

GEOGRAPHIC & ECOLOGIC FACTORS IN DISTRIBUTION OF NEOTROPIC HOMOPTERA

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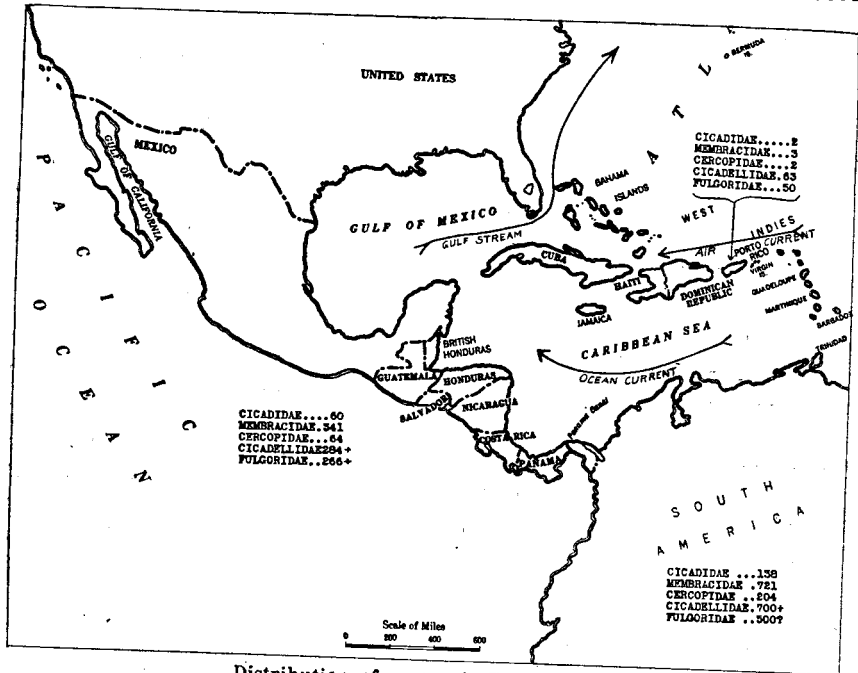
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A cursory review of the different groups of Neotropic Homoptera will reveal some quite puzzling questions and, while it may be as yet impossible to evaluate the factors concerned in the problem, there are certain phases which seem worthy of consideration, if for no other reason than to indicate the lines along which more intensive study is desirable. Why, for example, should the South American fauna include hundreds of species in the families *Cicadidae*, *Cercopidae* and *Membracidae*, and Puerto Rico have these families represented by only a very few species? To refer the paucity in these groups merely to differences in original distribution, to plant, hosts, or to land connections, recent or remote, does not seem to satisfy; and it is fair to give a general comparison of the relative abundance in species in the different sub-regions of the Neotropic realms. This question was brought forcibly to my attention in a rather extensive study of the Homopterous fauna of Puerto Rico after having given some attention to that of Cuba and the Central and South American regions. I could see no major reason why in Puerto Rico, with its very rich flora including many tropical trees and shrubs, and with ecologic conditions ranging from sea level to 3500 feet elevation, and from extremely humid to almost arid sections, that the Tree-hoppers, Frog-hoppers and Cicadas should be practically absent — two species of Cicadas, three of Cercopids and three of Membracids, and of these some totally different from South American representatives.

To bring out these differences let us make a little more detailed comparison of the numbers in different groups.

CICADIDAE.

The group *Cicadidae* which includes some of the largest of the Homoptera and which is very fully represented in the Oriental and Ethiopian Faunae is also very extensively represented in the South American region and also in Central America and Mexico, but the numbers of species fade out rapidly from west to east in the West Indies, a small number occur-



Distribution of neotropic Homoptera.

Fig. 1. — Map of part of the Neotropic realm showing relations of different divisions. The numbers used here are derived from various sources and in some case are doubtless far from indicating total species occurring. However the data for Puerto Rico is most recent and it may be assumed that further studies will only increase the differences between the South American and the Puerto Rican faunae.

ring in Cuba and but two species are known in Puerto Rico, As the group is certainly an ancient one and its evolution in South America undoubtedly extending over a long period, regardless of where we may look for its original center of evolution, there is reason to enquire as to what sort of fundamental factors should have been operative to prevent the dispersal of a greater number of the species throughout the Antillean region. One species known only from Puerto Rico and hence to be considered as probably endemic seems more likely to have developed from forms occurring to the west in the Antillean chain rather than to be associated with any of

the South American forms. The other species *Proarna hilaris* GERMAR has a wider distribution in the West Indies but here again the nearly related species would seem to be found in Cuba or Mexico rather than in South America.

MEMBRACIDAE.

This very large and widely distributed family has apparently a culmination of development in South America, the number of species accredited to this region in FUNKHOUSER's Catalogue running to at least 701, while a number of species recorded as locality unknown may very probably belong here. This enormous number for the family is carried well into Central America and even northward into Mexico and United States, but diminishes in a remarkable degree as we go eastward along the Antillean chain of islands. The situation seems to reach an extreme in Puerto Rico where a record of three species is given. Even if this should be increased by later collections the disparity is too great to be accounted for on any basis but some fundamental factor or factors of long duration and efficiency.

As these insects are largely tree inhabiting it seems evident that there would be far less opportunity for their transfer by human agencies than with some of the *Cicadellidae* which, living on cultivated crops, have a much better opportunity to be carried in with crop introductions. Hence we may assume that their distribution to the eastward along the Antillean chain has been prevented by certain natural forces operating probably in much the same manner as for the *Cicadidae* which present certain parallels in habit and restriction of host associations. These may be considered in connection with the discussion of the factors influencing dispersal.

CERCOPIDAE.

As with the preceding families the *Cercopidae* show a very remarkable disparity in numbers when the fauna of South America is compared with that of the West Indies and especially with Puerto Rico which occupies a somewhat exceptional location as the extreme eastern one of the larger islands of the Antillean chain. In this family again there is a very large representation of species in South America, 204 species according to LALLEMAND's list in the Genera Insectorum compared with 64 for Central America and only two for Puerto Rico. Here again there is a gradual lessening of numbers as we pass eastward along the West Indian Island, Cuba having much fewer than Central America or Mexico. A particularly striking comparison is seen in the genus *Tomaspis* which is so abundantly represented in south America and has one species for southern United States and Mexico but not one for Puerto Rico. Just what has been the barrier that

has interfered with the transfer from Trinidad or Venezuela along the Lesser Antilles to Puerto Rico is certainly an open question. While it may not seem reasonable to consider South America as the original home of the Frog-hoppers there can be no question as to their long existence in this region since we have such a wealth of genera and species and among them many genera not found in other regions. Here was evidently a center of evolution and distribution and the paths for their dispersal were evidently open to the north through the isthmian connection but closed at the eastern border.

CICADELLIDAE.

In the family *Cicadellidae* there is not so striking a discrepancy between the South American and the West Indian faunae as a whole, but some very striking differences are to be noted in certain subfamilies or genera.

In the *Bythoscopinae*, while there are numerous Agallias in Central and South America, there are very few in the West Indies, and these correspond more nearly with the species of Southern United States.

The species of *Macropsis* are scant in all of the Neotropics but for *Bythoscopus* where one is known for Cuba several occur in Mexico and Central America. *Idiocerus*, which is so very plentiful in the Nearctic realm, is but scantily known except for a few in South America and one recently noted for Puerto Rico.

The *Cicadellinae* are almost absent in Puerto Rico and these probably introduced with cultivated plants and while more occur in Cuba there is nothing to compare with the enormous number of species occurring in Central America and reaching a culmination with well over a thousand species in South America. Such as occur are more nearly related to the species of southern United States or Mexico than to those of South America.

In the *Gyponinae* especially in the genus *Gypona* in its wider sense we have scarcely any in the West Indies, none so far known for Puerto Rico, but many occur in Mexico and the genus has its center of greatest abundance apparently in northern South America where SPANGBERG alone recognized nearly 100 species and there are a number to be added to his records of a half century ago.

FULGORIDAE.

In the group of Fulgorids (often given super-family rank, as Fulgoroidea) we have a number of quite distinct divisions of subfamily or family rank but for our purpose they may be discussed together. All of the subdivisions are well represented in South and Central America but only one, the Delphacinae, are found in any considerable number of species in Puerto Rico. The group of large species including the lantern flies, the *Fulgorinae* and also

the *Dictyopharinae* and *Ricaninae*, have no species in Puerto Rico and the *Issinae*, *Tropiduchinae*, *Flatinae*, *Acanolinae*, *Cixiinae* and *Derbinae* but very few. It may be noted that these groups contain the larger species few of which are associated with cultivated crops or with grasses. The Delphacids are many of them cosmopolitan and associated with cultivated crops or with grasses. One Cixiid — *Oliarus franciscana*, also a grass or cane feeder, is found over wide areas of tropical and subtropical America. Evidently some if not all of the factors operating on the other groups of Homoptera have been effective here.

Considering now the possible factors that may have entered into the remarkable features of distribution that have been indicated here and recognizing that South America must have been in all probability the center of evolution for an enormous number of species in this group, it seems quite evident that no one factor can be credited with a sole or perhaps even a major influence in the conditions found.

We may assume an extended geologic period within which the separation of stock forms has been going on within the region as there has been not only a continuous succession of periods in which we may assume for this region the warmest if not the most tropical conditions of the western hemisphere but a range of temperature from tropical sea level to the boreal conditions of the upper Andean chain with certainly a great range of plant life and a great variety of ecological conditions. These would certainly give opportunity for much adaptation and the uniformity of conditions in definite areas the opportunity for the fixation of specific forms for definite host plants and local ecologic habitats.

The fact that a similar condition exists with all the major groups of Homoptera suggests that there must be some underlying factor or factors affecting all these groups and operating from the early stages of dispersal and establishment throughout the neotropic realm.

PALEOGEOGRAPHY.

If, as seems to be pretty generally accepted and supported by biologic as well as geologic evidence, there was land connection between South America and Africa as late as Jurassic or early Cretaceous period, we can readily understand certain fundamental affinities between African and South American animals and if this land connection was broken before or during the Cretaceous we have ample time for the evolution of many distinct forms in the two regions.

Also, if North and South America were divided by a wide stretch of ocean during Cretaceous and early Tertiary time we have ample reason for wide differences in the fundamental character of the Homopterous faunae in these, later connected, land areas.

Connection of North and South America by uplift in late Tertiary and

early Quaternary has given opportunity for dispersal between these areas but lack of such connection east of the Caribbean would account for the failure of South American forms to reach the Antillean chain.

Further, an examination of the ocean floor for the Caribbean sea and Gulf of Mexico has some very significant results bearing on the affinity of the West Indian fauna. Differences in elevation or subsidence of land areas in these regions might easily result in land connection between Honduras or Yucatan and Jamaica or other West Indian islands. However, it seems to me that this factor should be closely connected with another factor, that of water and air movement in the subequatorial belt.

CLIMATE.

The climatic factors of temperature and moisture have no doubt been operative as a distinct barrier to some lines of dispersal and in connection with available food plants and agencies of dispersal may have been a determining factor for certain groups. However, within the range of the tropics, except in connection with elevation, there would seem to be hardly sufficient climatic barrier to account for the faunal status.

The Homoptera are presumably all plant feeders or dependent on vegetable food, often quite restricted in kind, and therefore the extent of distribution dependent on distribution of plant species. Incidentally also the ready dispersal from one region to another will depend largely on the ability of the plants to secure means of dispersal.

OCEAN CURRENT.

Just how long a definite ocean current has been maintained from east to west through the Caribbean sea may be problematic but we can hardly doubt that it has been throughout the period we have in view and whether passing through open sea into the Pacific or later diverted through the Gulf of Mexico to form the Gulf Stream the effect as a barrier or as a possible means of carrying drift material from the South American coast in a westward direction is obvious.

AIR CURRENTS.

While the ocean current can readily be conceived as an effective barrier or as a means of carrying drift with possible insect passengers, there may be an equal or greater factor in the air movement in the equatorial region. The very continuous trade wind from east to west and the westward movement of storms through the West Indies can easily be conceived as a powerful agent in preventing the eastward movement of insects and also of carrying such insects as are present on the eastern islands to those to the westward. I have elsewhere discussed this possibility.

" It may be noted that the principal winds and particularly the tropical storms — hurricanes as well as regular trade winds travel from east to west and so far as wind agency is concerned, and probably surface currents with drift on the water, the direction of dispersal would be from east to west. "

HUMAN AGENCIES.

Finally we may consider the human factor as one which during recent time has had a distinct bearing on the dispersal of insect life and the Homoptera furnish some excellent examples.

Even a somewhat hasty comparison of the species represented in the different regions will show that the species most widely distributed and occurring in all parts of the Neotropic realm are those living on cultivated crops or on such plants as are most commonly distributed in commerce or by the activities of man.

RECENTLY INTRODUCED SPECIES.

Such introduced species as have come with cultivated crops, coffee, sugar cane, maize — and possibly a number of garden vegetables, and certainly some introduced grasses, Bermuda, Para, Natal and others, are to be accounted for as brought with their host plants and are limited by other than human agencies.

Examples are quite evidently such species as *Euscelis obscurinervis*, *Protalbra braziliensis*, *Deltocephalus flaviscosta*, all having been originally described from South America, but now known throughout tropical and much of subtropical Americas, with the preponderance of evidence favoring the belief that they were originally derived from the South American region.

The relation of the West Indian Homopterous fauna to that of Mexico or Central America was pointed out long ago by UHLER and possibly recognized by still earlier students of this fauna, but satisfactory explanation of this affinity has been lacking. The combination of factors here suggested may help in arriving at a more tenable solution.

To sum up in brief, we may say that there are some very wide differences in number of species of Homoptera in the different divisions of the Neotropic realm. Especially noteworthy in the *Cicadidae*, *Membracidae* and *Cercopidae*; that conditions of land connection or oceanic barriers, climate, vegetation, oceanic and air currents and finally human agency in commerce and plant introductions are to be combined in accounting for the existing faunal distributions.

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