PHYLOGENY OF THE HOMOPTERA AUCHENORHYNCHA

By Z. P. *Metcalf*

When one attempts to discuss the phylogeny of a group as large and as varied as the Homoptera he at once finds himself hedged about by so many restrictions that I thought I would be quite poetic and say that I found myself impaled on a trident. But after careful consideration I find that the limitations are so many times three times three that such an expression not only loses its scientific verity but it so far exceeds the bounds of poetic license as to lose all reality.

On the one hand we are confronted by the abundance of materials. The group as now recognized comprises no less than 2 cohors, 6 superfamilies, 43 families, 195 tribes, 3,200 genera, and about 30,000 species have been recorded. Of course no one individual can possibly know any such vast assemblage intimately enough to know whether these categories are valid or invalid. Assuming that the genera and species now known are all valid, the question naturally arises, are the species assigned to the right genera, and are the genera assigned to the right families, and so on into the higher groups. Both of these statements need varification before we proceed with our discussion of phylogeny but again we find ourselves in a strange dilemma. Further progress in the solution of the problem of correct assignment of genera and species is directly dependent upon the development of our knowledge of phylogeny. Thus science finds itself always in a state of unbalance as it inches its way forward. Science is always like a man walking who puts forward one foot to regain his balance only to find that he must put forward his other foot to balance himself on the other side. Thus the segregation of new genera and species may necessitate the rearrangement of some of the branches of our phylogenetic tree. And this phylogenetic rearrangement will call for a restudy of the included genera and species.

Turning in another direction we find our way barred to a complete understanding of the phylogeny of the group by the fact that our knowledge of this order of insects is as yet so incomplete. This defective record can be illustrated best by the consideration of a few concrete examples. Bruner and his associates collecting these insects in Cuba incidentally to their other duties have shown that a presumably limited faŭna of 57 genera and 125 species known from the island before 1920 is actually represented by at least 57 genera and 147 species, from the study of only 6 of the 30 families represented on the island. A single American soldier limited to collecting in a single valley in New Guinea during his spare time has collected no less than 900 species whereas previous to 1940 we knew only some 200 species from this vast tropical island. The records from other regions are similar.

Our knowledge of genera and species, especially in certain families, is fairly complete. Such regions as Europe and the United States have been fairly well studied for many groups. But, for other groups, even these regions are poorly known. The recent studies of three genera of North American leaf hoppers, *Empoasca, Typhlocyba* and *Erythroneura*, by such students as Beamer, De Long, Knull, Oman and others, illustrate the results that may be expected when other genera are as carefully studied. The species of these three genera are almost exclusively pale green insects, sometimes with varieties that are vittate, fasciate or spotted with bright red, but for the most part without evident external specific characters. Using the characters of the male genitalia as

criteria in the study of specific limits in these genera these students have revealed that what were considered as small genera with only a few species a quarter of a century ago, now stand revealed as genera with a large number of species. Gillette (1898) in his monographic study of this group of leaf hoppers described 28 species of *Empoasca* and 21 species of *Typhlocyba* and *Erythroneura*. In 1917 Van Duzee cataloged 32 species of the genus *Empoasca*, 11 species of *Typhlocyba* and 14 species of *Erythroneura*; but today we know no less than 99 species of *Empoasca*, 57 species of *Typhlocyba* and 296 species of *Erythroneura*. Therefore, any theories that are advanced today about genera and species of Homoptera are purely tentative and will be subject to constant revisions until that happy day when we know more thoroughly their taxonomic and geographic limits. Homoptera from the other regions of the world have been studied only superficially. Many genera have been poorly defined. This is in part due to a failure to appreciate true morphological characters. It is due in part, at least, to the fact that the generic characters inherent in phallic structures have not been recognized. And it arises from a lack of consideration of the importance of delineation of zoogeographic regions as fundamental characters in the definition of genera.

If we turn in still another direction we are faced with the same conditions. Comparative morphology is the corner stone of phylogeny but our knowledge of the comparative morphology of even the better known genera is very incomplete. This is said in spite of the fact that we have had fairly recent studies of the Homopterous head, of the male genitalia and the wings of these insects. Practically nothing has been done on the thorax recently. Most of these studies have been made from too limited a point of view to furnish satisfactory ground work for the discussion of the true phylogeny of this order of insects. Many of these studies have been made with the idea that the Cicadidae are the most primative of the Homopterous insects—a conclusion I believe I shall be able to disprove later. Then, too, in any study of comparative morphology we are confronted with the differential development of the various parts of the insect's body. Thus the head may be relatively primative, the wings highly developed, the legs simple and the genitalia complex in one group, whereas in another group we are confronted with a different combination of characters.

The fragmentary paleontological records are of no material assistance in the solution of our problem. Practically all the fossils which belong without question to the Homoptera are assigned to recognized recent genera or are very closely related to them. There are no intermediate forms which might help us solve some of the problems of phylogeny.

We are confronted with a similar problem when we turn to embryology to help us solve some of our most perplexing problems. Many years ago I made an extended study of the embryology of the periodical cicada (*Magicicada septendecim* Linne) in the hope that it would aid in the solution of the problem of the regions and sclerites of the head. But aside from reaffirming the well-known fact that insect mouth parts are developed from leg-like embryonic buds, the study led to no worth-while conclusions. In spite of these and other limitations, I am nevertheless inclined to advance some ideas in regard to the phylogeny of the group as a whole. Our present concepts of the phylogeny of the Homoptera is substantially the same as that established by Stål in the middle of the last century when we knew approximately 222 genera and 3,259 species over against the 3,200 genera and 30,000 species known today. Students in those days recognized five families; the present scheme lists forty-

three families. It can be readily seen therefore that we have made tremendous strides in taxonomy over the past century. But unfortunately our studies of phylogeny have not kept pace with this great development in taxonomy. Elsewhere I have expressed my dissatisfaction with our present concepts of genera (Metcalf 1947 a). But in the present instance I am concerned principally with the groups higher than the family. If we are to express ourselves clearly and distinctly about the phylogeny of this or any other order of insects we need a better terminology and a better understanding of the categories necessary. We need to appreciate the importance of this area of our phylogenetic tree. To this end I would like to propose the following phylogenetic categories as essential in many if not all cases to express our ideas of the evolutionary descent of insects of this order:

Order
Suborder
Legion
Phalanx
Cohors
Division
Section
Superfamily
Family
Subfamily
Tribe
Supergenus
Genus
Subgenus
Species

Now if we could get a toe hold on this phylogenetic stairway, if someone could define the word species in such a manner that it would be uniformly acceptable to all entomologists or if we had a set of tests so that entomologists studying an order of insects could apply the tests and determine whether previously described species were valid or whether a given specimen belonged to a species as yet undescribed, most of our problems would be solved and we could trip lightly up or down this phylogenetic stairway with the greatest of ease. But for the present at least, such a goal is so distant that you will pardon me if I do not dwell on this subject but hasten to outline the phylogenetic tree for the insects of the order Homoptera in bold strokes, leaving the details to be filled in by scientists of future generations in the slow laborious manner so characteristic of science.

There are certain basic principles which must be clearly understood before we can make much progress in studying phylogeny. The first of these is what I am pleased to call the purely tentative principle in science. We are apt to think of science as the product of the scientific method and to consist therefore of an accumulated body of facts. Unfortunately, this is not true. Even a cursory examination of the history of science covering only the years of the youngest of us here will show quite clearly how tentative are all our conclusions. Instead of discouraging us however, this discovery should stimulate us to ever greater and greater efforts to solve these mysteries. Parenthetically and facetiously may I inject here the idea that if the human race had waited until civilization was perfect we would still be swinging from our prehensile tails in a tropical jungle somewhere instead of finding ourselves in the middle of the Atomic

Age, and not knowing quite what to do about it. Yet in spite of this past history and the evident instability of our scientific knowledge we assume that our present knowledge is complete, whereas the only true progress that can be made is for this generation to do its best to produce a science that must be reconstructed by the next generation.

The basis for true phylogeny must be comparative morphology. The obvious pitfall here is that we misconstrue apparent or superficial characters and completely overlook basic but cryptic characters. There is a real and fundamental difference between making keys and constructing synopses. In making keys we are erecting guide posts to direct the traveller in a strange land. In constructing phylogenetic synopses we are attempting to direct the traveller's attention to the fundamental relationship of the people who live in these strange lands.

There is a fundamental principle in comparative morphology that is too frequently overlooked. This is that synoptic characters must apply to all members of a group. Thus they must be at one and the same time mutually inclusive and mutually exclusive.

There is another fundamental principle of comparative morphology that is frequently misconstrued. This is the fact that appendages and similar structures are always associated with the same sclerites or regions of the body. Any deviations from this rule are apparent only, not real. Thus in the fulgorids the sinus of the compound eyes is directed ventral and the antennae are ventral to the sinus. But in the tribe Bothriocerini the sinus is apparently directed cephalad and the antennae are situated apparently cephalad to the sinus due to the twisting of the head.

Regions and areas are often confused. Typically there are six surfaces on the insect's body: dorsal and ventral, two lateral and cephalic and caudal. The dorsal area of the head is the crown, the cephalic area is the face and the lateral areas are the cheeks. The crown may be composed largely or exclusively of the region we call the vertex, or largely of the region we call frons with the vertex concealed or even of the postclypeus with vertex and frons reduced or lost. In the same way the face may be composed in large part of anteclypeus, postclypeus, frons or vertex or by all sorts of combinations of these regions.

Each group must be analyzed for these factors and their interrelations understood before we can have a clear understanding of the true phylogenetic groups involved.

In a class as ancient geologically speaking as the Insecta, it might be assumed that most fundamental characters would be fixed. But unfortunately this does not seem to be the case. Not only are we bedeviled by the differential development of the various parts of the insect's body but also by the plasticity of protoplasm which is a fundamental, but too frequently unappreciated, property of this mysterious living substance. For example, wing venation of the Homopterous insects is perhaps better understood than any other area of comparative morphology of the Homoptera, but when we attempt to settle questions of phylogeny by appeal to wing venation we find in the Homoptera no less than three distinct types of tegmina: a very short fore wing with reduced venation, covering the basal segments of the abdomen only—*brachypterous*; or of moderate length covering most of the abdomen and with fairly well developed venation—*koeliopterous*; and lastly a fore wing usually longer than the abdomen, frequently much longer, with fully developed venation—*macropterous*. Not only are whole families characterized by one or another type of tegmina but sometimes all three types are found not only in the same family, but frequently in the same genus sometimes in the same species.

I hope that sometime our techniques will improve sufficiently so that comparative embryology may contribute its fair share to the solution of the difficult problems of phylogeny.

Then, too, I am sure that the center of origin theory and a restudy of zoogeography will clear up many otherwise obscure areas in the total picture. A very superficial study of certain genera of the Homoptera has proven the usefulness of this tool in the resolution of complex relationships and I hope that if it is properly used it will prove equally useful in the solution of the complex relationships of the higher groups.

And while I realize the limitations of the materials and ideas expressed here, I cannot help but attempt to bring the facts, as I see them, into a correlated system which I trust will stimulate others to improve on this effort which makes no other claim to fame.

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