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Chromosomal differences in populations of *Anopheles nuneztovari*

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Anopheles nuneztovari *from 3 localities in Brazil, 2 in Venezuela, and 1 in Colombia were subjected to chromosome analysis. The Venezuelan and Colombian populations, responsible for malaria transmission in certain areas of these countries, differ in an X-chromosome arrangement from the Brazilian specimens, the difference apparently being due to the fixation of an inversion in the homozygous state in one population. It was possible to identify 216 specimens from Venezuela and Colombia and 190 from Brazil by the X-chromosome.* A. nuneztovari *and its close relatives may be easily distinguished in this way. Diagnostic descriptions of the chromosomes and a standard map, based on the Brazilian population, are provided.*

The true facts concerning malaria transmission by certain species of *Anopheles* are sometimes obscured by problems involving the proper identification of the vector species. Much of the trouble is due to the fact that sibling species are quite common in mosquitos. Frizzi, in a long series of papers, established the chromosomal basis for the differentiation of the species of *A. maculipennis* complex (for a review see Kitzmiller et al., 1967). Colluzzi & Sabatini (1967, 1968, 1969) showed conclusively that the 5 sibling species of the *A. gambiae* complex could be distinguished chromosomally. The problem is that the anopheline mosquitos have evolved in a physiological sense without a corresponding degree of morphological differentiation. The *A. gambiae* complex illustrates the problem very well—obvious biological, physiological, genetic, and chromosomal speciation with little or no reliably consistent morphological differentiation.

The same problem evidently exists among the South American species of the subgenus *Nyssorhynchus*. In this group there are several interesting population problems many of which will undoubtedly be linked to problems of malaria transmission; one of these concerns *A. nuneztovari*.

A. nuneztovari was described on the basis of the male terminalia by Gabaldón (1940) from material collected at San Carlos, Cojedes, Venezuela. That author proposed a subdivision of the *A. albimanus* series—the " *tarsimaculatus* " series (Edwards, 1932) —of the subgenus *Nyssorhynchus*, also based on characteristics of the male terminalia. Rozeboom & Gabaldón (1941) concluded that the " *tarsimaculatus* " complex actually represents a group of closely related mosquitos including *A. oswaldoi*, *A. aquasalis*, *A. anomalophyllus*, *A. rangeli*, and *A. nuneztovari*, as well as some other species that have since been reduced to synonymy. The details of the taxonomy of this group will undoubtedly undergo a considerable amount of revision in the future, and are not especially germane to this paper, but it is clear that *A. nuneztovari* is closely allied to other members of the *A. oswaldoi* series.

The best estimate of the distribution of *A. nuneztovari* includes all of the Amazon basin; Guyana, French Guiana, and Surinam; Venezuela except for a strip along the northern coast; northern and eastern Colombia; some localities in Ecuador; and possibly considerable areas in Peru and Bolivia (Fig. 1). It is thus a wide-ranging species or species complex and appears to exhibit a considerable amount of variability in different parts of its range. Elliott (1972) summarizes the evidence for at least two populations, one of which is evidently responsible for the transmission of malaria in western Venezuela and northern Colombia.

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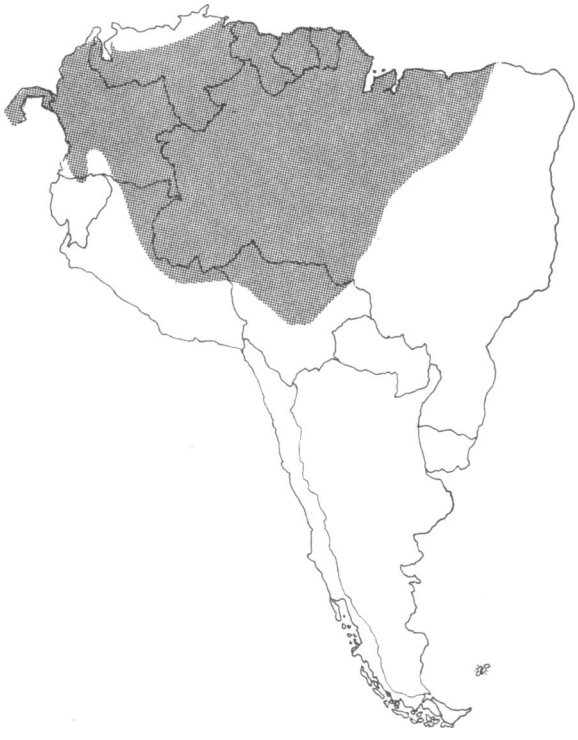

Fig. 1. Geographical distribution of *A. nuneztovari*.

One aspect of this variability apparently affects the vector capacity of the species. Throughout most of its range *A. nuneztovari* has not been incriminated as a vector of human malaria, but in parts of Venezuela and Colombia it is an important vector of the disease. Rey & Renjifo (1950) found naturally infected *A. nuneztovari* in Colombia in areas in which malaria was being transmitted. Gabaldón et al. (1963), in a detailed study of a malarious section of western Venezuela, clearly showed that considerable malaria transmission occurs in areas in which *A. nuneztovari* is found in large numbers, although both *A. darlingi* and *A. albimanus* are absent from these areas. Similarly, Pintos et al. (1968) reviewed the papers concerning salivary gland and stomach dissections of *A. nuneztovari* and added their own data on infected mosquitos found in western Venezuela. Elliott (1968) summarized the epidemiological and entomological data and suggested that *A. nuneztovari* actually exists as two sibling species one of which bites later in the night, inside houses, and is one of the main vectors of malaria in Colombia and Venezuela. It appears that the vector and nonvector populations might be sympatric in parts of those countries.

The lack of definitive morphological criteria raises the legitimate question whether these are in fact two distinct populations. One way of attacking this problem is to look at the salivary gland chromosomes and see if consistent chromosomal differences can be found that will serve to separate the two populations. Fortunately, *A. nuneztovari* is one of the anophelines with salivary gland chromosomes that are easily prepared. The present paper describes the salivary gland chromosomes of both populations. It has been possible to show that a consistent difference in the X-chromosome will distinguish the vector population in Colombia and Venezuela from the nonvector population in Brazil.

MATERIALS AND METHODS

Collections of *A. nuneztovari* were made at Tibú (Norte de Santander), Colombia, and in the state of Barinas, near San Antonio de Caparo, Venezuela, during the summer of 1969 (J. B. K. and E. T.), and at Manaus, Amazonas, Brazil, and along the Rio Doradas (Barinas) and Casigua (Zulia), Venezuela, during the summer of 1971 (J. B. K., R. D. K., and E. T.). Identification of this species is difficult in both larvae and adults. We used local taxonomic keys and relied heavily on the expertise of local entomologists, but our definitive identification of larvae was based on the morphology of the X-chromosome. Salivary gland preparations were made from fourth-instar larvae by standard methods (French et al., 1962) and were made permanent by the dry-ice method. Zeiss Einschlussmittel L-15 was used as a mounting medium and all final chromosome drawings were made by direct observation at 1 000× using a Zeiss phase contrast system. In the following descriptions of the chromosomes, specimens from Manaus were used as the standard.

DESCRIPTION OF THE CHROMOSOMES

The salivary gland chromosomes of *A. nuneztovari* have unmistakable homologies with the chromosomes of other members of the subgenus *Nyssorhynchus* and therefore the same numbered zones have been assigned to each arm. The X-chromosome thus contains zones 1–5; chromosome 2R contains zones 6–15; 2L, zones 16–25; 3R, zones 26–35; and 3L, zones 36–45. Within the numbered zones, letters have been arbitrarily assigned to subdivisions, but

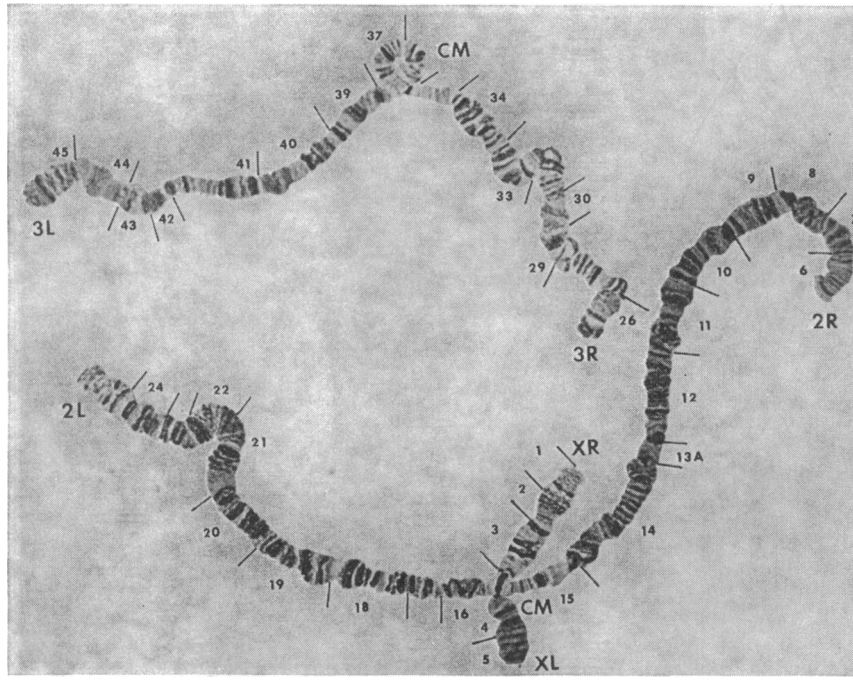

Fig. 2. *A. nuneztovari* salivary chromosome complement.

regions obviously similar to regions in species already mapped have been given the same letters.

The average lengths of the chromosomes, taken from 100 slides that appeared to be adequately but not excessively spread, were as follows: XR, 35 μm; XL, 25 μm; 2R, 205 μm; 2L, 155 μm; 3R, 147 μm; and 3L, 146 μm. All chromosomes were easily distinguishable by means of size and proportionate arm lengths. The X chromosome was submetacentric and short; the right arm of chromosome 2 was about 1.3 times the length of the left; and, in chromosome 3, both arms were equal in length.

Salivary chromosome complements are shown in Fig. 2 and the proposed standard chromosome map in Fig. 3.

X chromosome, right arm

Slightly longer than the left arm, the right arm of the X chromosome has 4 consistent recognition areas. The heavy pair of bands at the end of 1B, the dark series in 1C and 2A, the 3 dark bands in 3A, and the 4 dark bands in 3B can usually be recognized no matter how variable the other areas. Indeed, this variability in band intensity and in proportions would seem to be typical of the right arm. The banding pattern shown on the map can usually be seen in females; in males, the single X chromosome is usually thin, stretched, and twisted, with bands that stain with variable intensity.

Region 1A is often flared at the tip and sometimes appears to have one or two more bands than are shown. The 2 light bands at the beginning of 1B often stain more darkly and the 2 characteristic heavy bands at the end of 1B often appear as a single thick dark band, especially in slightly condensed chromosomes. Similarly, the dark bands in 1C and 2A stain with varying intensities. Often the 3 bands in 2A are just as dark as the 2 dark ones in 1C. In 1C the 2 dark bands at the beginning are generally as shown, but sometimes appear reversed—the first lighter, the second darker. The puff in 2C is extremely variable. It is shown on the map as a puffed area with 6 lightly staining bands; it is often not puffed and is sometimes much condensed; and the number of bands appears variable but these bands always stain lightly. When stretched, this area becomes quite thin but can always be recognized by its limiting 3 dark bands in 3A. These bands, in turn, often appear as 2, but in good preparations they may be clearly seen as 3. The rest of 3A is

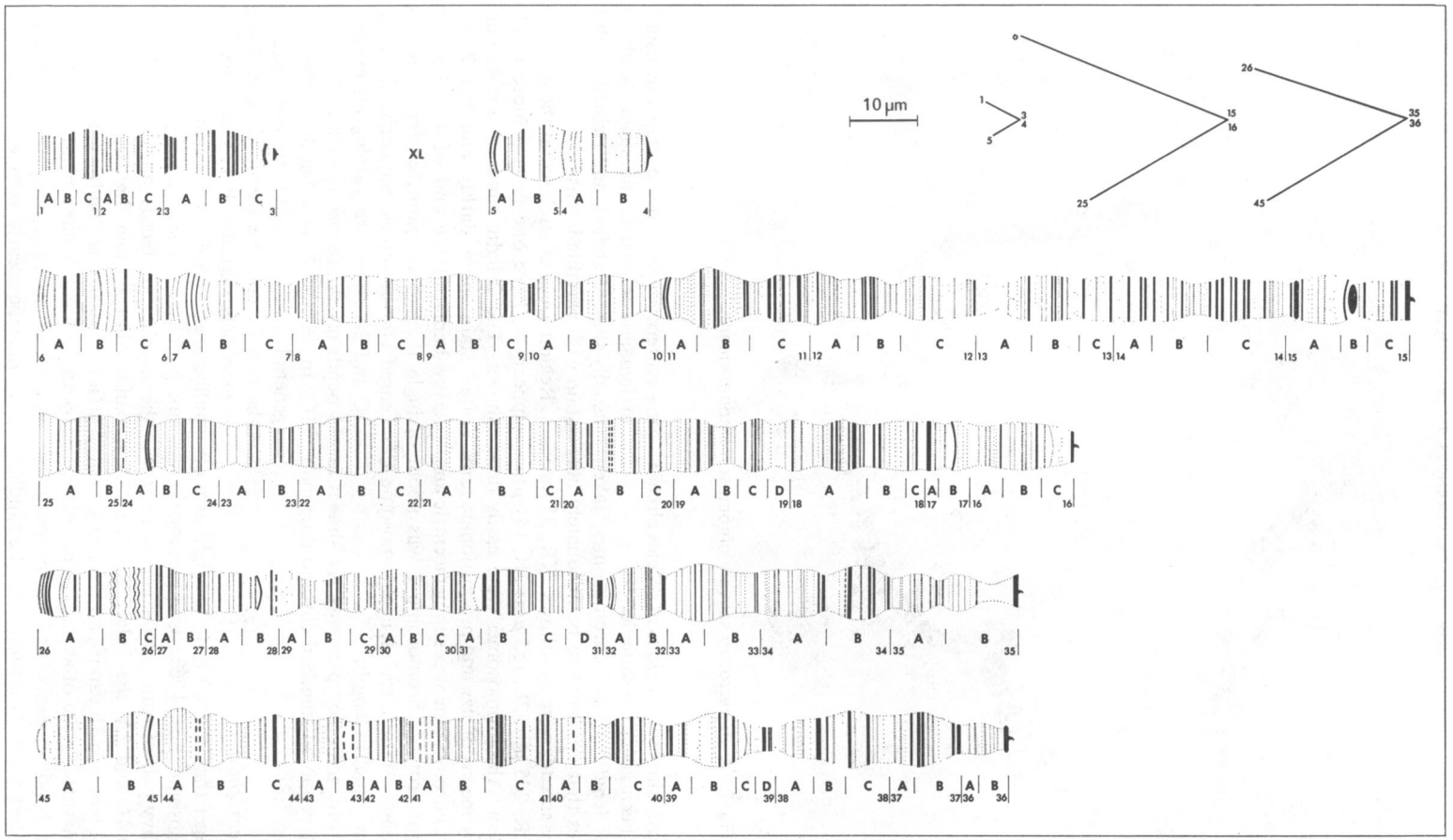

Fig. 3. *A. nuneztovari* salivary chromosome map.

also variable in the intensity of staining. On good slides they are as shown on the map but often the entire area appears to consist of lightly staining uniform bands. The 1–3 series of dark bands in 3B is generally consistent but the 3 closely spaced dark bands sometimes appear as only 2 in condensed specimens. 3C is usually stretched and connected by DNA-positive fibres to a darkly staining area in the nucleolus.

X chromosome, left arm

The shorter arm of the X-chromosome consists mostly of lightly staining variable bands. The dark bands in 5A, the 2 heavy bands in 5B, and the dark band at the beginning of 4B are the most consistent features. This arm is often condensed in females and is quite thin and nondescript in males. It is also connected with the nucleolus by darkly staining fibres.

Chromosome 2, right arm

Easily recognizable as the longest arm in the complement, 2R also contains positive recognition areas at the free end, at several points in the middle of the arm, and at the centromere end. The most obvious area is near the centromere, 15A–15C, an area also present in *A. aquasalis* and *A. darlingi*. A wide puff in 15A and 15B is bounded by thick dark bands at both ends with two lighter bands in the centre. Also typical is a pair of dark bands near the centromere in 15C. At the free end the most consistent bands are the 2 widely spaced dark bands in 6A, the 3 heavy bands in 6C, and the 3 thin dark bands in 7A. In 11C, 3 dark bands followed by 1 thick dark one are always present, as are the 4 thin dark bands in 12B. A long series of dark bands from 13B to 14A is usually distinct, as are the 7 dark bands in a puff in 14C.

This arm contains many areas of short-to-medium length that are notoriously and uniformly poor in staining quality. Only rarely do these areas stain well, and they are often weak, stretched, asynaptic, twisted, and indistinct. In other species such areas are characteristic of the break points of inversions. In *A. nuneztovari*, region 7B–7C is usually twisted, as is 8A. The band of medium intensity in the constriction at the end of 7B is visible only in the best preparations. 8B is often stretched, so that the light, bandless areas appear unusually long. Region 8C–9A is variable and often appears as a weakly staining, stretched area. The heavy band at the end of 9A is often double. 9B is another weak, indistinct area, as are 10A and 10B.

The 2 curved dark bands at the beginning of 11A are always blurred, and the centre of the expanded puff in 11B always appears as a dark area and only rarely are the individual bands as sharply delineated as indicated on the map. The constricted neck-like area between 11B and 11C is usually difficult to follow. Region 13A is invariably asynaptic and bandless, with twisted individual chromosomes visible. This feature is so consistent that it serves as a good point of orientation for this area of the arm. The variability continues up to and including 13B, although the bands here are visible in good specimens. 14B is usually narrow, twisted, and weakly staining.

Chromosome 2, left arm

Usually attached to the long right arm is the distinctively banded region 2L, which shows many similarities at the centromere end of the arm to 2L of *A. aquasalis*. At the free end the series of dark bands in 25A and 25B is characteristic, as is the triplet at the end of 24A. The thin dark bands in 24C are followed in 23A by a stretched, light area with few bands. A wide area of the arm, 22B–22C, contains a widely spaced series of dark bands. Three heavy bands in 21B are followed by a distinctly narrower area, lightly staining, which in turn is followed by a series of dark, heavy bands in region 20. The several dark bands in 19C often appear as a single dark area with one band often set apart. The dark bands in 18A and 18B are usually consistent, especially the thick band near the end of 18A, preceded by 1 thin dark band and followed by 2 such bands. Region 16 is variable, sometimes asynaptic.

Chromosome 3, right arm

The distinctive right arm of chromosome 3 contains many prominent recognition areas. A considerable portion of the arm is homologous with *A. aquasalis*. At the free end of the arm the somewhat spatulate tip contains a series of dark bands, followed by 4 consistent thin bands in 26A. Region 26B is always recognizable as a broad area, sometimes asynaptic, with a series of dark bands that always appear to be broken or wavy. These bands vary in spacing and staining intensity and their appearance is often unlike that shown on the map. They are followed by the 4 heavy dark bands in 27A, always wide, always in 2 groups of 2; these in turn are followed by a stretched, lightly staining, thinner area in 27B, then a series of dark bands as in region 28. The dark bands in 28B are always recognizable. Regions

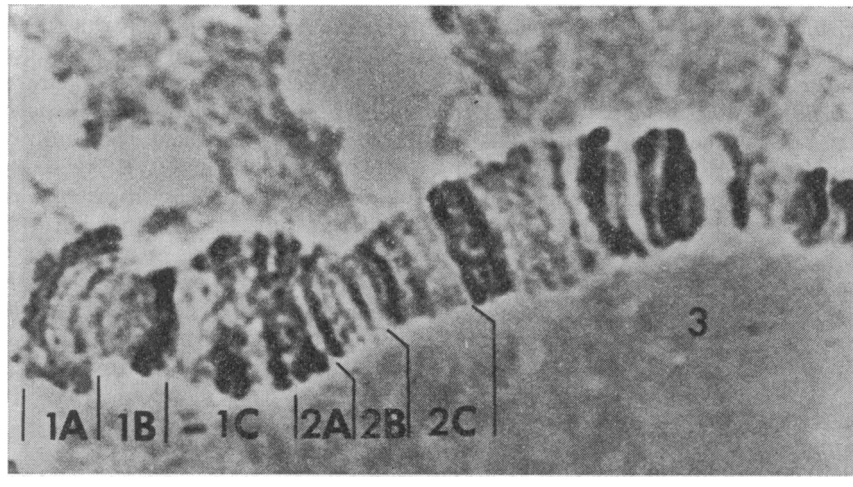

Fig. 4. X-chromosome, right arm, Manaus population.

29 and 30 are always difficult to follow and the bands are variably spaced and stained. Only rarely are they as sharp and distinct as shown on the map. The series of 5 bands in 31B unmistakably marks the middle of the arm. The puff in 32, with its thin, widely spaced dark bands and a heavy band at either end, is a consistent recognition area. From 34A to the centromere the banding pattern is clear, consistent, and apparently identical with that of *A. aquasalis*. The 2 thin dark bands at the end of 33B sometimes appear as a single thick one. The light area in 34A with several pairs of light bands is almost always identical with the pattern shown on the map. The wide puff in 34B is typical of the centromere end of the arm and, although the bands are sometimes variable and vacuolated, careful examination will usually reveal the pattern shown. The thin, stretched, lightly staining area in 35 extends to the centromere.

Chromosome 3, left arm

The distal fourth of 3L is lightly stained; there are many dark bands in the proximal three-fourths. At the free end, 45A–44B mostly stains lightly, the

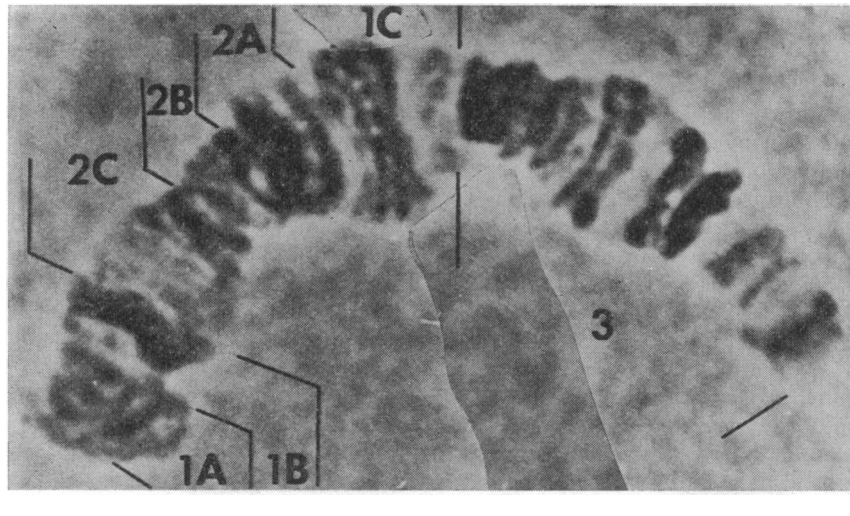

Fig. 5. X-chromosome, right arm, Casigua population.

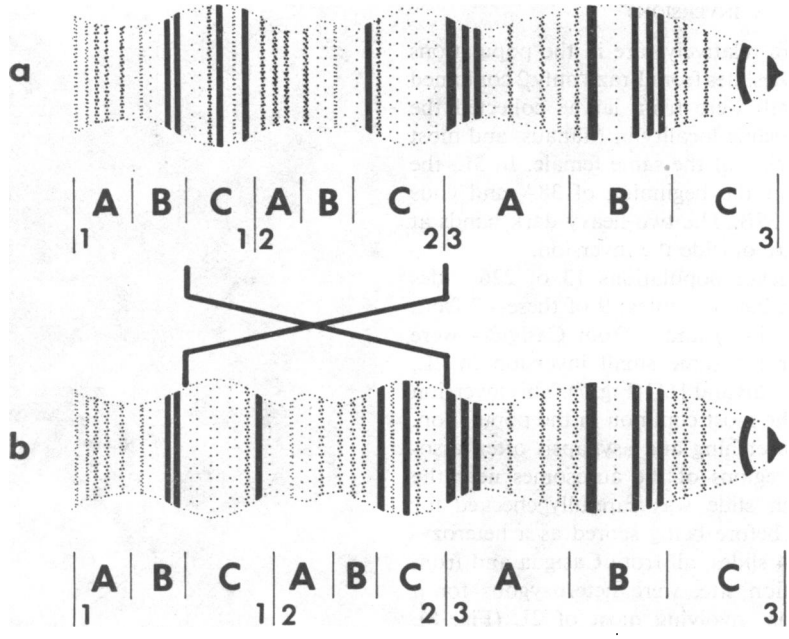

Fig. 6. Comparison of XR from Manaus (a) and from Casigua (b).

3 dark bands in 45B followed by a lightly staining puff in 44A are the best recognition areas. The thin area in 44B and 44C is always weak and lightly staining but the 2 heavy dark bands in 44C provide positive recognition. 43B–42B is also a poor area, with the dark bands always broken. The puff in 41A with 3 broken bands of medium intensity is one of the best landmarks in the arm and is followed in 41B by a long series of evenly spaced light bands. These, in turn, are followed by a series of dark bands in a 3–1–3 pattern in 41C. The dark band at the end of 40A is always twisted and broken, but is followed by 3 bands of medium intensity, then a light constricted area, always recognizable, at the end of 40B. The dark puff in 40C is a consistent recognition area, as are the 3 bands in 39A and the 3 in 39B. From 38A to the centromere the arm is often asynaptic and the bands stain with variable intensities.

CHROMOSOMAL DIFFERENCES BETWEEN THE POPULATIONS

The populations from Brazil and from Venezuela and Colombia may be distinguished with complete certainty by means of a homozygous rearrangement (inversion) in the right arm of the X-chromosome. Fig. 4 shows the Manaus arrangement, and Fig. 5 the arrangement from Casigua. Fig. 6 is a drawing of these two chromosomes, with the inverted areas indicated. The break points are between 1B and 1C and between 2C and 3A in the map (Manaus population). The two arrangements are easily distinguished in slides that may be quickly screened for one or the other arrangement. Thus 190 slides from Brazil (from Manaus, Alixia, and Itacoatiara, all in the state of Amazonas) all show the arrangement shown on the map and in Figure 6a, whereas 226 slides from Colombia (Tibú) and Venezuela (Casigua, Barinas) all show the homozygous inverted arrangement (Fig. 6b). All the Colombian and Venezuelan slides were made from material found in areas in which transmission is occurring.

Careful examination of the autosomes did not show consistent differences. The maps were drawn from specimens collected in Brazil, but were carefully checked against the Colombian and Venezuelan specimens. Except for individual differences in the intensity with which bands or chromosomal regions stain, there were no differences in the autosomes. The origin of the difference in the X-chromosome was presumably inversion, followed by fixation in one or the other population. It is of extreme interest that no inversion heterozygote involving the X-chromosome was ever found in either population.

INVERSIONS

Inversions were relatively rare in the populations studied. Of the 190 slides from Brazil only 2 contained an inversion. Both were from larvae collected the same day, at the same locality in Manaus, and most likely were offspring of the same female. In 3L, the inversion starts at the beginning of 38A and ends at the middle of 37B. The two heavy dark bands at the end of 37B are outside the inversion.

In the Venezuelan populations 13 of 226 slides showed inversion heterozygotes; 9 of these—7 from La Lengüeta (Barinas) and 2 from Casigua—were heterozygous for the same small inversion in 2L, involving regions 16B and 16C (Fig. 7). This inversion appeared to be the most common in the population. Because of the stretching and asynapsis often associated with the regions of the autosomes near the centromeres, each slide was carefully checked for banding pattern before being scored as a heterozygote. The other 4 slides, all from Casigua and from the same collection site, were heterozygous for a complex inversion involving most of 2L (Fig. 8). The details of this inversion remain to be worked out but it involves at least 3 arrangements, one of which is an included inversion. The inversion probably begins at the wide dark band at the end of 22A, although the 3 bands in the middle of 22A are sometimes involved. The 4 dark bands in 23B are certainly outside the inversion. Regions 21B, 21C, and 20A are synaptic within the inversion. Another included synaptic area extends from 18C to 16A. Regions 16B and 16C are asynaptic in all 4 slides and it is therefore probable that the 16B–16C inversion found in the 9 individuals from La Lengüeta is also involved in the complex inversion.

Chromosomal polymorphism in these populations of *A. nuneztovari* occurs at a low level. No heterozygous inversions were found (416 slides) in the X-chromosome, or in 2R or 3R. The lone inversion found in the 2 individuals from Manaus was not recovered from Venezuela or Colombia, nor was either of the Venezuelan inversions found in Brazil. If large population samples confirm the presence of these (or other) inversions in the two populations, this will be another way to separate them by chromosome analysis.

COMPARISONS WITH OTHER SPECIES

There are many autosomal similarities among the species so far studied within the subgenus *Nyssorhynchus*. The most obvious ones with *A. darlingi* are in

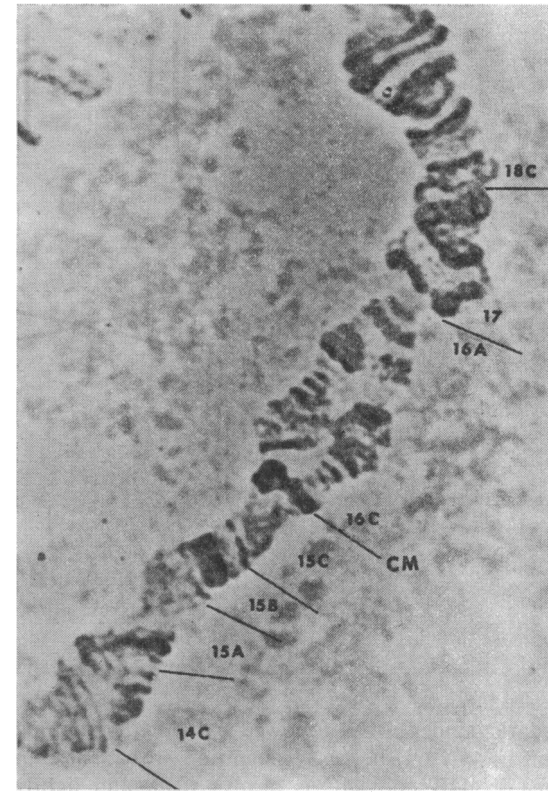

Fig. 7. Inversion in 2L, regions 16B–16C.

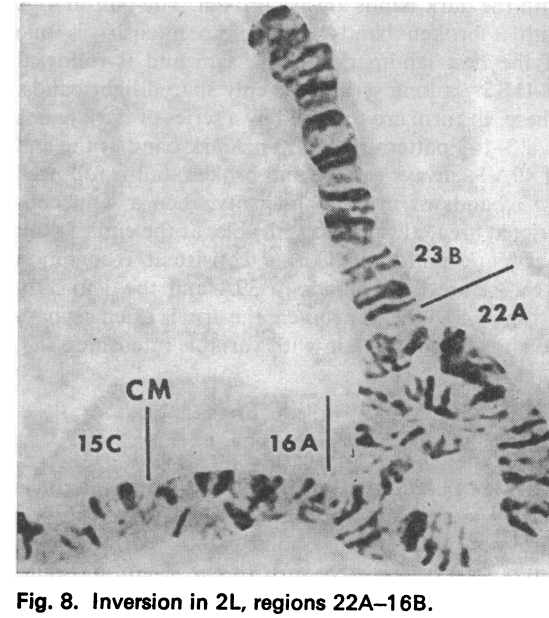

Fig. 8. Inversion in 2L, regions 22A–16B.

2R (Kreutzer et al., 1972) and these same areas are apparent in *A. nuneztovari*. At the free end of the arm, 6A–7B are apparently identical, or almost so, with 6A–8A of *A. aquasalis* and with 6A–8A of *A. darlingi*. At the centromere end of the arm, region 15 is identical in all 3 species. Region 14 is probably identical in *A. nuneztovari*, *A. darlingi*, and *A. aquasalis*, although this is less certain. The interior of the arm contains many areas that resemble areas in both *A. darlingi* and *A. aquasalis*, but the homologies have not been studied in detail.

In 2L the free end of the arm from 25A to the middle of 23A is almost identical in *A. nuneztovari* and *A. aquasalis*, but this area is very different from the free end of 2L in *A. darlingi*. At the proximal end of the arm fully one-third is apparently identical in *A. nuneztovari* and *A. aquasalis*, from 19C to 16C. In this region there are minor variations in spacing and in band intensities, but the homologies are certain. *A. darlingi* is less similar, but apparently homologous throughout region 16.

In 3R, regions 26A to 28A are identical in *A. aquasalis* and *A. nuneztovari* except for quite minor variations in staining intensities. At the centromere end of the arm, 34A–35B are identical in both species. There are no obvious homologies with 3R of *A. darlingi*. Except possibly for the extreme tip in 45A, there seem to be no similarities in 3L among *A. nuneztovari*, *A. aquasalis*, and *A. darlingi*.

There are also similarities between *A. nuneztovari* and *A. albimanus*, but they are not as striking as those between *A. darlingi* and *A. aquasalis*. The closest similarity is in 2R, in which 6A–7B and 14C–15C are similar in both *A. albimanus* and *A. nuneztovari*. There are possibly homologous areas at the free and centromere ends of 2L, but no apparent homologies at all in chromosome 3.

Thus the autosomal homologies are clearly the strongest with *A. aquasalis*, less so but still good with *A. darlingi*, and least of all with *A. albimanus*.

DISCUSSION

The X-chromosome differences between the Brazilian and the Venezuelan–Colombian populations provide at the moment the only sure means of separating the vectors from the nonvectors. The mosquitos from both areas are indistinguishable morphologically, and behavioural characteristics show considerable individuality and are subject to gross sampling errors. The chromosomal differences, however, are absolute and unmistakable. What remains to be done is to extend these data with collections from throughout the range of *A. nuneztovari* in both geographical areas, but especially in Colombia and Venezuela. Additional chromosomal data should delimit exactly the distribution of the two populations and should also define the zones in which they occur sympatrically.

Are these two chromosomally distinguishable populations really separate sibling species? If they follow the pattern so far obtained in other mosquitos, they most probably are distinct species. To establish this fact conclusively, the crosses between the two populations must be made to ascertain the amount, or lack, of gene flow between them. Models are already available in other species for such experiments.

From an evolutionary point of view, the case of *A. nuneztovari* is a most interesting one. Here is a widely distributed form, evidently composed of at least two (possibly more) subgroups that differ in many important physiological and behavioural aspects, yet have not evolved at all in a morphological sense. The chromosomal differences are also minimal. It would seem that this is a population that has just crossed an evolutionary threshold.

The picture becomes more interesting when the closely related species *A. oswaldoi*, *A. aquasalis*, *A. rangeli*, and *A. benarrochi* are considered. All these species may be separated in taxonomic keys (although often with great difficulty and uncertainty) but when large series of specimens from the field are examined it is immediately obvious that a wide range of variation exists. The morphological variation is considerable even among the offspring of a single female, and even wider among randomly collected specimens from nature. The variation extends to the key taxonomic characters, so that for a given specimen it is often difficult if not impossible to be certain of the specific identification. Certainly, this is a case of a species group whose members have obtained some slight measure of morphological individuality and can be distinguished with certainty only by chromosomal studies in conjunction with crossing tests.

There is no doubt about specific identification when the X-chromosomes are examined. *A. nuneztovari*, *A. aquasalis*, *A. oswaldoi*, *A. rangeli*, and *A. benarrochi* all have unique, easily identifiable X-chromosomes, readily distinguishable from one another. Admittedly identification is somewhat more difficult by means of chromosomes than by the external morphology, but if absolute identification of these species is required chromosomal studies are

still the only sure method. Whether or not these species will hybridize in the laboratory, and if indeed they do in nature, can be demonstrated only by a long series of experiments and careful study of the hybrid chromosomes, if any.

In addition to these most interesting evolutionary considerations, there are also important practical aspects. The fact that *A. nuneztovari* may be positively identified and separated from its close relatives by means of chromosome analysis is already an important step. It should be of practical interest to malariologists to identify, by this means, the anopheline responsible for transmission in a given area, and to take appropriate measures based on the data available from behaviour, ecology, and bionomics.

The case of *A. nuneztovari* is particularly striking. If crossing studies (which are no small or easy matter) substantiate the existence of two separate populations only one of which is involved in transmission, this will be an important advance indeed. Finally, if the X-chromosome differences prove to be operationally adequate to distinguish the vectors from nonvectors, chromosomal surveys can easily delimit the distribution and relative abundance of these two populations. Control measures can then be concentrated in areas of greater importance.

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RÉSUMÉ

DIFFÉRENCES CHROMOSOMIQUES ENTRE POPULATIONS D'*ANOPHELES NUNEZTOVARI*

Les chromosomes des glandes salivaires d'*Anopheles nuneztovari* comportent un chromosome X, comprenant les zones 1-5; un chromosome 2, dont le bras droit 2R contient les zones 6-15 et le bras gauche 2L les zones 16-25; un chromosome 3 avec un bras droit 3R (zones 26-35) et un bras gauche 3L (zones 36-45). Les analogies entre les chromosomes d'*A. nuneztovari* et ceux d'autres membres du sous-genre *Nyssorhynchus* sont décrites.

On a comparé les chromosomes de deux populations d'*A. nuneztovari*, l'une formée de moustiques vecteurs du paludisme récoltés à Tibu, Colombie, et dans les Etats de Barinas et de Zulia, Venezuela; l'autre de moustiques non vecteurs capturés à Manaus (Brésil), et noté, de façon constante, des différences dans la succession des bandes du chromosome X.

Si l'on prend comme séquence de bandes type celle du chromosome X de la population de Manaus, on voit que chez les populations d'*A. nuneztovari* de Colombie et du Venezuela la région 2A-2C du bras droit de ce chromosome est le siège d'un remaniement homozygote. Aucune modification hétérozygote du chromosome X n'a été décelée dans l'une ou l'autre des populations.

Dans les populations d'*A. nuneztovari* étudiées, le polymorphisme est relativement rare. Une seule inversion, intéressant les régions 38A-37B de 3L a été découverte parmi les spécimens de Manaus. Peu fréquentes également sont les inversions de la région 16B-16C de 2L chez *A. nuneztovari* de Barinas et de Zulia.

A. nuneztovari est particulièrement intéressant pour l'étude de l'évolution des espèces. Il est très répandu et comporte au moins deux sous-groupes qui diffèrent par leur physiologie et leur comportement, mais qui sont morphologiquement identiques et ne présentent que de faibles différences chromosomiques. Des espèces très voisines d'*A. nuneztovari*, comme *A. oswaldoi*, *A. aquasalis*, *A. rangeli* et *A. benarrochi*, difficilement discernables

morphologiquement, peuvent être néanmoins aisément distinguées grâce aux caractéristiques uniques de leur chromosome X.

Dans le cas d'*A. nuneztovari*, s'il se vérifie que les différences chromosomiques permettent la distinction entre espèces vectrices et non vectrices, on pourra préciser la répartition et la densité relative de ces populations.

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