WATERS, C. M., QUICK, D. T., OARD, H. C., and ALLEN, F. K. 1963. The 1961 outbreak of St. Louis Encephalitis in Pinellas, Manatee, and Sarasota counties. Fla. St. Board Health, Mon. 5:19–29.

WHITNEY, E. 1964. Flanders strain, an arbovirus newly isolated from mosquitoes and birds of New York State. Am. J. Trop. Med. Hyg. 13(1): 123–131.

YELLOW FEVER CONFERENCE. 1955. Yellow fever conference. Am. J. Trop. Med. Hyg. 4(4): 571–661.

THE COLONIZATION OF TEMPERATE NORTH AMERICA BY MOSQUITOES AND MAN*

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In attempting to understand the relationships between organisms occurring together in the same habitat, it is frequently helpful to know how the particular mixture of species came into existence. This is true of mosquitoes and man in the temperate part of North America. In this area (as in all other parts of the world permanently inhabited by man) man lives in many kinds of ecological communities and in each one of these communities man and a particular assemblage of mosquito species form an intimately related part of the ecosystem. One way of looking at this North American mosquito-man segment of the ecosystem is to try to determine when the various species reached this area, where they came from, and what has happened to them since. Information on these questions would explain one facet of the relationship between man and mosquitoes on this continent.

First let us consider the mosquitoes. There are slightly less than 150 species known from North America north of Mexico, out of the 2500 species known for the entire world. The questions we seek to answer about these 150 are: (1) where did they come from, (2) when did they reach this region? We can obtain reliable clues about these problems in only one way. First we need to know the family tree of all these mosquitoes; in other words, determine as reliably as possible how the different genera and species evolved. This is done by comparing detailed characters of all of them, determining which characters probably are primitive and from this deducing the order in which different character combinations evolved. This comparison should include all living and all fossil species. With mosquitoes, the fossils are too poorly preserved to show the minute characters that we need to see for such a study. After the family trees are worked out to the best of our ability, we can then superimpose geographic distribution on these and, in same cases at least, arrive at plausible explanations concerning the dispersal of each group. Using these methods, the following account outlines the results obtained by treating the North American mosquitoes genus by genus.

THE GENUS *Deinocerites*

Two of our most unusual mosquitoes are *Deinocerites cancer* and *mathesoni* that normally breed in the holes of land crabs. The genus *Deinocerites* is entirely American, restricted for the most part to the American Mediterranean region (Fig. 1). It is evident that the evolution of this genus has occurred primarily in the tropics. In each of two main lineages, however, a species became adapted to live in subtropical and even slightly temperate conditions. One of these is the species

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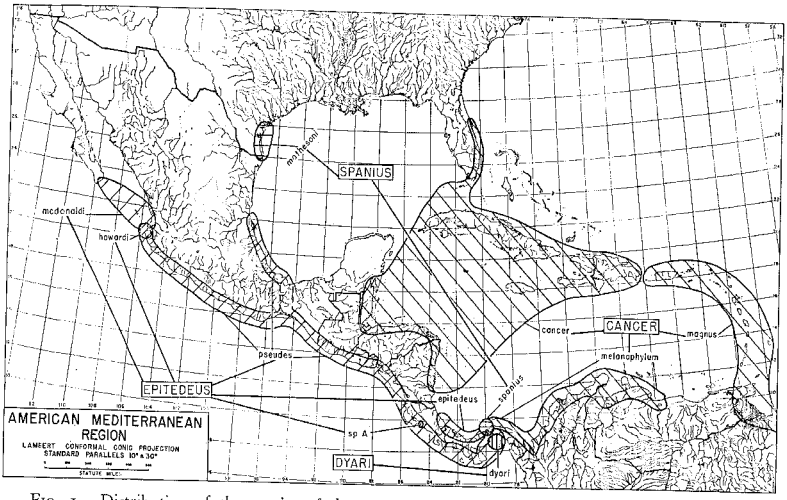


FIG. 1.—Distribution of the species of the genus *Deinocerites* (after Belkin and Hogue, 1959).

cancer, a tropical species whose range extends up the east coast of Florida; the other species is *mathesoni,* known only from extreme southern Texas, whose only close relative is the species *spanius* known only from the region of Panama. This means that the common ancestor of *spanius* and *mathesoni* once occurred between these distant points, its range became divided into a northern and a southern segment, the southern segment evolved into *spanius,* and the northern segment evolved into the subtropical and slightly temperate *mathesoni.*

THE GENUS *Wyeomyia*

Three species of this interesting little genus occur in North America. The genus belongs to a closely-knit tribe of mosquitoes called the Sabethini, primarily tropical in distribution, its species being restricted almost entirely to container-type breeding places such as water in the axils of bromeliad leaves or in pitcher plants. As at present understood, this tribe contains eight genera. Three of the genera, including *Tripteroides,* constitute a single branch of the tribe confined to the Old World tropics. The other five genera, including *Wyeomyia,* form an equally distinct unit of the tribe restricted to the New World. From this information it seems certain that at some time in the distant past, the common ancestor of these two units or tribes dispersed between the Old and the New Worlds, that later the intercontinental connection of this ancestral species was broken and that ever since the progeny of these isolated ancestral forms have evolved separately, one group within the Old World tropics, the other group within the New World tropics. Figure 2 is a simplified family tree of the American branch of the Sabethini. The names refer to the genera, the abbreviations refer to the subgenera of *Wyeomyia,* and each bar represents one existing species. Each unextended bar represents a species confined to the tropics. It is evident from this figure that these American Sabethini genera have evolved almost entirely within the tropical region. Only in the genus *Wyeomyia* has any exception to this occurred. In this genus two distantly related species, *vanduzeei* and *mitchelli,* have independently spread into the subtropical zone and now occur also in southern Florida. Two other species of the genus, *smithi* and *haynei,* occur only in the eastern part of the temperate zone. They evidently arose from a tropical spe-

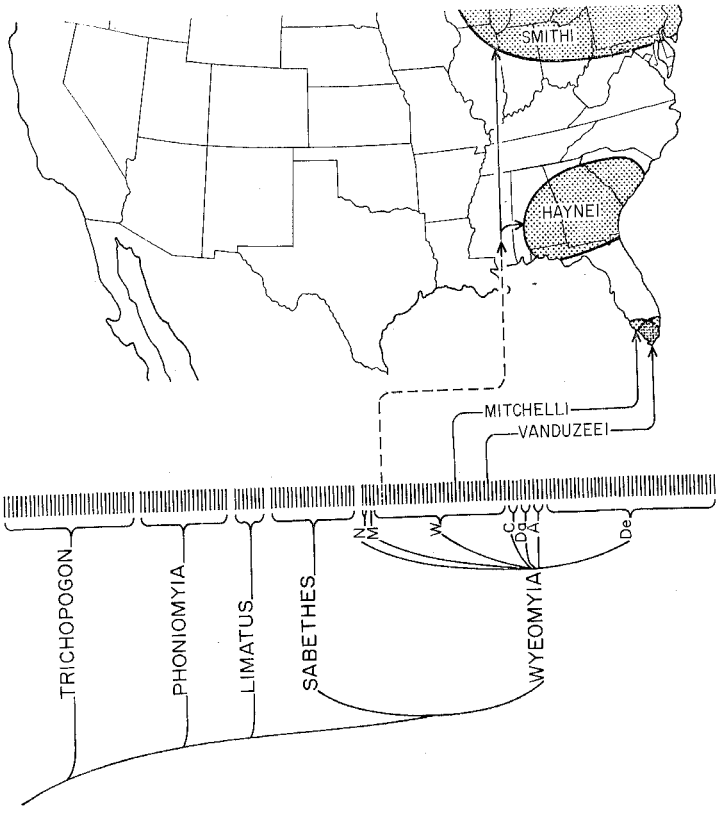


FIG. 2.—Diagram of relationships in the New World branch of the tribe Sabethini. Subgenera of *Wyeomyia* indicated by letters. Each short vertical bar indicates one tropical species (based on data from Lane, 1953).

cies that became subtropical and temperate, and spread into eastern North America. Subsequently the populations of this ancestral form occurring in the temperate region became isolated from the tropical populations and evolved into the only Sabethini now inhabiting the temperate zone.

THE GENUS *Mansonia*

The temperate American fauna of *Mansonia* superficially appears to parallel that of *Wyeomyia.* In North America there are two species of *Mansonia, titillans* and *indubitans,* found only in the extreme southern part of the United States, and a third species, *perturbans,* that occurs across the whole continent from southern Canada into Mexico. If, however, we plot the phylogeny and distribution of the world's species of *Mansonia,* Figure 3, we find that these species have a much different history. The genus forms two main branches, and each branch is divided into a pair of distinctive subgenera. In each of these pairs of subgenera (springing from ancestral forms B and C, respectively) one subgenus is confined to the Old World and one to the New World.

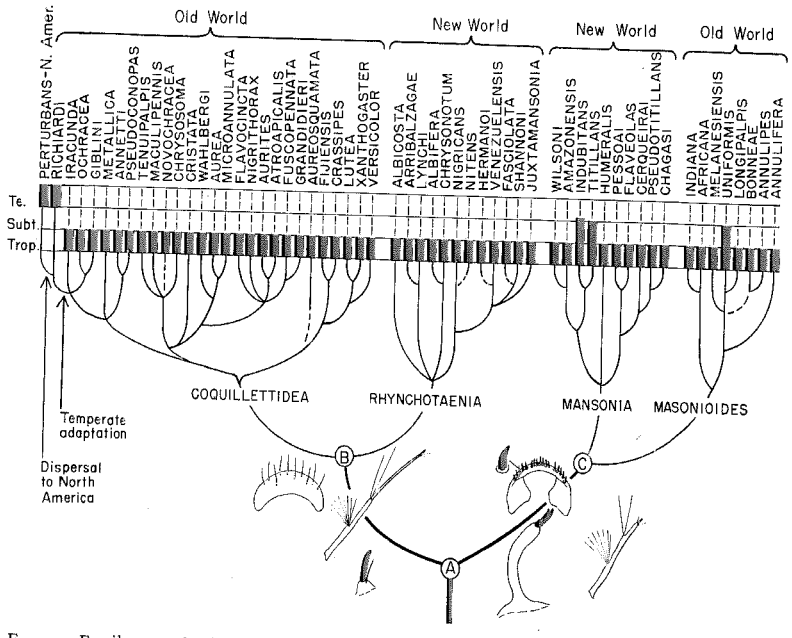


FIG. 3.—Family tree of subgenera and better known species of *Mansonia*. The distribution of each species is indicated by the black bars in the various levels. *Subt.*, subtropical; *Te.*, temperate; *Trop.*, tropical.

The great preponderance of tropical species shows that, as with the Sabethini, the evolution of the genus *Mansonia* occurred almost entirely within the tropics. These relationships also indicate that ancestral forms B and C spread between the New World and the Old World at some time in the past and that except for one species, there has been no intercontinental movement of the genus since. Looking first at the products of ancestor C, we find that the American branch, the subgenus *Mansonia,* is entirely tropical except for the two species *titillans* and *indubitans.* These two have become endowed with properties that have enabled them to extend their range into the subtropical and slightly into the temperate region of the United States. The Old World subgenus arising from ancestor C, *Mansonioides,* also remained primarily tropical but one species has become adapted to the subtropics and occurs in southern Japan.

Of the two subgenera arising from ancestor B, the American branch (the subgenus *Rhynchotaenia*) evolved only within the tropical region and none of its members spread into the United States. The Old World branch (the subgenus *Coquillettidea*) evolved into a large number of tropical species inhabiting Africa, India, southern Asia, and the Australasian region. One line, however, evolved into a temperate species, spread across the temperate areas of the northern hemisphere, and later gave rise to the temperate Eurasian species *richiardi* and North American species *perturbans.*

THE GENUS *Toxorhynchites*

There is only one temperate North American species of this genus, *rutilus.* The entire genus, like *Mansonia,* is almost completely restricted to the tropical regions of the world. Apparently there was an

ancient dispersal of the genus between the New and Old Worlds, because the two subgenera *Ankylorhynchus* and *Lynchiella,* totaling 14 species, are completely restricted to the New World and the third subgenus *Toxorhynchites,* totaling 43 species, occurs only in the Old World. The described differences between the various species make it difficult to reconstruct a detailed family tree but it is relatively certain that the American temperate species *rutilus* arose from the American subgenus *Lynchiella,* and probably is an offshoot of the tropical and subtropical species *theobaldi* that extends from Mexico to Argentina. Here again, a tropical species of mosquitoes evolved the ability to extend its range into the temperate region, and later the temperate population became cut off from the rest of the species, evolving into a distinctive member of the fauna of eastern North America.

THE GENERA *Uranotaenia* AND *Orthopodomyia*

Four species of *Uranotaenia* occur in the United States. The genus itself is large, world-wide, and almost entirely confined to the tropics. Characters available indicate that, like *Mansonia,* the genus may constitute two larger branches and each branch has dispersed between the New and the Old Worlds. On the basis of presently described characters it is difficult to extend the history of the genus much farther than this. The immediate origin of our United States species, however, is fairly clear. All of them represent extensions of New World tropical species into the north temperate region. The two species *lowi* and *sapphirina* are still in the first stages of this spread, occuring from the tropics northward into temperate United States. The other two, *syntheta* and *anhydor,* are apparently subtropical and temperate species that arose from a more ancient Central American ancestry.

In the genus *Orthopodomyia* it is even more difficult to find characters on which to base a detailed family tree for the 23 known species. These occur primarily in the tropics of both the Old and New Worlds. Of the three species occurring in temperate North America, *signifera* is a tropical species whose range extends into the temperate region, and the two wholly temperate species, the eastern and central *alba* and the far western *californica,* probably splintered off from ancestral *signifera* or some other species in the American tropics.

THE GENUS *Psorophora*

Up to this point we have treated what might be called the "tag ends" of the mosquito fauna of temperate North America. Now we come to something that is really serious, ten of our most vicious biters, the species of *Psorophora.* This genus occurs only in the New World. As can be seen from the family tree (Fig. 4) of all the better known species, the genus as a whole has evolved in the tropical region but several of these tropical species have become endowed with the ability to live far north into the temperate region. The species *pygmaea* has extended its range from the tropics into the subtropics of Florida. In addition, three species, *horrida, longipalpis* and *signipennis,* have evolved undoubtedly from tropical ancestors into species now restricted to the temperate zone. The tropical fauna of *Psorophora* has therefore served as a continuing source of new additions to the temperate mosquito fauna. This tree gives one the impression that eventually the entire genus *Psorophora* will move up into the temperate region and it is interesting to speculate how our comfort would be affected by the addition of the other eighteen species to our woodlands.

THE GENUS *Culex*

Although hundreds of species of *Culex* have evolved in the tropics, only 28 occur in the United States. Twenty-three of these belong to two large subgenera, *Culex* and *Melanoconion,* each primarily tropical. As would be expected, these 23 species are primarily invaders from the American

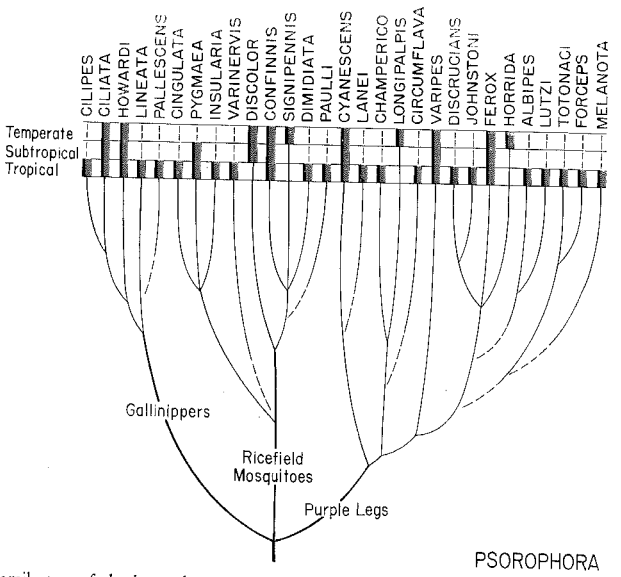


FIG. 4.—Family tree of the better known species of *Psorophora*, the distribution of each species indicated by the black bars in the horizontal strips.

tropics. This is shown dramatically by the subgenus *Melanoconion* which with the subgenus *Microculex* forms a single evolutionary branch of some 120 species restricted to the New World (Fig. 5). Four of these tropical species extend just into the United States subtropics (*atratus, opisthopus, mulrennani,* and *iolambdis*) and three others extend into and are common members of the temperate belt (*pilosus, erraticus,* and *peccator*). Two species, *abominator* in Texas and *anips* in California, have evolved from a *peccator*-like ancestor into distinctive subtropical-temperate forms.

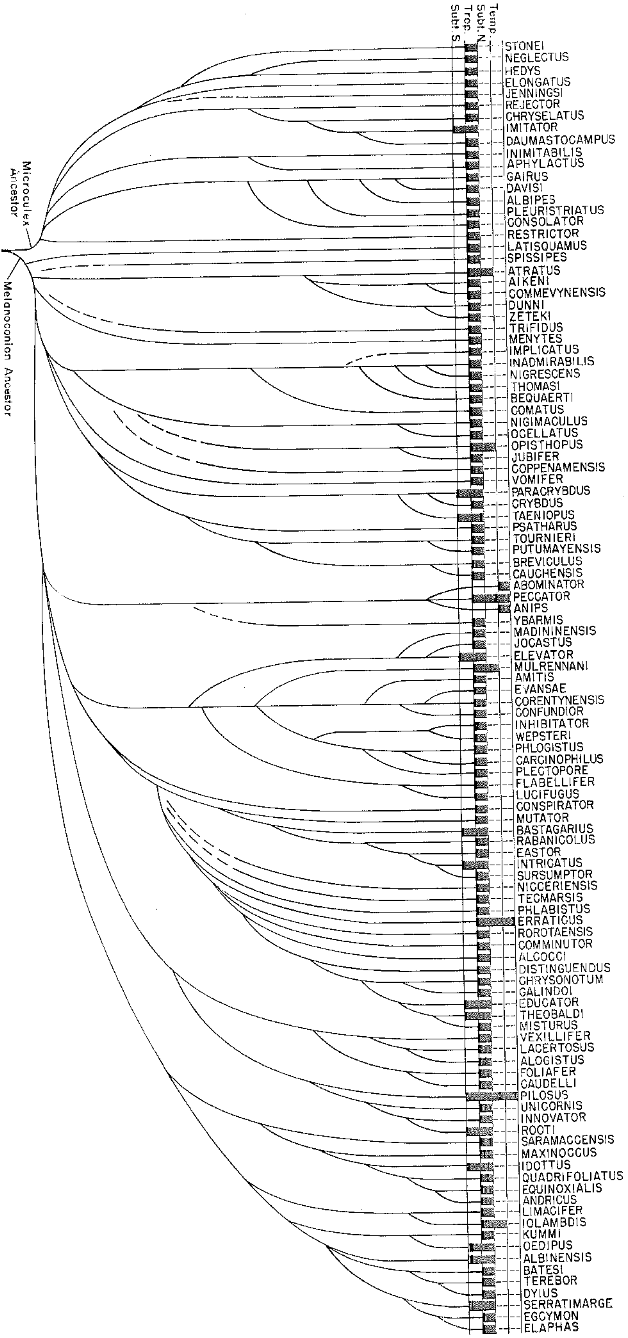
Of our species belonging to the world-wide subgenus *Culex,* represented in the American tropics alone by 100 or so endemic species, 12 represent either extensions of New World tropical species into this country or species that have evolved into subtropical or temperate species arising from such a tropical ancestor. These are shown in Figure 6. Two of our species, *pipiens* and *quinquefasciatus,* arrived here by boat, the former almost certainly from Europe, the latter probably from Africa.

The subgenus *Neoculex* is abundant in the Old World tropics, especially in Africa, but also has many species in the temperate part of Eurasia. Our species *territans* extends across this entire temperate area and undoubtedly evolved in Eurasia and dispersed into North America. We have also a cluster of endemic western species (*apicalis, arizonensis, boharti,* and *reevesi*) that likely evolved from a much earlier dispersal of a *territans*-like ancestor from Eurasia.

THE GENUS *Anopheles*

Our 13 species in this genus have varied origins (Fig. 7). The species *albimanus,* barely established in the subtropical cran-

FIG. 5.—Family tree of *Culex* subgenera *Microculex* and *Melanoconion.* Distribution of the species indicated by black bars in the horizontal strips. *Temp.,* northern temperate; *Trop.,* tropical; *Subt. N,* northern subtropical; *Subt. S,* southern tropical. (Based chiefly on Rozeboom and Komp., 1950).


Microculex Ancestor
Melanoconion Ancestor
Subt. S.
Trop.
Subt. N.
Temp.
STONEI
NEGLECTUS
HEDYS
ELONGATUS
JENNINGSI
REJECTOR
CHRYSELATUS
IMITATOR
DAUMASTOCAMPUS
INIMITABILIS
APHYLACTUS
GAIRUS
DAVISI
ALBIPES
PLEURISTRIATUS
CONSOLATOR
RESTRICTOR
LATISQUAMUS
SPISSIPES
ATRATUS
AIKENI
COMMEVYNENSIS
DUNNI
ZETEKI
TRIFIDUS
MENYTES
IMPLICATUS
INADMIRABILIS
NIGRESCENS
THOMASI
BEQUAERTI
COMATUS
NIGIMACULUS
OCELLATUS
OPISTHOPUS
JUBIFER
COPPENAMENSIS
VOMIFER
PARACRYBDUS
CRYBDUS
TAENIOPUS
PSATHARUS
TOURNIERI
PUTUMAYENSIS
BREVICULUS
CAUCHENSIS
ABOMINATOR
PECCATOR
ANIPS
YBARMIS
MADININENSIS
JOCASTUS
ELEVATOR
MULRENNANI
AMITIS
EVANSAE
CORENTYNENSIS
CONFUNDIOR
INHIBITATOR
WEPSTERI
PHLOGISTUS
CARCINOPHILUS
PLECTOPORE
FLABELLIFER
LUCIFUGUS
CONSPIRATOR
MUTATOR
BASTAGARIUS
RABANICOLUS
EASTOR
INTRICATUS
SURSUMPTOR
NICCERIENSIS
TECMARSIS
PHLABISTUS
ERRATICUS
ROROTAENSIS
COMMINUTOR
ALCOCCI
DISTINGUENDUS
CHRYSONOTUM
GALINDOI
EDUCATOR
THEOBALDI
MISTURUS
VEXILLIFER
LACERTOSUS
ALOGISTUS
FOLIAFER
CAUDELLI
PILOSUS
UNICORNIS
INNOVATOR
ROOTI
SARAMACCENSIS
MAXINOCCUS
IDOTTUS
QUADRIFOLIATUS
EQUINOXIALIS
ANDRICUS
LIMACIFER
IOLAMBDIS
KUMMI
OEDIPUS
ALBINENSIS
BATESI
TEREBOR
DYIUS
SERRATIMARGE
EGCYMON
ELAPHAS

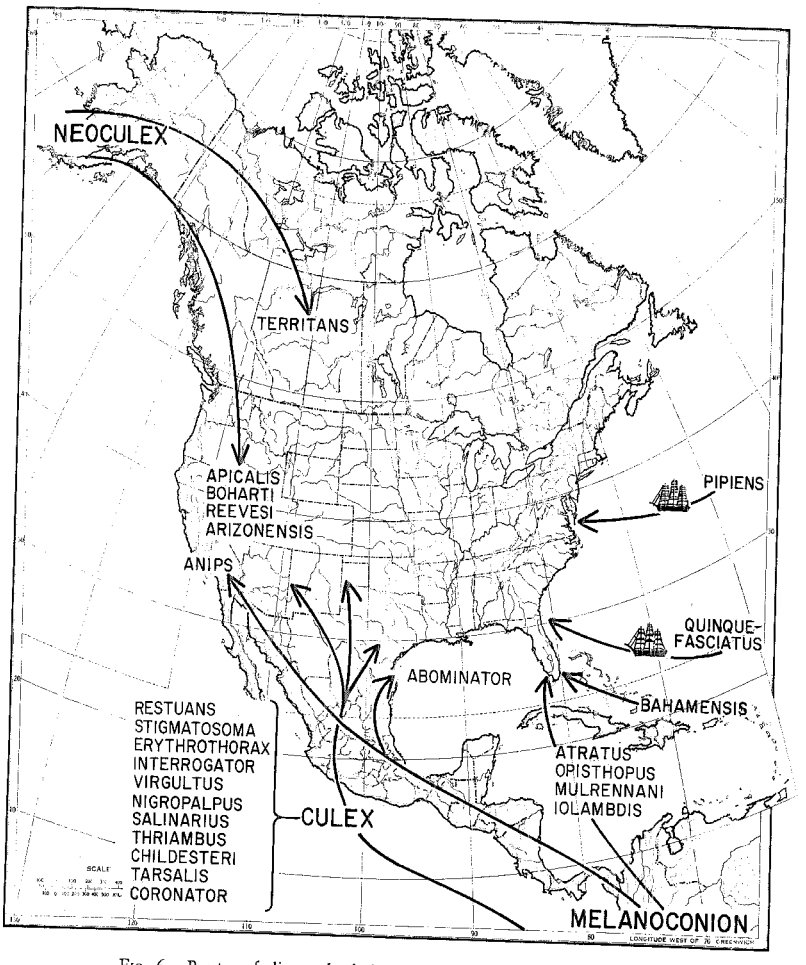


FIG. 6.—Routes of dispersal of the species of *Culex* into North America.

nies in Brownsville, Texas and the Florida Keys, is the only northward extension of the subgenus *Nyssorhynchus,* containing 25 species restricted to the New World tropics. Our other species belong to the world-wide subgenus *Anopheles* and seem to represent four phylogenetic lines of this large group. Our tree-hole species *barberi* belongs to the north temperate holarctic group of which the European *plumbeus* represents the other end. The southwestern *pseudopunctipennis* is our sole representative of a distinctive South American group. It is entirely possible that the remainder of our fauna represents two indigenous groups closely related to the European *maculipennis* complex. One of these, the North American *quadrimaculatus* complex, contains *quadrimaculatus, walkeri,* and *atropos.* The other, the North American *occidentalis* complex, contains *occidentalis, freeborni, earlei, punctipennis, bradleyi, crucians,* and *georgianus.* If these surmises are correct, then

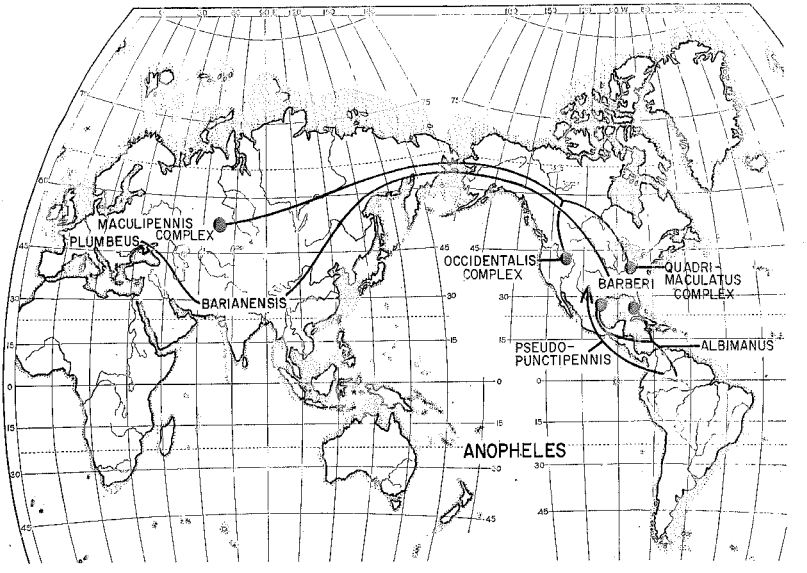


FIG. 7.—Routes of dispersal and centers of endemism for the North American fauna of *Anopheles*.

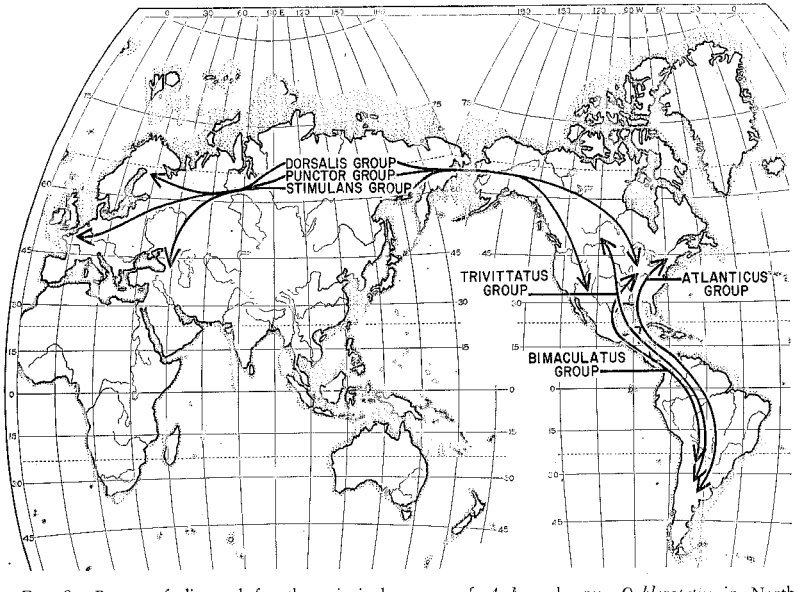


FIG. 8.—Routes of dispersal for the principal groups of *Aedes* subgenus *Ochlerotatus* in North America.

at some time in the past the common ancestor of the *maculipennis, quadrimaculatus* and *occidentalis* groups dispersed between Eurasia and North America; since that time the American range of this ancestor became isolated from the Eurasian portion, and evolved into the two complexes and ten species we have mentioned. I want to stress that these conclusions are highly tentative because we still lack a great deal of pertinent evidence concerning many species in the Old World and in Central and South America.

THE GENUS *Culiseta*

Our eight species of *Culiseta* represent the first truly temperate genus treated in this account. These eight species belong to three quite different phylogenetic lines. One, the subgenus *Climacura,* includes only our eastern species *melanura* and one or two New Zealand species. Another line, the subgenus *Culicella,* includes our eastern species *minnesotae,* the holarctic species *morsitans,* at least two European species, and several species from southern Australia. This type of dispersal would indicate that both of these subgenera are quite old in a geological sense. Our third line, the subgenus *Culiseta,* includes the holarctic species *alaskaensis,* a group of widespread North American species including *inornata,* all confined to the temperate regions, and several species occurring in temperate India and Europe.

From these distribution patterns it seems clear that the whole genus *Culiseta* has always been temperate to arctic and that the North American fauna has evolved from species that have dispersed between North America and Eurasia.

THE GENUS *Aedes*

The temperate and northern regions can well be characterized as "*Aedes* country" in a most intimate way. Roughly half of the temperate North American species belong here. The genus is world-wide in distribution and is divided into some 20 major species assemblages or subgenera. Only four occur naturally in temperate North America. Most of the subgenera are restricted to the tropics of either the Old or the New World. One of the largest, the subgenus *Stegomyia,* is restricted to the Old World tropics but one of its species, *aegypti,* has become introduced by man into the New World where it occurs as a local semi-domestic species.

Five of our species, *atropalpus, triseriatus, hendersoni, zoosophus,* and *varipalpus,* belong to the subgenus *Finlaya,* most of whose 180 species occur in the Old World tropics. A few occur in the New World tropics and a couple of dozen are found in the temperate regions of the northern hemisphere. Working out the exact phylogeny of these temperate species is difficult but some indication of the relationships of our North American forms can be made. Our species *atropalpus* appears to be an offshoot of a group of species occurring in north-eastern Asia. The four species *triseriatus, hendersoni, zoosophus* and *varipalpus,* seem to be a monophyletic cluster that evolved in temperate North America; affinities with certain east Asian species indicate that their ancestor came from that direction.

Our salt marsh mosquitoes and their allies (sometimes called the subgenus *Culicelsa,* including *sollicitans* and *taeniorhynchus*) appear to be a distinctive group that evolved in this country from a primitive member of the genus.

Mosquito-wise, the temperate part of North America is dominated by subgenus *Ochlerotatus,* whose 150 species are distributed in practically all regions of the world. Our temperate fauna belongs to a limited number of species groups very interesting geographically (Fig. 8). Two primitive groups, one containing only *thibaulti* and the other only *canadensis,* appear to be restricted to this country. Another primitive group, typified by *bimaculatus* and *fulvus,* is South American with these two species extending their ranges into the temperate regions of North America. Another primitive lineage, the *atlanticus* group, contains about eight

species, three of them in North America and the rest in South America. It appears that this group has evolved in the vicinity of what we might call the Central American interface of the New World. The next large lineage, the *trivittatus* group, contains about 10 species, three in North America and the remainder in the tropical region of the New World, again suggesting an evolutionary development along the Central American interface. The *bimaculatus, atlanticus,* and *trivittatus* groups are quite distinct from each other, yet possess sufficient characters in common to suggest that all three arose from a common ancestor distinct from that of other groups of the subgenus. If this is true, then they together represent a major branch whose evolution occurred entirely in the New World.

Another well defined lineage, the *dorsalis* group and its relatives, typified by *dorsalis, trichurus, intrudens,* and *diantaeus,* is confined almost completely to the truly temperate region. A few species occur only in North America, a few only in Eurasia, and about an equal number extend across the entire holarctic region. It is obvious that this group has evolved by alternate dispersals and isolations of species between North America and Eurasia. The next major lineage is the *punctor* group, including about 20 North American species of which *sticticus, communis,* and *punctor* are a few well known representatives. Here again we have a fair number of North American species, about the same number of Eurasian species, and a moderately large number of species extending across both North America and Eurasia. This group includes the great bulk of the typical arctic species of the far north. The last major lineage of *Aedes* subgenus *Ochlerotatus* is the *stimulans* group. Like the preceding two, it has several species restricted to North America, several restricted to Eurasia, and a number extending across both continents. The relationships of individual species within the last three lineages, the *dorsalis, punctor,* and *stimulans* groups, indicate that this entire large northern fauna has evolved by dispersals and subsequent range disjunctions, followed by species evolution and further dispersals, that have taken place around the top of the world. It is most remarkable, being the only large assemblage of mosquitoes whose evolution has occurred almost exclusively around the temperate-arctic interface. It therefore seems likely that the original ancestors of these three groups were tropical species which became adapted to cold climates many million years ago and since then each one has given rise to a large cluster of temperate and arctic species.

Evolution is a continuing process and this aspect is perhaps exemplified best by the last two species of mosquitoes on our list. First let us consider *Aedes cinereus,* our sole member of the subgenus *Aedes.* This subgenus contains over 75 species, all restricted to the Old World tropics except two (Fig. 9). One of these latter occurs in the temperate region of northern Japan. The other is *cinereus* which extends across the entire holarctic region. As with some of the species discussed earlier, so here again a tropical species evolved physiological adaptations to cold climates and has become a widespread and abundant species throughout the northern temperate and arctic regions. This could well be the first step in an evolutionary development that might eventually parallel the *punctor* and *stimulans* bursts. The last species is *vexans,* our sole representative of the subgenus *Aedimorphus.* This subgenus contains over 95 species, all but one restricted to the tropical and subtropical regions of the Old World (Fig. 10.) The exception, *vexans,* acquired the ability to live in temperate climates and has now spread throughout the temperate regions of the northern hemisphere. As with *cinereus,* so *vexans* could be an initial step in a potential burst of northern species.

WHEN IT HAPPENED

In review, the mosquito fauna of temperate North America represents many in-

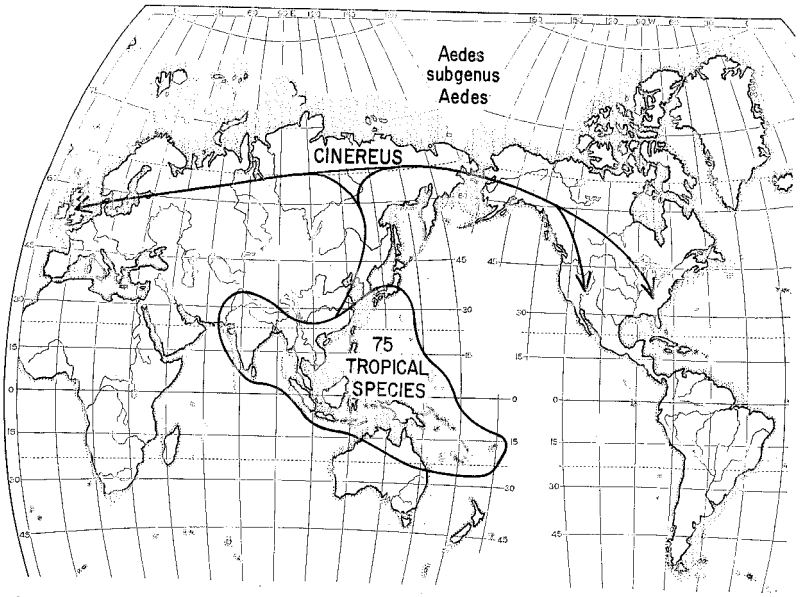


FIG. 9.—Distribution pattern of *Aedes* subgenus *Aedes*.

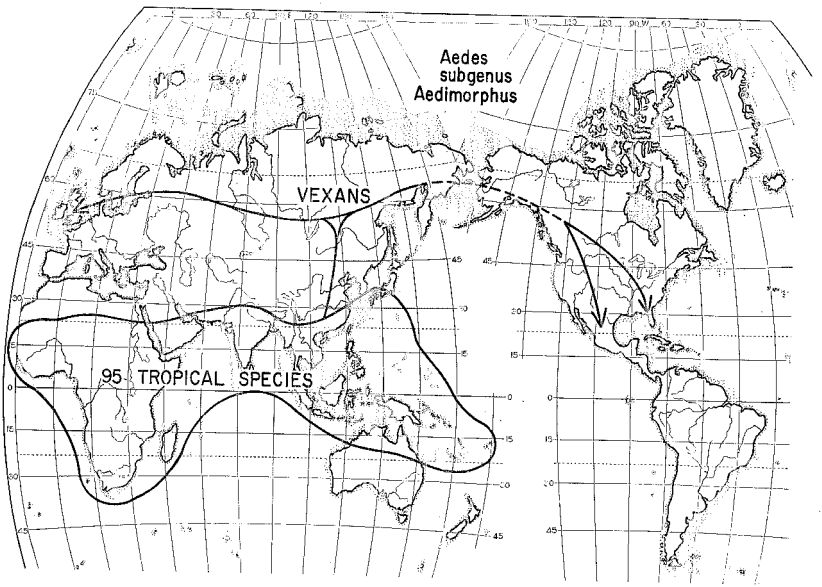


FIG. 10.—Distribution pattern of *Aedes* subgenus *Aedimorphus*.

dividual lineages that have spread into the temperate region from the South American tropics, from the temperate regions of Eurasia into this continent, or have evolved within the confines of North America. Many of these dispersals are impossible to date. We can say with assurance that *Wyeomyia mitchelli* and *vanduzeei* are tropical species that acquired the ability to live in the subtropics and for this reason have been able to colonize southern Florida, but it is impossible from this information alone to know when these species acquired their subtropical tolerances and when they got to Florida. The same reasoning applies to *Aedes cinereus,* which today occurs practically continuously across North America and Eurasia. With *Aedes vexans* we have the first type of clue concerned with time. *Vexans* occurs as far northwestward as the Yukon but has a gap in its range from there to some point in Eurasia. From this we can deduce that *vexans* probably spread from Eurasia into North America either during the last warm cycle of 9,000 years ago, or, less likely, during the last interglacial period, probably 50,000 years ago. At that time presumably the climate was slightly warmer than it is now, allowing *vexans* to live farther north and presumably to spread across Alaska into North America.

Instances in which tropical elements evolved into distinctive temperate species, such as *Psorophora horrida* and *Culex anips,* give some slight indication of time. Information from other insect groups indicates that it takes at least 30,000 years of isolation for a population to evolve into a species that is genetically distinct from other segments of the parental species. We have therefore fairly good evidence that these isolated temperate species of tropical origin have been here at least 30,000 years.

Another type of evidence concerns several species restricted to North America but occurring no farther north than southern Canada, and each with a closely related species occurring only in Europe. Examples of such North American species are *Orthopodomia signifier, Aedes triseriatus,* and *Mansonia perturbans.* Information from plant fossils indicates that the ancestor of each of these pairs of species probably spread between Europe and North America at a time when the temperate deciduous forest was continuous across this area, probably during the Miocene Epoch and perhaps 20 million years ago. It is possible that the ancestors of the *Aedes trivittatus* group together with the ancestors of other comparable groups spread into North America at the same time.

In various genera we pointed out that there were pairs of subgenera in which one member of the pair was in the American tropics, the other in the Old World tropics. From what is known of the past climates and land connections of the world, it seems certain that the intercontinental dispersals that produced these isolated units could have occurred no later than sometime in the Eocene Epoch, probably 50 million years ago. If members of the subgenera dispersed at this time, there is justification for believing that the ancestors of the genera themselves occurred during the Cretaceous period, anywhere from 70 million to 100 million years ago.

During the Eocene Epoch the area now covered by the United States was probably tropical or subtropical and many of the species now found in northern South America, Central America, and Mexico may represent forms that evolved in this southern area of North America and have since followed their tropical abodes southward with the gradual cooling of the midcontinental area.

Combining the relationships and dispersal patterns of the mosquitoes with these bits of information on the probable timing involved, there is good reason to believe that various lines of mosquitoes colonized North America at probably random intervals for the last 100 million years. Thus our mosquito fauna contains old lines that have been here for millions of years, other lines that have been here

for a few million years, and others that have been here for a few hundred thousand to a few thousand years. Some of the older lines evolved into clusters of species and some of these undoubtedly dispersed into our two neighboring land masses.

THE CHRONOLOGY OF MAN

How does man fit into this time table of mosquito evolution and dispersal? Man himself is fairly recent, probably being only 2 million years old. He didn't become a civilized creature until possibly 15,000 or 20,000 years ago. What sort of creatures were his ancestors during the Cretaceous period of 100 million years ago when mosquitoes remarkably similar to those that we know now had already evolved?

The primate lineage to which man belongs started out as a tree shrew or insectivore. Successive stages in the evolution from tree shrew to man are represented by the lemurs, tarsioids, monkeys, apes, and man. This entire primate lineage was a tropical one. It is thought that during the early part of Cretaceous time the tree shrews were the only representatives of this primate line. Lemurs and tarsioids were present during later Cretaceous and widespread in the Eocene. The monkey line probably differentiated sometime in the Eocene and it is possible that the ancestor of the New and the Old World monkeys dispersed between the New World and the Old World tropics during the Eocene in company with the progenitors of many of our tropical mosquito subgenera. We have good evidence that these mosquito companions included at least two species each of *Mansonia, Uranotaenia,* and *Culex,* at least one primeval sabethine, and at least one species each of *Anopheles, Aedes,* and *Orthopodomyia.* As with some of these mosquito subgenera, such as the American subgenera of *Mansonia,* the New World monkeys never spread back to the Old World and the Old World monkey and great apes lines never spread from the Old World into the New. A few million years ago, man eventually evolved as a tropical animal of the Old World, surrounded by an ever-diversifying mosquito fauna.

Man has a startling parallel with species such as *Aedes cinereus* and *vexans.* Like these two mosquitoes, man was the only member of his entire phylogenetic line to acquire the ability to spread into the temperate region. In the case of the insects, the basis of this ability was a genetic change in their physiological adaptations to climate. In the case of man, it was a change in behavior pattern, especially in what we call cultural artifacts. Because of these, including clothing, man spread into the temperate region and evolved into the northern races we now know. Some of these presumably spread into North America at an early date and gave rise to some of the aboriginal American cultures. The more advanced groups followed, some coming overland from Asia and others by ship from Europe and Africa.

From this outline it is plain that man first evolved in the midst of a well developed tropical mosquito fauna. When he spread into the temperate region he found that the mosquitoes had preceded him and had already become well adapted to the climate and habitats of the temperate region. These mosquitoes, furthermore, were not really strangers to man and his habits because they were sisters or cousins of the species he had grown up with in the tropics. This mosquito fauna presented temperate-inhabiting man with one of his greatest challenges in living successfully in the temperate habitat. If history is any guide, and if man persists long enough, more and more tropical mosquitoes will become adapted to cooler conditions and join him in the north.

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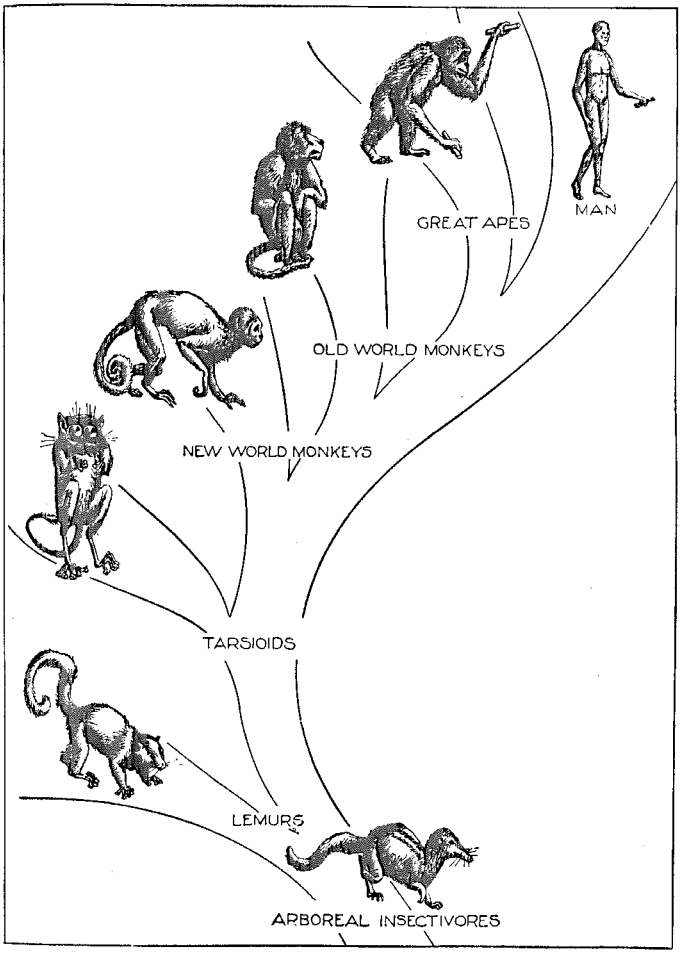

FIG. 11.—A simplified family tree of the primate branch. (From Romer, *The vertebrate story,* by permission of the University of Chicago Press.)

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Basic References

BARRAUD, P. J. 1934. The fauna of British India, including Ceylon and Burma. Diptera. V. Family Culicidae. London, Taylor and Francis. 463 pp.

BELKIN, J. N. 1962. The mosquitoes of the South Pacific (2 vols.). Berkeley, Univ. Calif. Press. 608 pp. and 412 pl.

BELKIN, J. N., and HOGUE, C. L. 1959. A review of the crabhole mosquitoes of the genus *Deinocerites* (Diptera, Culicidae). Univ. Calif. Publ. Ent. 14:411–458.

CARPENTER, S. J., and LACASSE, W. J. 1955. Mosquitoes of North America (north of Mexico). Berkeley, Univ. Calif. Press. 360 pp., 127 pl.

CHRISTOPHERS, S. R. 1933. The fauna of British India, including Ceylon and Burma. Diptera. IV. Family Culicidae: Tribe Anophelini. London, Taylor and Francis. 371 pp.

EDWARDS, F. W. 1922. A revision of the mosquitoes of the palearctic region. Bull. Ent. Res. 12:293–351.

———. 1924. A synopsis of the adult mosquitoes of the Australasian region. Bull. Ent. Res. 14:351–401.

———. 1941. Mosquitoes of the Ethiopian region. III. Culicine adults and pupae. London, British Museum (Natural History). 449 pp.

EVANS, A. M. 1938. Mosquitoes of the Ethiopian region. II. Anophelini adults and early stages. London, British Museum (Natural History). 402 pp.

HOPKINS, G. H. E. 1952. Mosquitoes of the Ethiopian region. I. Larval bionomics of mosquitoes and taxonomy of culicine larvae (2nd ed.). London, British Museum (Natural History). 355 pp.

LANE, J. 1953. Neotropical Culicidae, I, II. São Paulo, Univ. São Paulo Press. 1112 pp.

MARSHALL, J. F. 1938. The British mosquitoes. London, Wm. Clowes & Sons, Ltd. 341 pp.

NATVIG, L. R. 1948. Contributions to the knowledge of the Danish and Fennoscandian Mosquitoes. Norsk Ent. Tids., Suppl. I. 567 pp.

ROMER, A. S. 1959. The vertebrate story (4th ed.). Chicago, Univ. Chicago Press. 437 pp.

ROZEBOOM, L. E., and KOMP, W. H. W. 1950a. A review of the species of *Culex* of the subgenus *Melanoconion* (Diptera, Culicidae).

STONE, A., KNIGHT, K. L., and STARCKE, HELLE. 1959. A synoptic catalogue of the mosquitoes of the world (Diptera, Culicidae). Ent. Soc. Amer., Thomas Say Found., 6:1–358.

THURMAN, ERNESTINE H. B. 1959. A contribution to a revision of the Culicidae of northern Thailand. Univ. Md. Agr. Exp. Sta. Bull. A-100: 1–182.

SUSCEPTIBILITY OF SEVENTEEN STRAINS OF *AEDES AEGYPTI* (L.) FROM PUERTO RICO AND THE VIRGIN ISLANDS TO DDT, DIELDRIN, AND MALATHION

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INTRODUCTION. In 1963, the Communicable Disease Center established a program for the eradication of *Aedes aegypti* (L.) from the continental United States, Puerto Rico, and the Virgin Islands. The development of operational procedures for this program requires consideration of baseline data on insecticide susceptibility in the numerous areas of infestation. In both Puerto Rico and Florida resistance to DDT, dieldrin, and other chlorinated hydrocarbons by this species has been reported (Evans *et al.*, 1960; Fox *et al.*, 1960; Fox, 1961; Porter *et al.*, 1961). The following report describes the results of susceptibility tests with DDT, dieldrin, and malathion against larvae and adults of 13 strains of *A. aegypti* from Puerto Rico and 4 strains from the Virgin Islands.

METHODS. Temporary colonies for rearing and collection of F_1 eggs were established in San Juan from larvae collected during the period of May 28 to June 7, 1963, by personnel from the Public Health Service Quarantine Stations at San Juan and Miami. The eggs were shipped to Savannah, Georgia to provide larvae and adults of each of the 17 strains of *A. aegypti*. Test specimens were F_1 generation except for the St. John strain which was F_2. The standard procedures established by the World Health Organization were used to measure susceptibility to DDT, dieldrin, and malathion (Anon., 1960). Tests were replicated three or four times at each concentration of insecticide used.

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