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Wing deformation in an isolated Carpathian population of *Parnassius apollo* (Papilionidae: Parnassiinae)

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Summary. The last native population of *Parnassius apollo* (Linnaeus, 1758) in the Pieniny Mts. (Polish Carpathians) has been isolated for at least 20 years. In captive breeding, individuals with crippled or even missing wings were frequent. Crippled individuals were also observed in the field. However, while in the field only deformed males were found, in captivity the number of deformed females was about twice that of deformed males. Some genetic models for this situation are discussed.

Zusammenfassung. Die letzte Population von *Parnassius apollo* (Linnaeus, 1758) im Pienin (Karpathen, Poland) ist seit mindestens 20 Jahren genetisch isoliert. In einer Gefangenschaftszucht traten zahlreich Individuen mit verkrüppelten oder sogar völlig fehlenden Flügeln auf. Das Phänomen wurde auch im Freiland registriert. Während im Freiland jedoch nur deformierte Männchen beobachtet wurden, sind in der Zucht Weibchen doppelt so häufig deformiert wie Männchen. Hierzu werden einige genetische Modelle diskutiert.

Résumé. La dernière population autochtone de *Parnassius apollo* (Linnaeus, 1758) aux Monts Pieniny (Carpathes polonaises) a été isolée depuis au moins 20 ans. Lors d'un élevage en captivité, des individus à ailes malformées, voire même totalement manquantes, étaient fréquents. Des individus malformés furent également observés dans la nature. Toutefois, alors qu'à l'état sauvage seulement des mâles déformés ont été trouvés, en captivité le nombre de femelles déformées était le double de celui des mâles. Quelques modèles génétiques susceptibles d'expliquer cette situation sont discutés.

Key words: Lepidoptera, *Parnassius*, populations, teratology, genetics, Poland.

In the course of restoring a *Parnassius apollo* (Linnaeus, 1758) metapopulation in the Pieniny Mts. (Polish Carpathians) the last native population of that species was investigated (Witkowski & Adamski, 1996; Witkowski *et al.*, 1993). This population has been isolated for at least 20 years. At the beginning of the nineties its size did not exceed 20–30 individuals; hence, one may suppose that the long-term isolation and inbreeding connected with the small size of the population has lead to genetic degradation manifested in certain phenotypic characters.

Recovery measures on the population have included captive breeding based on individuals originating from that last isolated population. In captivity, a few phenotypic characters indicating genetic degradation were noticed (Allendorf & Leary, 1986; Chen, 1971):

- high mortality of pupae (>50% individuals) (Witkowski *et al.*, 1993),
- appearance of individuals with changed pattern of wing veins (Witkowski *et al.*, l.c.),
- considerable variation of egg hatching (with statistically significant difference between lines) (Witkowski *et al.*, l.c.),
- appearance of individuals with partially reduced or even vestigial wings (Witkowski *et al.*, l.c.).

As this last character was observed in both captive and wild populations, and has not appeared in the literature on *P. apollo* (recently such a phenomenon was reported from Turkey (Kovanci *et al.*, 1996)), it seems proper to present this question in detail.

Captive breeding was established in 1991, based on L3 and L4 larvae collected in the field. The second year commenced with eggs laid by two captive females and was completed with eggs obtained from two other females in the field. In that year the first individuals with deformed wings were observed in captivity. For experimental purposes, one wingless female was mated with a normal male. It appeared that wingless females were able to copulate, and eggs laid by them did not differ from the other females.

In two successive years (1993 and 1994), despite supplementary breeding using material from wild females, both mortality of captive population and fraction of wingless individuals increased (Budzik, unpubl. ms). In 1993, the fraction of wingless individuals amounted to about 16% of the captive population (Table 1).

The handicapped individuals form three groups (fig. 1). The first comprises wingless individuals. The second are individuals with deformed wings; these were unable to complete development (wing expansion); these wings are stuck together and are severely creased. The third group includes individuals that almost completed wing development (attained normal expansion) but whose wings were nevertheless creased. It is worthy of notice that single handicapped individuals like these were observed each year in the wild population, too. They were males that tried to fly, hopping? in long leaps much as cockchafers (Cicindelidae) do. Females in the wild were much less active and no handicapped individuals of this sex were found.

In 1994, the captive population was reinforced with wild individuals from a larger neighbouring population (Slovakian part of the Pieniny Mts.) and in subsequent years handicapped individuals appeared only sporadically.

In 1993, in the captive breeding population (before reinforcing it with the Slovakian individuals), a proportion of normally developed individuals to handicapped ones was as 601 to 175 (Table 1). The proportions of sexes among handicapped individuals were as follows:

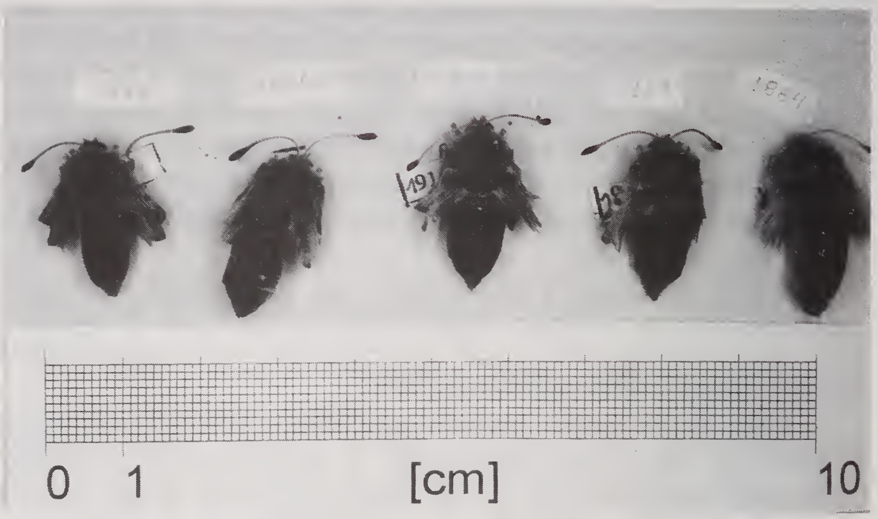
- group 1 (wingless individuals) — 74 females and 24 males;
- group 2 (deformed wings, unable to fly) and group 3 (deformed wings, able to make short leaps) — 29 males and 24 females (table 1).

These proportions point to some statistical regularities:

- In the group of wingless individuals the sex ratio markedly differed from 1:1 (Chi-square test for 2×2 2:2 tables = 4.27, $p < 0.0288$, H_0 = sex ratio not different from 1:1 was rejected).
- A difference between the sex ratio in wingless individuals and the sex ratio in individuals with deformed wings is also statistically significant (Chi-Square test = 4.81, $p = 0.0282$, H_0 = equivalent sex ratio in both cases of 1:1 was rejected).

Table 1. Number and percentages of normal and handicapped individuals of *Parnassius apollo* (Pieniny Mts. race) hatched during captive breeding in 1993

	Normal	Damaged	Wingless
	number of individuals		
male	286	29	45
female	315	24	77
	percentages		
male	79	8	13
female	76	6	19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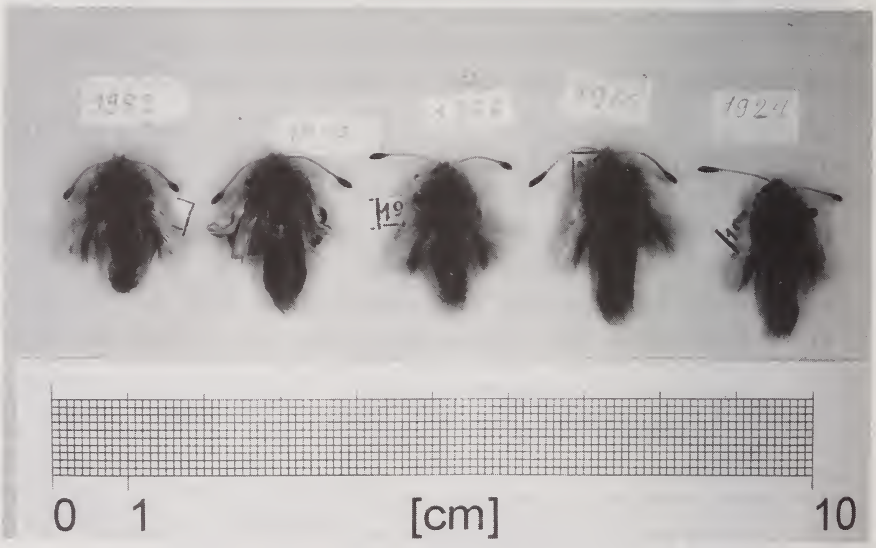
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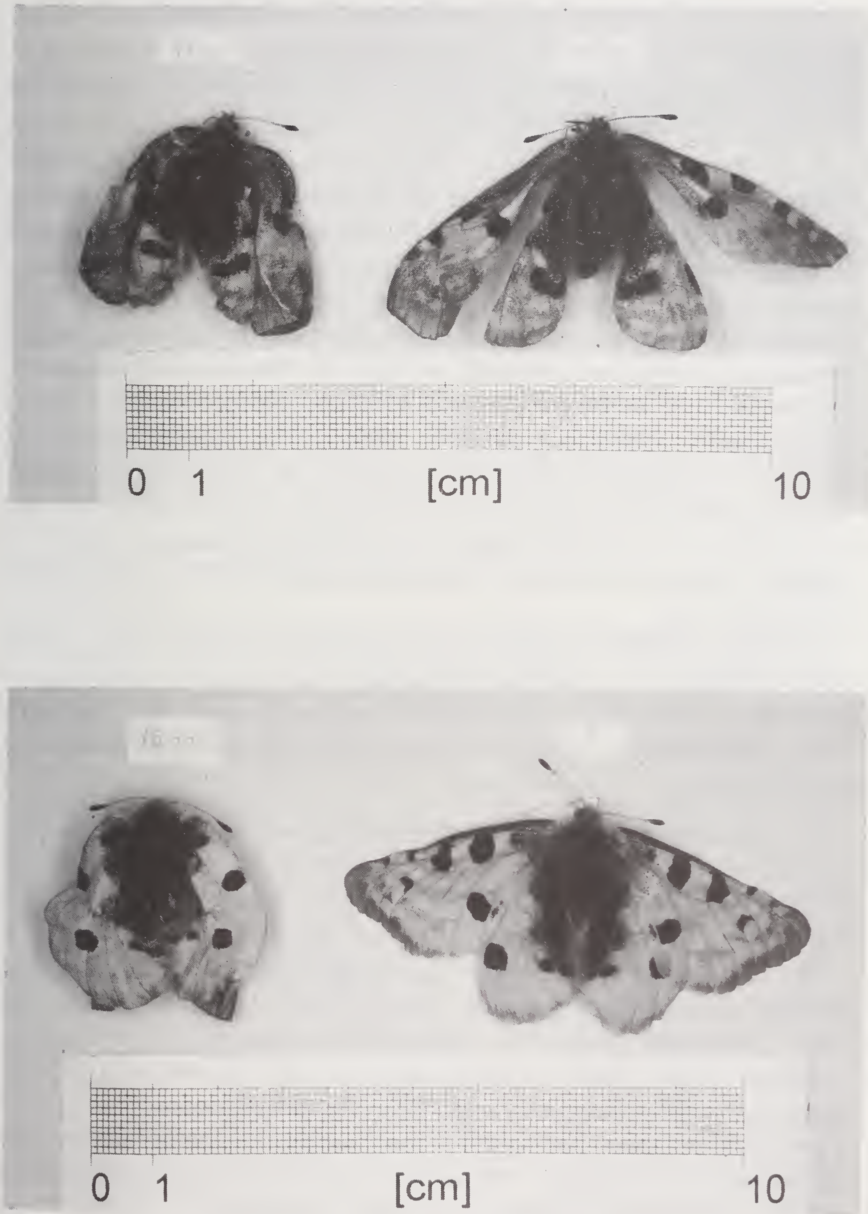

Fig. 1. Wingless (left) and deformed (right) individuals of *Parnassius apollo* during captive breeding of a restored metapopulation in the Pieniny Mts. (Polish Carpathians) (upper : females ; lower : males).

Since the fraction of handicapped individuals in captive population is ponderable, a hypothesis that the deformation of wings has a genetic background is very probable. Theoretically we may expect two possibilities:

1. *A quantitative polygenic inheritance.* Individuals with partially deformed wings were in captive breeding less numerous than completely wingless individuals. This suggests that the degree of wing development is not a quantitative character, which may assume values from the full development to the complete lack of wings. In such a case the wingless forms (the extreme morph) would occur least numerously or, at low frequencies of alleles, they would not be observed at all (Fisher, 1930). Wingless forms should occur with low frequency even in the case of significant differences in natural selection pressure on males and females.

2. *A qualitative single-locus inheritance.* In this situation we assume that the lack of wings is a qualitative character, but that defective wing expansion is a separate phenomenon regulated in a different way.

Another problem is the sex ratio of wingless individuals, which approximates 2:1 in favour of females (Chi-square = 0.34, p = 0.56, H_0 = sex ratio not different from 2:1 was not rejected). This phenomenon may be caused by one of the following alternatives:

A. The locus responsible for the wingless condition is located on the sex chromosome X. In this case a most fraction of phenotypes in which this locus becomes manifested should be expected in the heterogametic sex i.e. females (Haldane's rule).

B. Expression of the allele for "winglessness" is facilitated in females depending on genetic background. In this case the sex ratio diverging from 1:1 indicates the operation of natural selection which leads to differences in the expression of "winglessness" alleles between males (for which flightlessness is always a loss) and females (for which it may sometimes be an advantage) (Witkowski & Adamski, 1996). The fact that wingless individuals are not eliminated suggests that this character is "treated" by natural selection as at least a neutral mutation (Witkowski & Adamski, 1996).

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