d'un travail déjà publié [1], compte, à titre endémique, la sous-famille monotypique des *Paralichthodinae*, et, dans la famille des *Soleidae*, les 2 genres *Barnardichthys* et *Austroglossus*.

ZOOGEOGRAPHY OF THE HOMOPTERA

By Z. P. METCALF (Raleigh)

The practical completion of the card catalogue of the Homoptera of the World makes it possible to study the zoogeography of this suborder of insects in a manner not heretofore possible. In this catalogue the families are divided into sub-families, tribes, and genera according to our present concepts of their taxonomic relations and the species are arranged under the genera set off by small, colored metal tabs, which show geographical distribution very strikingly.

It is true that our catalogue is pratically complete for the described genera and species. However, it must be remembered that our knowledge of what constitutes valid genera and species and our knowledge of their distribution is far from complete. Then too, it is quite evident that as far as this order of insects is concerned, there is much yet to be discovered about the world fauna. My present belief is that we know approximately one-third of the genera and species of the world, this is based on the total number of species in rather extensive collections from such regions as Cuba, Brazil, Central America, Tanganyika, Java, and new Guinea in relation to the number of species now known from these regions.

Nevertheless, for the genera and species that we do know our knowledge of their distribution is now fairly complete and the sample is large enough, about 30.000 species in approximately 3.200 genera, to make any tentative conclusions worthy of consideration. The Homoptera are very valuable as geographic indices. In the first place they are insects of relatively small size, without strong powers of locomotion. This, together with the fact that for the most part species are limited to a single host plant or a very narrow range of food plants, results in their being limited typically to a very narrow range in nature. Many species not limited to a single species of host plant are limited to a relatively narrow range of host plants. Others not limited by food preference seem to be restricted by other ecological factors. This makes these insects, popularly known as cicadas, tree hoppers, leaf hoppers, plant hoppers and frog hoppers or spittle insects, excellent indicators of zoogeographic regions.

The author in a recent paper (METCALF, 1947 a) has stressed the importance of the center of origin concept in its relation to taxonomy and the close correlation that must exist between taxonomy and zoogeography. In the present paper I would like to look at the reverse side of this two-way relation and consider these matters from the standpoint of zoography.

1. *Bull. Inst. Océanogr.*, 908, 1947.

From our previous studies we believe that zoogeographic areas may be used to correct our ideas of systematic relationships and, vice versa, that our ideas of systematic relationships may be used to modify our concepts of zoogeographic mapmaking. These ideas may be expressed by the following parallel columns:

Zoogeographic Regions	Taxonomic Groups
Superrealm or Realm	Families
Realm or Subrealm	Subfamilies
Region	Genera and Subgenera
Subregion	Species and Subspecies

This classification, if correct, means that it should work both ways. Superrealms or realms should be defined by families; realms or subrealms by subfamilies; and genera should be confined to regions; species to subregions, et cetera. Now such a generalization does not mean that some species do not have a wider distribution than a subregion, or that some genera are not distributed over two, three, or more regions. Some species are found in more than one region; in some cases being distributed by man in connection with his cultivated crops. Thus, the corn plant hopper (*Peregrinus maidis* Ashmead) was described from Florida, and occurs in the southeastern states from New Jersey to Texas, and has been found wherever maize is grown in the tropical and warm temperate regions of the world-Mexico, Central America, West Indies to Brazil, Hawaii, Fiji, Micronesia, New South Wales, Queensland, New Guinea, through the East Indies to the Malay Peninsula, Formosa, Japan to India and Ceylon, Tanganyika to Cape of the Good Hope, West Africa, Nigeria, Gold Coast to Sierra Leone. Certain genera have a wider distribution than a single zoogeographic region. What I am trying to say is that the taxonomist and zoogeographers should look with suspicion on all such cases of wide distribution, especially of uncorrelated distribution. Genera may have isolated species in South America and in India, or in China and South Africa, but such cases are open to very grave suspicion. There may be cases of genera having species which have lost connections with their centers of origin as in the case of the elephant and horse tribes; but such cases should be established only by careful consideration of all the facts. At the present time we have many genera, especially the older established genera, which were very vaguely defined and which have become the dumping ground for a vast host of species simply because the generic descriptions are too all-inclusive. For example, the genus *Oliarus* Fieber, as at present constituted contains no less than 36 species in the Neartic Region, 67 species in the Paleartic Region, 31 species in the Ethiopian Region, 22 species in the Oriental Region, 12 species in the Caribbean Region, 4 species in the Neotropical Region, 16 species in the Australian Region, 1 species in the Austromalayan Region, and 9 species in the Oceanic Region. Now I have no more reason for believing that the genus *Oliarus* represents the correct systematic position of these species than that the genus *Cicada* represented the correct position of the 42 species described by Linnaeus in 1758. These 42 species are today distributed among 9 families and 16 genera. The correct solution of such taxonomic problems as presented by the complex genus *Oliarus* awaits a better understanding of taxonomic

characters, zoogeographic distribution, et cetera. It is, of course, barely possible that this genus is a very ancient one of world-wide distribution ; but it is certainly a safer assumption that it represents a vague complex with poorly defined and very generalized characters of polyphyletic origin. All such cases should be carefully reconsidered and the boundaries of such taxonomic groups should be redefined and modernized. By these and similar methods only will it be possible to make taxonomy a more exact science.

This belief that there is a mutual interrelation between valid taxonomic groups and real zoogeographic regions is dependent upon our definition of both terms. That both terms need clearer definitions requires no extended argument at this time.

Now I do not believe that it is possible for us to have clear definitions for the various categories in taxonomy or in the field of zoogeography without some understanding of the center of origin theory. This theory may be stated briefly as follows :

If the terms genus and species are phylogenetic as well as systematic concepts, the species composing the genus will be closely related. They will have similar morphological characters, not merely similar appearing characters. In other words, if living organisms have evolved from pre-existing organisms, or if evolution be accepted as a natural law in the organic world, and if there is any reality in the taxonomist's concepts of the individual, the species, the genus, the family, the order and phylum ; then there is a spot on the earth's surface where each category originated. For the lowest category, we call this place the birthplace of the individual. For the higher categories, we call this area the center of origin for the group under consideration, be it species, genus, family, order or phylum. Each species will have a center of origin and each genus will also have a center of origin. These centers of origin will bear the same relation to the species or the genus zoogeographically as his birthplace bears to the history of the individual. The center of origin of a group has a geographic location, which will be more definite for the lower categories, such as species and genera, than it will be for the higher categories, such as families and orders ; just as the birth place of an individual, if it can be determined, is more definite than the center of origin for a species even if the center of origin can be approximated. In the same way, in general, the center of origin for a species will be more recent, geologically speaking, than it will be for the higher groups.

Usually the center of origin for a species will be within the present range of the species, but not necessarily so. The center of origin of a genus may be within the range of the known species ; but is more apt to be beyond the range of the included species, than the center of origin for a species is apt to be beyond the known range of this species.

In the highest categories the center of origin is frequently very remote geologically and geographically ; and may have no apparent relation to the present distribution of the recent forms. In fact only a very few of these racial histories have been traced. But the generalized histories of the horse family and the elephant family make one of the most interesting chapters in paleontology. These somewhat fictionalized histories are developed in the illustrations and are repeated here not because they are not well known ; but only because

they may help us to an understanding of the zoogeography of these animals and furnish a basis for a better understanding of the zoogeography of other groups.

In the same way the spread of certain introduced species may help us to a better understanding of zoogeography. The spread of the English sparrow, the starling, and the cotton boll weevil, reveal the same fundamental pattern. For a period after introduction there is very little spread, then gradually the rate of spread increases and reaches a climax when the animal has occupied all the territory available to it, that is, to all the territory to which it is adapted ecologically. With the cotton boll weevil this would mean all that area in the southeastern United States where cotton is grown except certain upland areas where either winter temperature or low humidity seems to be a determining factor. From this climax of wide distribution there may be a gradual recession until the species occupies only the most favorable islands in the territory that is has occupied. Eventually, the enemies of this species may gain the upper hand and it may disappear entirely from the territory that it once occupied.

There are usually seven fairly distinct stages in the spread of introduced species. First, a period when it is becoming established, typically restricted to a very limited area; then a period when it commences to spread; third, a period of increased dispersal; fourth, a period of maximum development; fifth, a slight and gradual recession; then a period of rapid recession; and finally a period of great reduction in range and complete elimination.

It may be argued that these accidental introductions have no resemblance to the dispersal of a species in nature. That in the latter case the spread is slow; occupying periods that are measured by geological epochs not in years; but let's not be too sure that this is the case. Is it not possible that the spread of species in nature is fully as rapid as that of introduced species? Introduced forms which find themselves in a new but favorable environment usually find no great numbers of enemies arrayed against them. May this not be equally true of newly evolved forms? I rather suspect, if we knew the complete history of a species, that we would find that it runs about the same course that we have seen repeated in the United States by several introduced forms.

From its center of origin a species will spread in a manner similar to an introduced species until it occupies all the territory, ecologically speaking, to which it is adapted. But sooner or later any species in its dispersal will meet with impassible barriers: the ocean for terrestrial species, high mountains for lowland species, temperate climates for tropical species; and many other ecological and physical barriers. Within the continental range of a species there will be many areas which a highly modified species cannot occupy. If the species is restricted to a single host plant species, obviously it will not be able to live on other host plant species of the same genus which may be available. If the given species is restricted to a single ecological niche, then other ecological niches are available in the area occupied by the species under consideration. Other species may develop for the food plants which are not used or the ecological niches which are not occupied. In this way an area may support many closely related species. Such a group of species would constitute a phylogenetic genus. The geographic extent of such a phylogenetic group becomes of special interest not only to the systematist but to the student of zoogeography, for

it too will have a center of origin. Tentatively we will advance the idea that the extent of such a genus would be bounded by a zoogeographic region. If this is true, a group of genera may be used to delimit a zoogeographic region and a zoogeographic region may be used to define a genus. Any such concept must be used in the broadest sense until we are much surer of our facts than we are at the present time.

Such a concept is based upon a number of assumptions which may or may not be true. Some of the assumptions may apply to animals with limited powers of locomotion, such as the Homoptera, and not to other animals like birds with practically unlimited powers of flight. Some of the assumptions on the other hand may not be true for recently evolved groups like the mammals which may be in a state of flux, evolutionarily speaking, but could be true for animals like the ancient insects with their external armor of inflexible chitin which may have settled into evolutionary grooves. Some may apply to animals which have only limited powers of adaptation to the environment while not applying to other animals which have a wide range, ecologically speaking. If the center of origin theory will help us understand phylogenetic and taxonomic relations, it will also aid us in our understanding of zoogeography.

For the present, at least, it is my belief that it is not possible to develop a single zoogeographic map for all groups of the animal kingdom. The attached map has been developed during the past twenty-five years and fits my present classification of the Homoptera better than any other scheme I have been able to advance.

This would not be the regions of the world for mammals or any other group of animals which have better methods of locomotion, or different sets of ecological factors limiting their ranges, or different centers of origin, or different rates of spread. It should be recalled, also, that it is difficult to locate boundaries between regions in nature. Regions for land animals unless separated from each other by large bodies of water, merge gradually into each other. Therefore, on this map I have drawn the boundaries as broad areas in certain parts of the world, and by narrow lines in other places. This lact of definiteness may be due also to lack of knowledge, for it must be emphasized repeatedly that our knowledge of the Homoptera is far from complete. This map differs from the conventional map in the following respects : New regions proposed are Caribbean, embracing Mexico, Central America and the West Indies; Malaysian, embracing the Sunda Islands, the Philippines and Celebes; Austromalayan, comprising New Guinea, Solomon Islands, New Hebrides and New Caledonia ; Maorian, including New Zealand and the nearby islands.

Whether any of these regions are real zoogeographic regions in the best sense of the word must depend upon more evience than is now at hand.

In studying this map it must be borne in mind that nature draws no hard and fast lines. The low tide mark may be the extent of the spread of a strictly terrestrial species but no land area is separated from a contiguous land area by sharp boundaries. In such areas species from adjoining areas may tend to overlap, and all boundaries on the map are subject to modification as more evidence is produced. But as indicated on the map there are three great areas where it is practically impossible to define boundaries with our present know-

ledge of the Homoptera. These areas are indicated on the map by solid black. One is the boundary between the Neartic Region and the proposed Caribbean Region. This is a semiarid region with many high mountains. Many Mexican species extend northward into the southwestern United States and on the other hand many species from the southwestern United States, especially in the mountains and I suspect equally along the gulf coast, tend to extend into Mexico. On the other hand, if we are to establish a Carribbean Region, its southern border is equally hard to define. The great valley of the Orinoco has many close ties with the Carribean Region but many species from the Amazon subregion tend to extend northward into the valley of the Orinoco.

The other trouble spot on our zoogeographic map is the area in southeastern Asia including southern China, Formosa and Hainan Island where it is difficult to draw a boundary between the Oriental Region on the one hand and the Paleartic Region on the other. Elsewhere this boundary seems to be fairly sharp across the Himalayas and Persian Desert.

Most of the other boundaries seem fairly stable with our present knowledge of the Homoptera. The oceans and deserts dividing the great geographic regions are usually effective barriers against land animals such as the Homoptera. Narrow straits, on the other hand, may not be effective barriers to the spread of strictly terrestrial species. The Straits of Florida and Malacca Straits, separating the Nearctic from the Carribean and the Oriental from the Malaysian, are examples. The southern tip of Florida shows some Carribean elements and the southern end of the Malay Peninsula contains a mixture of Oriental and Malaysian elements. But what will emerge from the studies now in progress of extensive collections from the Malaysian Regions and Austromalayan Region, is a matter of conjecture. In fact, further studies may eliminate both the Caribbean Region and the Malaysian Region entirely but for the present they are useful concepts.

If this concept of zoogeography be accepted, it makes it possible for us to restudy the distribution of various groups of animals based on a better understanding of taxonomic relations, phylogeny including center of origin, ecology, and morphology of the forms involved. Thus it might be possible for us to arrive at a closer approximation of the truth, the goal of all science.

APPENDIX

Superrealm Paragea
- Realm Arctogea
  - Subrealm Holartic
    - Region Paleartic
      - Subregions European
        - Mediterranean
        - Siberian
        - Mongolian
        - Japanese
    - Region Neartic
      - Subregions Canadian

Alleghanian
Cordilleran
Californian

Subrealm Palaeotropical
Region Ethiopian
Subregions Guinean
Sudanese
Mozambican
Caffrarian
Malagasian

Region Oriental
Subregions Indian
Ceylonese
Siamese

Region Malaysian
Subregions Sunda omit ian
Philippine
Celebesian

Realm Neogaea
Region Neotropical
Subregions Andean
Amazonian
Pampean
Orionocian

Region Caribbean
Subregions Aztecan
Mayan
Antillian

Superrealm Teleagea
Realm Notogaea
Region Australian
Subregions Carpentarian
Victorian
Aurian
Tasmanian

Region Austromalayan
Subregions Papuan
Melanesian

Realm Nesogaea
Region Maorian
Region Oceanian
Subregions Polynesian
Micronesian
Hawaiian