Tests for linkage and other interactions in the honey bee

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WITH 16 linkage groups expected to be found in the honey bee, *Apis mellifera* L., only two linked pairs of visible mutants are known[6]: chartreuse eye with hairless[5], and cream eye with pearl eye[1]. The present work was conducted as a contribution to the establishment of the honey bee's linkage groups, even though no new linkages were found. The present paper reports 31 new tests and 4 repeated tests between visible mutants and 5 new tests to the X locus. The tests were conducted primarily with the eye mutants eyeless (*e*), and garnet (*g*), and the wing mutants short (*sh*), truncate (*tr*), and wrinkled (*wr*); also, to a less extent, with the body color mutants black (*bl*), and cordovan (*cd*), and the eye color mutants brick (*bk*), chartreuse-1 and brown (*ch[1]* and *ch[1]*, *m*), chartreuse-2 (*ch[2]*), cream (*cr*), ivory (*i*), pearl (*pe*), and snow (*s*).

Materials and Methods

Linkage tests between visible mutants were conducted by counting the drone progenies of queens heterozygous for various pairs or trios of mutant genes. Drone segregations give gametic ratios, because drones develop from unfertilized eggs. The mutants were combined usually in trans combination, but a few were cis, as indicated in Table II. Also, in Table II, the first two categories include the parental types, which are followed by the recombination types.

Linkage tests between visible mutants and the sex alleles (X locus) were conducted by self insemination of heterozygous queens each with her own mutant drones[4]. Outcrossed comparisons were made for some of the mutants tested by backcrossing heterozygous mutant queens to less closely related mutant drones. The worker progenies of these backcrosses were classified and counted (Table I).

Results and Discussion

No new linkages between visible mutants were apparent (Table II), even though only 1 of the 39 crosses did not deviate from independent assortment. Perhaps some loose linkages (over 40 percent recombination) were hidden by the incomplete penetrance of *wr* or by the differential survival of certain mutant types.

No new linkages were discovered between mutants and the sex alleles (Table I). Selfed *pe[+]/pe* × *pe* fit 1:1 segregation.

The departures from expected segregation of *tr*, *sh*, and *g* are probably due to subviability of the mutant and/or *g[+]* (wild type). Two of the four *wr* matings departed from expected 1:1 segregation, presumably due to incomplete pentrance of *wr*. Whereas no outcrossed comparison was conducted for *sh*, the findings here compare to other data[2] and survival of *sh/sh* workers is similar to that of *sh* drones. Likewise the *wr/wr[+]* × *wr* worker progenies are similar to drone progenies of *wr/wr[+]* queens (Tables II and III, also Laidlaw et al.[2]).

Selective mortality of mutant phenotypes was a striking feature of the drone segregations, and is summarized in Table III. The most severe mortality was suffered by *tr*, *sh*, and *e*, whose numbers were invariably significantly less than wild type. Next in levels of mortality were *g*, *cd*, and *bl*, in which subviability was significant for only some of the crosses, perhaps reflecting variable genetic load. Selective mortality was very severe with certain double mutants: *e-tr*, *bk-tr*, and *e-sh*. The subviabilities found here were similar to those already reported for *e[3]*, and for *sh* and *tr[1,2]*. This is the first report of subviability for *bl*, *cd*, and *g*. However, except for *bk-tr*, significant subviability was not found with *bk* or *s*, as earlier reported[1,5].

I have proposed a polygenic basis for subviability in which a few to many genes act jointly to produce one death[7]. With a greater stress, such as *tr*, fewer genes would be required for death than with a lesser stress, such as *cd*.

I am persuaded to this hypothesis by the periodicity of selective viability, especially within individual progenies, but still observable in the array of data in Table III. However, the present data are inadequate to further detail the hypothesis, in view of the complex development of the bee with the possi-

Table I. Tests for linkage of some mutants to the sex alleles. Segregations in worker progenies of backcrossed heterozygous queens, outcrossed or self inseminated

| Mutant | Selfed or outcrossed | Numbers of worker progeny | | χ^2 |
		mutant	wild-type	
garnet	outcrossed*	2223	2281	0.75
	outcrossed	1444	1307	6.82**
	outcrossed	19	31	2.88
	selfed	85	78	0.30
	selfed	508	467	1.72
	selfed	114	82	5.22*
	selfed	266	342	9.50**
pearl	selfed	388	416	0.98
	selfed	920	917	0.01
short	selfed	22	23	0.02
	selfed	53	77	4.43*
	selfed	58	90	6.92**
	selfed	348	484	22.23**
	selfed	64	449	288.94**
truncate	outcrossed	816	1183	67.38**
	outcrossed	968	1770	234.80**
	outcrossed	313	1729	981.91**
	selfed	39	77	12.45**
	selfed	376	774	137.74**
wrinkled	selfed	157	189	2.96
	selfed	654	747	6.17*
	selfed	172	156	0.78
	selfed	335	451	17.12**

* Deviation from expected 1:1 ratio, $P < 0.05$
** Deviation from expected 1:1 ratio, $P < 0.01$

bility of death at many points, such as hatching of the egg and at each of six molts.

As earlier reported[1,2], the incomplete penetrance of *wr* was of variable magnitude (Table III).

Epistatis of two sorts occurred: the eyeless phenotype precluded the appearance of the mutant eye colors *bk, ch², cr, g, i,* and *s*. Also, *cr* and *i* were each epistatic to *g*.

The phenotypes of certain genic combinations could not be identified properly. Among the eye-color mutants, *bk-g* could not be distinguished from *bk;* also *ch¹, m-g* and *ch¹-g* could not be distinguished from *ch¹, m.* Double wing mutants *sh-tr* could not be distinguished from *tr.* Moreover, the distinctions between *sh-wr* and *sh,* and between *tr-wr* and *tr* were by no means certain.

Summary

No linkages were found in 31 new combinations of visible mutants, nor in 5 new combinations with the X locus, conducted mainly with eyeless (*e*), garnet (*g*), short (*sh*), truncate (*tr*), and wrinkled (*wr*). Eyeless was epistatic to eye colors; cream (*cr*), and ivory (*i*) were epistatic to garnet (*g*). Selective mortality was invariable with *e, sh,* and *tr,* and occasionally with *bl, cd,* and *g.*

Table II. Tests for linkage and other interactions among visible mutants

Queen's genotype	Phenotypes and numbers in drone progenies				Linkage?*
$bl^+;bk/bl;bk^+$	150 bk;	179 bl;	158 bl-bk;	174 +	A
$bl^+;e/bl;e^+$	277 e;	419 bl;	280 bl-e;	473 +	B
$bk^+;e/bk;e^+$	1214 e (& bk-e);		856 bk;	891 +	C
$ch^+;e/ch^2;e^+$	274 e (& ch²-e);		326 ch²;	291 +	C
$cd^+;e/cd;e^+$	422 e;	616 cd;	360 cd-e;	582 +	C
$cr^+;e/cr;e^+$	2391 e (& cr-e);		1436 cr;	1500 +	C
$e;g^+/e^+;g$	132 e (& e-g);		127 g;	120 +	C
$e;i^+/e^+;i$	1347 e (& e-i);		1037 i;	1033 +	C
$e;sh^+/e^+;sh$	343 e;	675 sh;	135 e-sh;	1035 +	D
$e;s^+/e^+;s$	661 e (& e-s);		483 s;	473 +	C
$e;tr^+/e^+;tr$	402 e;	249 tr;	56 e-tr;	704 +	D
$e;wr^+/e^+;wr$	252 e;	195 wr;	133 e-wr;	459 +	D
$bl^+;g/bl;g^+$	1061 g;	1227 bl;	1061 bl-g;	1234 +	B
$bk;g^+/bk^+;g$	1162 bk & bk-g;		536 g;	604 +	D
$cr^+;g/cr;g^+$	491 g;	1122 cr (& cr-g);		572 +	D
$g;sh^+/g^+;sh$	258 g;	212 sh;	187 g-sh;	336 +	B
$g;tr^+/g^+;tr$	406 g;	292 tr;	206 g-tr;	437 +	B
$g;wr^+/g^+;wr$	1796 g;	490 wr;	318 g-wr;	1772 +	C
$bl^+;sh/bl;sh^+$	1193 sh;	1669 bl;	756 bl-sh;	1846 +	D
$i^+;sh/i;sh^+$	228 sh;	384 i;	222 i-sh;	352 +	B
$sh;tr^+/sh^+;tr$	667 sh (& sh-tr?);		385 tr;	773 +	D
$sh;wr^+/sh^+;wr$	783 sh (& sh-wr);		587 wr;	1201 +	D
$sh;wr^+/sh^+;wr$	87 sh;	105 wr;	79 sh-wr;	162 +	D
$bl^+;tr/bl;tr^+$	109 tr;	512 bl;	91 bl-tr;	535 +	B
$bk^+;tr/bk;tr^+$	54 tr;	213 bk;	3 bk-tr;	198 +	C
$ch^+;tr/ch^2;tr^+$	139 tr;	880 ch²;	134 ch²-tr;	829 +	B
$cr^+;tr/cr;tr^+$	360 tr;	1139 cr;	375 cr-tr;	1197 +	B
$s^+;tr/s;tr^+$	258 tr;	485 s;	281 s-tr;	468 +	B
$tr;wr^+/tr^+;wr$	317 tr;	725 wr;	365 tr-wr(?);	820 +	D
$tr^+;wr^+/tr;wr$	618 +;	229 tr-wr(?);	237 tr;	361 wr	C
$cr;wr^+/cr^+;wr$	233 cr	157 wr;	159 cr-wr;	252 +	B
$cd^+;e;g/cd^+;e^+;g^+$	284 e (& e-g); 168 cd-g;	233 cd-e (& cd-e-g);	166 cd;	146 g; 179 +	C
$cd;e;tr^+/cd^+;e^+;tr$	164 cd-e; 23 e-tr;	167 tr; 133 cd-tr;	162 e; 21 cd-e-tr;	255 cd; 278 +	B
$cr^+;e;g/cr;e^+;g^+$	718 e (& cr-e; e-g; cr-e-g); 197 g;		429 cr (& cr-g); 264 +		D
$e;g;i^+/e^+;g^+;i$	600 e (& e-g;e-i; e-g-i); 212 g;		404 i (& g-i); 191 +		D
$e;g;sh^+/e^+;g^+;sh$	171 e (& e-g); 110 g-sh;	126 e-sh (& e-g-sh);	104 sh;	140 g; 171 +	D
$e;g;tr^+/e^+;g^+;tr$	315 e (& e-g); 76 g-tr;	38 e-tr (& e-g-tr);	146 tr;	218 g; 277 +	D
$ch^+;m^+;g/ch^1;m;g^+$	1675 ch¹-m & ch¹-g & ch¹-m-g; 650 ch¹;			994 g; 1315 +	D
$cd;cr;wr^+/cd^+;cr^+;wr$	320 cd-cr; 157 cd-wr;	194 wr; 184 cr-wr;	352 cr; 166 cd-cr-wr;	314 cd; 390 +	B

* A = no significant deviation from independent assortment
B = no significant deviation from expected proportions between combined parental and combined recombinant classes
C = no significant deviation from equality between 1 selected parental and 1 selected recombinant class
D = recombinant + is so high as to suggest no close linkage

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Table III. Survival, penetrance, epistasis and confused phenotypes for the mutants tested*

	bl	bk	cd	ch¹	ch²	cr	e
bl	—	91/ 86	—	—	—	—	59/ 59
bk	91/103	—	—	—	—	—	x68/x68
cd	—	—	—	—	—	83/ 92	62/ 73 65/ 80 58/ 59
ch²	—	—	—	—	—	—	x47/x47
cr	—	—	83/ 81	—	—	—	x80/x80 x68/x68
e	59/ 89	x68/ 96	62/106 65/ 93 58/ 92	—	x47/112	x80/ 96 x68/ 81	—
g	86/ 99	z91/ z?	94/ 93	z85/ 99	—	x98/x98 x81/x81	x55/x55 x79/x79 x68/x68 x79/x79 x50/x50 x57/x57
i	—	—	—	—	—	—	x65/x65 x79/x79
sh	41/ 90	—	—	—	—	—	13/ 33 37/ 50
s	—	—	—	—	—	—	x70/x70
tr	17/ 96	2/108	48/ 92	—	16/106	31/ 95	8/ 57 8/ 61 7/ 57
wr	—	—	67/ 81	—	—	81/ 96 69/ 92	69/ 59

	g	i	sh	s	tr	wr
bl	86/ 86	—	41/ 65	—	17/ 20	—
bk	z91/ 89	—	—	—	2/ 27	—
cd	94/82	—	—	—	48/ 60	67/ 67
ch¹·	z85/ 76	—	—	—	—	—
ch²	—	—	—	—	16/ 17	—
cr	x98/ 86 x81/ 75	—	—	—	31/ 30	81/ 77 69/ 66
e	x55/106 x79/ 91 x68/ 75 x79/111 x50/ 91 x57/ 79	x65/100 x79/x106	13/ 65 37/ 63	x70/102	8/ 35 8/ 60 7/ 53	69/ 60
g	—	x106/x106	56/ 63 64/ 61	—	47/ 67 27/ 53	30/43
i	x106/111	—	63/ 65	—	—	—
sh	56/ 77 64/ 82	63/109	—	—	z43/ 50	z?/ 66 z95/ 79
s	—	—	—	—	60/55	—
tr	47/ 93 27/ 79	—	z43/z43	60/104	—	z107/ 94 z98/ 74
wr	30/ 93	—	z?/z44 z95/z62	—	z107/ 44 z98/ 48	—

* Survival is stated as percentage of wild type. The percentage of the double mutant is to the left of /, the mutant heading the column alone on the right. The percentages under the column wr are for penetrance, and the row following wr are for penetrance on the left and for survival on the right. Epistasis is indicated by x, and confused phenotypes by z; the percentages following these were calculated from the expected proportions of the aggregate phenotypes. Percentages in bold face type differ significantly from wild type