

INHERITANCE OF ASSEMBLY PHEROMONE RESPONSIVENESS IN ARGAS (PERSICARGAS) PERSICUS (OKEN)

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Abstract. Experimental hybridization of two populations of *A. persicus* originating from Czechoslovakia (Cc) and Azerbaijan (Aa) and exhibiting a different responsiveness to assembly pheromone demonstrated the matrocliny in the inheritance of the strong responsiveness in F_1 generation and its gradual disappearance in F_2 generation. It is assumed that the responsiveness to assembly pheromone is directed by a polygenous system the replication rates of which may be reversibly affected by experimental hybridization, which results in the matrocliny in the F_1 generation. A gradual restabilization of the original replication rates in subsequent hybrid generations then affects the gradual disappearance of the matrocliny.

Although the genetics of mites and ticks was widely studied in the past, the studies dealt particularly with the cytogenetics, genetics of resistance against acaricides, and population genetics based mainly on experimental hybridization (Balashov 1979, Goroshchenko 1962, Oliver 1967, 1983, etc.). The heredity of quantitative characters was studied rather exceptionally. Some authors observed the matrocliny in ticks in heredity of some morphological (Panova 1967) and biological (Hunt and Drummond 1983, Dusbábek 1985a, b) characters, but mostly without any attempt to evaluate this phenomenon more deeply.

During the studies of the responsiveness to assembly pheromone in two populations of *Argas (Persicargas) persicus* (Oken), a weakly responding population from Azerbaijan and strongly responding population from Czechoslovakia, the matrocliny was observed in the inheritance of a strong responsiveness to assembly pheromone in F_1 hybrid males (Dusbábek 1985c). In order to answer the question whether this matrocliny is the manifestation of the extranuclear heredity or whether another genetic phenomenon is involved, we have studied the assembly pheromone response also in F_2 hybrids. The results are summarized in this paper.

MATERIALS AND METHODS

A. persicus from laboratory breeding of the Institute of Parasitology, Czechoslovak Academy of Sciences, České Budějovice, originating from Ipelský Sokolec, district of Lévice, Czechoslovakia, collected in henhouses on June 28, 1972 and May 4, 1982, and from villages of Arad and Shlelyan, district of Yevlakh, the Azerbaijan SSR, collected in henhouses on October 16 and 22, 1979, were used for experimental hybridization. The ticks were kept at $27 (\pm 1)^\circ\text{C}$ and $75 (\pm 5) \%$ RH in darkness and fed on chickens and hens 1 month after moulting using common methods (Dusbábek 1985a). Non-mated virgin specimens obtained from nymphs II and III were chosen for the hybridization.

The multiple-choice method in Petri dishes (Leahy et al. 1973) was used for the tests of the responsiveness to assembly pheromone under conditions described before (Dusbábek 1985c). A group of 10 virgin males was tested in five replications to the pheromone of their own hybrid combination and in other five replications to the pheromone of an opposite combination. For example, the responsiveness in Ca \times Ac hybrids was tested using paper discs contacted previously for one month with

males of $Ca \times Ac$ combination and filter paper discs contacted with $Ac \times Ca$ combination etc. Maximum aggregations in the sector with pheromone-marked disc during the first 6 h of experiment were considered.

The significance of differences in the aggregation score between the groups was compared by means of the χ^2 (chi-square) test.

The following abbreviations are used in the text and tables:

Aa — progeny of ♀ from Azerbaijan and ♂ from Azerbaijan
 Ac — progeny of ♀ from Azerbaijan and ♂ from Czechoslovakia
 Ca — progeny of ♀ from Czechoslovakia and ♂ from Azerbaijan
 Cc — progeny of ♀ from Czechoslovakia and ♂ from Czechoslovakia

RESULTS

The response to assembly pheromone of *A. persicus* engorged males of homozygous P and heterozygous F_1 generation is summed up in Table 1. The results of homogamic and heterogamic crosses show that the response of males from $Cc \times Cc$ or $Cc \times Aa$ crosses is significantly higher ($P < 0.001$) than that of males from $Aa \times Aa$ or $Aa \times Cc$ crosses and that the reciprocal crosses are nonidentical. Significant ($P < 0.01$) is also the difference between the homogamic and heterogamic crosses. A comparison of crosses with identical females reveals that there are no significant differences ($P > 0.10$) in the response of the progeny of Aa females and only probably significant difference ($P < 0.05$) in the response of the progeny of Cc females. However, there is a highly significant difference between the response of the progeny of Aa females and that of the progeny of Cc females ($P < 0.001$). A contrary situation is in the crosses with identical males. The differences in the response of the progeny of Aa males are probably significant ($P < 0.05$) and in those of the progeny of Cc males are even highly significant ($P < 0.001$), whereas the differences in the response of the progeny of Aa males compared to that of Cc males are insignificant. Heterozygous F_1 hybrid males respond therefore in a similar manner as males from homozygous population from which the mother of heterozygous F_1 hybrids originated. Consequently, the inheritance of the responsiveness to assembly pheromone is markedly matrilineal.

Table 2 summarizes the responses of males from the F_2 generation of brother-sister crosses. No statistically significant differences were found even if the aggregation score of parental and hybrid generations within the groups were compared ($P > 0.10$). Only the comparison of parental $Aa \times Aa$ and $Cc \times Cc$ generations revealed the probably significant difference in their aggregation score ($P < 0.05$). Nevertheless, even here the effect of matrocliny was evident in the increase in the aggregation score in relation to the increase in the genetic similarity of females to the homozygous parental Cc population.

The response to assembly pheromone of engorged F_2 males of reciprocal backcrosses is apparent from Table 3. The reciprocal backcrosses were identical in all cases except the crosses $Ac \times Cc$ and $Cc \times Ac$, i.e. in backcrosses of Ac heterozygous with Cc homozygous populations, where the aggregation score of the progeny of homozygous females was significantly higher ($P < 0.025$). The differences in backcrosses with identical females were insignificant ($P > 0.05$). Similarly insignificant were the differences in the summary aggregation score between the progeny of females of different genotypes. Like in F_2 brother-sister crosses (Table 2), also here the effect of matrocliny was manifested in the tendency to the increase in the aggregation score with the increase in the similarity of the genotype of female progeny to the genotype of homozygous parental Cc generation. In backcrosses with identical males, the aggregation score of the progeny of Aa males ($P < 0.05$) and Ac males ($P < 0.001$), i.e. the progeny of males distant in their genotypes from the genotype of the homozygous Cc population, was significantly different. On the other hand, no significant differences

Table 1. Assembly pheromone response of *A. persicus* engorged males from homozygous P and heterozygous F_1 generation

Homogamic and reciprocal heterogamic crosses		Crosses with identical females		Crosses with identical males		χ^2
		Hybrid combination (n = 100)	Aggregation (n = 200)	Hybrid combination (n = 100)	Aggregation (n = 200)	
$Aa \times Aa$	60	20.37	148	$Aa \times Aa$ 7.16	2.44 109	
$Cc \times Cc$	88			$Aa \times Cc$ 74	32.14	
$Aa \times Cc$	49	13.20	128	$Cc \times Aa$ 88	6.37 162	
$Cc \times Aa$	74			$Cc \times Cc$		
				$Aa \times Cc$ 49	4.43	134
				$Cc \times Cc$ 88	35.25	137

Table 2. Assembly pheromone response of *A. persicus* engorged males from P and F_2 brother-sister crosses

Comparison according to genotype similarity		Comparison of P and F_2 generations		χ^2
		Hybrid combination (n = 100)	Aggregation (n = 200)	
$Aa \times Aa$	56	0.18	116	
$Ac \times Ac$	69			
$Ca \times Ca$	61	1.41	130	2.37
$Cc \times Cc$	69			
		$Aa \times Aa$ 56	56	3.61
		$Cc \times Cc$ 69	69	125
		$Ac \times Ac$ 61	61	0.08
		$Ca \times Ca$ 69	69	120

Table 3. Assembly pheromone response of *A. persicus* engorged males from reciprocal backcrosses and backcrosses with identical females and males in F_2 hybrid generation

Reciprocal backcrosses		Backcrosses with identical females		Backcrosses with identical males	
		χ^2	Aggregation (n = 200)	χ^2	Aggregation (n = 200)
<i>Aa</i> × <i>Ac</i>	50	99	<i>Aa</i> × <i>Ac</i> 0.02	115.5	<i>Ac</i> × <i>Aa</i> 0.49
<i>Ac</i> × <i>Aa</i>	49		<i>Aa</i> × <i>Ca</i> 65.5	0.21	<i>Ca</i> × <i>Aa</i> 66
<i>Aa</i> × <i>Ca</i>	65.5	131.5	<i>Ac</i> × <i>Aa</i> 10.81	111	<i>Aa</i> × <i>Ac</i> 50
<i>Ca</i> × <i>Aa</i>	66		<i>Ac</i> × <i>Cc</i> 0.73	2.03	<i>Cc</i> × <i>Ac</i> 77.5
<i>Ac</i> × <i>Cc</i>	62	139.5	<i>Ca</i> × <i>Aa</i> 0.73	125	<i>Aa</i> × <i>Ca</i> 65.5
<i>Cc</i> × <i>Ac</i>	77.5		<i>Ca</i> × <i>Cc</i> 2.67	3.37	<i>Cc</i> × <i>Ca</i> 65
<i>Ca</i> × <i>Cc</i>	59	124	<i>Cc</i> × <i>Ac</i> 0.76	142	<i>Ac</i> × <i>Cc</i> 62
<i>Cc</i> × <i>Ca</i>	65		<i>Cc</i> × <i>Ca</i> 0.76	0.19	<i>Ca</i> × <i>Cc</i> 59

were found in the progeny of *Ca* and *Cc* males. This indicates the positive effect of males of F_1 generation of the *Cc* and *Ca* genotypes on the increase in the pheromonal responsiveness of the progeny of F_2 generation. The differences in the total aggregation score of the progeny of males of different genotypes were not significant and not even there was a tendency to the increase in the aggregation score with the increase in similarity of the genotype of males to the genotype of homozygous *Cc* population as in the case of females.

DISCUSSION

Our previous experiments showed that the responsiveness of engorged males of the Azerbaijan population of *A. persicus* to the assembly pheromone is significantly lower than the score of the Czechoslovak population and that this lower responsiveness is not due to a different quality or quantity of the released pheromone, but to different perceiving and treating of the pheromone signal and reacting to pheromone stimuli (Dusbábek 1985c). Consequently, the different responsiveness to assembly pheromone stimuli in both populations may be one of the series of adaptations to the local living conditions of each population in different latitudes. The random genetic drift, change in gene frequency resulting from the dispersive process due to the isolation of wild populations may be involved as well.

The experimental hybridization of Azerbaijan and Czechoslovak populations of *A. persicus* also demonstrated the non-identity of the aggregation score in males from reciprocal crosses in F_1 generation. The engorged males of F_1 hybrid generation responded in a similar manner as males from a homozygous population from which the mother of heterozygous hybrids originated. In that way, *Ca* cross-bred males responded similarly as *Cc* males and *Ac* cross-bred males similarly as *Aa* males. A matrocliny feature in F_1 hybrid generation was therefore confirmed (Table 1). In F_2 hybrids of brother-sister crosses (Table 2), the differences in the reactions to the assembly pheromone were no more statistically significant; a probably significant difference ($P < 0.05$) occurred only between the homogamic crosses *Aa* × *Aa* and *Cc* × *Cc*. However, even here was the tendency to the increase in the aggregation score with the increase in similarity of the genotype of hybrids to the genotype of *Cc* homozygous population. The reciprocal backcrosses of F_1 hybrid generation with the parental form, however, were identical and yielded a similar aggregation score in all combinations, with the exception of the backcross of the hybrid *Ac* form with the parental *Cc* form, which was markedly non-identical (Table 3). The higher aggregation score of *Cc* × *Ac* hybrids, compared to *Ac* × *Cc* score, shows the effect of matrocliny even in the backcrossed F_2 generation. This is indicated also by the tendency to the increase in the aggregation score with the increase in the similarity of the genotype of the progeny of hybrid females to the genotype of homozygous *Cc* population in backcrosses with identical females. Although this tendency is not supported by statistical significance, the difference in the summary aggregation score of the progeny of females from backcrosses of *Cc* populations with hybrid males in comparison with backcrosses with *Ca* females lies at the limit of significance ($\chi^2 = 3.37$, $P < 0.10$) and seems therefore to be biologically significant. After all, the difference between the summary aggregation score of the progeny of these females and the aggregation score of the progeny of *Aa* or *Ac* females is statistically significant ($\chi^2 = 7.66$, $P < 0.01$ or $\chi^2 = 10.34$, $P < 0.005$). The tendency to the increase in the aggregation score with the increase in similarity of the genotype of hybrid males to the genotype of homozygous *Cc* population in backcrosses with identical males is not so distinct as in the case of crossing with identical females, but it cannot be completely

excluded for the time being. The fact that statistically significant differences in the aggregation score in this type of backcrosses were found only in the progeny of Aa or Ac males in combination with Ca or Cc females and not in the progeny of Ca or Cc males suggests that the effect of matrocliny is more pronounced or occurs solely in the combinations of F_2 hybrids, where the genotypes of parent males resemble only minimally to the genotype of homozygous Cc population. In an opposite case no matrocliny occurs in the inheritance of the high responsiveness to assembly pheromone, which indicates the effect of males of Ca and Cc genotypes on the increase in the aggregation score. Nevertheless, our results do not provide a sufficient evidence of this statement for the time being.

It may be stated that the matrocliny in the inheritance of the responsiveness to assembly pheromone, which is very strong in F_1 generation, occurs also in the hybrids of F_2 generation, but it is much weaker in them. In some cases, also the genotype of male may have an influence on the matrocliny making it less pronounced and gradually disappearing. In this gradual disappearing of the matrocliny the results of our experiments resemble the manifestations of persistent modification (Dauermodifikation) described by Jollos (1921, 1939). It may be supposed that the responsiveness to assembly pheromone of *Argas (P.) persicus* is directed by a polygenic system of plasmon and chromosomal genes. The experimental hybridization can probably affect the replication rates of this system which results in greater involvement of genetic units contained in the cytoplasm resulting in matrilineal inheritance of the ability to react to pheromone stimuli in F_1 generation. In further generations, this system probably returns to the original replication rates, which is manifested by a gradual disappearance of the matrocliny. However, this hypothesis based on the Michaelis's (1948, 1954) explanation of the mechanism of reversible and irreversible changes in the genotype (modifications, persistent modifications, and mutations) caused by the effect of the outer environment should be supported by another evidence (see also Harwood 1985).

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НАСЛЕДСТВЕННОСТЬ РЕАКТИВНОСТИ НА ФЕРОМОН СКОПЛЕНИЯ У КЛЕЩЕЙ *ARGAS (PERSICARGAS) PERSICUS* (OKEN)

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Резюме. При помощи экспериментальной гибридизации двух популяций клещей *A. persicus* из Чехословакии (Cc) и Азербайджана (Aa), обладающих различной реактивностью на феромон скопления, была показана матротинность в наследственности сильной реактивности у генерации F_1 и ее постепенное исчезновение у генерации F_2 . Автор полагает, что реактивность на феромон скопления управляема полигенной системой, репликационные отношения которой могут быть обратимо нарушены экспериментальной гибридизацией, вследствие чего возникает матротинность у генерации F_1 . Постепенная рестабилизация оригинальных репликационных отношений у следующих генераций гибридов оказывает влияние на постепенное исчезновение матротинности.

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VII International Congress of Acarology

International Congress of Acarology, already the seventh in order, held on August 3—9, 1986 at the exquisite environment of the international West End Hotel in Bangalore, Karnataka, India. It has been sponsored by Acarological Society of India, Bangalore, Indian Council of Agricultural Research, New Delhi and University of Agricultural Science, Bangalore. Prof. G. P. ChannaBasavanna, Professor at University of Agricultural Science, Bangalore and the leading personality in Indian acarology, acted as the President of the Congress.

The Congress sessions were divided into 12 sections and three symposia, including evening posters presentations. In Section I — Ecology and Behaviour of Ticks under the chairmanship of A. Liebisch nine papers were read, two of which were devoted to the bionomics and life cycles of ticks of the genera *Hyalomma* and

Otobius, three papers were faunistic communications and two papers dealt with the transmission of *Theileria annulata* and Kyasanur Forest Disease. The last two papers were devoted to the comparative studies of local *Argas persicus* populations and characterization of cells from tissue cultures of *Dermacentor variabilis*. In Section II — Soil Mites ten papers were presented, directed mainly to the problems of decomposition process in soil, microbial and fungal association of oribatid mites and to the problems of taxonomy, ecology and bionomics of oribatid and mesostigmatic soil mites. The section was leaded by J. A. Wallwork. Section III — Systematics and Taxonomy of Acari, leaded by G. W. Krantz, included besides purely taxonomic studies also papers on fossil Devonian mites in the U.S.A., evolution of the family Tetranychidae and Tenuipalpidae as