HOMOPTERA AUCHENORHYNCHA

Z. P. METCALF
University of North Carolina[1]

Reprinted from *A Century of Progress in the Natural Sciences—1853–1953*

As I contemplate the literature devoted to the suborder Homoptera Auchenorhyncha on file in my laboratory, I am more and more impressed with the progress that has been made during the last century.

There are in this library about 12,000 different items: all of the books and papers, bulletins and circulars that have been printed about the Homoptera, except fifty, more or less. These fifty, to which I find some reference in the literature, are not to be found in the great American libraries, nor in any of the great European libraries, so far as I can discover. Many of the earlier works are in Latin, and not a few in Chinese and Japanese, which are, as far as I am concerned, knowledge securely locked up. I wish that each of these books and the important papers might pass in review so that the reader might comprehend the history of the science of entomology as it refers to the Homoptera. Here are the great classics of ancient times that tell of the struggle of a beginning science called entomology; also the more recent monographs devoted to single families or even to single genera—the work of a whole host of men deeply interested in our science. What a marvelous tale they have to tell also of far away places and strange faunas! Places about whose people we know very little sometimes contribute the most to our science; the upper reaches of the Congo River, Tanganyika, South Africa, Tibet, Java, Sumatra, Celebes, New Guinea, the great interior of Australia, the high mountains of Peru, Ecuador, the upper reaches of that greatest river basin of them all, the Amazon, with its marvelous fauna.

As I realize that this group has grown, since 1758 when Linneaus described one genus and 42 species, to a group composed of 45 families, about 3,500 genera, and approximately 30,000 species, I am convinced that no one should attempt to understand the suborder as a whole, let alone attempt to describe the progress that has been made over a century of time.

If history is simply the lengthened shadow of the great men who made it, then in discussing the history of a group of insects one must perforce devote most of his time to a discussion of the men who made that history. In a short paper such as this to cover more than the mere outline of the development of the study of the Homoptera is impossible.

When we think of progress in a field of biology we perhaps think first of progress in the field of taxonomy because here we have in the number of genera and species discovered a convenient measure of progress.

For the century beginning with 1850, it is convenient to recognize three periods. Up to about 1850 most of the students of insects were entomologists who studied more than one order of insects. About 1850 the study of entomology began to show a good deal of specialization so that by the beginning of the century 1853–1953 there were a number of students of the group Hemiptera, including both the Heteroptera and the Homoptera.

---

1. North Carolina State College of Agriculture and Engineering.

At the beginning of this century Stål, a great Swedish hemipterist, commenced his work. Perhaps no student of the order Homoptera has had a better grasp of the fundamental groups and the fundamental phylogeny. He was ably assisted by a fairly large group of students of Homoptera in Europe, including Walker and Marshall of England, Signoret of France, and Fieber of Germany. Most of these men had ceased publication by the end of the second decade of the century. In America at this same time the most outstanding student of this order was Fitch in New York.

Walker worked on the extensive collections in the British Museum and described many new genera and numerous new species from all parts of the world. Unfortunately, he did not seem to have a clear concept of taxonomic units. He made numerous mistakes in assigning species to genera, and formerly it was quite the fashion to condemn his work universally; however, recent students in restudying his material have had a better appreciation of his work. Marshall worked on a taxonomic review of the species then known from Great Britain and contributed a sound foundation on which future students of the British fauna could work. Signoret's studies were most extensive in his reviews of the genus then known as *Tettigonia* and related genera, and of the species which he considered closely related to the genus *Acoccphalus*. Fitch's catalogue of the specimens in the State Cabinet of Natural History, with careful descriptions of the species known to him, was the foundation for future studies by American homopterists.

After this first period in the development of taxonomy in relation to the Homoptera, the large number of workers as well as their increased specialization makes it difficult to summarize the contributions of each student. I have simply listed these workers, therefore, together with the years during which they made their principal contributions, and will leave it to the individual student to make his own summary.

The next three decades showed a large increase in the number of students who devoted their primary energy to this order. During the first two decades these students devoted their time principally to the larger and more conspicuous species. Beginning about 1870 more emphasis was placed upon the local faunas of the various European countries, and of the United States and Argentina in particular. Some of the outstanding students of this time and the periods of their contributions were the following: Ashmead, 1880–1900; Berg, 1879–1899; Distant, 1878–1920; Edwards, 1877–1928; Horváth, 1871–1931; Lethierry, 1869–1894; Melichar, 1896–1932; Puton, 1869–1899; Scott, 1870–1886.

From 1900 on there has been a great tendency to discuss or to review single genera and their species, usually from a restricted area: Baker, 1895–1927; Ball, 1896–1937; de Bergevin, 1910–1934; Breddin, 1896–1905; Buckton, 1889–1905; Davis, 1885–1942; Fowler, 1894–1909; Funkhouser, 1913–1951; Goding, 1890–1939; Jacobi, 1902–1941; Kirkaldy, 1899–1913; Lallemand, 1910 to date; Matsumura, 1898 to date; Osborn, 1884 to date; Edmund Schmidt, 1904–1937; Swezey, 1903–1942; Van Duzee, 1888–1940.

Since about 1920 more and more studies have appeared on the internal male genitalia as the court of last resort in defining species. Some of the principal workers of this era are the following: Beamer, 1924 to date; China, 1923 to date; De Long, 1916 to date; Esaki, 1922 to date; Evans, 1931 to date; Fennah, 1939 to

date; da Fonseca, 1926 to date; Kato, 1925 to date; Kusnetzov, 1925–1938; Lindberg, 1923 to date; Muir, 1906–1934; Nast, 1933 to date; Oman, 1930 to date; Ossiannilsson, 1934 to date.

I have listed above the men who have been chiefly responsible for our present-day concepts of the systematics of the group. Many other students of morphology, phylogeny, fossil insects, physiology, ecology, and especially economic entomology have contributed greatly to our knowledge, but their numbers are so large that it is not possible to evaluate here their contributions.

Our next purpose is to summarize very briefly the developments that have taken place in the study of the Homoptera. Before 1853 most students of entomology devoted themselves almost exclusively to the larger and more conspicuous insects; and the Homoptera, particularly the smaller-leafhoppers, planthoppers, and froghoppers, were largely neglected. The larger and more conspicuous singing cicadas and a few of the more conspicuous treehoppers, particularly those from South America, received some attention.

More and more attention, however, has been devoted not only to the smaller Homoptera of Europe and North America in particular but from various parts of the world. It was in this period also that Fieber, studying the smaller European planthoppers of the family Araeopidae, emphasized the importance of a careful study of the details of the male genitalia. Fortunately, in this family there are abundant characters in the external male genitalia for determining most species, and it is not necessary to make elaborate dissections and clear these parts in order to appreciate the importance of these characters.

Unfortunately, however, Fieber's contribution was almost completely neglected for fifty years, while students devoted themselves to the finer and finer details of the external anatomy of the insects of this order and did not study the internal genitalia. Increasing attention was given, for example, to the relative proportion of parts, particularly the length and breadth of the face, of the crown, of the pronotum, of the mesonotum; some attention was paid to wing venation and some to the external characters of the male and female genitalia, particularly the last ventral plate of the female in the leafhoppers and the proportions of the valve in the male. But beginning about 1920 students of Homoptera placed increasing emphasis on the details of the various structures revealed by careful dissection and clearing of the male genitalia. In this connection one may point out that perhaps too much emphasis has been placed upon the fine details of the aedeagus. Subsequent studies may show, however, that even greater emphasis is needed on the study of this structure and that what we now consider good genital characters for the differentiation of species are of generic, not specific, value. On the other hand, perhaps too little emphasis has been placed upon the general picture of the male and female genitalia as generic characters. And I believe that one of the developments for the future will be in this particular area.

In other areas, however, the study of the Homoptera has not kept pace with the development of taxonomic studies. Fairly comprehensive studies have been made in the general morphology of the head, of the wings, and of the male genitalia. Still more detailed work needs to be done in all of these areas and particularly in the morphology of the thoracic sclerites before we have a comprehensive view of the morphology of this interesting group of insects.

Other morphological structures have been greatly neglected. The internal morphology of a few of the larger species has been studied, but more careful studies of the internal morphology of many of the smaller species are needed. I feel safe in saying that we do not have sufficient knowledge of the morphology of enough representatives of the various families, tribes, and subtribes to generalize about the phylogeny of the group as a whole.

The study of the physiology of the Homoptera has been woefully neglected. We have perhaps a beginning of comprehension of their methods of feeding, and a little knowledge about their digestion, especially in some of the vectors of plant diseases. A startling discovery by Ossiannilsson that all these insects, and not the cicadas alone, are singing insects, is perhaps one of the most interesting developments. Except some minor contributions on the secretion of wax, honeydew, the formation of froth in the froghoppers or spittlebugs, there is little of real importance in the study of the physiology of these insects. The study of many other physiological aspects awaits better techniques than any now available, especially for the investigation of the smaller forms.

In the field of ecology most of the contributions have been on the food plants of the various species. One would gather the impression that these insects were almost exclusively confined to a single host plant or to a very limited order of host plants, and that only a few species are rather general feeders. My own impression from limited study would lead me to believe that the exact opposite may be true and that the limiting factor is perhaps the sum total of all the physical and biological features of the environment. Thus a species, if it finds other favorable physical and biological factors, may transfer its attention from one host plant to another belonging perhaps to an entirely different group of plants. Now such an assertion as this is exceedingly difficult to prove because, in the first place, we cannot at present be even reasonably sure what the physical or biological factors in the environment are or what is the insect's ability to adapt itself to their extreme ranges. Neither can we be sure that we know the most important physical and biological factors in the environment of these insects. We assume that temperature, humidity, and food plants rate very high, but we have very little evidence of their importance.

As illustrations of these two points I have only to report three limited observations. What is apparently the same species of small planthopper was described originally from *Spartina* grass growing on the high dunes of Long Island, and has been taken also on a species of *Uniola* growing on the high dunes along the North Carolina coast. Here we have, apparently, two different regions with approximately the same physical factors harboring the same species of insect. In Northern Michigan, however, I observed another larger species of planthopper living in the sheltered beach pools on rushes, whereas this planthopper was not found along the shores of the lake where the rushes were subject to high winds. Every student of this order who has collected extensively in the field has had this experience. Two nitches, which are as far as can be judged identical in the more important biological and physical factors, are vastly different in regard to the total population of Homoptera; for the one will yield a large number of specimens whereas the other seems to have none. What then are the factors that make such conspicuous differences? Whether any of these observations will stand the test of carefully planned experiments with

accurate measurements of all of the known factors in the different environments should command the study of future students.

That the field of ecology has been too much neglected is abundantly evidenced. I need point out only a single example. Our studies of the great grassy plains of the Missouri and Mississippi valleys have largely neglected the leafhoppers and planthoppers which occur in a normal grasslands area. Yet Osborn's studies showed many years ago that the total population of these insects is of the order of one to two million individuals per acre. Now such an important observation as that cannot be neglected in studying the sum total of all of the factors, physical and biological, in the environment.

There is great need for more careful studies in ecology from all parts of the world. The inference of such studies on the development of the science of ecology and of the economic control of insect pests is incalculable. Careful studies such as are now being made by two Finnish homopterists, Lindberg and Nuorteva, should be initiated by students in all parts of the world.

Until about fifty years ago very little attention was given to the economic importance of the Homoptera. However, a few species received some notice; chief attention was given to the spectacular appearance of the seventeen-year and the thirteen-year cicadas and little attention to the conspicuous but relatively inconsequential damage done by the so-called buffalo treehopper. But starting about fifty years ago a sequence of events impressed upon entomologists the importance of the Homoptera in relation to crop damage. One of the earliest and most spectacular of these incidents was the great destruction wrought to the sugarcane fields of Hawaii by the sugarcane planthopper imported from Australia or New Guinea and its control by introduced parasites. Also relatively early was the damage caused by the sugarcane froghopper in Trinidad. Following this was the destruction by the potato leafhopper of potatoes, beans, and peanuts, and the damage caused by the sugarbeet leafhopper to the growing of sugarbeets in the western United States. More recently, the damage caused by the alfalfa froghopper has again emphasized the importance of these insects as pests of agricultural crops.

Concurrently with the foregoing, or nearly so, there developed the appreciation of the economic importance of these insects, particularly the apple leafhopper complex; various species of cotton leafhoppers in Africa, India, and Australia; the importance of the grape leafhopper in the United States; of leafhoppers on cranberries in New Jersey; and of leafhoppers and planthoppers on rice, particularly in Japan. Other economic pests perhaps should be mentioned, but most of these are pests of minor crops or are of only local consideration at present.

Another development is the importance of these insects as vectors of certain diseases of crop plants. Recent important summaries of these have been published, and mention should be made of such important diseases as curly-top of sugarbeets and other types of curly-top transmitted by *Circulifer tenellus*, of peach yellows by *Macropsis trimaculata*, of the phloem necrosis of the elm by *Scaphoideus*, and of various mosaic diseases and several kinds of yellows transmitted by leafhoppers.

The life histories of many of the economic pests belonging especially to the leafhopper group have been studied but there are many other forms which

have received only cursory attention. The life history of the seventeen- and thirteen-year cicadas in North America is well known owing to the comprehensive studies of Marlatt. Osborn and Ball made very great contributions to the life histories of the leafhoppers in Iowa many years ago, and Osborn studied the life histories of the leafhoppers of Maine and the froghoppers of the same region. More recently some contributions have been made to the life history of the alfalfa froghopper. Some general studies of the life histories of the treehoppers were made many years ago by Funkhouser, and some of the economic pests in this group have been rather generally studied. Much still remains to be done, especially in the tropical regions of the world. The fulgorids have been rather generally neglected; the life histories of only a few species have been studied and these rather incompletely.

The phylogeny of the group as a whole is rather poorly understood. Most of our present-day discussions are based upon the studies of Stål, made nearly 100 years ago. Less than 500 of the present known 3,500 genera and perhaps less than 4,500 species of the known 30,000 species were then known. Stål conceived the group as comprising four families and for the most part we now consider these of superfamily or even higher rank. Basing our studies of the group's phylogeny on such a small area of the total population would be like basing our studies of geography on the knowledge of geographers of the world before the discovery of America by Columbus, or basing our studies of history on only the history known before the beginning of the Christian era.

Fairly comprehensive studies of the genera of Fulgoridae by Muir and others, of the Cercopidae by Lallemand, of the jassids by Evans, Oman, and others, and of the Membracidae by Funkhouser give a rather firm basis for comprehensive study of the phylogeny of these groups. Perhaps what is most needed now is research on the phylogeny of the families and of the groups higher than the families. For the present I believe that the knowledge of the subfamilies, perhaps of the tribes, of most of the groups is fairly comprehensive.

What, then, of the future? What the future holds for the field of taxonomy is anybody's guess. Whether other characters will influence the taxonomy of the group as profoundly as the discovery of the importance of male genitalia has influenced it in the last quarter century remains unknown. Yet I believe that other characters quite as important as the morphology of the male genitalia will be discovered in the not too far distant future.

The present tendency is to confine taxonomic studies to a single genus restricted to a limited area of the world's surface. Perhaps this is the best method for making progress. It is unfortunate, however, that so few students are sufficiently interested in the suborder as a whole to devote their time and attention to the groups higher than genera. Very little progress in taxonomy is going to be made until we have a thorough restudy of at least the external morphology of these interesting insects, correlated perhaps with a study of the internal morphology, of physiology, embryology, ecology, and zoogeography. This, indeed, sounds like a comprehensive program but as long as our knowledge of taxonomy is based upon the phylogenetic concepts of Stål of one hundred years ago and as long as we confine the insects of this group to four or five families, just so long will our taxonomic concepts be inadequate, for the consideration not only of the species already described, but of the genera and species not yet described.

We hear on all sides complaints about the rapidly changing nomenclature, and the International Commission is engaged apparently in an attempt to stabilize our nomenclature by decrees fixing certain names. How futile this is can be appreciated from a number of apparent facts. First, it is doubtful whether we know more than a third of the genera and species of the Homoptera Auchenorhyncha now living in the world. Second, until recently we have had no comprehensive bibliography of this group. Third, only about a fifth of the families have been covered with an up-to-date catalogue of the genera and species. It might be remarked in passing that although I spend a considerable portion of my time on the current literature, I can just barely keep pace with it. Yet I am foolhardy enough to believe that any attempt to fix names is going to fail utterly; first, because there are not enough workers to study all of the literature of the past and to fix names with accuracy, and second, because the names that are fixed are bound to change with our increased knowledge of the real taxonomy of the group.

The changes in nomenclature in systematic zoology are no more drastic than the changes in the nomenclature of any other science, biological or physical, which is developing rapidly. There is something amusing, if not ridiculous, in reading biological papers and noting how carefully the writer has checked every factor involved except the accepted nomenclature of the day.

If evolution is an explanation of the facts of the biological world, then the center of origin theory must be accepted. That is, there must be for each species and each genus a center on the earth's surface where these units of the animal kingdom have arisen. It follows, therefore, that a clear understanding of the zoogeography of the animals of a group is a necessary prerequisite to an understanding of the taxonomy, ecology, phylogeny, and other areas of the field of biology. A great deal of progress has been made in the study of the zoogeography of the Homoptera. Of course, much more than has already been discovered awaits the inquiring mind of the future student. Most of the facts of zoogeography are so patent that they would seem to need little argument for their support. Except where nature has been interfered with by man and his commerce, we would naturally expect that species would spread from their center of origin gradually, perhaps more rapidly than we think, to other areas to which they can adapt themselves. A firm foundation for our study of zoogeography was established by many different workers working on local lists of the countries of Europe, the states in the United States, South Africa, India, Japan, Australia, various countries in South America, and other regions.

The real purpose of a short history such as this is to call attention to the great areas of study which await the nimble fingers and keen minds of future research workers. For these alone can develop the techniques which will push forward the frontiers of our knowledge of one of the larger orders of the insect kingdom and one which contains some of the most bizarre animals known to man.