is basically genetic in nature. This view is corroborated by the fact, in addition, that there is a sharp jump in the relative frequencies of the morphs within a comparatively narrow zone located in central Sweden at about latitude 63°N, from which point on the relative frequencies of the morphs turn out to change towards those typical for the Finnish population (Voipio 1961: 120).

Viewed against these facts, the following observations offer a still more direct indication that the differences are hereditary. Examination of the head-shield patterns of 20 pregnant females and their 151 fetuses showed that the frequencies of the morphs among the young grouped according to the type of mother differed in the direction to be expected if heritability is assumed (Table 3). Even though, in this case too, the direct effect of the environmental factors similarly affecting both the females and their offspring having developed, with parallel results, under the same environmental conditions, cannot be totally ruled out, this result, together with the knowledge obtained from the geographical patterns of variation indicated above, fairly firmly speaks for inheritability rather than against it. This, in turn, strengthens the view on the interrelations, through the mediatory role of the rectangular patterns, between the anterior and posterior part of the pileus.

It is to be noted, finally, that Dely (1978:25, 1981:45) and Dely & Sohl (1982:101) also seem to be inclined to consider the cross, and particularly the transversal, constellation of the praefrontalia, as belonging to a different category of deviations than the others representing anomalies sensu stricto. This interesting point of view is based, partly, on the considerably higher percentage occurrences of the former than of the latter. In other words, the prefrontal patterns do not represent the results of mere disturbances in individual morphogenesis characterized with a high degree of anomalies including asymmetry, but rather they reflect a phenomenon deeply anchored in the phylogeny of the species and even of the whole group of *Scincomorpha* displaying parallel evolution in regard to the prefrontal pileus variation (of which e.g. *Anguis fragilis* is an example, see later). On these grounds Dely & Stohl (1982:101) remarkably point to the genotypic basis, i.e., to the populationally varying gene pool determining the appearance of the prefrontal pileus patterns with relative frequencies varying geographically.

5. A survey of the principal results

The following results should be considered in assessing the share of factors acting on the morphogenesis of the pileus as a whole:

1) The differences in the prefrontal pileus pattern are probably hereditary.
2) The relative frequencies of the prefrontal morphs appear to change in relation to environmental conditions suggesting different relative viabilities of the pileus types in different ecological situations.
3) The postfrontal anomalies are much more common among individuals with the rectangular pattern than among the other types, the former thus possibly being connected with some specific system of disturbance particularly susceptible to anomalies.

As a consequence, it seems evident that

4) There are genetically determined interrelations between the anterior and posterior part of the pileus through the mediatory role of the rectangular pattern. Being associated with the relative viabilities of the prefrontal morphs, it links, at least in part, the posterior pileus and its irregular variation with the ordinary polymorphism of the prefrontal pileus.

Table 3. Comparison of frequencies (%) of different morphs in females and their offspring.

Females Morph	n	Offspring Median	Cross	Transversal	Rectangular	n
Median	15	73	10	9	8	105
Cross	4	58	15	18	9	33
Transversal	1	46	15	23	15	13
Total	20	67	12	12	9	151

6. Discussion

6.1. Anterior and posterior pileus as targets of the action of genetic vs. environmental factors

It has been suggested (Dely & Stohl 1982, Dely & Böhme 1984) that the median pileus pattern would be the basic type, whereas the other variants, the cross and transversal patterns, were to be considered mere deviants from the normal. This opinion is based, not only on the fact that the median pileus pattern occurs as the most common type among the lacertids in general, but also on the overall relative frequency (about 75 %) of the median pattern among the 239 *Lacerta vivipara* specimens collected from the huge distribution area of the species extending from western Europe to Manchuria.

In proportion to the area of collecting, the size of the sample, however, cannot be particularly representative and apparently does not tell too much about the real circumstances prevailing in separate parts of the distribution area, including Europe. This appears e.g. from the fact indicated above (p. 88), that in the collection of as many as 158 specimens studied (Voipio 1961) from South and Central Sweden, all but one individual represented the median ("basic") type (comp. also Wermuth 1955), whereas in the collection of 89 specimens available from Finland till then, the relative proportion of the median pattern appeared to be quite different (73 %). Further, the cross and transversal morphs taken together were represented by a percentage at least twice as great (<25 %) in Finland compared to the sample collected from the whole of the species area (10 %, according to Dely & Böhme, 1984:363). Finally, the remaining anomalous deviations from the presumed basic type displayed considerably lower percentages, i.e. from 3 to 6% at the most. From all this it appears that the three ordinary prefrontal patterns, median, cross and transversal, represent a quite different phenomenon, viz. ordinary polymorphism the phases of which cannot be considered mere phenodeviants of a more or less stochastic nature.

In the present study, therefore, the head-shield constellations of the anterior and posterior pileus have been considered two different kinds of variation. The *anterior pileus* displays a clear-cut geographical variation not only

1) as changes in the relative frequencies of the morphs in certain direction regionally (Wermuth, 1955, Voipio 1961, Dely & Böhme 1984:376), but also
2) as a strong dissimilarity of the polymorphic structure of the separate nearby populations presumably living in about similar ecological conditions (Sweden and Finland) and, finally,
3) as a sharp jump in the relative frequencies of the morphs in Central Sweden where two populations, presumably coming from different geographical directions, meet (Voipio 1961).

The variation of the *postfrontal pileus*, on the contrary, shows no features of this kind but is to the greatest extent, both individually and populationally (comp. Dely 1978, 1981), stochastic in its general occurrence, notwithstanding the fact that also on the prefrontal pileus disturbances leading to anomalies can occur within individual populations subject to environmental stress (see p. 91 of this study and Zakharov 1981, 1989). It is worth repeating that the Finnish population appears to be conspicuously stable as regards the prefrontal pileus.

Consequently, while the differences in the relative frequencies of the prefrontal morphs, within the populations of Fennoscandia, can be explained on the basis of their distribution history, the occurrence of considerable differences between individual local populations calls for a choice between genetic and environmental factors as a basis of the phenomenon. That none of the prefrontal patterns can be considered a phenodeviant from the third, the median one, together with the apparent heritability of this variation, suffices to eliminate the environmental factors as a sole cause of the frequency changes between the populations in general and within the peat-bog population studied in particular. The decision is to be made, thus, between selective factors due to different viabilities of the morphs and the possible effect of drift. Though comparison between separate populations living in similar conditions are still needed, there seems to be no doubt, however, that the main problem here is essentially genetic, in contrast to the postfrontal pileus variation, which basically relates to the problem of environmental influence in terms of development stability.

6.2. Development stability and environment

Into the theory of disturbances occurring in the morphogenetic processes enters the concept of the extreme phenotype. There is some ambiguity in regard to this term in that there is a continuous scale of disturbances of varying extent, and it is difficult, if not impossible, to judge where the point lies from which on one can safely apply the attribute "extreme". Besides, we cannot know, for example, the extent of invisible physiological disorder(s) behind the morphological macroscopic variation, however small the latter might be.

Occurrences producing an extreme phenotype might be reasonably classified in the following three categories (Soulé & Cuzin-Roudy 1982):

1) error or accident(s) in the developmental process,
2) environmental stress during development, and
3) an extreme genotype.

Notwithstanding the different sources of these agents giving rise to disturbances in development, they are all characterized, in regard to the nature of their effect(s), by a great amount of stochasticity. The stochastic component of variation refers to randomness in development (of which developmental error, noise and accidents are synonyms) as has been stated by Soulé (1982). This term has been used for the "residual component of variation which cannot be ascribed to either genetic or environmental factors". In other words, following Soulé (1982), although the developmental disturbances manifesting as anomalies and asymmetries are not (necessarily) hereditary, there is some amount of additive genetic variation affecting, at the cellular level (?), the very elementary (rudimentary) events which normally guarantee the stability of the developmental trajectory designated for the normal structure. Leaving the question of the residual genetic variation aside for a while, I will concentrate on the problem of environmental stress first.

6.2.1. Possible role of environmental stress

In regard to the concept of the stress-abnormality-asymmetry syndrome (Soulé 1982) the problem (implication) of environmental stress is substantial. As is well known, environmental conditions deviating considerably from those normally met with by the animals generally affect their morphology, indicating stress directed at the morphogenetic processes during ontogeny (see e.g. Soulé 1979, 1982, Zakharov 1981, 1984, 1989, Pankakoski 1985, Pankakoski & Hanski 1989). As regards the common lizard, in particular, low temperatures do have an effect on the onset and duration of the embryonal development (Voipio 1968:321). This observation must be considered relevant with respect to stress. Though doubts have been expressed (Soulé 1982:758) about whether animals adapted to developing in a fluctuating environment really experience low temperatures as developmentally stressful, it has been demonstrated clearly, with experimental support applied to another lacertid species, e.g. *Lacerta agilis* (Zakharov 1981, 1989), that there are stages during the development which are particularly sensitive to such departures. Such occurrences can be expected especially in such cases where the population lives in suboptimal conditions. The peat-bog mentioned earlier may well be considered to be a habitat where 'temperature lows' can occasionally reach almost lethal values during the period of embryonal development. If such conditions really bring out developmentally stressful effects, it would be expected that the incidence of the anomalies increase considerably, not only among the ordinary pileus morphs, but in particular among individuals of the rectangular type manifestly liable, as reported above, to suffer from disturbances leading to anomalies.

Examination of the 30 specimens of the peat-bog population as described above (p. 88) confirmed this expectation. In addition to the considerable changes in the frequencies of anomalies, other signs of heavy disturbances were also to be seen in the posterior pileus: two of the three individuals possessing rectangular pileus were anomalous, one of them displaying the heaviest disturbance known to me in that both of the frontoparietalia were cut off by an oblique cleavage running in the medio-lateral direction and, in addition, in that the scutum frontale (within the prefrontal pileus!) was also cut off transversally.

Interestingly, the vulnerability of the middle area of the pileus indicated above (p. 87) was also clearly revealed from the increased amount of disturbances affecting shields located within, or in close vicinity to, that area: beside bipartition of the scuta frontoparietalia, there is an extra little shield between the parietalia in two cases, a strong anomaly in the structure of the interparietale and occipitale simultaneously, an extra transversal cleavage running across the frontale as mentioned above, and, finally, an anomalous frontonasale added with an extra shield at its medio-anterior edge.

6.2.2. Share (implication) of the residual genetic variation

Following the train of thought by Soulé, it is to be expected that if some additive genetic variation is normally present in a population, the irregularities or anomalies — disregarding those caused by extreme genotype due to, for instance, the intrusion of foreign individuals (see below) — should occur, among the different pileus types, with about equal relative frequencies. This is, indeed, the case when median and cross types are considered. Among these, the anomaly percentages (14.3 and 14.7 resp.) are equal (see Table 4). This holds good, interestingly, also for the transversal and rectangular pattern taken together: they yield approximately the same percentage of anomalies as each of the two remaining morphs, viz. 17.4 % (Table 4). In addition, among the anomalous individuals with more than one kind of anomalous shield, presumably representing the most extreme cases of disturbance, the transversal and rectangular patterns combined yield about the same percentage value (4.3 %) of seriously affected individuals as each of the other two patterns (Table 4).

Table 4. Frequencies (%) of anomalous and seriously affected individuals in different morphs.

Morph	Anomalous	Affected	*n*
Median	14.3	2.9	237
Cross	14.7	3.2	61
Transv. + rectang.	17.4	4.3	69
Total	14.9	3.3	367

Variability between morphs: $\chi^2 = 0.064$, $P = 0.97$.

From this point of view, the problem of the relationship between the rectangular pattern, a part of the prefrontal pileus, and the stochastically varying postfrontal pileus gets new light as to the possible causal mechanisms. Considering the rectangular pattern as an anomaly and representative of some kind of extreme phenotype loses its credibility (likelihood) both for its clear-cut morphology and for its comparatively high and rather constant relative frequency within most of the species area. The problem thus turns out to be (-again) that of the residual variation. It seems that the rectangular condition, without itself being an anomaly, releases the effect of the additive (residual) genetic variation manifesting itself as a relatively high frequency of anomalies, as has been ascertained for this pattern. Testing this assumption, intended to explain the disproportionately high susceptibility of the rectangular pattern to disturbances, however, presupposes that its heritability can be demonstrated. This has not been possible so far, unlike the indications referring to the other patterns; no pregnant females of the rectangular type are known to me so far. There is, however, indirect evidence for that, viz., first, the fact just mentioned that the representation of the rectangular pattern is rather constant within the populations, and, second, that there are indications of some connection between the morphogenesis of the rectangular and transversal pattern. This is reflected in that these patterns together behave, as seen above, as though they were one and the same morph manifesting itself either in a transversal or rectangular (rarely) fashion for so far unknown reasons.

6.2.3. Extreme genotypes and morphogenesis

The question of extreme genotypes as a source of disturbances in morphogenesis certainly has relevance to the common lizard, even though the direct evidence for it is lacking so far. This claim is justifiable for the following reasons. First, the susceptibility of the rectangular type to anomalies, as has been demonstrated above, can be considered indirect evidence for the general sensitivity of the pileus formation to the prevailing genetic milieu at any given time. Second, as has been shown in my previous studies (Voipio 1962, 1968) on the European Slow-worm *Anguis fragilis* displaying parallel geographical variation of pileus polymorphism, there are clear indications of incompatibilities arising at the meeting of populations of different geographical origins. This appears from the considerable and statistically significant increase of the anomalous shield-patterns (which are not necessarily the same as in *Lacerta*) within the zone of the secondary contact located in Central Europe (see Voipio 1962:15 and Fig. 4; see also Dely 1981b:246). It can thus be expected that the same will occur, on a smaller scale, in those particular cases where individuals originating from microgeographically sufficiently remote populations intrude on another more or less isolated local population equipped with a harmoniously adjusted genotype of its own.

Recent studies by Zakharov (1981, 1989) have convincingly shown that this expectation, amply supported by investigations on population genetics and microsystematics by decades, rests on a sound basis. While comparable demonstration for lacertids is lacking so far, it has been shown by experiment on a fish, a species of stickleback (*Gasterosteus aculeatus*), that freshwater populations exposed to migrant flow from foreign sea populations experienced a considerable increase of phenodeviants as a result of genetic interference (Zakharov 1981, 1989). Analysis of hybrid populations of some other fish species (Zakharov 1987, Leary & Allendorf 1989) has given principally the same results.

6.3. Some inferences and prospects

Considerations discussed provide a theoretical framework generating testable predictions on expected changes in the morphogenetic processes. In sum, the following predictions can be made:

1) If the existence of the residual genetic variation within the natural populations is a norm or a rule, some amount of morphogenetic disturbance of a stochastic nature should occur in the pileus formation in about equal frequencies irrespective of the morph type.
2) If an individual morphic type provides an exceptional genetic milieu under which the morphogenesis advances during ontogeny, a deviating frequency of disturbances is to be expected for that morph.
3) If foreign gene complexes immigrate to a population, a local upset of morphogenetic balance manifesting an increased amount of anomalies, along with that of the asymmetries is to be expected.
4) If a population lives in an extreme or suboptimal environment, the incidences of the morphic characters will change due to the altered selection regime, and/or the frequency of phenodeviants is increased due to the environmental stress during ontogeny.

More extensive studies may provide conclusive tests for these predictions so far representing preliminary attempts only on the basis of some empirical data from the field. Studies on several separate populations large enough to eliminate the effect of genetic drift and originating from ecologically different environments are still necessary. Sets of relevant experiments performed by using varying environmental conditions paralleling those met with in the field are also important.

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