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Ivory: A Recessive White-Eyed Tryptophan Metabolism Mutant with Intermediate F_2 - and R_1 - Progenies in the Flesh Fly *Sarcophaga barbata*

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Summary. The recessive autosomal gene *ivory* (i) causes white eyes in the flesh fly *Sarcophaga barbata*. The mutation completely blocks the synthesis of formylkynurenine. *Ivory* larvae and *ivory* imagoes are able to synthesize xanthommatin if formylkynurenine and kynurenine respectively are provided with the food. The eye colour of the F_2- and the R_1-mutants respectively is intermediate because these animals have taken up xanthommatin precursors that were excreted by the *wild*-type larvae. The white eye colour is not influenced by temperature. The viability of the *ivory* stock is somewhat lower than that of the *wild*-type stock. The mutation *ivory* is homologous to the mutation *vermilion* of *Drosophila melanogaster* and to the mutation *green* of *Musca domestica* respectively.

Key words: Formylkynurenine - Kynurenine - Uptake of Excreted Xanthommatin Precursors

Introduction

Eye colour mutants have been observed quite often in insects (see: Wagner and Mitchel 1955; Egelhaaf 1963; Ziegler 1961, 1969; Dickinson and Sullivan 1975). Extensive data have been collected concerning the action of numerous genes, especially in the case of the genus *Drosophila*. With other Diptera - especially with the genus *Musca* - a number of eye colour mutants have also been found (Milani 1967; Heath 1970; Nickel and Wagoner 1970, 1974), but, unlike *Drosophila*, there is hardly any detailed information on the function of the genes in question. This paper deals with the action of the gene *ivory* in the flesh fly *Sarcophaga barbata*.

Materials and Methods

The flesh fly *Sarcophaga barbata* Thomson was kept at 25°C, 16/8h l/d and fed on beef liver. In such conditions, 12 days pass between pupariation and adult emergence. In most of the feeding experiments only the i-larvae received a special diet; the eyes of the i-flies were investigated in the first few hours after emergence. The diet for the mutant larvae in detail: tests 1 to 3 as well as 18 to 20: only fresh liver; test 4: liver on which *wild*-type larvae had been fed before = +-liver; test 5: liver on which mutant larvae had already been fed = i-liver.

In the tests 6 to 17 the young i-larvae were at first fed on fresh liver for one day and at the beginning of the second day put on the following diets. Tests 6 to 8: respectively 3, 6 and 9 days old *wild*-type pupae. Tests 9 to 11: respectively 3, 6 and 9 days old mutant pupae. (With *wild*-type flies eye pigmentation begins 7 days after pupariation.) In each test about 100 pupae were squashed, together with the puparium and 30 i-larvae were put on to the squashed pupae. Test 12: 50 one-day-old decapitated *wild*-type flies were squashed and given to 10 i-larvae. Tests 13 to 17: 20 five-day-old i-pupae were dissected out of the puparium and squashed. To this pulp, somewhat thickened with bread-crumbs, the following substances were added. Test 13: 50 squashed heads of one-day-old +-flies. Tests 14 to 17: 1 or 10 mg crystalline N-formyl-L-kynurenine or DL-kynurenine. 10 i-larvae were put on to each medium, taking up this food completely.

In 5 additional experiments, every 10 i-flies received the following diet in their first ten days of life (larval food: liver). Test 2: sugar. Test 3: sugar and liver. Test 18: sugar and a pulp of 9-day-old +-pupae. Tests 19 and 20: sugar and 10 mg formylkynurenine or kynurenine on moistened filter paper.

The tests 1 to 11 were carried out at least twice with at least 25 flies each; the tests 12 to 18 were carried out once and the tests 19 and 20 twice with 10 flies each. The emergence rate of the adult flies was 90%. The flies which emerged in tests 6 to 17 had reached a medium size.

The eye colour was determined by means of the Ostwald Colour Chart (edition A, 1939). The eyes were squashed in insect Ringer and examined microscopically. The pigment content of the pigment-bearing cells was estimated from at least 5 eyes each.

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Results

In the winter 1973/74, in a mass breeding of *Sarcophaga barbata* (Trepte 1976), some flies emerged whose eyes were distinctly lighter than the reddish-brown eyes of the normal flies. The eye colour of these imagines covered a range from yellow over orange to light-red (collective name: "orange-eyed").

The mating of the orange-eyed flies with each other resulted in only white-eyed imagoes in the following generation, irrespective of the fact that the parents' eyes had been yellow, orange or light-red. In the later generations of these 3 lineages with the yellow-eyed to light-red-eyed progenitors there were also only white-eyed flies. This proved that the character white-eyed is hereditary and as it may be specified best as ivory, the homozygous mutant stock was called *"ivory"* (i).

The reciprocal crosses of the *wild*-type stock (+/+) with the i-stock (i/i) gave only normal red-eyed phenotypes in the F_1 (see: Table 1). The F_2 gave red-eyed and orange-eyed phenotypes in the proportion of 3:1 in both sexes. The backcrosses of the F_1 with the flies of the i-stock gave red- and orange-eyed phenotypes in the proportion of 1:1 in both sexes. The eyes of the orange-eyed F_2- and R_1-flies respectively were always at least beige-yellow, mostly they were orange and often light-red. All the shades of light-yellow to light-red were represented in each F_2 and R_1 respectively; the eyes of these flies were never as light, i.e. white, as those of the i-stock. The backcrosses with heterozygous F_1-♀♀ (♀+/i × ♂i/i) as well as the backcrosses with heterozygous F_1-♂♂ (♀i/i × ♂+/i) gave orange-eyed progenies; and these flies did not show whether they were bred from a heterozygous father or a heterozygous mother.

The crosses of the orange-eyed F_2- or R_1-flies with each other or crosses between orange-eyed and white-eyed flies always gave white-eyed imagoes again. The character *ivory* is thus determined by an autosomal recessive allele (i). The orange-eyed flies in the F_2 and R_1 are homozygous i/i.

The eyes of *S. carnaria* contain the eye pigment xanthommatin (Butenandt et al. 1960; Linzen 1967). In the primary pigment cells (ppc) as well as in the ocelli of *S. barbata*, the pigment occurs in the oxidized (yellowish-brown) form and in the secondary pigment cells (spc) in the reduced (red) form. When treated

Table 1. Inheritance of the mutant *ivory* (i) of *Sarcophaga barbata* (number of the F_1-, F_2-, and R_1-progenies)

Cross	Number of F_1-, F_2-, and R_1-flies			
	♀♀		♂♂	
	+	i	+	i
I: P-♀ +/+ × P-♂ i/i	247	-	297	-
II: F_1-♀ +/i × F_1-♂ +/i	366	108	366	126
P[a] for 3:1	0.26		0.76	
III: F_1-♀ +/i × ♂ i/i	279	252	267	271
P for 1:1	0.40		0.86	
IV: F_1-♂ +/i × ♀ i/i	210	194	204	212
P for 1:1	0.42		0.40	
V: P-♀ i/i × P-♂ +/+	489	-	551	-
VI: F_1-♀ +/i × F_1-♂ +/i	354	105	384	108
P for 3:1	0.30		0.14	
VII: F_1-♀ +/i × ♂ i/i	337	303	310	308
P for 1:1	0.18		0.94	
VIII: F_1-♂ +/i × ♀ i/i	74	75	63	70
P for 1:1	0.93		0.52	

[a] Estimated by the Chi^2-test

with $Na_2S_2O_4$ and $K_3Fe(CN)_6$ respectively, these pigments show the redox reaction typical of ommochromes: change of colour to the red or yellow form (see: Butenandt 1957).

On the seventh day after the pupariation in the eyes of the normal flies the first signs of a beginning eye pigmentation are clearly visible, macroscopically and microscopically. In unfixed squash preparations of the pale-yellow eyes very fine yellow granules may be observed in the ppc by a magnification of 1000x. The ocelli, too, already contain the yellow pigment. In the spc the yellow pigment is clearly visible only on the eighth day. Until the eleventh day the concentration of the yellowish-brown pigment increases in the ppc and spc, as well as in the ocelli, the pigment granules obtaining a diameter of just under 1 µm. About 10 hours before the adult emergence the eyes only contain the yellowish-brown form of the xanthommatin. The pigment of spc is reduced to the red form only a few hours before the adult emergence; thus the newly emerged flies exhibit the yellow xanthommatin in the ppc as well as in the ocelli and the red one in the spc. The retinula cells show traces of a diffuse yellow pigment. The same applies to *Calliphora erythrocephala* (Tate 1948). Whether the adult wild-type flies still produce xanthommatin in the pigment cells could not be decided by means of squash preparations. With the testes sheaths, the deposition of the yellowish-brown pigment only begins on the tenth day, i.e. 3 days later than in the eyes.

The ivory eye colour of the i-imagoes corresponds fairly well to the shades 1ea to 2ea of Ostwald's Colour Chart. A lighter tinge of yellow may be observed quite often. In squash preparations very light traces of a yellow pigment may be seen in the area of the ppc. This is the yellow xanthommatin occurring in very small concentrations. In the spc no pigment may be detected by this method. The ocelli, too, contain little or no pigment at all. In the retinula cells there is no yellow pigment either. With age, the eyes of the i-imagoes darken only very slightly.

The testes of the i-males are also colourless. The colouring of the malpighian tubules changes slightly during development. And there is no distinct difference between the mutants and the *wild*-types.

The fecundity of the i-stock appears reduced compared with the one of the +-stock. It was striking with the first 15 generations that the white-eyed ♀♀, in contrast to the red-eyed ♀♀, regularly deposited a large number of eggs, from which no larvae emerged. For example, 20 i-♀♀ gave no progenies at all and in another case 30 i-♀♀ only gave 130. Obviously, the reason is to be found with the i-♀♀, for these layed undeveloped eggs, irrespective of whether they had been mated with i-♂♂ or +-♂♂. On the other hand, +/+-♀♀ or +/i-♀♀ which had been mated with i/i-♂♂ showed no distinct reduction of fecundity. With this mutant of more than 30 generations, the decrease in fecundity does not seem to be as pronounced as at the beginning, for there is no longer such a striking number of decayed eggs in the spawn of a culture. With respect to the duration of the larval and pupal stage as well as the period until the first larval deposition, there are no remarkable differences between mutant and *wild*-type.

How may the interdediate eye colour of the F_2 and the R_1 be explained? The eyes of the homozygous i-flies of an R_1 are orange, irrespective of whether the mother or the father was heterozygous. Therefore, it may be excluded that the intermediate eye colour was possibly caused by a predeterminative influence of the +-allele in the not yet reduced +/i-oocyte. Moreover, the egg or the embryo could not have taken up enough xanthommatin precursors from the surrounding tissues of a heterozygous mother.

Therefore, it should be examined if and in which way the +/i-larvae of an R_1 may have an influence on the eye-colouring of the i/i-flies. Thus, in three tests every 20 one-day-old R_1-larvae were isolated and raised individually. Only red-eyed and white-eyed imagoes emerged in the proportion of 1:1. In three other tests about 50 one-day-old larvae of the +-stock and of the i-stock each were put into a culture box and raised together. Only red-eyed and orange-eyed flies emerged in the proportion of 1:1.

These experiments show that the +-allele influences the eye pigmentation with the i-flies neither during the oogenesis nor during the embryogenesis. Obviously, only the proximity of i/i- and +/i- and +/+-larvae respectively caused orange-eyed i/i-flies. It may be supposed that the +-larvae excrete substances which can be taken up by the i-larvae and used for the synthesis of eye pigments.

This idea is supported by the following findings. If i-larvae are fed on liver which had before been

Table 2. The influence of different diets[a] on the pigmentation of the eyes, ocelli, and testes of the *ivory*-imago of *Sarcophaga barbata*

Test number	Diet for		Eye colour mainly	Colour class[b]	Pigment content in % of the normal content (estimated)			
	larva	imago			ppc[c]	spc	oce	tes
1	liver		ivory	2ea 2ca 3ea	< 5	0	< 5	0
2	liver	sugar	ivory	3ea 2ea 3ea	< 5	0	< 5	0
3	liver	sugar liver	pale yellow	3ea 3ea 3ga	5	0	5	0
4	±-liver		pale yellow	3ea 2ea 3ic	5	0	5	0
5	i-liver		ivory	2ea 2ca 3ea	< 5	0	< 5	0
6	±-pupae 3 days old		light red brown	5pc 5pc 6pe	40 - 60	< 5	20 - 40	5 - 10
7	±-pupae 6 days old		red brown	6pc 6pe 6pc	40 - 60	< 5	20 - 40	10 - 20
8	±-pupae 9 days old		red orange	5na 5la 5pc	40 - 60	< 5	20 - 40	< 5
9	i-pupae 3 days old		chalky	2ca 2ca 1ea	0	0	0	0
10	i-pupae 6 days old		chalky	2ca 2ca 1ea	0	0	0	0
11	i-pupae 9 days old		chalky	2ca 2ca 1ea	0	0	0	0
12	±-imagoes without heads		red orange	5na 5na 4pc	40 - 60	5 - 10	20 - 40	< 5
13	i-pupae with ±-heads		orange	3na 3na 5na	20 - 40	< 5	10 - 20	0
14	i-pupae and 1 mg formylkyn.		orange	4la 3na 4la	20 - 40	< 5	10 - 20	0
15	i-pupae and 10 mg formylkyn.		red brown	7pe 7pe 7pe	60 - 80	40 - 60	40 - 60	5 - 10
16	i-pupae and 1 mg kynurenine		light red brown	5pc 5pa 5pc	40 - 60	< 5	20 - 40	5 - 10
17	i-pupae and 10 mg kynurenine		red brown	7pe 7pe 7pe	60 - 80	40 - 60	40 - 60	40 - 60
18	liver	sugar ±-pupae 9 days old	orange	3ga 3ga 3la	5	0	< 5	0
19	liver	sugar and 10 mg formylkyn.[d]	orange	3na 3na 4na	20 - 40	0	10 - 20	5 - 10
20	liver	sugar and 10 mg kynurenine[e]	light red brown	5pc 5pc 5pc	40 - 60	0	20 - 40	20 - 40

given to ±-larvae, then imagoes resulted with pale-yellow to honey-yellow eyes. However, ivory eyes were produced when the i-larvae were fed on liver from which i-larvae had eaten previously. The idea that the mutant can take up pigment precursors from the food to use them for the synthesis of xanthommatin was supported by another experiment, namely be feeding 3 or 6 day-old, i.e. white-eyed *wild*-type pupae. The eyes of the i-flies fed on ±-pupae as larvae were of a deeply reddish brown colour. Squash preparations from the eyes of these yellow-eyed and red-eyed i-imagoes showed that the ppc as well as the ocelli contained many pigments, on the other hand the spc showed relatively few pigments (see: Table 2). So the ppc, for example, had taken up about 40 to 60 %, whereas the spc had taken up, at most, 5 % of the normal amount of pigment. The testes sheaths, too, showed a smaller proportion of pigment than the ppc.

In contrast to this, the eyes of the i-imagoes having been fed on i-pupae appeared white, i.e. chalky. Not even the slightest traces of the yellow pigment could be found in unfixed squash preparations. This differs from the position of the i-flies fed on liver, whose ivory eyes always contained small concentrations of the yellow xanthommatin in the ppc.

These findings show that with the i-flies a link in the synthesis chain from tryptophan over formylkynurenine, kynurenine, 3-hydroxykynurenine to xanthommatin is blocked. However, the orange-eyed i-flies indicate that the pigment synthesis is continued from a certain point and that the xanthommatin in the pigment cells of the i-flies may be bound into the structures specific for it, for these obviously are untouched by mutation.

The eye colour mutant *vermilion* of the fruit fly *Drosophila melanogaster* has lost its ability to synthesize formylkynurenine and thus fails to produce xanthommatin. This failure may be compensated by adding formylkynurenine to the larval diet (Green 1955). As a first approach to the problem of which point, in *S. barbata*, is the synthesis chain to xanthommatin blocked, 3-day-old i- and ±-pupae, respectively, were squashed and mixed in a proportion of about 1:1 with the medium for the *vermilion* mutant. The ocelli of the *vermilion* flies fed on *wild*-type pupae showed distinct amounts of the yellowish-brown xanthommatin in the squash preparations. The ocelli of the *vermilion* flies fed on *Sarcophaga* mutants contained no pigment. Hence the i-mutant of *S. barbata*, like the v-mutant of *D. melanogaster*, also is not able to synthesize formylkynurenine.

These conclusions were supported by tests, in which the i-flies were fed on formylkynurenine and kynurenine respectively. It was shown that the larvae as well as the imagoes can take up the precursors of xanthommatin supplied with their food and change them into the pigment, for the eyes and the testes sheaths of the flies contained the brown pigment. Curiously, the spc of the mutant remained practically colourless when the pigment precursors were applied only with the imaginal food. The retinula cells of the i-mutant fed on *wild*-types or supplied with doses of formylkynurenine and kynurenine remained colourless.

In the feeding experiments the eye colour, i.e. the amount of pigment of the i-mutants, was always quite homogeneous, whereas with the F_2- or R_1-mutants the intensity of the colour mostly covered a relatively wide range between yellow and red. These differences may be due to the fact that i-flies with more intensively coloured eyes had eaten dead *wild*-type larvae.

At low temperature the w-mutant of *C. erythrocephala* is able to produce small amounts of xanthommatin (Tate 1947; Hanser 1959). i-flies of *S. barbata*, which as 3, 5, 6, 7, 8, 9 or 10 day-old pupae had been kept at 4°C for six weeks and subsequently at 25°C until adult emergence, only showed ivory eyes. i-pupae kept at 11°C or 15°C when they were six days

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[a] Quantity, composition, and preparation are described in chapter materials and methods
[b] After Ostwald (1939). In the first place is listed the most frequent, in the second place the lightest, and in the third place the darkest value. *Wild*-types show the value 7pc.
[c] ppc primary pigment cells, spc secondary pigment cells, oce ocelli, tes testes
[d,e] The supplied quantity was not fed completely.

old, i.e. shortly before the time when the pigment synthesis normally starts, developed as far as mature pharate imagoes and imagoes, respectively. The eyes of these flies were also ivory. Similar results were obtained by keeping the i-pupae at 21°C, 30°C and 36°C. As far as could be judged from squash preparations, there was no significant difference in eye colour or pigment concentration between the mutants kept at different temperatures and those kept at 25°C.

The imaginal emergence rate of the pupae kept between 15°C and 36°C showed no striking differences from the standard value of 90 to 95 % of the flies kept at 25°C, neither with the *wild*-type nor with the mutant flies. On the other hand, pupae of the i-stock cannot be kept at 4°C for as long as those of the +-stock. With i-pupae, which after the first 2 to 2.5 days of life at 25°C were put at 4°C, the emergence rate was reduced to less than 50 % after a 6 to 8 week stay at 4°C, while +-pupae could be kept for 8 to 12 weeks at 4°C, without a noticeable reduction of the emergence rate under 90 %. Most of the flies that did not emerge had developed up to the mature pharate imago but had not left the puparium; their cuticle had tanned within the puparium.

Discussion

The i-mutant of *Sarcophaga barbata* cannot form formylkynurenine and consequently no xanthommatin. Therefore, the eyes and the ocelli of the mutant are white, just like the testes. The reason why the formylkynurenine synthesis is blocked is not known. The lack of pigment may almost completely be compensated for by feeding the mutant with formylkynurenine or kynurenine. This explains the fact that homozygous i-flies of an F_2 or an R_1 are orange-eyed, if one assumes that these flies have taken up a precursor of the xanthommatin with their food. This may by kynurenine which as a product of the tryptophan metabolism is also excreted. So the kynurenine may be excreted by the *wild*-type larvae in an F_2 or an R_1 and taken up again by the mutants.

In the eyes of the liver-fed i-flies small amounts of the yellow xanthommatin could always be detected. In contrast to this, the eyes of the mutants fed on mutant pupae did not contain any pigment. The pigments in the eyes of the i-flies may therefore not be interpreted as an indication that the formylkynurenine synthesis is merely slowed down to a considerable extent, but rather it is completely blocked. For the xanthommatin synthesis the "liver flies" were obviously provided with precursors of the pigment which could only have resulted from the tryptophan metabolism of the liver.

The eyes of the blow fly *Calliphora erythrocephala* contain about 80 µg xanthommatin per fly (Butenandt et al. 1960). If each larva is supplied with 1 mg formylkynurenine or kynurenine in its food, the eye colour of the mutant may not or only with difficulty be distinguished macroscopically from that of the wild-type. Squash preparations, however, showed that the pigment cells only contained half or three quarters of the normal amount of pigment, i.e. less than one tenth of the supplied pigment precursors has been used for the synthesis of xanthommatin.

These, together with the other feeding experiments show that in a heterozygous ♀ the +-allele of a growing oocyte will certainly not be able to provide for sufficient xanthommatin precursors for the synthesis of a visible amount of the pigment. Besides, the test with isolated larvae have also shown that neither the oocyte nor the embryo of a heterozygous mother take up any amount of xanthommatin precursors worth mentioning to store them for pigment synthesis.

In all feeding experiments it was striking that the spc of the orange-eyed mutants deposited less pigment than the ppc. Even the testes sheaths did not contain anything like the amount of xanthommatin which would correspond to the amount of the pigment appearing in the eyes. This may be an expression of sequential xanthommatin deposition, beginning one day earlier in the ppc than in the spc and three days earlier than in the testes. In the later stages, the supplies of pigment precursors merely taken up with the food have obviously been largely exhausted. It seems remarkable that even the imago can still synthesize xanthommatin from the newly taken up pigment precursors.

The heads of the house fly *Musca domestica* contain neither kynurenine nor tryptophan (Laudani and Grigolo 1969). Provided that the conditions are equivalent with *S. barbata*, the mutants fed on *wild*-type heads should have developed their eye pigment from the xanthommatin of the normal flies.

The following fact gives an indication of how soon a new mutation may be discovered in mass breeding. In September 1973, the mass breeding was divided into two strains and in December 1973 the first orange-eyed, i.e. homozygous *ivory* flies, appeared in one of the two strains. This was the F_2 of the newly founded stock. This means that the mutation must have arisen in the original generations of the new stock at the latest, but certainly not much earlier than, two generations before it. In the other stock no white-eyed flies have yet occurred.

A comparison with other eye-colour mutants shows that the mutant *ivory* of *S.barbata* is homologous to the mutant *vermilion* of *D.melanogaster* (see: Green 1955). More than 20 eye-colour mutants of the house fly *M.domestica* have been described (Milani 1967), but hitherto, only in the mutants *green* and *ocra* is it known what caused the change of phenotype. Both of the mutations influence the metabolism of the xanthommatin precursors. In the case of *green* the synthesis of the formylkynurenine is blocked (Ward and Hammen 1957; Bodenstein 1959). On the other hand, *ocra* cannot synthesize 3-hydroxykynurenine (Laudani and Grigolo 1969).

With the mutant *snow* of *Apis mellifera* (Green 1955) and the mutant a of *Ephestia* kühniella (Kühn 1956), again the same link of the pigment synthesis chain is blocked as with *vermilion* of *Drosophila* and *ivory* of *S.barbata*. The mutant *lemon* of *C.erythrocephala* (Ullerich and Langer 1974) may possibly take up xanthommatin precursors from the food like *S.barbata* and use it for the pigment synthesis. A detailed investigation of this observation is in preparation (Ullerich, pers. communication).

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