CORRECTIONS AND ADDITIONS CONCERNING THE GENETICS OF *COLIAS ERATE POLIOGRAPHUS* (PIERIDÆ)

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KOMAI and AE (1953) published a paper on "Genetic studies of the Pierid Butterfly, *Colias hyale poliographus*." REMINGTON (1954) has suggested that certain items in the paper of KOMAI and AE be clarified. In the present paper, the junior author of the 1953 paper, with the approval of the senior author, will undertake the clarification of those items, together with the presentation of some additional data which were collected in 1952-1953 at the Catholic University of Nagoya, Honshu, the main island of Japan.

At the outset, the subspecies *poliographus* Motschulsky has been transferred from the species *C. hyale* Linné to the species *C. erate* Esper, and so will be referred to below as *C. erate poliographus*.

THE SEX-LIMITED "ALBA" GENE

Proof that the sex-limited "alba" gene, which controls female dimorphism in *Colias,* is autosomal, not sex-linked with female heterogamety, requires that both female forms appear among the daughters of a cross between an "alba" female and a male known to be homozygous for the recessive allele.

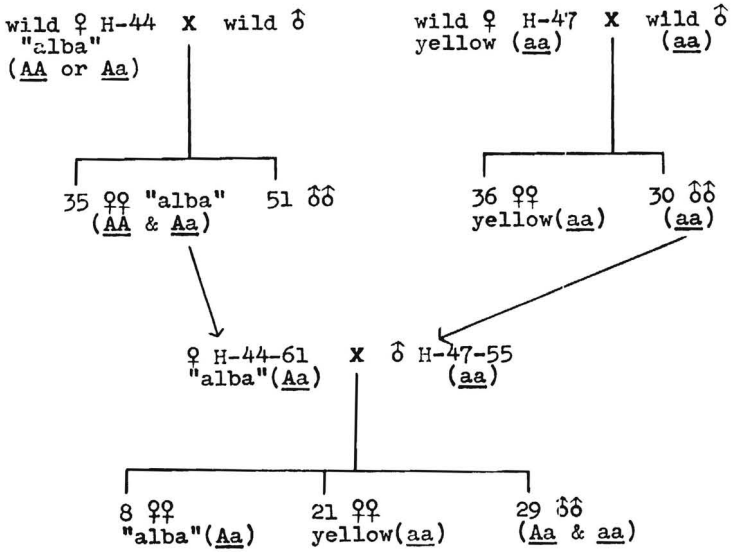

Fig. 1. Genealogy of an "alba" female brood.

This had been proved for *Colias eurytheme* Bdv. and *C. philodice* Latr. (Remington 1954). Dr. REMINGTON also pointed out that "Brood 44-61 of Komai and Ae (1953) for *Colias erate poliographus* Motsch. is probably another

example of this cross, but the published data are inadequate for certainty." The writer presents here more detailed data which actually prove it for *C. erate poliographus*. The mother of Brood H-44-61 (referred to as Brood 44-61 by REMINGTON) was from Brood H-44 from a wild "alba" female. Brood H-44 consisted of 35 "alba" females and 51 males. The father of Brood H-44-61 was from Brood H-47 from a wild yellow female. Brood H-47 consisted of 36 yellow females and 30 males. Therefore it is clear that the father of Brood H-44-61 had an *"aa"* genotype. *W-w* alternative symbols for the white ("alba") and yellow alleles in the 1953 paper are replaced here by *A-a* as suggested by REMINGTON (1954). Brood H-44-61 consisted of 8 "alba" females, 21 yellow females, and 29 males (Fig. 1).

Twenty-five "alba" females were sent from the University of Hokkaido, Sapporo, Hokkaido, the most northern island of Japan, to the Biological Laboratory of the Catholic University of Nagoya by Mr. SHOZO EHARA in fall 1952. Eleven of them laid eggs, and the larvæ from these eggs were raised at the laboratory. Table I shows the results. Broods 0-2, 0-4, 0-5, 0-6, 0-9, and 0-10 may be presumed to be all "alba" broods without much doubt. Brood 0-3, consisting of 39 "alba" females and 8 yellow females, may be the result of $Aa \times Aa$ mating and probably shows the low viability of *"aa"* individuals, just as in the Kyoto district of Honshu. From the matings of the butterflies of the above broods (one wild male from the Nagoya district was also used), it was proved that Broods 0-4, 0-5, 0-9, and 0-10 had carried the *"a"* gene also. Sex ratios in a few cases in Table I are far from expected 1 : 1; however, facilities did not give an opportunity to examine this phenomenon.

WHITE AND PALE MALES

Dr. REMINGTON pointed out that no further rearings, of the broods in which white males appeared, were mentioned by KOMAI and AE (1953). The relatives of No. 1 and No. 2 white males of the 1953 paper are as follows:

No. 1:— Brood K-2 from a wild faded female (yellowish, but much paler than ordinary yellow females) consisted of 44 "alba" females and 62 yellow males ($aa \times AA$). Two sib matings were obtained from this brood. Brood K-2-6 and Brood K-2-16 were obtained from these sib matings. Brood K-2-6 consisted of 1 white male, No. 1, and 1 yellow male and no females. Brood K-2-16 consisted of 16 "alba" females and 17 yellow males. No further mating was obtained because of the winter season. Therefore, the genotype of this No. 1 white male for "alba" gene could be *AA, Aa,* or *aa.* Consequently the sentence "All his sisters were white." at the fourth line from the bottom of page 68 in KOMAI and AE (1953) is wrong and must be corrected.

No. 2:— Brood B-2 from a wild "alba" female consisted of 55 "alba" females and 63 males, and Brood B-4 from a wild "alba" female consisted of 28 "alba" females and 19 males. From the mating between an "alba" female of Brood B-4 and a male of Brood B-2, Brood B-4-8a was obtained which consisted of 7 "alba" females and 1 white male, No. 2, and 1 yellow male. Therefore, the genotype of No. 2 white male for "alba" gene may possibly

TABLE I. Offspring of 13 Japanese wild "alba" ♀ ♀ of *Colias erate poliographus*

Brood Number[1]	Parents ♀ ♀	Parents ♂ ♂	Offspring "alba" ♀ ♀	Offspring yellow ♀ ♀	Offspring ♂ ♂[2]	Total
0-1	wild	wild	7	0	6	13
0-2	wild	wild	16	0	29	45
0-3	wild	wild	39	8	58	105
0-4	wild	wild	42	0	43	85
0-5	wild	wild	30	0	30	60
0-6	wild	wild	23	0	12	35
0-7	wild	wild	8	5	10	23
0-8	wild	wild	7	0	8	15
0-9	wild	wild	26	0	54(1)	80
0-10	wild	wild	47	0	53	100
0-11	wild	wild	7	0	25	32
0-3-14[3]	"alba"	0-3-10	7	0	4	11
0-3-15	"alba"	0-3-11	5	0	12	17
0-4-3	"alba"	0-4-1	17	0	33	50
0-4-8	"alba"	0-4-6	17	0	25	42
0-4-32	"alba"	0-4-29	2	1	5	8
0-4-37	"alba"	0-4-31	6	0	11	17
0-5-17	"alba"	wild	7	3	19	29
0-6-8	"alba"	0-6-2	4	0	23	27
0-6-10	"alba"	N-4-34-7	15	0	24(1)	39
0-6-26	"alba"	0-9-52	48	0	63(36)	111
0-7-6	yellow	0-9-46	27	21	58	106
0-10-9	"alba"	0-10-2	8	0	6(1)	14
0-10-10	"alba"	0-10-5	18	0	24	42
0-10-19	"alba"	0-10-15	5	2	1	8
0-10-57	"alba"	0-10-53	23	0	15	38
0-10-34	"alba"	0-9-12	20	0	26	46
0-10-49	"alba"	0-7-1	51	0	34	85
0-6-26-49	"alba"	0-6-26-29	23	0	17(7)	40
N-3	wild	wild	9	0	12	21
N-4	wild	wild	7	9	25	41
N-3-21	"alba"	N-3-20	11	0	10(3)	21
N-4-34	yellow	N-3-20	5	0	7	12

[1]The prefix 0 of the brood number is used for stocks from wild ♀ ♀ from Sapporo, Hokkaido; N for stocks from Mt. Myoko, Niigata Pref., Honshu. 0-4-3 means 3rd butterfly emerging in Brood 0-4; if this individual was a ♀ from which a brood was then raised, this whole brood received the same designation, i.e. 0-4-3. All wild females were "alba".

[2]( ) Number of males with pale yellow cell spots on the upper side of the hind wing.

[3]For this and the next seventeen 0- broods, and for broods N-3-21 and N-4-34, the designation of the female parent is the same as the brood number.

be *AA* or *Aa*. No. 2 failed to harden his veins, and no further mating was possible. His relatives produced a total of 26 "alba" females, but no yellow females, and 33 yellow males, but no white males.

Several pale males, of which the yellow ground color was reduced toward white, were obtained among the laboratory males. They emerged at the Catholic University of Nagoya in the winter of 1952-1953. The cages were placed at the window side of the laboratory which the sunshine reached well. The room temperature was usually between 5°C and 15°C in January and February, 1953. Six color grades were set up by an arbitrary standard. Grade 6 is the grade of a typical yellow male, and grade 1 is pure white. Four intermediate grades, which were equally divided according to paleness, were applied for pale males. Consequently grade 5 (slightly paler) in this standard is rather common among early or late season males in the wild as well as laboratory. The No. 1 white male above mentioned has grade 1, and No. 2 has grade 2. Table II shows these arbitrary color grades of male butterflies which emerged between October and March in Broods 0-5 and 0-11, both of which included pale males.

TABLE II. Arbitrary color grades of ♂♂ of two broods containing pale ♂♂

Brood Number	Month of Emergence	Color Grades* 6	5	4	3	2	1
0-5	October	1	3	—	—	—	—
	November	2	—	—	—	—	—
	December	1	—	—	—	—	—
	January	—	—	1	—	—	—
	February	1	4	—	3	—	—
	March	1	1	—	—	—	—
0-11	October	11	—	—	—	—	—
	November	1	2	—	—	—	—
	December	—	—	—	—	—	—
	January	—	2	—	1	—	—
	February	—	2	—	1	—	—

*Grade 6 indicates typical yellow male; grade 1 would be pure white.

All of the white and pale males above mentioned had no distinguishable differences in the melanin coloration (usual dark markings) from other yellow males. It is clear that the environment has some effects on this pale color, and at the same time it is possible to presume hereditary effects, because the majority of males of Broods 0-5 and 0-11, and many other broods, emerged under the same conditions as the pale males, yet these others kept their yellow color. The cell-spot on the upper side of the hind wing of these pale males was usually orange, although its color was somewhat lighter. No yellow female emerged in the midwinter.

CELL-SPOT ON THE HIND WING

The difference in color of the cell-spot on the upper side of the hind wing seems to be determined on a monogenic basis, orange dominant over pale-yellow (KOMAI and AE, 1953).

A further study was done in 1952-1953. Only one pale-yellow spotted male, 0-9-52, appeared among the 54 males of Brood 0-9 (Table I). This male was mated with an "alba" female, 0-6-26. The sib mating of Brood 0-9 was completely unsuccessful. The Brood 0-6-26, from the above mentioned mating, consisted of 27 orange spotted males, 36 pale-yellow spotted males, and 48 females. One male, 0-6-26-29, among the above 36 pale-yellow spotted males, was mated to one of his "alba" sisters, 0-6-26-49, and the resulting brood consisted of 10 orange spotted males, 7 pale-yellow spotted males, and 23 "alba" females. This brood was raised in an incubator which was controlled between 27°-29°C. In this case the cell spots of 23 "alba" females were also divided into 11 orange and 12 pale-yellow, although a few of them are close to the intermediate between orange and pale-yellow (Table I and Fig. 2).

One "alba" female, N-3, collected at Mt. Myōkō, Niigata prefecture, Honshu, by the writer, left a progeny of 9 "alba" females and 12 orange spotted males. A sib mating (N-3-21 × N-3-20) from this brood produced 11 "alba" females, 7 orange spotted males, and 3 pale-yellow spotted males. The father of this sib-mating was again mated with a yellow female, N-4-34, from another brood from Mt. Myōkō and produced 5 "alba" females and 7 orange spotted males. One of these orange spotted males, N-4-34-7, was mated with an "alba" female, 0-6-10 of Brood 0-6, and left a progeny of 15 "alba" females, 23 orange spotted males, and 1 pale-yellow spotted male (Table I and Fig. 2). Brood 0-10-9 derived from a sib mating of Brood 0-10 consisted of 8 "alba" females, 5 orange spotted males, and 1 pale-yellow spotted male (Table I).

Differences between orange and pale-yellow cell spots in males are very clear in summer broods and in Brood 0-6-26-49, which was raised in the incubator at 27°-29°C. However, it is not perfectly clear in fall broods, as in 0-6-26. Many of the pale-yellow cell spots in Brood 0-6-26 had slightly orange coloration, which may correspond with "pale semi-orange" of REMINGTON in *C. philodice* (1955). Seven of them may be listed as "semi-orange," and two with orange cell spots may also be close to "semi-orange." Some of the others with orange cell spots may correspond with "deep semi-orange." The males of Broods 0-9-52 and 0-6-26-29 may be classified as "pale semi-orange." However, Brood 0-6-26-49, whose father was 0-6-26-29, produced a clear-cut, 10 orange : 7 pale-yellow (yellow of REMINGTON, 1955). Therefore the writer presumes it is reasonable to divide the males of Brood 0-6-26 into two genetic classes, orange and pale-yellow, assuming that several individuals are somewhat intermediate in color due to environmental or minor hereditary variation.

Cell spots of "alba" females of Brood 0-6-26, raised in the laboratory in uncontrolled conditions, show a continuous variation. However, if they

are roughly divided into 4 groups, the results are 11 orange (although not so deep as males), 19 light orange, 12 lighter orange, and 2 pale egg-yolk color, (4 were lost out of 48 females). The mother of Brood 0-6-26-49 was from the orange group. This brood, raised in the incubator at 27°-29°C., included 23 "alba" females which fell into two distinct groups (referred to, above, as "orange" and "pale-yellow"): 11 light orange and 12 pale egg-yolk color.

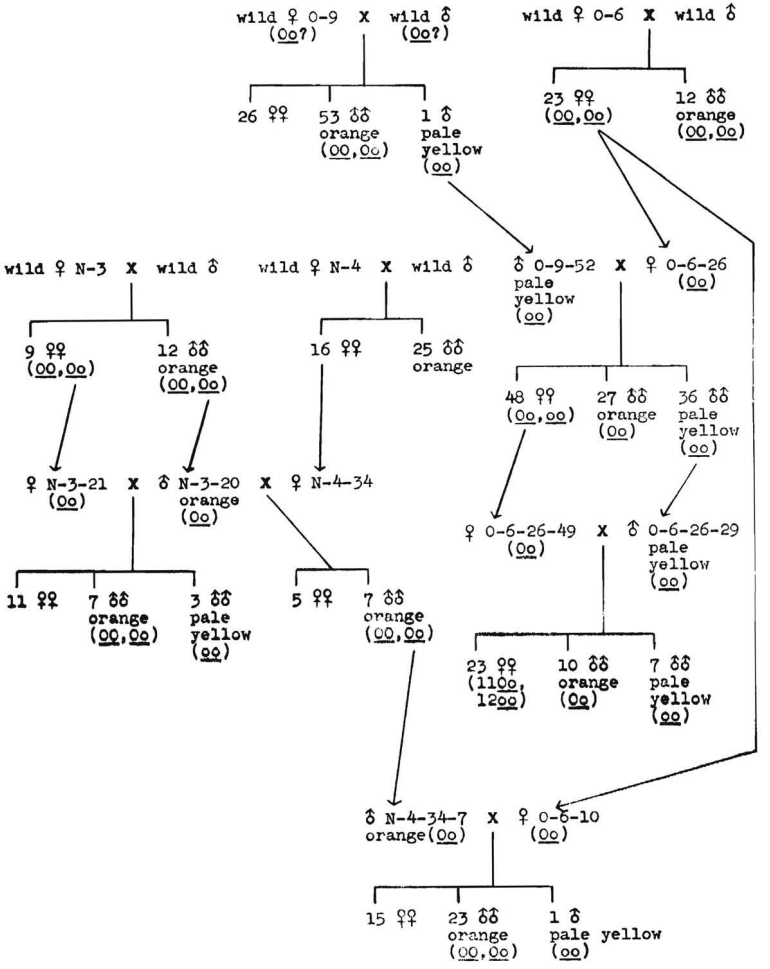

Fig. 2. Genealogy of one pale yellow cell-spotted line.

Correlation in hereditary factors in cell spots between male and female may be suggested by the above data. However, more studies are necessary to clarify this point.

It is difficult to interpret 53 orange : 1 pale-yellow and 23 orange : 1 pale-yellow ratios. A reduced penetrance of genes for pale-yellow cell spot in homozygous individuals can be considered, as well as a low viability of them. However, in general, it is most probable that a recessive gene which is fairly common in nature is controlling the heredity of pale-yellow cell spot. In Fig. 2, *O* - *o* alternative was used as *O* for orange and *o* for pale-yellow.

CORRECTIONS OF FIGURES IN TABLES

The following corrections are necessary for the tables of KOMAI and AE (1953).

Table 1, group 1: $\chi^2 = 0.46$ instead of "2.22"; $0.3 < P < 0.5$ instead of "$0.1 < P < 0.2$."

Table 3: %w in female at Tokiwa is 77.3 instead of "77.2" and at Arakawa is 73.5 instead of "72.2."

Table 4: %w in June-August in 1949 is 68.6 instead of "69.9."

SUMMARY

1. It was proved that the sex-limited "alba" gene, which controls female dimorphism in *Colias erate poliographus,* is autosomal, not sex-linked with female heterogamety.

2. Laboratory breeding of the progeny from 11 "alba" females of *C. erate poliographus* from Hokkaido, Japan, was carried on.

3. The relatives of 2 laboratory white males in the 1953 paper were described to show the relation between these two white males and "alba" genes.

4. A number of pale males of *C. erate poliographus* were produced among the butterflies raised in the laboratory in winter.

5. A further study of the hereditary basis of the orange and pale-yellow cell spots on the upper side of the hind wing of *C. erate poliographus* was made, and its monogenic basis was confirmed.

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