MUTANTS IN *AEDES ALBOPICTUS* (DIPTERA: CULICIDAE) [1]

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In recent years, a very substantial amount of research has been performed on the formal genetics of mosquitoes. However, attention has been directed largely to *Aedes aegypti* (L.) and the *Culex pipiens* complex. For example, more than 80 mutants are known in *Aedes aegypti* (VandeHey, 1964). About 30 mutants have been isolated in *Culex pipiens,* largely in the laboratories of H. Laven and J. B. Kitzmiller. In *Anopheles,* a few mutants have been found in such species as *An. albimanus* (Rozeboom, 1963), *An. quadrimaculatus* (French & Kitzmiller, 1964) and *An. gambiae* (G. Mason, personal communication).

Although there are about 800 species of *Aedes,* genetic work in this genus has been limited to *A. aegypti.* It would seem that genetic studies of other *Aedes* could make valuable contributions in the development of a comparative genetics for mosquitoes. The example provided by *Drosophila* genetics is instructive here. Our knowledge of evolution and of genetic systems has been greatly enhanced by in-depth studies of *D. melanogaster* and comparative studies of other species in the genus.

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Aedes albopictus (Skuse) is a member of Group C of subgenus *Stegomyia.* It is widely distributed in the Oriental Region, Oceania, Australia and Malagasy. The species is a container breeder and, like *A. aegypti,* is often found associated with man. *A. albopictus* is a major vector of dengue and, perhaps, other viral diseases. The species is an excellent laboratory subject and can be used for almost all the biological and physiological experimentation for which *A. aegypti* has been used.

In view of the importance and laboratory adaptability of *A. albopictus,* it seems rather remarkable that it has not been studied from the genetic point of view. Perhaps the closest approach has been the attempts of many workers to hybridize *A. aegypti* and *A. albopictus.* However, Leahy (1962) demonstrated complete reproductive isolation between the two species.

Mutants and marker genes are the first prerequisites for establishment of a formal genetics. Therefore, a search for mutants was initiated in *Aedes albopictus.*

MATERIALS AND METHODS

Three geographical populations of *A. albopictus* are maintained at the Mosquito Genetics Project, University of Notre

Dame. Visible mutations were sought in these strains.

The populations were:

1. AL-MAUR: Laboratory colony of G. A. H. McClelland, who received the strain field-collected from R. Mamet, Mauritus, in 1962.
2. AL-MAD: Laboratory colony of G. A. H. McClelland, received field-collected from A. Grijebine, O.R.S. T.O.M., Tananarive, Madagascar, 1961.
3. AL-ISR: Laboratory colony of the senior author, maintained at the Israeli Institute for Biological Research, Ness Ziona, collected in India, site unknown, in 1957.

The rearing methods used were generally similar to the standard procedures for *A. aegypti* described by Craig and VandeHey (1962). The most important departure was in the egg stage, in that *A. albopictus* requires 72–96 hours for complete embryonation. Eggs of *A. aegypti* are completely embryonated in 48–72 hours after deposition and can be dried very soon thereafter. Eggs of *A. albopictus* must be held on moist paper at least 3 days before drying. If held in an environment with high humidity, the dried eggs remain viable for 3–5 months.

Eggs from each population were hatched with deoxygenated water. The larvae were reared in a constant environment room with a temperature 27±2° C., and relative humidity of 80±5 percent. They were fed Liver Powder, N. F. (Nutritional Biochemicals Corp., Cleveland, Ohio). Pupae were segregated by sex, the female being larger than the male. As the adults emerged they were held in separate containers and were provided with sugar cubes. The females were offered a blood source from an anesthetized mouse. The sugar cubes were removed 24 hours prior to blood feeding in order to insure complete engorgement.

For microscopic examination, mosquitoes were anesthetized with ethyl ether. Virgin mosquitoes, 1–3 days old, were examined through a stereoscopic microscope. A magnification of 12 diameters was employed. The mosquitoes were handled with a No. 5 watchmaker's forceps.

Each adult mosquito was thoroughly examined for any morphological deviation from the wild type appearance. Attention was paid only to gross morphological variations found in the adult mosquito. The structure and pattern of the immature stages as well as those of the bristles and body scales of the adults were not given special attention.

Each variant form found was mated to a sib, usually in a single-pair cross, although some mass matings were employed. The line was then reared for two generations. A complete failure to recover the variation even in the second generation was considered to be an indication for its non-genetic basis. However, if the variation was recoverable the mutant was maintained both by mass mating and in inbred lines. Stock cultures of each of the mutants isolated are currently available from the Mosquito Genetics Project, University of Notre Dame. Many recessive mutants are present in populations at low frequency in the heterozygous condition. The presence of such mutants can be revealed by inbreeding, as was done by Craig and VandeHey (1962). Several of the mutants isolated in the present work originated from lines which had been inbred by single-pair brother-sister matings for several generations.

MUTANTS

Proboscipedia (*prb*). This mutant was isolated from the AL-MAUR strain. The mutant phenotype results in conversion of the labella into two tarsal segments, including claws (Fig. 1). In addition, the palpi are converted into a second set of antennae. This mutant is analogous to proboscipedia in *Drosophila melanogaster,* which was discovered by Bridges and Dobzhansky in 1932. In both cases, mouthparts were modified into leg-like and antenna-like appendages.

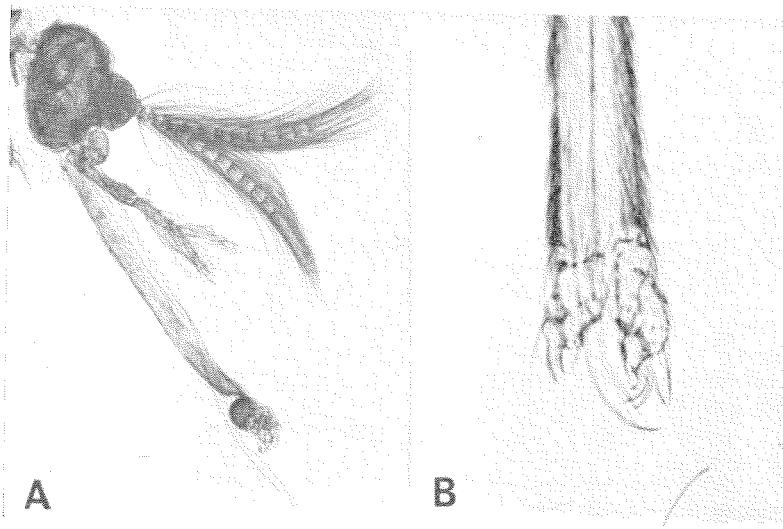

FIG. 1.—The mutant proboscipedia in *Aedes albopictus*. (A) Head of male, showing modified labella and antenna-like palps. (B) Enlarged view of the apical portion of the proboscis, showing modification of labella into two tarsal segments with paired claws.

This is the first homeotic mutant to be described in mosquitoes. Homeotic mutants are brought about by a change in the direction of the development of embryonic anlagen of a body segment into new channels, so that they differentiate into organs normally characteristic of other segments (Stern, 1955). Such mutants in *Drosophila* include aristapedia (arista of antenna changed to a leg) and bithorax (halteres changed to wing-like appendages) as well as proboscipedia. Among the homeotic mutants of *Musca domestica* are aristapedia, antennapedia and abdominal legs. H. V. Daly (personal communication 1965) has recently discovered labiopedia in *Tribolium confusum*.

There is some variation in expression of proboscipedia in *A. albopictus*. In its most extreme expression, the proboscis of the female may be very short because the apical region is contracted into a twisted bulb. However, the tarsal claws at the apex of the proboscis are usually visible. The altered palp of both sexes may occasionally carry a single 'tarsal' claw. In the male, the modified palp is reduced to two segments and is antenna-like, although less hairy than the normal antenna. The modified palp of the female is similar to that in the male. Sometimes the true antennae are shortened or compressed and this modification may be asymmetric.

The mutant results in sterility in females because they are unable to take a blood meal. Males are viable and fertile. Both sexes are able to feed on sugar solutions. Mosquitoes fed on sugar and a dye showed abundant color in the midgut. However, females did not feed on a solution of heparinized blood and sugar. Occasionally, both sexes die during adult emergence, probably because the modified distal portion of the proboscis is caught in the pupal case.

Since females showing *prb* are sterile, maintenance of homozygous stocks is impossible. Lines were maintained by crossing homozygous males to their heterozygous sisters in every generation.

To determine the mode of inheritance, crosses were made between wild type fe-

males (+/+) and proboscipedia males (*prb*/*prb*). The F_1 were all wild type. The following results were obtained from 20 F_2 pairs:

♀ wild type	451
♀ proboscipedia	51
♂ wild type	349
♂ proboscipedia	145
Total:	996 (+58 dead pupae)

The ratio of wild type to proboscipedia was 800:196. This is the general sort of result one would expect from genes with some lethality. The expected segregation for a 3:1 ratio would be 747:249; the actual results give a Chi-square value of 11.5 ($P<.001$). Thus, the results do show a departure from a 3:1 ratio. Fifty-eight dead pupae were observed. If all of these were *prb*/*prb*, one would have a segregation ratio of 800:254. The Chi-square value would be 0.4 and the hypothesis of a 3:1 segregation would be upheld. Following these assumptions, one might suggest that in this cross, only about 77 percent of proboscipedia homozygotes reached adulthood.

The data show differential segregation according to sex. In culicine mosquitoes, sex seems to be determined by a single gene, *m*, which is homogametic in females (*m*/*m*) and heterogametic in males (*M*/*m*). Moreover, crossover occurs in both sexes. Thus, the pattern for sex-linked inheritance is somewhat different from that expected in *Drosophila*-type segregation. Table 1 shows the pattern that would be expected if proboscipedia were linked to sex. If one applies this scheme to the data obtained, a crossover value of 20.3 ± 2.0 is obtained. Certainly, this cross should be repeated to confirm this value. At any rate, the data are compatible with the hypothesis that *prb* is linked to sex. The linkage group with sex and, tentatively, proboscipedia, is here designated as group I in *Aedes albopictus*.

As a further check on the mode of inheritance, F_1 females (+/*prb*) were backcrossed to proboscipedia males (*prb*/*prb*). Results were as follows:

♀ wild type	209
♀ proboscipedia	124
♂ wild type	212
♂ proboscipedia	203
Total:	748 (+38 dead pupae)

Following the sex-linkage hypothesis, a ratio of 1:1 would be expected for both sexes. A ratio of 1:1 is evident in males (Chi-square=0.194, $P>.80$) but there is a significant deficit in proboscipedia females (Chi-square=21.5, $P>.001$). The sex ratio in *A. albopictus* is close to 1:1; the number of wild type females is in line with the number of males. One might hypothesize that about 80 proboscipedia females died in the developmental stages, giving a survival rate of about 60 percent for mutant females. The disparity between this figure and that obtained from the F_2 data calls for further investigation of lethality in this mutant.

Because *prb*/*prb* females are unable to take blood, stock maintenance is difficult.

TABLE 1.—The scheme of crosses made to demonstrate the mode of inheritance of *prb*, based on the assumption that this gene is linked to the factor for sex determination (*mm*=♀, *Mm*=♂).

Generation	Genotypes		Phenotypes *
Parental	$\frac{m +}{m +} \times$	$\frac{M\ prb}{m\ prb}$	♀ wild type ♂ proboscipedia
F_1	$\frac{m +}{m\ prb}$	$\frac{M\ prb}{m +}$	All wild type
F_2 non-crossovers	$\frac{M\ prb}{m\ prb}$	$\frac{M\ prb}{m +}$	♂ wild type: ♂ prb
	$\frac{m +}{m\ prb}$	$\frac{m +}{m +}$	♀ wild type
crossovers	$\frac{M +}{m +}$	$\frac{M +}{m\ prb}$	♂ wild type
	$\frac{m\ prb}{m +}$	$\frac{m\ prb}{m\ prb}$	♀ wild type: ♀ prb

* Frequency of crossover $= \frac{(2 \times \text{prb ♀♀})}{\text{total ♀♀}} \times 100$.

At the suggestion of Prof. K. S. Rai, an attempt was made to incorporate *prb* into an autogenous line (see below). Autogenous females (+/+) were crossed to proboscipedia males (*prb/prb*). The F_1, which were obtained without blood feeding, were wild type in appearance. An F_2 was also obtained without blood. However, there were only a few proboscipedia females in the F_2 and these failed to oviposit. Nevertheless, this method offers interesting possibilities for obtaining a homozygous line of proboscipedia. These crosses should be repeated using larger numbers of individuals.

The effect of temperature on survival of proboscipedia has been studied (Table 2).

TABLE 2.—Effect of larval rearing temperature on survival of proboscipedia.

Larval rearing temperature	Initial number *	No. adults of phenotype: Wild type ♀	Wild type ♂	Proboscipedia ♀	Proboscipedia ♂
27° C.	250	55	57	49	53
34° C.	250	28	36	..	1

* 250 newly hatched larval, reared in lots of 50, from the backcross of ♀ +/prb × ♂ *prb/prb*.

Larvae from a backcross were reared at 27 and 34° C. At the lower temperature, about half of the emerging adults were proboscipedia. At 34°, only 1 proboscipedia male was recovered, indicating differential sensitivity of the phenotypes. The segregation data at 27° support the earlier hypothesis concerning mode of inheritance, since they fit the 1:1:1:1 segregation expected.

Individuals homozygous for proboscipedia take longer to reach adulthood. In an F_2, 232 progeny were obtained, 61 proboscipedia and 171 wild type. On the second day of adult emergence, 50 percent of the wild type individuals had emerged, compared to 15 percent for proboscipedia. Similar figures on the fifth day give 97 percent vs. 66 percent.

Yellow larva (*y*). The body color of normal larvae in *A. albopictus* is dark, generally much darker than that of *A. aegypti*. This color is caused by granules deposited in the fat body. Paler, yellowish larvae were discovered in AL-ISR and in the F_1 of a cross between AL-MAD × AL-MAUR. Individuals showing the yellow phenotype were selected and a strain was maintained. Macroscopically, one can distinguish yellow individuals readily, both by general color and by the apparent lack of distinct separation between abdominal segments.

The yellow larvae in *A. albopictus* superficially resemble the mutant yellow found in *A. aegypti* by Craig and Gillham (1959). These authors examined several thousand larvae in each of several other *Aedes*, including *A. albopictus*, but did not find the yellow phenotype. Adhami (1964) confirmed earlier observations that the yellow mutant in *A. aegypti* is due to absence of the uric acid granules which are found within the cells of the fat body of wild type larvae.

Larvae of both *A. aegypti* and *A. albopictus* were sectioned and stained with the hexamine-silver method for uric acid (Pierce, 1961). In *A. aegypti*, wild type larvae stained deeply and yellow larvae gave no reaction. In *A. albopictus*, however, the difference between the phenotypes is quantitative. The yellow mutant has much less uric acid than the wild type, although a histochemically demonstrable quantity is definitely present.

Crosses to elucidate the mode of inheritance of yellow gave anomalous results. Crosses of wild type × yellow usually gave wild type in the F_1. However, a 3:1 segregation was not always evident in the F_2. Some F_2's approximating 1:1 were observed. Crosses of yellow x yellow usu-

ally gave all yellow offspring, although occasional progeny had some dark individuals. These results differ from those in *A. aegypti,* where yellow is inherited as a simple recessive factor on linkage-group II. In *A. albopictus,* the mode of inheritance of yellow is still uncertain and further investigation is needed.

Black palp (*blp*). This mutant, isolated from AL-MAUR, reduces the silver scaling of the palpi of both sexes. In wild type females the dorsal surface of the apical segment of the palp is covered with silver scales. The mutant palp is largely black-scaled, although some silver scales may remain on the dorso-medial surface. Wild type males have a ring of silver scales at the base of palpal segments 2–5. In mutant males, the silver scales are almost absent in segment 2 and are much reduced on segments 3–5. At the time of initial isolation, expression of the mutant was not uniform. Subsequent selection has led to the development of a strain with all individuals showing palps almost entirely black.

Reciprocal crosses were made between wild type and individuals with black palp. F_1 progeny were wild type. Results from backcrosses seem to show that the gene is recessive and, possibly, sex-linked. In a backcross hypothetically $\frac{\text{blp m}}{\text{blp m}} \times \frac{+ \text{ M,}}{\text{blp m}}$ the following progeny were obtained:

♀ wild type	86
♀ black palp	47
♂ wild type	44
♂ black palp	128
Total:	305

If *blp* is indeed linked to *m,* these data would give a crossover value of 33 ± 3.5.

Additional crosses are needed to confirm the hypothesis that *blp* is sex-linked. It is of interest to note that proboscipedia was first discovered in the F_2 of a cross of wild type × *blp.* Subsequent selection of various lines for *blp* has often resulted in re-isolation of proboscipedia. These results might be expected if both genes are, indeed, in linkage-group I. In *Aedes aegypti,* a similar mutant, also called black-palp, occurs in linkage group III. It is doubtful that the loci are homologous in the two species.

Bulb (*b*). This mutant was isolated from a stock with proboscipedia. It is expressed only in males; the apical segment of the palp is reduced to a knob or club-like structure. Expression is often asymmetric, sometimes being limited to a curve in the apical segment. The strain is maintained by crossing of bulb males to their sisters.

A similar mutant named bulb is found in *A. aegypti* (VandeHey and Craig, 1962). However, this factor is a dominant. Moreover, the bulb in *A. aegypti* is usually found in the middle of the apical segment; its counterpart in *A. albopictus* is at the base of this segment and the segment never extends beyond the bulb. Similar mutants have been found in *Culex pipiens.*

From the meager data available to date, it seems that bulb is a sex-limited recessive. Cross of a wild type female with a bulb male gave all wild type in the F_1 and the following in the F_2:

Females	116	
Wild type males	121	
Bulb palp males	37	(9 on one side only)
	274	

White proboscis (*wp*). This mutant was also isolated from a line containing proboscipedia. The scales on the ventral surface of the labium of wild type individuals are entirely black. In the mutant white proboscis, a cluster of white scales occurs at the base of the venter of the labium. Expression is more pronounced in males. A similar mutant, also called white proboscis, occurs in *A. aegypti.* In the latter species, expression is more pronounced in females; in addition, a medial line of white scales may extend to the apex of the proboscis.

Mode of inheritance is unknown. A line selected for *wp* shows a high propor-

tion of white proboscis in every generation, whereas this character is never seen in other stocks of *A. albopictus*. However, crosses of *wp* × *wp* usually have a few wild type offspring. Reduced penetrance may be involved.

Wart (*wa*). This mutant affects the palps of both sexes. In the male, there is a bulb at the joint between segments 3 and 4. The bulb appears as a wart-like protuberance on the ventromedial surface of the palp. In the female, the apical segment of the palp is shorter and more pointed than in wild type. A similar mutant in *Aedes aegypti* occurs in linkage-group 2 and has been designated wart-palp by VandeHey and Craig (1962). However, this mutant affects the junction between segments 2 and 3. Kitzmiller (1958) describes a similar mutant in *Culex pipiens*. Mode of inheritance is unknown. The mutant occurred in sequential generations in a selected line.

Dark scutum (*ds*). This mutant was isolated from *AL-ISR*. It is expressed as increased dark scaling and a reduction of the width of the median silver band on the mesonotum. In addition, all scales of the prescutellar area and the caudal quarter of the median silver band are entirely black instead of the normal silver. On both thorax and abdomen, the silver scales that remain are slightly dull, lacking the normal metallic sheen. Expression is more conspicuous in females. This mutant is reminiscent of dark scutum in *Aedes aegypti* (McClelland, 1962) in that both mutants diminish the silver lines and spots of the mesonotum.

Mode of inheritance is unknown. Frequency of the phenotype was high during four generations of selection.

Autogeny. Autogenous reproduction (egg maturation without an exogenous source of protein) was first observed in our laboratory by Mrs. M. K. Adhami in 1963. Adults of the AL-MAUR strain were fed only on sugar and raisins, yet they produced a few eggs. These eggs were hatched and the resulting F_1 adults were again held without blood meal. Again, eggs were produced. This process of selection was continued in sequential generations. Autogenous reproduction was observed for 12 generations.

Elaborate precautions were taken to eliminate experimental error as an explanation of these observations. Cages with double screening were used and all potential blood sources were excluded. In addition, batches of eggs were divided into three parts and were hatched and reared simultaneously in three different laboratories. Autogenous reproduction was obtained from each of the three groups.

Autogenous reproduction was found in other strains. Table 3 gives an indication of the rate of egg production in several

TABLE 3.—Occurrence of autogeny in several strains of *Aedes albopictus*.

Strain	No. ♀♀ *	Eggs produced without blood meal		
		Total number	Number embryonated	% of embryonated eggs hatching
AL-MAD	50	118	65	74
AL-ISR	50	168	143	92
AL-MAUR-Unselected	50	135	92	78
AL-MAUR-F_8, selected for autogeny	50	246	223	82
AL-MAUR-F_8 selected for autogeny	50	220	94	85
AL-MAUR-F_8, selected for autogeny	50	157	102	71

* 50 ♀♀ and 50 ♂♂ placed in 2 cages and fed with raisins and sugar. No blood was provided at any time.

strains and in the selected line. In this experiment, 50 newly-emerged mosquitoes of each sex were placed in a gallon container and were fed on raisins and sugar. All eggs were deposited within 2 weeks, although the females remained alive up to 3 months. It is evident from Table 3 that the autogenous eggs were not defective. The rates of embryonation and hatching are typical for *A. albopictus*.

The rate of ovulation was always low, even in the selected lines. The unselected AL-MAUR averaged about 2.7 eggs per female; after five generations of selection, the rate rose to 4.4 eggs per female, but dropped to 3.1 in the F_9. Thus, attempts to improve this character by selection were unsuccessful.

Attempts were made to increase the rate of autogeny by inbreeding. Single-pair matings were made with 30 pairs of autogenous individuals. Three of these produced 11, 7 and 6 eggs, respectively. None of these eggs were embryonated.

The first report of autogeny for *Stegomyia* mosquitoes was by Lea (1964). He developed an autogenous line of *Aedes aegypti* by selection, combined with special diets for larvae and adults. In our laboratory, autogeny has been observed in BRAZZA, a strain of *Aedes aegypti formosus*. A line of this strain was reared for three generations without a blood meal. No dietary modification was involved. Our attempts to obtain autogeny from numerous other strains of *A. aegypti* were unsuccessful. Our attempts to increase autogeny in *A. albopictus* with Lea's special diets were also unsuccessful.

A number of workers have demonstrated genetic control of autogeny in *Culex pipiens*. Although autogeny has been demonstrated in several *Aedes*, very little is known about the genetic basis of the character in this genus.

Abnormalities of uncertain origin. A number of structural abnormalities were observed during the course of this study. However, heritability of these modifications could not be confirmed since they were not recovered in subsequent generations.

Among the most interesting abnormalities was an individual with a deep cleft running longitudinally through the mesonotum. A more or less complete mesonotal pattern was evident on each side of the cleft. In addition, a leg-like structure protruded from the cleft. From the dorsal aspect, the thorax appeared to be doubled. A similar abnormality has been observed several times in *A. aegypti* but attempts to establish a line with this abnormality have not been successful. This malformation is probably of teratological origin.

One gynandromorph was found. This individual had the head and left side of the thorax female, the rest of the body being male. To our knowledge, this is the first report of a gynandromorph in *Aedes albopictus*. It seems probable that this individual was formed by fertilization of an egg with two sperm, as was demonstrated by Rai and Craig (1963) for *Aedes aegypti*.

Several thousand larvae were reared at high temperature (34° C.) in the hope that mutants of low penetrance might be better expressed. Among the adults obtained were individuals with modifications resembling mutants in *Aedes aegypti*, including compressed antenna, short palp, broken legs, and blistered or notched wing. However, these were probably phenocopies, since none were recovered in later generations. Among the heat-treated individuals was one intersex. All of the dimorphic parts of this individual were intermediate between male and female. Craig (1965) has isolated a mutant, intersex, in *A. aegypti*. In lines homozygous for this autosomal mutant, rearing of larvae at high temperature feminizes males but does not affect males. Perhaps there is an homologous locus in *A. albopictus*.

DISCUSSION

It is evident that mutants in *A. albopictus* are not particularly uncommon. Earlier workers suggested that morphological mutants in mosquitoes are rare.

However, Craig, VandeHey and Hickey (1961) demonstrated vast genetic variability in *Aedes aegypti*. The gene pool of this species contains a great many morphological mutations, most of them concealed as heterozygous recessives. The present work suggests that a similar situation exists in *Aedes albopictus*. Assays of genetic variability, similar to that of VandeHey (1964) with *A. aegypti*, should prove profitable.

It is interesting to note the similarity between most of the mutants described here and those previously reported for *A. aegypti*. Only proboscipedia has no counterpart. The two species have similar phenotypes in yellow larva, black palp, bulb palp, white proboscis, wart palp and dark scutum. This similarity seems remarkable in view of the complete reproductive isolation which exists between these species. Linkage relationships of these characters should be determined in *A. albopictus*. A comparison of linkage maps for the two species should prove instructive in determining evolutionary relationships.

Craig (1963) has suggested that *Aedes aegypti* might be controlled by genetical manipulation of field populations. Genetic control might be effected through mass production and release of individuals carrying sex ratio distorters, deleterious genes, sterility factors or genes modifying ability to transmit disease. Continued genetic study of *Aedes albopictus* will most probably results in development of factors in this species which might be used in similar programs of genetic control.

SUMMARY

A formal genetics has been initiated for *Aedes albopictus*. Several morphological variants have been isolated, demonstrated to have a simple genetic basis and established in culture. Among these is proboscipedia, the first homeotic mutant in mosquitoes. Other mutants include yellow larva, black palp, bulb palp, white proboscis, wart palp and dark scutum. Similar mutants have been described in *Aedes aegypti*. In addition, autogeny has been demonstrated in *A. albopictus*.

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