

GENETICS OF *Aedes albopictus*¹

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ABSTRACT. *Aedes albopictus* is an important vector of dengue fever and dengue hemorrhagic fever in Southeast Asia. Its distribution extends from Madagascar to Hawaii and is currently expanding. From its proposed origin in Southeast Asia, *Ae. albopictus* has migrated as far as Mauritius and Madagascar to the west and Korea, Japan, Guam, Hawaii and other Pacific Islands to the east. In the continental United States, it was originally reported in the Texas area in August 1985 and is now well established in several states.

This paper reviews information on distribution, cytology and genetics of *Aedes albopictus*. In addition, it includes comments on its competitive interaction with several other species. Relevant information on evolutionary genetics of certain other related sibling species is also included for comparative purposes.

INTRODUCTION

Because of the importance of several species as pests and vectors of human disease, few mosquito genera have attracted as much attention in the laboratory and the field as *Aedes*. Genetically, the yellow fever mosquito, *Ae. aegypti* (Linn.) has been the most thoroughly studied species although more recently the emphasis has shifted to other species in *Stegomyia* and a few other subgenera (Rai and Hartberg 1975, Rai et al. 1982).

The subgenus *Stegomyia* contains approximately 110 described species divided into seven groups including the *Scutellaris* group which is divided into the *scutellaris* and the *albopictus* subgroups consisting of 34 and 11 species respectively (see list in Rai et al. 1982). The former subgroup is largely allopatric in distribution, while the latter is predominantly sympatric. During the last 10 years, our laboratory has pioneered genetic studies in this group.

Because of their unique zoogeography, the *scutellaris* subgroup species have received particular attention in the area of evolutionary genetics through the use of: (a) experimental hybridization (Woodhill 1950, 1954; Hitchcock and Rozeboom 1973, Hoyer and Rozeboom 1977, Hilburn and Rai 1981, Dev and Rai 1982, 1985, Sherron and Rai 1983), (b) mate-choice tests (McLain et al. 1985), (c) chromosomal studies (Dev and Rai 1984, Sherron and Rai 1984a, 1984b), (d) electrophoretic studies of allozymes (Townson et al. 1977, Hilburn and Rai 1981, Pashley and Rai 1983, Pashley et al. 1985) and, (e) analyses of the molecular evolution of the genomes (McLain et al. 1986). Many of these studies

included *Ae. albopictus* (Skuse) for comparative purposes.

Since 1983, the focus of our genetic studies has been on the *Aedes albopictus* subgroup with major emphasis on *Ae. albopictus* in view of its very large and expanding distribution and its importance as a vector species. The primary objective of our current work is to elucidate genetic correlates of geographic differentiation and vector competence in *Ae. albopictus*.

This paper briefly reviews information concerning distribution, range extensions and various aspects of the genetics of this species including competitive interaction with certain related species.

DISTRIBUTION AND RANGE
EXTENSIONS

Aedes albopictus is presumed to have originated in Southeast Asia, also the indigenous home of the dengue viruses (Smith 1956). From its native home, the species moved to the west and east quickly. Currently, it is widely distributed in an area from Madagascar in the west, through the Indomalayan and the Oriental regions, China, Japan, the Pacific islands and extending as far east as Hawaii (Huang 1972, Ho et al. 1973, Knight and Stone 1977). In 1962, *Ae. albopictus* was absent from the South Pacific (Belkin 1962). Yet as Elliott (1980) and Pashley and Pashley (1983) have shown, it has considerably expanded its range recently into various locations in the South Pacific including the Solomon and Santa Cruz islands. These range extensions are obviously brought about by human transport since the species has a rather limited flight range and does not normally travel more than 200 yards (180 m) in its life time (Bonnett and Worchester 1946).

Historically, the establishment of *Ae. albopictus* even in Hawaii is a relatively recent event occurring through human transport sometime between 1830–96 (Hardy 1960, Joyce 1961).

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Aedes aegypti was introduced in Hawaii around the same time as *Ae. albopictus*. The former species is no longer present there although the latter is quite common. On Guam, *Ae. albopictus* first appeared in 1944 and has flourished since (Joyce 1961).

Eads (1972) reported that *Ae. albopictus* larvae and pupae were found in tires shipped to Los Angeles from Vietnam. In June 1983, an adult female of this species was recovered from a light trap in Memphis, Tennessee (Reiter and Darsie 1984). In August 1985, the species was detected in relatively large numbers in Harris County, Texas (Sprenger and Wuithiranyagool 1986). Currently the species occupies a wide range in the United States and is well established in Texas, Louisiana, Tennessee, Alabama, Florida (Sutherland 1986) and has even reached the midwestern states of Ohio and Indiana (C. Moore, personal communication).

Aedes albopictus is a remarkably successful colonizer, able to move easily through commerce routes. Apparently, it gains a foothold in new locations at least initially through its ability to exploit disturbed habitats such as scrap yards, tires and discarded containers. Since a good many of such habitats abut wooded areas, as is the case in and around Houston and New Orleans, the species, in time, will be likely to adapt its breeding to tree holes as well. Once this happens, the species becomes a permanent part of the local fauna.

For the continental United States, the potential public health importance of this species becomes even greater when one realizes that this species is considerably more cold tolerant than *Ae. aegypti*. In Japan and China, where its distribution reaches just about 40°N latitude (Belkin 1962, Huang 1972) and in the Oriental region (North India, West Pakistan, Nepal), it can withstand long periods of freezing. Thus in the United States, it may be expected to become established in more northern (midwestern) states where *Ae. aegypti* cannot exist.

GENETICS

A. CYTOGENETICS

1. *Chromosome Karyotype*: The chromosomal complement of *Ae. albopictus* is composed of three pairs of metacentric chromosomes which can be easily distinguished from each other based on their overall length (Rai 1963). Although actual measurements of chromosome lengths among various geographic populations have not yet been made, there appear to be considerable differences among the same (Rao

1985²). Bianchi et al. characterized heterochromatin (1971), chromosomes (1972a) and replication of chromosomes (1972b) in cell lines in this species.

2. *C-Banding*: The two homologues of the smallest or the sex pair can be distinguished from each other based on their distinctive Giemsa C-banding patterns. The female-determining chromosome possesses an intercalary heterochromatic band in one arm which is absent in the male-determining chromosome (Motara and Rai 1978). The two larger autosome pairs possess centromeric C-bands only.

Steiniger and Mukherjee (1975) described a modified technique for G- and Q-banding in an established cell line of *Ae. albopictus*. More recently, Marchi and Rai (1986) have compared three different types of bands, Q-, H-, R- in *Ae. albopictus* with those of two related species, *Ae. aegypti* and *Ae. mascarensis* MacGregor. The results indicated the presence of structural homology (a G-C rich intercalary region) in the sex-determining chromosome of the three species. They also observed considerable intrachromosomal polymorphism in the width of heterochromatic bands.

3. *Meiosis and Spermatogenesis*: Comparative studies of meiosis and chiasmata frequencies in *Ae. albopictus* and four other related species in the subgroup [*Ae. flavopictus* Yamada, *Ae. pseudalbopictus* (Borel), *Ae. seatoi* Huang and *Ae. unilineatus* (Theobald)] have been examined by Rai and Herman (1985). The chiasmata frequencies ranged from 2.95 per primary spermatocyte at diplotene in *Ae. pseudalbopictus* to 4.50 in *Ae. unilineatus*, with a value of 3.97 in the Tana strain of *Ae. albopictus*. Earlier, Smith and Hartberg (1974) described the process of spermatogenesis in *Ae. albopictus*.

B. *FORMAL GENETICS*: Bat-Miriam and Craig (1966) isolated 7 mutants from three laboratory strains of *Ae. albopictus*. Of these, *Proboscipedia*, a homoeotic mutant, was shown to be sex-linked recessive. Studies on the mode of inheritance were not undertaken in the case of *White proboscis*, *Wart palp*, *Dark scutum* and *Yellow-larva*. *Black palp* was recessive and "possibly sex-linked" and *Bulb palp*, a sex-limited recessive mutant, expressed only in males. An extensive phenogenetic analysis of the female-sterile, proboscipedia, was presented by Quinn and Craig (1971).

Tadano et al. (1980) and Tadano (1981)

² Rao, P. N. 1985. Nuclear DNA and chromosomal evolution in mosquitoes. Ph.D. Dissertation, University of Notre Dame, Notre Dame, Indiana, 96 pp.

have described the mode of inheritance of *White-body* and *Brown-eye* and linkage relations of a dominant mutant, *Frosty-body* and a recessive, *Pigmented pupa* respectively. Eleven morphological mutants have been described in this species, and each of the three linkage groups are marked with at least one locus: sex and *Proboscipedia* on linkage group 1, *Frosty body* and *pigmented pupa*, and *Brown-eye* on the two autosomes.

C. EVOLUTIONARY GENETICS

1. *Biochemical genetics and allozyme differentiation.* Yong et al. (1981, 1982, 1983) undertook formal and population genetic analyses of glucose phosphate isomerase, phosphoglucomutase and glycerol-3-phosphate dehydrogenase in three natural and a laboratory population of *Ae. albopictus* from Peninsular Malaysia.

Pashley and Rai (1983) compared allozyme relationships among 10 species in the *albopictus* and the *scutellaris* subgroups utilizing 25 enzyme systems and horizontal starch gel methods. For the *albopictus* subgroup this study included four strains of *Ae. albopictus* and one of *Ae. seatoi*. Allele frequencies for each locus and each species were calculated and used as input for genetic distance calculations and subsequent clustering and tree-building algorithms and for a principal component analysis. Results obtained were largely in agreement with established taxonomic classifications. Members of the *scutellaris* and *albopictus* subgroups clustered independently.

In order to examine morphological differentiation, Pashley and Rai (1983) also conducted a numerical taxonomic survey in the same two *albopictus* subgroup species using 22 adult, 25 larval and 5 pupal traits from written descriptions of species by Huang (1972, 1975) and Huang and Hitchcock (1980). Results of a principal component analysis indicated that *Ae. albopictus* was intermediate between *Ae. seatoi* and the *scutellaris* subgroup species indicating much greater divergence among the two *albopictus* subgroup species than among the *scutellaris* subgroup species. Thus, with morphology as with mating behavior and experimental hybridization, there is greater divergence within the largely sympatric *albopictus* subgroup than within the allopatrically distributed *scutellaris* subgroup species.

When allozyme differentiation was compared with morphological differentiation, allozymes were more congruent with systematic relationships than morphology, especially adult traits.

More recently, we have begun an allozyme analysis of geographic populations of *Ae.*

albopictus with particular emphasis on the United States strains to decipher their origin. Data on allele frequencies at 8 loci and level of heterozygosity in 13 populations (8 from Texas, 4 from Louisiana and 1 from Tennessee) are being collected. Preliminary data indicate that mean heterozygosity in the Tennessee (Memphis) strain was approximately one-third of that in other U.S. populations suggesting that the former population was founded by a small number of individuals arising from either Houston or New Orleans. Furthermore, considerable differentiation was observed among neighboring populations in Houston and New Orleans. It appears that within each of the two cities populations become established from a few individuals with the result that drift creates local genetic differentiation (Black, Ferrari, Rai and Sprenger, 1986).

2. *Nuclear DNA amounts:* Through the use of quantitative cytophotometry of Feulgen-stained primary spermatocytes, haploid (1c) nuclear DNA amounts have been determined for four species in the *albopictus* subgroup and in ten strains of *Ae. albopictus* (Rao 1985²). These values ranged from 0.95 to 1.29 picograms for the four species and from 0.88 to 1.32 picograms among the ten *Ae. albopictus* geographic strains. Strains from islands had higher DNA amounts than those of continental origins. These amounts are 4–5 times higher than those of *Anopheles* sp. (Jost and Mameli 1972) and 5–7 times higher than that of *Drosophila melanogaster*. (Rasch et al. 1971).

It is possible that the observed differences in DNA amounts among various strains of *Ae. albopictus* are associated with divergence. The Indo-Malayan region, where *Ae. albopictus* is widely distributed, is presumably the center of its origin. Strains from this region possess relatively lower DNA amounts. The expansion of this species to the various island regions is apparently associated with increase in nuclear DNA amounts. Similar correlation exists between nuclear genome sizes and historical migration of the species in the *Ae. scutellaris* subgroup (Rao 1985²).

3. *Molecular differentiation:* In order to compare the molecular organization of the genomes and to investigate if the observed changes in genome sizes result from amplification of repetitive elements, two approaches are being employed in our laboratory.

a. *Variation in abundance and distribution of families of repeated DNA sequences.* This project involved isolating genomic DNA from a strain, digesting it with the appropriate restriction enzymes, cloning the fragments in the drug-resistant *E. coli* plasmid pUC12, identifying

clones containing repetitive elements and hybridizing the same to genomic digests of different geographic strains of *Ae. albopictus* and other species in the group. Numerous recent studies in other taxa have revealed repetitive DNA elements to be evolutionarily labile, making this class of DNA a useful tool for analysis of evolution within closely related taxa (Peacock et al. 1981, Flavell 1986).

Eight highly repeated DNA sequences isolated from a Hawaiian (Oahu) strain of *Aedes albopictus* were hybridized to total genomic DNA from 14 other strains and 6 sibling species to determine the extent of intra- and interspecific variation in sequence abundance. Variation in abundance was as great within as between species and frequently represented the amplification or diminution of hundreds of thousands of sequence copies. A principal components analysis was performed using the abundance of each of the eight sequences. It resolved two clusters: one consisting of seven island species and strains [*Ae. albopictus* strains from Hawaii (3), Japan, Taiwan, Hong Kong, *Ae. flavopictus*, and *Ae. pseudoscutellaris* (Theobald)] and one containing eight species and strains including six from Malaysia and adjacent areas (*Ae. albopictus* strains from Pune (India), Madagascar, Indonesia, Malaysia, *Ae. pseudalbopictus*, *Ae. malayensis* Colless, *Ae. seatoi* and *Ae. hebrideus* Edwards). This clustering may represent the selective conservation of sequence abundance profiles. Extensive sequence variation was suggested in some species and strains by the failure of probes to hybridize at high stringency but to hybridize at low stringency. This also suggests a concerted molecular evolution in which some sequence variants within a highly repeated family have been lost while others have been amplified (McLain et al. 1986). Highly repeated sequences may have been responsible for some of the more than two-fold increase in genome size reported for these sibling species. Furthermore, this class of DNA may play an indirect role in local adaptation and even speciation through effects on frequency and localization of recombination and developmental rates (Peacock et al. 1981, Macgregor and Sessions 1986, Flavell 1986).

b. *Genome organization*: In order to compare molecular organization of the genome among various strains of *Ae. albopictus* and related species in terms of the relative proportion of unique, middle and highly repetitive sequences of DNA, the methodology of Britten et al. (1974) is being employed. DNA from two strains, Calcutta and Mauritius possessing the smallest (0.86 pg) and the largest (1.32 pg) genome sizes respectively, has been characterized. The results indicate that 17.23% of the

genome (or 0.149 pg) consists of highly repetitive DNA, 37.45% middle repetitive and 35.07% unique in the former and 27.59% (or 0.364 pg), 32.52% and 30.53% respectively, of these same classes in the latter strain (Black and Rai 1986). Thus, the Mauritius strain possesses approximately 2½ times as much repetitive DNA as does the Calcutta strain.

4. Reproductive differentiation

a. *Experimental hybridization*: The extent of insemination, embryonation and egg hatch rates and hybrid viability observed in intra- and interspecific crossing experiments is important in determining levels of differentiation within and among species, especially when used in combination with other measures. In addition, experimental hybridization allows insights into the possible isolating mechanisms that prevent or restrict gene flow among populations. Crossing relationships among 8 geographic strains of *Aedes albopictus* (Mauritius, Japan, Hawaii, Indonesia, India, Malaysia and United States) and five species in the subgroup (*albopictus*, *flavopictus*, *seatoi*, *pseudalbopictus* and *unilineatus*) have been examined.

Interstrain crosses yielded relatively high egg hatches except Mauritius females, which produced completely infertile, unembryonated eggs, when mated with males of the other strains. The reciprocal crosses, involving males of the Mauritius strain and females from the other strains tested, produced egg hatches ranging from 62 to 98 percent (Rai, unpublished). Such unidirectional incompatibility is quite common among certain species in the *Aedes scutellaris* subgroup but has not been reported earlier among *Ae. albopictus* geographic strains.

Data from interspecific crosses among five species in the subgroup have revealed that species with overlapping ranges are reproductively isolated from each other. For some species pairs (*albopictus* ♀♀ x *pseudalbopictus* ♂♂, and *pseudalbopictus* x *seatoi* in reciprocal crosses), there was no sperm transfer. *Aedes flavopictus* which is allopatric with all species except *Ae. albopictus* is bidirectionally compatible with *Ae. pseudalbopictus* and unidirectionally with *Ae. seatoi* producing relatively high egg hatches ranging from 70 to 98%. Except for *Ae. unilineatus*, these results are in keeping with the distribution of the species. Sympatric species have evolved strong premating isolation whereas species with no overlap have not been subjected to such selection and produce viable F₁ progeny. Meiotic analyses of the species hybrids have shown little chromosomal divergence among the parental species (Rai and Herman 1985).

b. *Mate-choice tests*: Ethological (behavioral) isolation tests were undertaken to determine if sympatry has promoted premating reproductive isolation in the *Ae. albopictus* subgroup utilizing three southeast Asian species including six geographic strains of *Ae. albopictus* (McLain and Rai 1986). These tests were conducted by providing females with a simultaneous choice between conspecific males and males of another species.

Fifteen males or females of each of two species/strains were placed with 15 individuals of the opposite sex but from only one of the species/strains. Pairs were removed from the case upon initiation of mating and their specific status identified using morphological markers (from keys of Huang 1972) and/or fluorescent dusting with different colors. Isolation indices were used to assess the significance of the mate choice patterns observed. These indices varied from -1 (complete preference for the other species) to 1 (complete isolation).

Females of *Ae. albopictus* from Borneo and Malaysia sympatric with *Ae. pseudalbopictus* and females from Thailand sympatric with *Ae. seatoi* exhibited strong intraspecific mating preferences. Females of three *Ae. albopictus* strains (Madagascar, Mauritius, Korea) allopatric with populations of *Ae. seatoi* and *Ae. pseudalbopictus* failed to discriminate between males of their own species and those of the other species. Statistically, sympatry was significantly associated with strong behavioral preferences and allopatry with weak or no premating isolation. These results suggest that reinforcement of ethological isolation has evolved in sympatry.

Ethological isolation tests between strains of *Ae. albopictus* revealed no significant isolation and indicate that no divergence in male characteristics evolved in sympatric populations in response to putative changes in female preference.

Viability of interspecific hybrids was assessed through egg hatch and embryonation rates. These results suggest that fitness of interspecific hybrids is zero. Hybrid inviability may have provided the selective pressure favoring ethological divergence (McLain and Rai 1986).

VECTOR COMPETENCE

Work is underway at our laboratory to catalogue variation among geographic strains of *Ae. albopictus* to oral infection, disseminated infection (infection beyond the midgut) and transmission of dengue viruses. Particular emphasis is being placed on strains from known dengue endemic, non-endemic and epidemic areas. Sixteen low passage lyophilized strains of dengue virus, from various parts of

the world, have been obtained from the Yale Arbovirus Research Unit. They are being maintained by intrathoracic inoculations in the Oahu strain, which we have designated as the reference strain.

Preliminary results using dengue 1 virus from Fiji showed considerable variation in disseminated infection rates among the five strains tested (2 from Malaysia, 2 from Hawaii and 1 from Texas). The Houston strain showed the lowest (34%) infection rate and a Hawaiian strain the highest (91%). The transmission rates of mosquitoes with disseminated infection ranged from 36 to 46% (Boromisa and Rai, unpublished data).

For an extensive review of data on vector competence, reference should be made to a paper by Don Shroyer in this issue.

COMPETITIVE DISPLACEMENT

There is extensive literature concerning competitive interactions of *Ae. albopictus* with the following *Stegomyia* and other species:

A. Aedes aegypti. *Ae. aegypti* became established in Southeast Asia towards the end of the last century (Rudnick 1967). Historically, *Ae. aegypti* largely displaced *Ae. albopictus* in Calcutta during the period 1907-32 (Senior-White 1934) and in Kuala Lumpur during approximately 1916-26 (Stanton 1920). Similarly in urban Bangkok *Ae. aegypti* has almost completely replaced *Ae. albopictus* (Rudnick 1965).

The reverse is true in Hawaii. *Aedes aegypti* was widespread there in 1892. As mentioned earlier, *Ae. albopictus* was introduced in Hawaii sometime between 1830-96. "By 1912 *Ae. albopictus* had become dominant and during . . . 1943-44, 85% of the day-time mosquitoes were *Ae. albopictus* and 15% *Ae. aegypti*" (Gilotra et al. 1967). Observations in Guam are more or less similar. *Aedes albopictus* arrived there in 1944 and by 1951 it was present all over the island while *Ae. aegypti* was almost completely displaced (Hull 1952). The use of insecticides to control *Ae. aegypti* both in Hawaii and Guam may have in part helped in this displacement.

In experimental analyses involving larval competition in Calcutta, Gilotra et al. (1967) have shown that *Ae. aegypti* is favored in urban premises and *Ae. albopictus* in the outdoor environment of suburban and rural areas, while in urban gardens the two species exist in a state of equilibrium. In studies conducted in Singapore City, Chan et al. (1971) have suggested that "*Ae. aegypti* in the city is favored by rapid and extensive urbanization and by the higher fecundity and short life cycle of the species."

A critical question which needs to be an-

swered regarding the introduction of *Ae. albopictus* into the continental United States concerns the outcome of its possible competition with the native *Ae. aegypti* and/or *Ae. triseriatus* (Say). Mosquito workers in Houston, New Orleans and Memphis are already observing that locations in and around these cities which yielded *Ae. aegypti* in previous years are now producing primarily *Ae. albopictus* (D. Sprenger, G. Carmichael, B. Kelly, personal communication).

B. Aedes guamensis Farner and Bohart. Rozeboom and Bridges (1972) compared the relative densities of larval populations of *Ae. guamensis*, a species native to Guam and *Ae. albopictus* which was introduced there in 1944, with an earlier survey and showed that "as the population density of *Ae. albopictus* increased, that of *Ae. guamensis* decreased by as much as about 95% in artificial containers and by 30% or more in natural breeding habitats" in Guam.

C. Aedes polynesiensis MARKS. Competition between populations of *Ae. polynesiensis*, a major vector of nonperiodic filariasis in Polynesia and *Ae. albopictus* resulted in elimination of *Ae. polynesiensis* in relatively small, 1 cubic foot cages (Gubler 1970) and in a large walk-in cage, where conditions of the habitat of the two species were simulated (Rozeboom 1971). Two hundred male and 200 female *Ae. albopictus* were introduced in the walk-in cage which was producing approximately 4,000 *polynesiensis* adults per week. In small confined space, *Ae. albopictus* males readily inseminate *polynesiensis* females but the eggs are infertile. Such cross insemination sterility was considered to be an important factor in competitive displacement in Gubler's cages. However, in the case of the large, walk-in cage where steady decrease in *Ae. polynesiensis* paralleled an increase in *Ae. albopictus*, and where after 41 weeks *Ae. polynesiensis* was reduced to approximately 5% of its original density, Rozeboom (1971) interpreted the replacement of *polynesiensis* by *albopictus* as resulting from "the higher reproductive rate of the latter species, which permitted it to monopolize the ecological niche provided by the large cage."

Whatever the mechanism, competitive displacement of one species by another was proposed as a method for replacing a vector or an insect pest by a non-vector or an innocuous form. A preliminary field trial on a small island in the Pacific utilizing this approach and the above mentioned two species was conducted by Rosen et al. (1976). However, the results were inconclusive.

D. Other species. The absence of *Ae. albopictus* from Africa and Australia is highly puzzling in view of its success as a colonizing species

elsewhere. Obviously *Ae. aegypti* originated in Africa and migrated to Southeast Asia with the dhow traffic, where *Ae. albopictus* was already native. What prevented the migration of *Ae. albopictus* to Africa? The eggs of *Ae. albopictus* must have been taken from its indigenous home in Southeast Asia to the African coast on the dhows on their reverse journey. But perhaps the other native *Aedes* species in Africa have not permitted the occasionally introduced *Ae. albopictus* to share the same micro- and/or macrohabitats. Lounibos (1981) has elegantly documented habitat segregation among 14 *Aedes*, 3 *Culex*, 3 *Eretmapodites* and 2 *Toxorhynchites* species among African treehole mosquitoes and the possible "evolutionary role of competition in shaping this community of mosquitoes."

In conclusion, considerable variability exists between geographic populations of *Ae. albopictus* in various genetic parameters tested. The emphasis of the work to date has been largely on evolutionary genetics although considerable information exists in areas dealing with cytogenetics and formal genetics also. Much additional work needs to be done in other areas and to explore those features of its genotype which determine its success as a colonizing species. Furthermore, the possible genetic basis of its ability to serve as an efficient vector of dengue and other virus diseases should be investigated. We are in the process of genetically characterizing strains from dengue endemic and non-endemic areas.

A thorough understanding of the genetic biology of this species will be an essential prerequisite to design strategies for its future management in the United States.

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