A MODEL FOR POLYGENIC INHERITANCE OF ABDOMINAL TERGAL SCALE PATTERN IN *AEDES AEGYPTI*[1]

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ABSTRACT. There is much variation in the amount of white scaling on the abdominal tergites of *Aedes aegypti*. The genetic basis for this white scale pattern was investigated in two laboratory strains established by selection from the CARN Strain of *Ae. aegypti*. These experimental strains were crossed in all possible directions in single pair matings. Based on analysis of their progeny it is proposed that genes at three separate independently assorting loci control abdominal tergal scale pattern. Correlation of observed data and expected data was high. Since the abdominal tergal scale pattern in *Ae. aegypti* appears to be controlled by one major polygenic system with modifiers, it is proposed that it is better to consider differences in ethology, physiology, and reproductive behavior as the bases for separation of the species into intraspecific groups.

INTRODUCTION

Aedes aegypti (Linn.) imagoes have a black to brownish cuticle with black, silver, matte-white, or gold scales appearing in an assortment of patterns on various body parts. The abdominal tergites have black or brownish background scaling with light (silver or matte-white) scales appearing in lateral spots and basal bands; sometimes additional white scales extending from the basal bands are present on the tergite proper. The abdominal tergal scale pattern has been used as the primary basis for classification of this species into subspecies and varieties (Mattingly 1957).

Based on scaling of abdominal tergites, Mattingly (1957) recognized three forms of *Ae. aegypti*. These are: *Ae. aegypti*, the type form, with pale scaling on the first abdominal tergite and/or a distinctly paler or browner body than the blackish African subspecies *formosus* (Walker); *Ae. aegypti formosus*, which never has any pale scales on the first abdominal tergite, has a markedly blackish appearance, and is confined to Africa south of the Sahara; and *Ae. aegypti* variety *queenslandensis* (Theobald), which has increased white scaling on the abdominal tergites beyond the first, and/or has a lighter mesonotal color. Mattingly's (1957) classification system stressed the presence of pale scales on the first abdominal tergite as a good diagnostic character of frequent occurrence; however, he also noted that it was not completely constant.

A wide range of abdominal tergal scale pattern exists even within distinct populations of *Ae. aegypti*. McClelland (1960) examined abdominal tergal scaling in *Ae. aegypti* hatched from eggs collected from filter paper-lined water pots in Kenya. In selected matings, imagoes with abdominal tergal scale pattern corresponding to the nominate form produced progeny representative of subspecies *formosus* and the nominate form. Parental *formosus* phenotypes produced both *formosus* and nominate form offspring. Paler forms, i.e., those representative of variety *queenslandensis*, resulted in *queenslandensis* progeny. These results were substantiated by Hartberg (1969), who examined progeny of field-collected females for abdominal tergal scale pattern and also found that females corresponding to subspecies *formosus* produced offspring representative of *formosus* and the nominate form; nominate form females gave offspring of both *formosus* and nominate form appearance. McClelland (1974) analyzed 74 samples from 69 different populations for abdominal tergal scale pattern. Again, his data showed a wide range of variation in abdominal tergal scale pattern. Mogi et al. (1984) also showed a wide range of variation in abdominal tergal scale patterns in eight populations of *Aedes aegypti* from the Philippines.

Since there is variation in abdominal tergal scale pattern even within the three subdivisions of *Ae. aegypti*, this variation is probably genetic and heritable. The genetic mechanism for the inheritance of abdominal tergal scale color has long been a subject of speculation. McClelland (1960, 1967, 1974) proposed a multifactorial mode of inheritance for abdominal tergal scale color; VandeHey et al. (1978) presented data that suggest a polygenic system of inheritance. Other investigators suggested a monofactorial scheme. Johnston and Hartberg (1981) presented a polygenic system of inheritance for variation in scale pattern of the abdominal sterna of the mosquito *Eretmapodites quinquevittatus* (Theobald).

[1] This investigation was supported in part by a research grant to the first author from the Georgia Southern College Faculty Research Fund.

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The purpose of the present investigation is to propose a genetic mechanism for inheritance of abdominal tergal white scale pattern in *Ae. aegypti*.

MATERIALS AND METHODS

Several strains of *Aedes aegypti* were obtained from Dr. G. B. Craig, Jr., Vector Biology Laboratory, University of Notre Dame, and were examined for variability in the pattern of white scales on the abdominal tergites. The CARN strain exhibited the most variability and therefore was chosen as the experimental strain for this study. CARN-DARK and CARN-LIGHT strains were selected from the CARN strain (Table 1).

The CARN-DARK strain was obtained by selecting from the CARN strain males and females with the least amount of white scales on the abdominal tergites and inbreeding 10–15 selected pairs. At each generation, offspring were examined and again darkest individuals (10–15 pairs) were selected and allowed to mate and oviposit. Individuals with no, or very few, white scales appearing on the abdominal tergites are hereinafter referred to as "dark." The procedure of selecting darkest individuals and inbreeding them was carried through the third generation for CARN-DARK. By the third generation, most CARN-DARK specimens had no white scales on the abdominal tergites (except in basal bands) and no specimens had white scales on tergites II-VII. A typical CARN-DARK F_3 female is shown in Fig. 1A.

The CARN-LIGHT strain was established by the same method as the CARN-DARK strain, except that males and females with the greatest number of white scales on the abdominal tergites were selected from the CARN population and at each subsequent inbred generation. Inbreeding and selection for increased white scaling of the abdominal tergites was carried through six generations, at which time white scaling on abdominal tergites became essentially uniform. Individuals with completely or predominantly white scaled abdominal tergites are hereinafter referred to as "light."

The majority of single pair matings for this investigation were carried out with CARN-LIGHT F_2 individuals and CARN-DARK F_3 individuals. Use of CARN-LIGHT F_2 instead of later generations was necessary because poor viability and low fecundity in this strain did not allow sufficient numbers of F_3 or later generations for crosses (except as noted below). Similar difficulties in inbreeding strains of *Ae. aegypti* were noted by Craig and Hickey (1967). However, later in this study, the "inbreeding barrier" was pierced and some experimental crosses were made with CARN-LIGHT F_6

Table 1. *Aedes aegypti* strains utilized in this investigation.

Strain	Strain history
CARN	Received November, 1972, from Monsieur P. Carnevale, En tomologie Medicale, Centre ORSTROM, Brazzaville, Rep. du Congo, as eggs of a local strain (5 batches total).
CARN-LIGHT	Selected from CARN strain by C. K. Meeks for maximal white scaling on abdominal tergites. Inbred to the F_6 generation with selection for increased white scaling at each generation. By F_6, expression of white scaling on abdominal tergites uniform.
CARN-DARK	Selected from CARN strain by C. K. Meeks for minimal white scaling on abdominal tergites. Inbred to the F_3 generation with selection for minimal white scaling at each generation. By F_3, most CARN-DARK specimens had no white scales on abdominal tergites (except in basal bands) and no specimens had white scales on tergites II–VII.

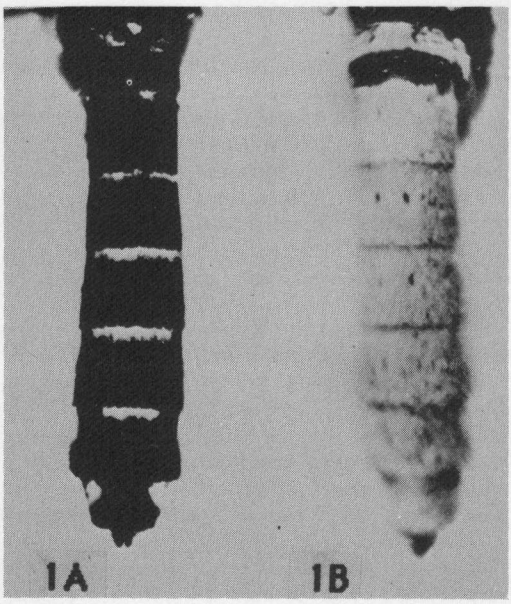

Fig. 1. Dorsal aspect of adult *Ae. aegypti* females: Fig. 1A. Typical CARN-DARK female, CKM "0"; Fig. 1B. Typical CARN-LIGHT female, CKM "7".

individuals (Fig. 1B). No significant differences were noted between these crosses using CARN-LIGHT F_6 and those using CARN-LIGHT F_2. Both sexes of the F_6 CARN-LIGHT strain are essentially identical to each other with regard to abdominal tergal scale pattern.

Rearing methods were essentially those described by Craig and VandeHey (1962) for genetic research with *Aedes aegypti*. All mosquitoes were reared in an insectary with a temperature of 26° ± 3°C and ambient relative humidity. Larvae were fed on a suspension of liver powder in tap water (12 cc/liter). Pupae were segregated by sex and placed in emergence cups. After emergence adults were rechecked for sex to ensure that females used in crosses were virgins.

For single pair matings, etherized virgin adults were examined with a stereo-dissecting microscope and appropriate males and females selected. Each single pair was placed in a cage made from a pint-sized cardboard container. A shell vial lined with absorbent brown paper toweling and ¾ filled with water was inserted in the cage to provide an oviposition site and prevent desiccation. A sugar cube was provided as a carbohydrate source. Females were offered a blood meal from an anesthetized white mouse 4–5 days after emerging. Oviposition usually occurred 4–5 days after the blood meal.

Adult mosquitoes to be examined for abdominal tergal scale pattern were removed from emergence cups within 24 hours postemergence to prevent loss of scales due to rubbing and scraping against each other and/or against the emergence cup. Adults were anesthetized with ether and transferred to an examination container for classification. An Olympus stereo-dissecting microscope with a high-intensity light source and heat filter was used in the examination of all mosquitoes. To eliminate classification error, it was necessary to orient all imagoes in the same direction, since individuals improperly oriented reflected light differently, and thus obscured the tergal scale pattern. Two pairs of Inox No. 5 watchmaker's forceps were used to separate the wings and expose the abdominal tergites for examination.

McClelland (1960, 1974) described a system for classifying *Ae. aegypti* according to abdominal tergal scale pattern based on the number of tergites that have a continuous medial band of white scales from the apical to the distal end. The number of the most posterior tergite with such scales is used to denote the degree of paleness; in general, all tergites anterior to this tergite are as pale or paler than it is, and those posterior to it, especially the adjacent one, have scattered pale scales (McClelland 1960). McClelland arbitrarily assigned a letter (F, G, H, J, K, L, M, N, O, P, or Q) to denote eleven color grades, "F" representing a mosquito that had no white scales except in basal bands (as in subspecies *formosus*, through "Q," representing the most extreme expression of variety *queenslandensis*, where only speckled black scales appeared on the tergites (McClelland 1974). Since there was so much variation in tergal scale pattern, McClelland (1974) expanded the system to cover 30 basic patterns by subscripting each letter with a digit to indicate the number of tergites with white scales. Thus, McClelland in his later work incorporated both the amount of white scaling and the number of tergites with white scales to form a "pattern value" method for mosquito classification.

It became apparent early in our investigation that the number of tergites with white scales, rather than the amount of white scaling on the tergites, was a better criterion for classification. This prompted the formulation of the CKM system of classification. In the CKM method, only the number of tergites with white scales (except in basal bands) is considered regardless of the number of white scales on the tergites. Since abdominal segments VIII-X are modified as genitalia in mosquitoes, only segments I-VII were considered for classification. When white scales were present on any given tergite, they always appeared on all tergites anterior to the given tergite. Additionally, the amount of white scaling usually decreased from anterior to posterior end of the abdomen.

There are eight possible classes in the CKM system: "0" if no white scales appear on the tergites (except in basal bands), "1" if only the first tergite has white scales, "2" if the first two tergites have white scales, up to "7" if all seven tergites being considered have white scales. The eight classes of the CKM system are equated to McClelland's pattern value classes in Fig. 2. All mosquitoes examined in this study were classified according to both McClelland's original system and the CKM system developed during the present investigation.

According to McClelland (1974), some subjectivity in determining the pattern value of individuals scored is unavoidable since all types of intermediates exist, but he states that subjectivity is unlikely to cause an error of more than one pattern value unit. This error is avoided in the CKM method, since one can easily determine whether white scales are present or absent on any given tergite. One possible source of error in classification in the present study might have been the loss of white scales due to mosquitoes rubbing against each other and/or rubbing against the emergence cup. Since imagoes were examined as quickly as possible after emergence, it is believed that

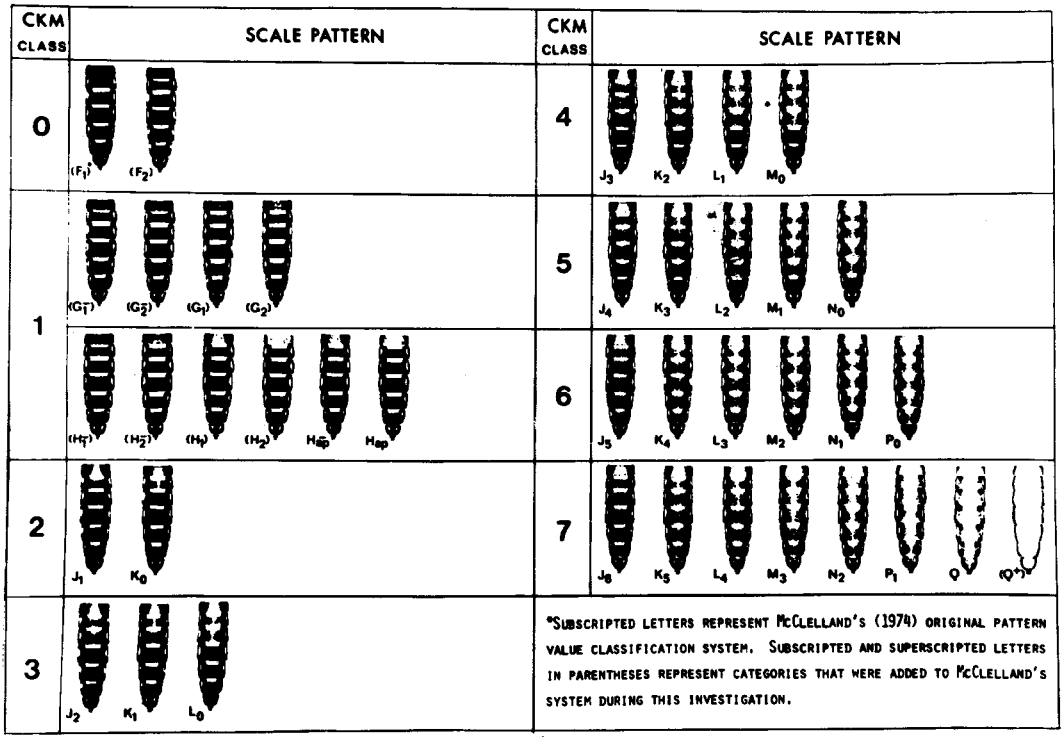

Fig. 2. Diagrammatic representation of correspondence between CKM classification system and McClelland's pattern value system.

the number of mosquitoes so damaged was too small to be of any significance with regard to the data collected.

RESULTS

Although males as well as females of each single pair cross were scored, for clarity of data analysis, only those data from female offspring are considered in this investigation (Table 2). McClelland (1974) implied that when males and females are analyzed together, little more information is gained than if only females are scored and that there is probably little justification in scoring males as a routine. Observations during the course of this investigation support earlier findings that males tend to be darker than females (Connal 1927, Craig and VandeHey 1962, Lewis 1945, Mattingly 1957, McClelland 1960).

Exclusion of males from the data is justified. Females are more consistent in their scaling patterns and are easier to score. Using just females is equivalent of working out of any sex-linked or sex-influenced genetic system, such as feather pattern in birds. As long as one can predict what the female offspring will look like from a cross, what the males will look like is inconsequential for the genetic model being considered.

Single pair crosses in all possible directions were made in this study ("light" × "light," "light" × "dark," "dark" × "dark," and "dark" × "light"). Of the 113 single pair matings attempted in this investigation, only 39 (34.5%) yielded viable offspring. In most unsuccessful crosses, parents died before mating and/or ovipositing. Poor viability of parental "light" individuals seemed to account for many of the unsuccessful crosses; only 26% of crosses involving "light" males yielded viable offspring, while 56% of the crosses with "dark" males were successful. McClelland (1960) noted declines in fecundity and viability of mosquitoes that had been selected through four generations for increased light scaling of abdominal tergites.

Results from single pair matings are shown grouped according to parental types, and within these groups according to distribution of offspring (Table 2). In single pair crosses where both parents were CKM "0", female offspring of both classes "0" and "1" were produced. These results are similar to those of McClelland (1960) and Hartberg (1969). An

Table 2. Correspondence between CKM classification and computer model classification (Computer Model Values) for female offspring of single pair matings.

Cross number	Classification of parents*		Number of female offspring, CKM classification**								Number of female offspring, computer model classification							Sample size
			0	1	2	3	4	5	6	7	0	1	2	3	4	5	6	
12	7(6)	7(6)								271							271	271
55	7(6)	7(6)								30							30	30
73	7(6)	7(6)								24							24	24
77	7(6)	7(6)								71							71	71
20	7(6)	6(6)								36							36	36
49	0(0)	6(6)						1	7	11						8	11	19
42	0(0)	6(6)							3	20							23	23
1	0(0)	6(6)						6	1	11						7	11	18
3	0(0)	5(6)								42							42	42
66	1(0)	7(6)	1						1	5	1						6	7
67	1(0)	6(6)	6						1	4	6						5	11
32	0(0)	0(0)	79	43							79	43						122
31	0(0)	0(0)	36	14							36	14						50
34	0(0)	0(0)	51	17							51	17						68
37	0(0)	0(0)	72	51							72	51						123
39	0(0)	0(0)	88	34							88	34						122
101	0(0)	0(0)	19	19							19	19						38
10	7(6)	0(0)		22	1		4	1	5	15	23			5		20		48
7	7(6)	0(0)		13		3	3	2		26	13			8		26		47
6	7(6)	0(0)		24			1			14	24				1		14	39
9	7(6)	0(0)		2						4	2						4	6
22	7(6)	0(0)		19						21	19						21	40
27	7(6)	0(0)		109						123	109						123	232
60	7(6)	0(0)		3					2	4	3						6	9
8	7(6)	0(0)								12							12	12
26	7(6)	0(0)							37	100							137	137
24	7(6)	0(0)							30	69							99	99
28	7(6)	0(0)								21							21	21
29	7(6)	0(0)							51	21							72	72
30	7(6)	0(0)						2	8	9							19	19
84	7(6)	0(0)							10	118							128	128
90	7(6)	0(0)								29							29	29
81	7(6)	0(0)								38							38	38
110	7(6)	6(6)		2						5	2						5	7
108	7(6)	6(6)	18	8						74	26						74	100
106	7(6)	6(6)	2	1						10	3						10	13
112	7(6)	6(6)	16	17						79	33						79	112
107	7(6)	6(6)	4	11						78	15						78	93
113	7(6)	6(6)	8	5						17	13						17	30

* First number represents CKM classification of individuals crossed; number in parentheses represents computer model classification. Female parent listed first.

** Under CKM classification, actual observed data are given; under computer model classification, observed data are shown grouped for Chi-square analysis of model fit due to the putative overlap of categories (Fig. 2).

individual scored as CKM "0" is representative of *Ae. aegypti formosus*, while one scored as CKM "1" corresponds to the type form. Although male data are not included in this report, the majority of males that resulted from these crosses were classified as CKM "0"; only a few CKM "1" males were observed from "dark" × "dark" crosses. Of the twenty "dark" × "dark" crosses attempted, six (30%) were successful.

"Light" × "dark" matings were the most successful of all types of crosses made in this study. Thirty such single pair matings were attempted; sixteen (53%) of these produced offspring. Although these parents appeared phenotypically alike (i.e., all females "light" and all males "dark"), variation was exhibited by the offspring of the various crosses. Three of the crosses (cross numbers 6, 7, and 10) yielded offspring ranging from a CKM "1" to a CKM "7." Four crosses (cross number 9, 22, 27, and 60) gave some dark offspring (CKM "1") and some light offspring (CKM "6" or "7"). The remainder of these crosses resulted in light progeny (CKM "5" – "7").

Variability in progeny classes was also observed in matings of "dark" × "light." In cross numbers 1, 3, 42, and 49, offspring were phenotypically light. Cross numbers 66 and 67 differed slightly from the former crosses' parental types, and produced both light and dark offspring. Of the thirty "dark" × "light" crosses attempted, only six (20%) of these yielded offspring. Decreased success in these crosses was thought to be due to poor viability of parental CARN-LIGHT individuals.

Two kinds of "light" × "light" crosses were attempted. The first group (cross numbers 12, 20, 55, 73, and 77) involved parental CARN-LIGHT and resulted in all CKM "7" progeny. The other group (cross numbers 106–113), involved F_1 individuals obtained from a single pair "light" × "dark" (cross number 90), in which all 29 female progeny were CKM "7" and all 27 male progeny were CKM "6." The six successful crosses of these eight attempted resulted in both dark (CKM "0" and "1") and light (CKM "7") female offspring. Although the parents in these crosses (cross numbers 106–113) were all phenotypically light, both light and dark offspring appeared in the F_2 generation. The overall success of both kinds of "light" × "light" crosses was 33%. However, there was a great difference in the two groups of "light" × "light" crosses when each group was considered separately. The success rate for the first group was only 20% while 75% of the crosses in the second group (F_2 individuals from single pair 90) were successful. The striking success of this second group of crosses may be an exemplification of some type of heterosis.

Based on results of the single pair matings, it is proposed that genes at three separate independently assorting loci control the pattern of white scaling on the abdominal tergites in *Ae. aegypti*. The first of these loci determines whether white scales can or cannot appear on the tergites, and is designated "tergite-white" (*Tw*). In the homozygous recessive state (Tw^+Tw^+), this locus is epistatic to genes at the other two loci and prevents the appearance of white scales on the tergites. In the homozygous dominant (*TwTw*) and heterozygous ($TwTw^+$) forms, this locus allows for white scaling of the tergites, but does not contribute to or influence the amount of white scaling. The second locus is occupied by a series of multiple alleles which largely determine the amount of white scaling on the tergites. These genes are termed "white-scaling" and are symbolized by L_1, L_2, and *1*. L_1 produces more white scaling than does L_2; *1* in a homozyous state produces no white scaling. At the third locus appears a gene pair that intensifies the effect of the series of *L* alleles, producing increased white scaling of the tergites except in the homozygous recessive form. This is the "white-intensifier" locus, *I*. A summary of these postulated gene pairs, their computer symbol, the computer model value assigned to each, and the effect of each pair on abdominal tergal white scaling is given in Table 3.

When the "white-intensifier" genes (*II* or *Ii*) appear with the genes for "white scaling" (L_1L_1, L_1L_2, L_2L_2, L_11, or L_21) and where the epistatic genes for "tergite-white" are not present to block their effect, the result is a mosquito with increased white scaling on the abdominal tergites. But when the "white-intensifier" genes (*II* or *Ii*) appear with the recessive alleles for "white-scaling" (*11*), no intensification of white scaling results, as the *11* alleles produce no white scales. Therefore, it would be possible to have "white-intensifier" genes present in a parent generation, and to have these genes passed to progeny, even though the parent generation had no genes for white scaling of the tergites.

From the combinations of the two different alleles at the *Tw* locus, the two different alleles at the *I* locus, and the three different alleles at the *L* locus fifty-four possible genotypes (3 × 3 × 6) were generated; "Computer Model Values" were assigned to each genotype (Table 4), for use in the computer analysis described below.

From the 54 possible genotypes proposed in the genetic model, 2,916 hypothetical matings (54 × 54) could occur. However, a number of

Table 3. Postulated gene pairs, their computer symbol, their computer model value, and their effect on abdominal tergal white scale pattern.

Gene pair	Computer Symbol	Computer model value	Effects of tergal scaling
TwTw	SS	0	Allows white scaling.
TwTw$^+$	ST	0	Allows white scaling.
Tw$^+$*Tw*$^+$	TT	0	Epistatic to L_1, L_2, and *I*; allows no white scaling.
L_1L_1	LL	4*	Produces extreme amount of white scaling.
L_1L_2	LM	3*	Produces large amount of white scaling.
L_2L_2, L_1l	MM,LN	2*	Produces intermediate amount of white scaling.
L_2l	MN	1*	Produces minimal amount of white scaling.
ll	NN	0	Produces no white scaling.
II,Ii	II,IJ	2*	Intensifies white scaling if *Tw* and L_1 or L_2 are present.
ii	JJ	0	No intensification of white scaling.

* These values are only used when the gene pairs *TwTw* or *TwTw*$^+$ are present in the genotype. In the presence of the gene pair *Tw*$^+$*Tw*$^+$ these values *are not* used and the computer model value would be 0, since *Tw*$^+$*Tw*$^+$ is epistatic to these genes.

these crosses are reciprocal crosses, and thus yield no additional information since these characters do not appear to be influenced by sex-linkage. The number of distinct possible crosses, eliminating reciprocal crosses, is 1,485 [n(n+1)/2], where n equals the number of parental genotypes. These crosses can be represented as follows:

Cross parent #1 with parents #1 through #54
Cross parent #2 with parents #2 through #54
Cross parent #3 with parents #3 through #54
.
.
.
Cross parent #54 with parent #54.

This crossing scheme eliminates reciprocal crosses so that each cross is unique.

These 1,485 crosses can produce 64 different gametic combinations (progeny), since individuals with three pairs of independently assorting genes produce eight types of gametes

Table 4. Possible genotypes and their computer model values (C.M.V.).

Genotype	C.M.V.*	Genotype	C.M.V.	Genotype	C.M.V.
Tw$^+$Tw$^+$11ii	0	TwTw$^+$11ii	0	TwTw$^+$L$_2$L$_2$Ii	4
Tw$^+$Tw$^+$11Ii	0	TwTw$^+$11Ii	0	TwTw$^+$L$_2$L$_2$II	4
Tw$^+$Tw$^+$11II	0	TwTw$^+$11II	0	TwTw$^+$L$_1$1Ii	4
Tw$^+$Tw$^+$L$_2$1ii	0	TwTw11ii	0	TwTw$^+$L$_1$1II	4
Tw$^+$Tw$^+$L$_2$1Ii	0	TwTw11Ii	0	TwTw$^+$L$_1$L$_1$ii	4
Tw$^+$Tw$^+$L$_2$1II	0	TwTw11II	0	TwTwL$_2$L$_2$Ii	4
Tw$^+$Tw$^+$L$_2$L$_2$ii	0	TwTw$^+$L$_2$1ii	1	TwTwL$_2$L$_2$II	4
Tw$^+$Tw$^+$L$_2$L$_2$ii	0	TwTwl$_2$Iii	1	TwTwL$_1$1Ii	4
Tw$^+$Tw$^+$L$_2$L$_2$II	0	TwTw$^+$L$_2$L$_2$ii	2	TwTwL$_1$1II	4
Tw$^+$Tw$^+$L$_1$1ii	0	TwTw$^+$L$_1$1ii	2	TwTwL$_1$L$_1$ii	4
Tw$^+$Tw$^+$L$_1$1Ii	0	TwTwL$_2$L$_2$ii	2	TwTw$^+$L$_1$L$_2$Ii	5
Tw$^+$Tw$^+$L$_1$II	0	TwTwL$_1$1ii	2	TwTw$^+$L$_1$L$_2$II	5
Tw$^+$Tw$^+$L$_1$L$_2$ii	0	TwTw$^+$L$_2$1Ii	3	TwTwL$_1$L$_2$Ii	5
Tw$^+$Tw$^+$L$_1$L$_2$Ii	0	TwTw$^+$L$_2$1II	3	TwTwL$_1$L$_2$II	5
Tw$^+$Tw$^+$L$_1$L$_2$II	0	TwTw$^+$L$_1$L$_2$ii	3	TwTw$^+$L$_1$L$_1$Ii	6
Tw$^+$Tw$^+$L$_1$L$_1$ii	0	TwTwL$_2$1Ii	3	TwTw$^+$L$_1$L$_1$II	6
Tw$^+$Tw$^+$L$_1$L$_1$Ii	0	TwTwL$_2$1II	3	TwTwL$_1$L$_1$Ii	6
Tw$^+$Tw$^+$L$_1$L$_1$II	0	TwTwL$_1$L$_2$ii	3	TwTwL$_1$L$_1$II	6

* Note that *Tw*$^+$*Tw*$^+$ is epistatic to L_1, L_2, and *I* and allows no white scaling; therefore C.M.V. is 0 when *Tw*$^+$*Tw*$^+$ is in the genotype.

with equal frequencies. Crossing of two such individuals yields 64 (8 × 8) possible combinations of these gametes. These gametic combinations (progeny) may or may not be genotypically distinct. Those genotypes producing similar phenotypes are grouped by the computer so that phenotypic ratios for each mating are readily apparent.

The obvious plethora of possible matings (1,485) and progeny (95,040) necessitated computer analysis. The computer program was written so that grouping of crosses by expected phenotypic distribution of offspring was possible. This allowed the rapid identification of hypothetical crosses which would produce results similar to those observed, thus facilitating comparison of observed data to theoretical data. The computer program was written in FORTRAN EXTENDED for a Control Data CYBER 70 model 74. Since the program uses extensive character manipulation, it is highly dependent on the extended features of Control Data FORTRAN.

The basic design of the computer program involves the creation of three tables: (1) A table consisting of six character patterns representing the fifty-four possible genotypes. This table is created one time only. (2) A table of corresponding "Computer Model 1 Values" assigned to the 54 genotypes. This table is created one time only. (3) A table of frequencies, i.e., each entry is a count of the number of times the corresponding genotype would occur when all 64 possible offspring from a given cross are examined. This table is created and results are printed for each of the 1,485 possible crosses. As stated in the previous paragraph, the crosses are grouped by expected distribution of offspring, thus making comparison of observed to expected results for each cross easier to complete.

Following are a few selected crosses from the computer printout to illustrate how the expected results are displayed. To the right of the cross the Computer Model Value for the parents crossed is in parentheses. The genotypes of the parents and offspring are given in their computer symbols (see Table 3 for gene symbols). The expected frequency of the offspring for each Computer Model Value is listed under each category. It should be noted that the crosses between phenotypically similar, but genotypically different, parents can give divergent results.

In order to quantify the degree of white scaling on the tergites, numerical values were assigned to the proposed alleles. These numerical values are referred to as "Computer Model Values" (Tables 2, 3, and 4). Since the *Tw* locus only determines whether white scales can or cannot appear on the abdominal tergites and does not contribute to the amount of white scaling, this gene pair was assigned a computer model value of zero. The series of *L* genes and the *I* genes were assigned computer model values as shown (Table 3). Genotypes with a computer model value of 0 or 1 would appear dark, with few if any white scales except in basal bands, which are always present on tergites II-VII and may or may not be present on tergite I. Intermediate genotypes, i.e., with amount of white scaling between dark and light, have computer model values ranging from 2 to 4. The light genotypes, where white scaling was maximal, have either a 5 or 6 computer model value. Often in these latter genotypes dark scaling was limited to a few black scales speckled along the lateral part of the tergites.

These computer model values for the proposed alleles were then equated to the CKM method of classification, where classification is based solely on the number of tergites having white scales (Fig. 3). It will be noted that any one computer model value may be representative of two or three CKM categories. This overlap of categories may be attributable to various factors: several modifier genes may affect expression of white scaling; different kinds of gene interaction may result in different phenotypic expression of alleles; and, the computer model values are only numerical estimates of the amount of white scaling that can be expected. Thus, any one category of classification may contain a very few individuals of the category immediately adjacent to it on either side. It is believed, however, that the majority of individuals fell in the proper category of classification, with a few extremes falling into adjacent categories. For example, a mosquito with a genotype resulting in a computer model value of zero may in fact have a few white scales on the first tergite, appearing to be a CKM "1" instead of a "0". Or, due to a different effect of modifier genes or different gene interaction, a genotype with a computer model value of "5" may appear to be a CKM "6."

It is felt that this overlap of categories is justifiable since, as Mather (1942) has pointed out, the interaction of the genes of organisms and nonheritable agencies can contribute to the lack of completely unambiguous phenotypic classes for polygenic traits.

Data from female offspring of the 39 successful single pair matings are grouped in view of this proposed overlap of categories (Table 2). From these grouped data, the expected computer model ratio of offspring phenotypes was determined (Table 5). Chi-

TTMNIJ x TTMNII (0 x 0)

0	1	2	3	4	5	6
TTNNIJ 8						
TTNNII 8						
TTMNIJ 16						
TTMNII 16						
TTMMIJ 8						
TTMMII 8						

STMNJJ x SSMNJJ (1 x 1)

0	1	2	3	4	5	6
STNNJJ 8	STMNJJ 16	STMMJJ 8				
SSNNJJ 8	SSMNJJ 16	SSMMJJ 8				

TTLNJJ x STLNJJ (0 x 2)

0	1	2	3	4	5	6
TTNNJJ 8		STLNJJ 16		STLLJJ 8		
TTLNJJ 16						
TTLLJJ 8						
STNNJJ 8						

TTMNIJ x SSLMIJ (0 X 5)

0	1	2	3	4	5	6
	STMNJJ 4	STMMJJ 4	STMNIJ 8	STMMIJ 8	STLMIJ 8	
		STLNJJ 4	STMNII 4	STMMII 4	STLMII 4	
			STLMJJ 4	STLNIJ 8		
				STLNII 4		

TTLNJJ x STLMIJ (0 x 5)

0	1	2	3	4	5	6
TTMNJJ 4	STMNJJ 4	STLNJJ 4	STMNIJ 4	STLNIJ 4	STLMIJ 4	STLLIJ 4
TTMNIJ 4			STLMJJ 4	STLLJJ 4		
TTLNJJ 4						
TTLNIJ 4						
TTLMJJ 4						
TTLMIJ 4						
TTLLJJ 4						
TTLLIJ 4						

STLLII x STLLII (6 x 6)

0	1	2	3	4	5	6
TTLLIJ 16						STLLII 32
						SSLLII 16

SSLLJJ x SSLLII (4 x 6)

0	1	2	3	4	5	6
						SSLLIJ 64

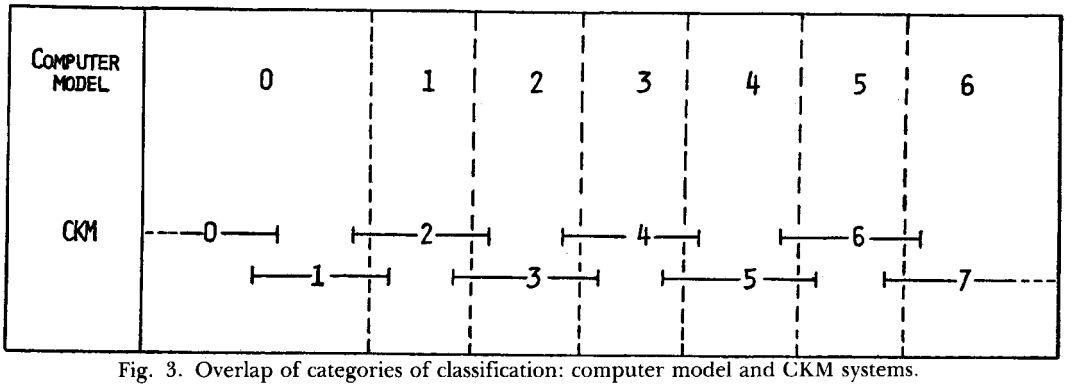

Fig. 3. Overlap of categories of classification: computer model and CKM systems.

square analysis of deviation of observed data from expected ratios was performed for each cross. The Chi-square value and the probability that deviations from the expected are due to chance alone are given (Table 5).

Several times during the course of this study, a light-colored cuticle and light background scaling were observed. The lightness of this cuticle and scale color was striking when compared to the normal black or brownish-black cuticle of most *Ae. aegypti*. A description of the light cuticle and background scales was penned at the time as "light brown" or "very light" brown—almost yellowish." This phenomenon was noted in later selections of the CARN-LIGHT strain and in heavily white-scaled progeny of some single pair matings where parental CARN-LIGHT individuals were used.

Observations during the course of this study substantiate earlier findings that males appear darker than females (Connal 1927, Craig and VandeHey 1962, Lewis 1945, Mattingly 1957, McClelland 1960). Males generally fell a full category of classification below (darker than) females except in crosses where all progeny were extreme darks or extreme lights. Lightest males observed in this study were classified as CKM "7," but no male with white scales covering the entire abdomen was ever observed. The first six tergites of the males in point were completely clad in matte-white scales, the white pattern ending abruptly with the white apical band of tergite VII. This is in sharp contrast to the white scale pattern in CKM "7" females, where white scales usually extended without interruption to the distal end of the tergite VII. In males, randomly scattered white scales appeared on the seventh tergite, the number of white scales being extremely variable. The white scales of this tergite were never observed to form any pattern. Neither were they concentrated on any particular area of the tergite. In the CARN-LIGHT F_6 population males differ from each other only in the number and random arrangement of white scales on the seventh abdominal tergite.

CARN-LIGHT females also differ from each other in scaling of the seventh tergite. Generally this tergite, like all those anterior to it, is completely covered in matte-white scales. In many specimens, however, black scales in varying numbers are present on the apical portion of tergite VII. When present, black scales form rough triangles on either side of the tergite. These triangles of black scales begin at the apex of the tergite and meet the lateral margin of the tergite at about one-third the length of the tergite. The black scales do not fuse in the center of the tergite, so that the appearance of these two small black antero-lateral triangles results. Females vary less in regard to scaling of tergite VII than do males.

DISCUSSION

All experimental crosses except one (cross number 7) support the proposed genetic mechanism at the 0.05 or greater level of significance. This exceptional cross yielded a small number of individuals; thus, small sample size and/or human error in choosing parental types or in scoring progeny may be responsible for failure of this cross to support the proposed genetic model.

Until rather recently there has been a basic assumption that any quantitative trait must be controlled by a large number of polygenes. Reexamination of this assumption by Thompson (1975, 1977, 1979) shows that only a small number of loci are involved. The present investigation supports his view since only three loci are involved in the genetic system proposed and supported in this study.

Several mutant genes are known to affect abdominal tergal scale pattern in *Ae. aegypti*. The mutations white abdomen (*W*) and lateral silver spot (*s*), which when present increase the amount of white scaling on the tergites, were described by Craig and VandeHey (1962). Craig and Hickey (1967) list spot (*s*) and

Table 5. Chi-Square analysis of results of single pair matings.

Cross number	Classification of parents*	Expected computer model value ratio							Model fit	
		0	1	2	3	4	5	6	χ^2 value	P
12	7(6) 7(6)							1	0	0.99
55	7(6) 7(6)							1	0	0.99
73	7(6) 7(6)							1	0	0.99
77	7(6) 7(6)							1	0	0.99
20	7(6) 6(6)							1	0	0.99
49	0(0) 6(6)						1	1	0.47	0.30
42	0(0) 6(6)							1	0	0.99
1	0(0) 6(6)						1	1	0.89	0.30
3	0(0) 5(6)							1	0	0.99
66	1(0) 7(6)	1						3	0.43	0.50
67	1(0) 6(6)	1						1	0.09	0.70
32	0(0) 0(0)	5	3						0.26	0.50
31	0(0) 0(0)	3	1						0.24	0.50
34	0(0) 0(0)	3	1						0	0.99
37	0(0) 0(0)	5	3						0.82	0.30
39	0(0) 0(0)	3	1						0.54	0.30
101	0(0) 0(0)	1	1						0	0.99
10	7(6) 0(0)	4			1		3		0.43	0.70
7	7(6) 0(0)	4			1		3		8.22**	0.01
6	7(6) 0(0)	4				1		3	4.15	0.10
9	7(6) 0(0)	1						1	0.17**	0.50
22	7(6) 0(0)	1						1	0.10	0.70
27	7(6) 0(0)	1						1	0.84	0.30
60	7(6) 0(0)	1						1	0.44	0.50
8	7(6) 0(0)							1	0	0.99
26	7(6) 0(0)							1	0	0.99
24	7(6) 0(0)							1	0	0.99
28	7(6) 0(0)							1	0	0.99
29	7(6) 0(0)							1	0	0.99
30	7(6) 0(0)							1	0	0.99
84	7(6) 0(0)							1	0	0.99
90	7(6) 0(0)							1	0	0.99
81	7(6) 0(0)							1	0	0.99
110	7(6) 6(6)	1						3	0.07	0.70
108	7(6) 6(6)	1						3	0.53	0.70
106	7(6) 6(6)	1						3	0.03	0.70
112	7(6) 6(6)	1						3	1.19	0.20
107	7(6) 6(6)	1						3	3.44**	0.05
113	7(6) 6(6)	1						3	0.53	0.30

* First number represents CKM classification of individuals crossed; number in parentheses represents computer model classification. Female parent listed first.

** Yates' correction factor used on these data.

pale-abdomen (*pa*) as causing increased white tergal scaling. A gene designated as black tergite (Bt^+)[5] (VandeHey et al. 1978) controls white scaling of the first abdominal tergite; its allele, *Bt*, produces no white scales on the first tergite. These genes may serve as modifiers to the presently proposed polygenic system for inheritance of abdominal tergal scale pattern in *Ae. aegypti*.

A strikingly different pattern of scaling of the seventh tergite in CARN-LIGHT was observed during this investigation. So far as can be determined, these observations have not previously been reported in the literature. The scale pattern of this tergite may be influenced by a genetic system other than the one controlling the scaling of the first six tergites. Such an influence would not be completely unexpected since tergite VII serves as somewhat of a housing for the terminalia which in both sexes are formed from modifications of segments VIII-X. Tergite VII may therefore be influenced by genes which control development of the terminalia in both sexes, as well as

[5] Machado-Allison, C. E. 1971. Genetic differences among subspecies of *Aedes aegypti* and their evolutionary implication. Ph.D. Thesis, University of Notre Dame, Notre Dame, IN.

by those genes which control rotation of the terminalia in males. That the seventh tergite appears to be more greatly affected in males than in females suggests the possibility of a secondary sex characteristic or a sex-influenced characteristic. It was beyond the scope of this investigation to determine the genetic system controlling the scale pattern of the seventh tergite in particular; it is not known if such control is mediated by a number of genes or by a single gene as has been shown for tergite I[5] (VandeHey et al. 1978).

The present system of *Ae. aegypti* taxonomy proposed by Mattingly (1957) separates the species into two types: mosquitoes without white scales on the first tergite, and those with white scales on at least the first tergite. As previously noted, the scaling of this tergite is controlled by the *Bt* locus. The great variability of abdominal tergal scaling led McClelland (1967) to suggest that the species be interpreted as a polymorphic rather than a polytypic one. McClelland's suggestion was further supported when he observed that a continuous range of abdominal tergal scale pattern existed in some populations of *Ae. aegypti* (McClelland 1974). Scott and McClelland (1977) proposed a model to explain polymorphism in *Ae. aegypti*. Their model included an indoor ecotype and an outdoor ecotype, and three possible habitats: human, peridomestic and natural. The indoor ecotype consisted of mosquitoes with increased white scaling of abdominal tergites, while mosquitoes with predominantly dark scaling on abdominal tergites comprised the outdoor ecotype. The model indicated that polymorphism of *Ae. aegypti* in East Africa was a result of three factors: (1) the presence of a dry season during which breeding occurs only in the human habitat; (2) greater fitness of the indoor ecotype in the human habitat and of the outdoor ecotype in the natural habitat; and (3) less than random movement between human and natural habitats (Scott and McClelland 1977). Paterson et al. (1976) proposed that since the indoor and outdoor ecotypes exist sympatrically and yet remain distinct types, they must be different species. Scott and McClelland (1977) disagreed with Paterson et al. (1976) on this point. Furthermore, there has been little or no evidence of reproductive isolation in subspecies of *Ae. aegypti* (Hartberg and Craig 1968, McClelland 1967, Scott and McClelland 1975).

Under the present system of *Ae. aegypti* taxonomy, taxonomic characters can be altered by single genes such as black tergite[4] or by expression of alleles at one or two loci which determine lightness according to the polygenic system proposed herein. These facts seem to indicate that reevaluation of the bases for *Ae. aegypti* taxonomy is needed. It is not disputed that indoor and outdoor ecotypes exist sympatrically, and also as distinct allopatric populations. However, it appears that too much emphasis has been placed on abdominal tergal scaling patterns as the taxonomic criterion. Regarding the presently accepted system of classification of *Ae. aegypti* based on Mattingly (1957), Craig and Hickey (1967) state that it is significant that taxonomic characters can be altered by single genes. Results of the present study support the above statement, as abdominal tergal scale pattern can be influenced greatly by any one of the three genetic loci proposed in the genetic model, or probably even by any one or more of the several listed possible modifiers. Abdominal tergal scale pattern may be useful as a tool in distinguishing populations, but may not be valid as the exclusive taxonomic basis for classification of the species.

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