

THE SOLUTION OF A LONG OUTSTANDING PROBLEM IN THE GENETICS OF DIMORPHISM IN *COLIAS*

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The interest in the dichroism of white and orange females of the butterfly genus *Colias* has been revived by the recently recognized importance of polymorphism as involved in the problems of population genetics and evolution (Ford, 1945). The problem of the genetics of this dichroism is as old as the rediscovery of the laws of heredity itself. Already in 1901 FROHAWK reported the results of breeding four wild white females of *Colias croceus* Fourc. (= *edusa*). He had obtained 110 white and 125 orange individuals, *i.e.* a ratio of 1:1. When later, in 1905, 52 white and 13 orange individuals, *i.e.* a ratio of 3:1, were obtained from one wild white female by MAIN and HARRISON, it was fairly established that a monohybrid cross of a dominant allele for white and a recessive one for orange was involved. It is likely that the report of this brood remained unnoticed since it was subscribed by "Anonymous". Anyway, it was not until 1911 that it was proved by GEROULD, who based his conclusions on numerous results of broods and crosses of the North American species *Colias philodice*, that the gene for white is wholly dominant over the gene for orange. But since white males appear neither in nature nor in experimental crosses (neither with the AA nor Aa genotype), GEROULD maintained the gene for white to be recessive in males. However, in 1923 he concluded correctly that a pair of autosomal genes were involved, their manifestation being sex-controlled. GEROULD as well as HOVANITZ and REMINGTON used for this phenomenon the term "sex-limited inheritance". The same situation is known to apply in the dimorphism of *Argynnis paphia* var. "valesina", where the allele for the dark colour is expressed only in females, as proved by GOLDSCHMIDT (1922). Evidently, this might hold for all cases of female dimorphism in butterflies.

Besides the sex-controlled or sex-limited inheritance some irregularities in the supposed $Aa \times Aa$ crosses were found by GEROULD: instead of the expected 3:1 ratio he obtained in some broods good 2:1 ratios, whereas the 3:1 ratio was found to appear only rarely. Hence he deduced that the AA combination was lethal. Twelve years later, however, he changed this hypothesis by supposing one separate lethal gene linked with the gene A or a. Only in this way could he explain the shortage of white

females in the 3:1 ratios as well as the complete lack of homozygous orange females in one cross where a ratio 3:1 was expected.

The question of the dimorphism in the genus *Colias* was thus found unsolved twenty years ago. HOVANITZ was the first to be struck by this. The ecological significance of the dimorphism in question was amply studied by him. He observed, too, in the crosses with a very similar species *Colias eurytheme* Boisd.* that many 2:1 proportions appeared instead of 3:1. His interpretation of the anomaly is similar to that first employed by GEROULD, with the additional attempt to alleviate the lethality of the homozygous AA combination by sublethality and a certain modifying influence of the genic environment. Later studies of the geographic distribution of white and orange females, however, turned his attention to the possibility of the more important part being played by the environment rather than by genic modifiers, white colour was more frequent northwards and orange southwards, furthermore, the white form was more active at lower temperature and orange at higher ones. In the same sense REMINGTON, who carried out a critical review of all the broods and crosses in the genus *Colias* so far (1954), concluded that there were no convincing arguments for the hypothesis of lethality, the different viability of the genotypes in different environmental conditions being a more plausible alternative. The lethality, or disadvantage of the double dose, however was considered later by HUXLEY (1955, 1956) as a possible explanation of the maintaining of polymorphism in populations. But this is perhaps an unnecessary duplication in explaining phenomena.

The first of the authors of the present paper could not obtain convincing evidence of the existence of lethality in broods of *Colias croceus* reared by him during 1941-1951 period, since the frequency of ratios 1:0, 3:1 and 1:1 in 8 broods coincided with the percentage of white and orange females in the natural population of the surroundings of Zagreb. The proportion was in one backcross nearer to 2:1 ($X^2 = 0.666$) than 1:1 ($X^2 = 0.942$) but this could be fairly easily ascribed to the low number of individuals (16:11). In another case of a greater probability of 2:1 than 1:1 the number of individuals was still smaller (15:9) but the genotype was unknown (Lorković & Herman, 1958).

In order to solve the question definitely it was decided to carry out the necessary number of relevant types of crosses with *Colias croceus*.

* In fact, owing to the very incomplete genetical reproductive isolation between *C. philodice* and *C. eurytheme* as established by HOVANITZ (1943), *C. eurytheme* cannot be considered as a true species but only as a semispecies.

The first experiments in 1957 were unsuccessful because of a sudden chill which destroyed all the food plants available. The experiments were started anew in August 1958 and were finished in April 1959 after 6 subsequent generations had been bred.

MATERIALS AND METHODS

Three white and three orange females of *Colias croceus* Fourc., already mated with unknown males of the same species, were captured in Istria at the end of July 1958 and brought to the laboratory.

On July 28th, 1958, two white and three orange females already mated in nature were captured on šalata in Zagreb. They were prepared for laboratory breeding.

All captured females were very young, not more than 3 to 5 days old. All were laying eggs onto young alfalfa plants (*Medicago sativa* L.) in cages sized $25 \times 25 \times 40$ cm. During oviposition, the females were fed on beet sugar in water. The caterpillars were constantly fed on young alfalfa. Prepupæ hung themselves onto the walls of the cages resting there until the imago got out. The butterflies after they had left the pupæ were separated into special cages owing to sex and phenotypes.

The males were fit for copulation the second day after eclosion and the females immediately after having got dried. There were obtained a lot of copulæ. The majority consisted of natural copulæ in the large cage ($40 \times 50 \times 60$) or in the large window. Some copulæ were artificial according to LORKOVIĆ's method (1948) and some semi-artificial where the female was held onto by the wings with a pair of forceps and posed near the male. When there was no sunlight a 200W bulb was used.

Of wild females from Istria and Zagreb six successive laboratory generations were bred from the end of July 1958 to the beginning of May 1959.

The results were elaborated statistically using the chi-squared test (Fisher, 1948).

RESULTS

The first laboratory generations of wild "alba" females from Istria yielded ratios of white and orange daughters that conform to the supposition 1:1 with a high probability. (See table A, broods No. 1, 2, 3.) Hence all three white mothers were of the *Aa* genotype and the unknown males they had mated with in nature had probably been of the *aa* genotype.

Table A. The obtained ratios and their statistical elaboration.

Brood	Month & year	Proportion white : yellow		Theoretical proportion	χ^2	P
1	8	17	22	1 : 1	0,64102	$0,30 < P < 0,50$
2	8	35	37	1 : 1	0,05554	$0,80 < P < 0,90$
3	8	51	58	1 : 1	0,44954	$0,50 < P < 0,70$
4	8	0	85	0 : 1		
5	8	0	100	0 : 1		
6	8	0	59	0 : 1		
7	8	21	27	1 : 1	0,75000	$0,30 < P < 0,50$
8	8	55	55	1 : 1	0,00000	100
9	8	0	149	0 : 1		
10	8	23	28	1 : 1	0,49019	$0,30 < P < 0,50$
11	8	0	101	0 : 1		
2A	9	55	14	3 : 1	0,81622	$0,30 < P < 0,50$
2B	9	0	39	0 : 1		
2C	9	47	40	1 : 1	0,56320	$0,30 < P < 0,50$
2D	9	5	2	3 : 1	0,04760	$0,80 < P < 0,90$
3A	9	27	23	1 : 1	0,32000	$0,50 < P < 0,70$
3B	9	20	10	1 : 1	3,33333	$0,05 < P < 0,10$
3C	9	29	34	1 : 1	0,39682	$0,50 < P < 0,70$
3D	9	28	34	1 : 1	0,58064	$0,30 < P < 0,50$
3E	9	35	36	1 : 1	0,01408	$0,90 < P < 0,95$
3F	9	21	19	1 : 1	0,10000	$0,70 < P < 0,80$
7A	9	29	2	3 : 1	5,08816	$0,02 < P < 0,05$
7B	9	23	4	3 : 1	0,54320	$0,30 < P < 0,50$
8A	9	54	19	3 : 1	0,04109	$0,80 < P < 0,90$
8B	9	34	11	3 : 1	0,07406	$0,70 < P < 0,80$
8C	9	0	45	0 : 1		
8D	9	23	15	1 : 1	1,68420	$0,10 < P < 0,20$
8E	9	13	4	3 : 1	0,06371	$0,80 < P < 0,90$
8F	9	29	19	1 : 1	2,08333	$0,10 < P < 0,20$
8G	9	28	27	1 : 1	0,01818	$0,80 < P < 0,90$
8H	9	0	43	0 : 1		
8K	9	0	47	0 : 1		
8L	9	12	15	1 : 1	0,33332	$0,50 < P < 0,70$
8M	9	0	15	0 : 1		
41	11	20	6	3 : 1	0,05128	$0,80 < P < 0,90$
42	11	27	0	1 : 0		
43	11	12	0	1 : 0		
44	11	30	23	1 : 1	0,92452	$0,30 < P < 0,50$
45	11	5	0	1 : 0		
46	11	3	0	1 : 0		
47	11	2	0	1 : 0		
48	11	15	11	1 : 1	0,61538	$0,30 < P < 0,50$
49	11	30	0	1 : 0		
51	11	38	11	3 : 1	0,17006	$0,50 < P < 0,70$
52	11.1958.	5	1	3 : 1	0,22221	$0,50 < P < 0,70$
A	1.1959.	12	0	1 : 0		
B	1.1959.	15	0	1 : 0		
C	1.1959.	15	0	1 : 0		
A1	3.1959.	1	0	1 : 0		
A1A	4.1959.	19	0	1 : 0		

The three orange mothers from Istria produced only orange daughters in their progeny (table A, broods 4, 5, 6). Thus they were of the *aa* type, and the males they had mated with in nature had been of the same type as well.

The two white females captured on Šalata in Zagreb yielded in their progeny white and orange daughters in a fair relationship 1:1 (table A, broods 7 and 10). They were thus of the *Aa* genotype and the males they had mated with of the *aa* genotype.

One orange female on Šalata (table A, brood 8) yielded 55 white and 55 orange daughters. This is the exact ratio of 1:1. The mother was of the *aa* genotype whereas the wild father ought to have been of the *Aa* genotype.

The remaining two orange females from Šalata yielded in their progeny only orange daughters (table A, broods 9 and 11).

Table A demonstrates clearly the ratios obtained and their statistical elaboration. Table B shows the genotypes according to their groups.

The second laboratory generation has been bred from fertilized females of broods 2, 3, 7 and 8.

From brood 2 eight females mated with brothers of the same brood. Of these there is a further progeny of two white females (broods 2 D and 2 A) and the offspring of two orange females (broods 2 C and 2 B). See scheme 1.

Five white and two orange (daughters) females have been obtained from brood 2 D. Due to the small number, the result cannot be considered as a sure evidence that their parents belong to the genotypes $Aa \times Aa$.

Brood 2 A — mother "alba" — yielded an excellent result of 55 white: 14 orange females (daughters). X^2 is only 0.81622. The parents were $Aa \times Aa$ (table BV and table A).

Brood 2 C — mother orange — yielded a good ratio 1:1. Thus the mother was *aa* and the father *Aa*.

Brood 2 B is of the type $aa \times aa$, since only orange daughters have been obtained.

Of the total of four copulæ two were $Aa \times Aa$, one of them was $Aa \times aa$ and the other $aa \times aa$. This fact has been confirmed on the supposition that the obtained genotypes *Aa* and *aa* in brood 2 are in the ratio of 1:1, since in five butterflies there have been found the genotype *Aa* and in three the genotype *aa*, of the total of 8 tested ones.

Brood 3 (see scheme 2) produced a total of seven matings of sisters and brothers. The progeny of three "alba" and three yellow mothers was used (Nos. 3 A, 3 B, 3 C, 3 D, 3 E and 3 F) for breeding.

Table B. The genotypes according to their groups.

I. ♂♂ <i>aa</i> × ♀♀ <i>aa</i>			
Brood	♂♂	white ♀♀	yellow ♀♀
4	84	0	85
5	124	0	100
6	67	0	59
9	168	0	149
11	99	0	101
2B	38	0	39
8C	44	0	45
8H	36	0	43
8K	53	0	47
8M	10	0	15

II. ♂♂ <i>aa</i> × ♀♀ <i>Aa</i>			
1	48	17	22
2	79	35	37
3	94	51	58
7	48	21	27
10	49	23	28
3A	46	27	23
3C	83	29	34
3D	55	28	34
48	22	15	11
8F	53	29	19
8L	28	12	15

III. ♂♂ <i>aa</i> × ♀♀ <i>AA</i>			
6°-1957	45	54	0

* Brood of previous experiment.

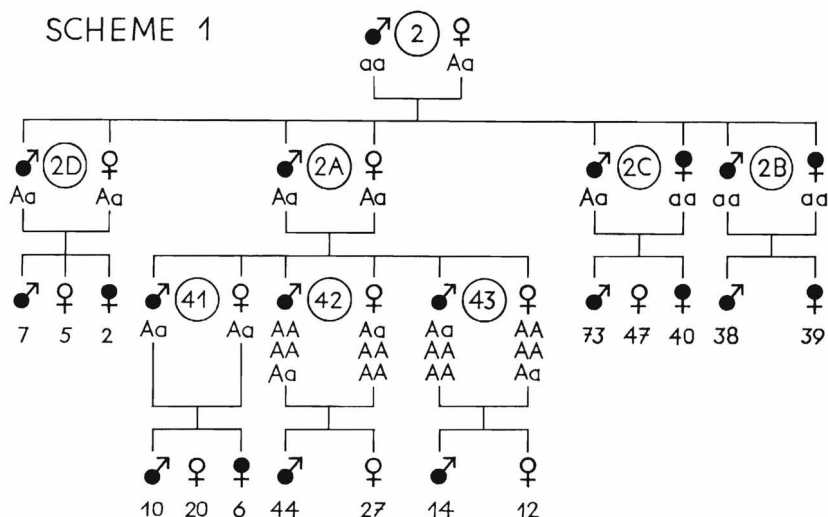
IV. ♂♂ <i>Aa</i> × ♀♀ <i>aa</i>			
Brood	♂♂	white ♀♀	yellow ♀♀
8	125	55	55
2C	73	47	40
3B	21	20	10
3E	42	35	36
3F	24	21	19
8D	32	23	15
8G	60	28	27
44	50	30	23

V. ♂♂ <i>Aa</i> × ♀♀ <i>Aa</i>			
8A	63	54	19
8B	55	34	11
8E	17	13	4
2D	7	5	2
2A	76	55	14
41	10	20	6
7B	30	23	4
7A	38	29	2
51	49	38	11
52	10	5	1

VI. ♂♂ <i>AA</i> × ♀♀ <i>aa</i>			
C	19	15	0

VII. White ♀♀ and one parent homozygous <i>AA</i>			
42	44	27	0
43	14	12	0
45	7	5	0
46	3	3	0
47	2	2	0
49	21	30	0
A	12	12	0
B	26	15	0
A1	3	1	0
A1A	20	19	0

SCHEME 1



In broods 3 A, 3 C, 3 D — mother “alba” — there are good 1:1 ratios (table B II), thus the parents were $aa \times Aa$.

In broods 3 B, 3 E, 3 F — mother orange (table B IV) — there have been obtained good 1:1 ratios, hence their parents were $Aa \times aa$.

Of the total of 12 butterflies tested for their genotype, six are of the Aa genotype and the remaining six of the aa genotype. That is the accurate ratio 1:1 which confirms the supposition that the butterflies of brood 3 were of the genotypes Aa and aa in the relationship 1:1. This is of course comprehensible, since they are the progeny of the crossing of the Aa mother and the orange aa male.

From brood No. 7 (scheme 3) there are five pairings. For further breeding there have been used the progeny of two “alba” females (No. 7 A and 7 B). Brood 7 B yielded a good ratio 3:1 and breed 7 A ratio 3:1 with an insignificant probability rate. The parents were thus $Aa \times Aa$.

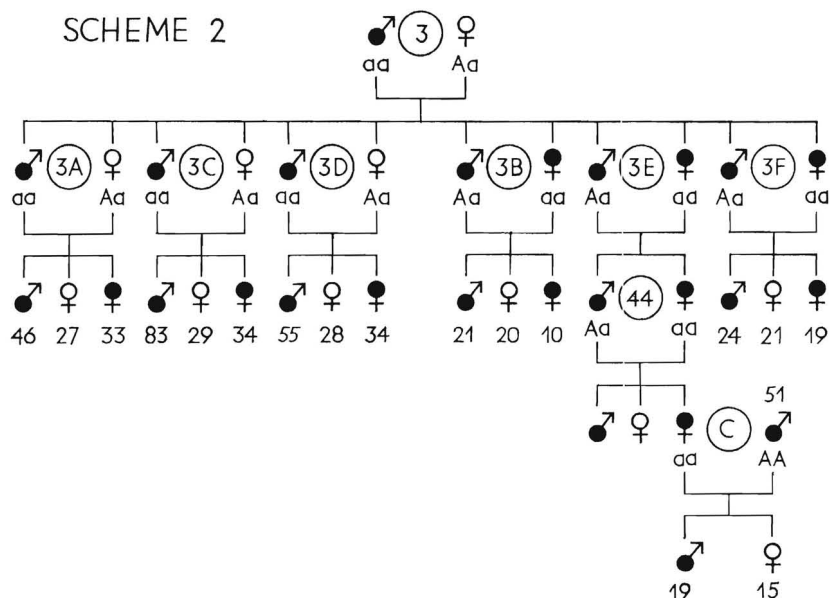
Brood No. 8 yielded altogether 17 copulæ. We used for breeding the progeny of 5 “alba” females (scheme 4) No. 8 A, 8 B, 8 F, 8 L and 8 E and six orange females No. 8 D, 8 G, 8 C, 8 H, 8 K and 8 M.

Broods 8 F and 8 L — mother white — produced good 1:1 ratios (table B II), hence the parents were $aa \times Aa$.

Broods 8 A, 8 B, 8 E — mothers white — yielded good 3:1 ratios (B V), the parents were $Aa \times Aa$.

Broods 8 D and 8 G — mother orange — yielded good 1:1 ratios (B IV), the parents were $Aa \times aa$ (B I).

Broods 8 C, 8 H, 8 K and 8 M — mother orange — yielded good 0:1 ratios (B I), the parents were $aa \times aa$.



Of the total of 22 butterflies tested for their genotype in brood 8, there were 10 genotypes Aa and 12 genotypes aa , which is again a proof for the supposition that brood No. 8 was composed of genotype Aa and aa in relationship 1:1.

The third laboratory generation has been bred from the progeny of females from brood No. 2 A, 3 E, 7 B and 8 E. All females mated with males of the proper brood.

Broods 41, 42, 43 were derived (scheme 1) from "alba" females of brood No. 2 A mated with males of brood 2 A.

Brood 41 yielded a good ratio 3:1 (B V), the parents were $Aa \times Aa$.

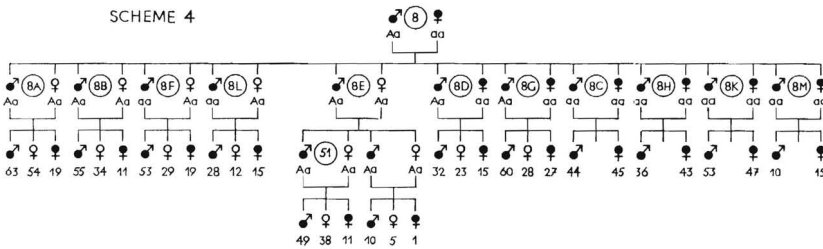
Broods 42 and 43 produced the ratio 1:0. There are 3 probabilities for the genotypes of the parents $AA \times Aa$, $AA \times AA$, $Aa \times AA$.

If we count with the fact that all butterflies of brood 2 A were of the genotype $AA : 2Aa : aa$ (since they are the offspring of the crossing $Aa \times Aa$) then there should be given preference to the supposition that one brood was of type $AA \times Aa$ and the other type $AA \times AA$. Such ones belong to table B VII of white females with one homozygote parent.

Brood 44 (parents $3E \times 3E$) — mothers orange — (scheme 2) produced a good ratio 1:1. The parents were $Aa \times aa$ (B IV).

Broods 45, 46, 47, 48 and 49 derive from white females of breed 7 B mated with males from breed 7 B.

Brood 48 yielded a good relationship 1:1. The parents were $aa \times Aa$. Broods 45, 46 and 47 yielded the ratio 1:0 with a small probability rate,



brood 49 yielded the ratio of 1:0 with a considerable probability since there emerged the total of 21 ♂♂ : 30 “alba” ♀♀ and not a single orange ♀. There are again 3 probabilities — $AA \times Aa$, $AA \times AA$, $Aa \times AA$.

If we consider ratio $AA : Aa : aa$ as the ratio 1 : 2 : 1, then we may suppose that one copula was of type $AA \times AA$, two of type $AA \times Aa$ (resp. $Aa \times AA$), one of type $Aa \times Aa$ (which could be in brood 46 or 47, since it may be due to the small number) 3 males : 3 females, resp. 2 males : 2 females — orange females failed to emerge, one being certainly of type $aa \times Aa$.

Broods 51 and 52 have been derived from “alba” females in brood 8 E mated with males from the same brood. Both broods yielded good 3 : 1 ratios, i.e. those crossings are $Aa \times AA$.

The fourth laboratory generation has been bred from:

- a) Two “alba” females from brood (ancestors No. 7 Šalata) mated with males from brood 42 (ancestors No. 2 from Istria, scheme 3). These are broods A and B.
- b) From an orange female from brood 44 (ancestors from Istria) mated with a male from brood 51 (ancestors from Zagreb). This is brood C (scheme 2).

Broods A and B yielded good 1:0 ratios (table B VII).

Brood C also produced a good 1:0 ratio (table B VI). That is the proof that there are homozygote orange males of genotype AA .

The fifth laboratory generation bred from a white female from brood A mated with a male from brood A. That is brood A 1 (scheme 3). It yielded only three males and one “alba” female. This “alba” female mated with a male — her brother. Her progeny is:

The sixth laboratory generation in which there were 20 males and 19 white females (brood A 1 A).

Since in the genealogy of brood A 1 A there was no segregation in 5 successive generations, we are likely concerned with the mating $Aa \times AA$. Both parents are homozygote dominant as to the observed characteristic. This, unfortunately, we have not been able to prove by means of further breeding.

DISCUSSION

With our crossings of white and orange butterflies of *Colias croceus* we have attempted to obtain all those combinations of crossings indispensable for the explanation of the question concerning the viability of homozygote white AA genotypes. In fact, all ratios have been yielded which are possible in monohybrid autosomal crossing, *i.e.* in 11 broods the ratio of white : yellow females = 1:0 has been obtained, in 10 broods 3:1, in 19 broods 1:1, and in 10 broods 0:1. In not one single crossing have unexpected ratios been obtained, this being particularly important for the ratios 3:1 and 1:0. All ten 3:1 ratios could have been obtained only if such a ratio was expected because the parents were all from families with an equal (1:1) distribution of Aa and aa genotypes. In such a family (8) we succeeded in breeding a progeny of 11 inbred matings of which three yielded a ratio of progeny 3:1, four the ratio 1:1 and four 0:1, thus an ideal relationship of the three possible combinations from crosses of $Aa \times Aa$ and $aa \times aa$. Moreover, in the broods with the ratio of 3:1, there were also homozygote AA individuals. This has been proved by 8 inbred matings (42, 47, 49, 49 A, 49 B), each with a ratio in their progeny of 1:0; hence one parent had to be homozygote. Such could have been the "alba" females being chosen for mothers, but the males as well. This latter has been proved by cross C (scheme 3), where a yellow (thus homozygote aa) mother and a father from a family with 3:1 ratio produced 19 "alba" females and not a single yellow one; thus the male must have been a homozygote AA.

Against the hypothesis of lethality or sublethality of the homozygote combination AA, postulated by GEROULD and later by HOVANITZ, argues the fact that the 3:1 ratios in laboratory broods are not rarer than is to be expected on the ground solely of genotypes in a series of generations. The fact that 3:1 ratios are yielded only exceptionally in progeny of wild "alba" females, while the proportion 1:1 is more frequent, is quite comprehensible due to the much lower percentage of "alba" females in nature. Therefore, instead of genetic F_2 generations, the backcross having the ratio of 1:1 occurs the most frequently, as we have already stressed in our previous study (1958).

In addition, it is very characteristic, that in our crossings among 17 with 1:1 proportions there are 14 very good ones with a mean value of $P = 70$, whereas only two crossings approach slightly the ratio 2:1 (though even these have a lesser probability of this ratio than of 1:1). One single crossing produced the ratio 2:1, being in fact precisely 20:10. It is just this ratio that had led to the idea of lethality of the dominant homozygote. But in this case not only is the genealogy not in support

of this hypothesis, it even argues against it. The 2:1 ratio was obtained in cross 3 B, where the ratio of 3:1 is ruled out, since the mother was yellow (thus pure *aa*) whereas the father owing to his origin had to be *Aa*; hence the expected ratio could be only 1:1. Thus, in interpreting this 2:1 brood, we are not concerned with the absence of the homozygote *AA*, but with a double surplus of *Aa* genotypes.

This conforms to the fact that in 2 cases of expected 3:1 ratios the white phenotypes exceed by far the value 3 (3.74 in cross 7 A and 3.40 in 7 B). Therefore we are not at all allowed even to think of a lower viability of homozygote *AA* genotypes and even less of their lethality.

CONCLUSION

The current opinion that the dimorphism of "alba" and orange females of *Colias croceus* Fourc. is dependent on a pair of autosomal alleles with the dominant gene *A* for "alba" has been confirmed by our experiments. The phenotypic manifestation of this gene is strongly sex-controlled, for it is expressed only in the females even though males can also be *Aa* and *AA*. All this is known to apply in the North American species *Colias philodice* Latr. and *Colias (philodice) eurytheme* Boisd.* Our results can provide no support for the hypothesis of lethality of the dominant combination *AA* nor for the existence of a recessive lethal gene linked to the genes *A* or *a*. A certain excess of the white or orange form can most simply be explained by REMINGTON's hypothesis of the unequal vitality of the two genes in different environmental conditions, especially in different temperatures. Current investigations in our laboratory give support to this hypothesis and will contribute to the better understanding of the ecological side of *Colias* dimorphism with the hope that this example of morphism can be used more for population genetics.

SUMMARY

Extensive breeding and crossing with the species *Colias croceus* Fourc. have been performed in order to elucidate finally the genetics of dimorphism of white ("alba") and orange females of the genus *Colias*.

Experiments have confirmed the previous conception, that we are concerned with an autosomal pair of alleles, with the dominant gene producing white. This character is phenotypically sexually controlled, since it manifests itself only in the female.

On the other hand, no support whatsoever could be given to the hypothesis of lethality of the homozygous combination *AA*, nor of a recessive lethal gene closely linked to the genes *A* or *a*.

* The designation of a semispecies proposed by KIRIAKOFF and LORKOVIĆ (latest 1958).

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