

EVOLUTION IN THE HOMOPTERA

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UNTIL COMPARATIVELY RECENTLY all systematic studies were regarded by many biologists as an arid occupation of little scientific worth, but of a potentially high nuisance value due to the confusion which is sometimes caused in the literature when the names of well-known organisms are changed.

When, however, Huxley (1940) introduced the term 'New Systematics' the discipline acquired an apparent scientific respectability, not only because of the methods of approach of the New Systematics but because of its dissociation from the 'Old Systematics'.

Mayr (1942) has defined the two sorts of systematics as follows: 'The old systematics is characterised by the central position of the species. No work or very little is done on infraspecific categories. A purely morphological species definition is employed. Many species are known only from a single, or at best, a very few specimens; the individual is therefore the basic taxonomic unit.'

In the new systematics

The importance of the species as such is reduced, since most of the actual work is done with sub-divisions of a species such as subspecies and populations. The population, or rather an adequate sample of it, the 'series' of the museum worker, has become the basic taxonomic unit. The purely morphological species definition has been replaced by a biological one, which takes ecological, geographical, genetic and other factors into consideration. The material available for generic revisions frequently amounts to many hundreds or even thousands of specimens, a number sufficient to permit a detailed study of the extent of the individual variation.

The nature of a contribution which a follower of the 'old' systematics can make to an understanding of some of the many unresolved problems of evolution is clearly very different from that of a 'new' systematist and even more so from that of a geneticist. A geneticist may be able to furnish reasons for the evolutionary changes which take place in his short-term laboratory cultures and a 'new' systematist to associate differences and discontinuities in his material with ecological and other factors. A systematist of the 'old' school can provide no explanations, based on experimental evidence, for the phenomena he observes, nor can he have much, if any, knowledge of biological factors associated with the abundant material he handles. Nevertheless, the wide sweep of his vision, both in

time and in space, may, in part, compensate for his deficiencies in these respects.

For a period of over thirty years I have been interested in a sub-order of plant-feeding insects, the Homoptera, which comprise groups such as cicadas, aphids and scale insects. In particular, I have studied a group known as 'leafhoppers' (Cicadelloidea) of which some 1,500 genera have been described. Also I have been fortunate enough to have had the opportunity of examining abundant fossil material.

In this contribution I proposed to measure some observations which have been made during the course of systematic work of the 'old' school against what I understand, possibly not always correctly, to be current views on evolution. The sweep of time involved is some two hundred million years and the area, the present land surface of the earth.

Pre-Tertiary Developments

Although the wings of certain insects discovered in Carboniferous strata have been ascribed to the Homoptera, no undoubted representatives of this sub-order have been recorded from earlier than Lower Permian times. Nevertheless, because of the abundance of forms known from the Permian and the fact that by then the two sub-orders of the Hemiptera (Homoptera and Heteroptera) had become differentiated, it can be accepted that the order had its inception during the Carboniferous.

It is assumed that there will have existed at some time during the late Carboniferous, insects which will be regarded as the starting point for the purpose of this discussion and which will have had, among others, the following characteristics: piercing and sucking mouthparts; three ocelli; a laterally expanded prothorax; two pairs of wings similar in size, texture and shape, but not coupled together during flight; an abdomen lacking cerci and, in female insects, three pairs of valvifers.

During Permian times there will have existed Homoptera which lacked a median ocellus and lateral prothoracic expansions; had fore and hind wings which differed from each other in size, shape and texture and were coupled in flight; had a transverse line of weakness in the forewing enabling it to be apically flexed in a downwards but not upwards direction and sound-producing organs in the nature of tymbals, actuated by abdominal muscles. Contemporaneously, there will have existed other Homoptera which retained the lost characteristics mentioned above but which had not acquired the additional ones.

The most striking distinguishing feature of the Homoptera, and one which they share with insects in the sub-order Heteroptera, is the possession of piercing and sucking mouthparts. This type of mouthparts is undoubtedly derived from mandibulate ones such as are possessed by most insects at the present day. An apically flexible forewing, while a character restricted to certain lines of Homopterous descent (e.g. cicadas), is one likewise shared with no other group of insects, as are also structural features associated with tymbal sound production. All these three characteristics merit discussion because of their unique nature, as does also one

other, although of wide occurrence in representatives of most insect orders. This is the coupling apparatus which enables the fore and hind wings to move in unison during flight.

There are several groups of insects other than those comprised in the order Hemiptera which have piercing and sucking mouthparts. One has only to think, for example, of a mosquito, or a flea. In these groups, however, the mouthparts are rigid and associated externally with the head capsule. In the Hemiptera, on the other hand (and also in the Thysanoptera), the mandibles and maxillae are flexible and internally articulated with the head by means of transverse levers.

While it is possible to visualize a change taking place by a process of slow evolutionary stages from biting to sucking mouthparts in both mosquitoes and fleas, it is not easy to visualize this for the Hemiptera, and embryology, comparative anatomy and the fossil record provide no clues as to the sequence of events involved.

Sewertzoff (1931) distinguishes evolutionary changes which result in an increase of energy or 'life activity' from those changes which do not have such an effect. He called the change in organization involved in the former 'aromorphosis' and it is suggested that the acquirement of sucking mouthparts in the Hemiptera was in the nature of an 'aromorph'. That is to say, the change from mandibulate to suctorial feeding which may have taken place very rapidly and not been the result of an accumulation of minute differences over a very long period of time will have paved the way for further rapid evolutionary changes.

The acquisition of a 'nodal line', as the transverse line of weakness in the forewings of certain Homoptera is called, may also be another example of a rapid evolutionary development. An insect wing is subject to considerable stress and it is difficult to visualize the gradual initiation of the changes involved, which consist of the modification in structure of several veins.

Tymbal sound production is mentioned for the purpose of contrasting it with another Palaeozoic development. The problem of the origin of tymbal muscles has recently been discussed by Pringle (1957) and the possible significance of sound production by the same author and myself (Evans, 1957).

Whilst, very possibly, sound production was universal among Palaeozoic Homoptera, and as well an accomplishment of both sexes, the development of complex organs for sound perception, accompanied by the loss of ability to 'sing' in the female sex, which are characteristics found only in the family Cicadidae, may not have taken place until late Mesozoic times.

Auditory tympana might be regarded as a 'need' for insects capable of producing sound and their acquirement a response to such a need. However, those groups of Homoptera which possess functional tymbals but lack tympana are very much more numerous than those which have both the former and the latter.

The benefit conferred by ability to perceive calls at a distance is obvious, since it enables the assembling together of the sexes. Hence the progressive improvement of auditory tympana, which in cicadas consist of a modifica-

tion of the first abdominal segment, will doubtless have been the result of selection.

The synchronization in flight of fore and hind wings is of great benefit for flight purposes. Accordingly modifications of both wings, which make synchronization possible, are also characters with selective value. As with tympana, so the acquisition of wing retinacula might seem to be a response to a 'need' but unlike tympana retinacula are situated in the one position where they can be of functional significance.

While tymbals are peculiar to Homoptera, tympana and wing coupling devices are not, but are of wide occurrence amongst insects generally. If the development of a simple retinaculum was due solely to the effect of a chance mutation one would expect to find among the multitude of insect forms some evidence of the production of meaningless structural developments of neutral significance. Seemingly, however, these do not occur. Mayr (1942) has stated 'that while a gene never mutates in response to a need, it is nevertheless premature to assert with too much positiveness that all gene mutation is strictly random'.

From the beginning of the Upper Carboniferous until the end of the Permian period represents a period of some sixty million years and approximately two hundred million years have elapsed since the end of the Permian. During Palaeozoic times some of the evolutionary changes affecting the Homoptera were apparently greater in magnitude than any which have occurred subsequent to that period. Consequently it would seem as if the tempo of evolution may have changed. Moreover, during the Palaeozoic, new characteristics were acquired which involved considerable changes in organization, while subsequent developments have been essentially ones of loss and of modification of existing structures.

One group of Homoptera in particular which has shown no striking changes in structure since Upper Permian times is the Cicadelloidea. With these insects the greatest apparent change has been the reduction of the veins which support the apex of the forewing from seven to four in number and this reduction has been achieved in three different ways in separate Families. Apart from certain secondary anomalies of venation the only departure from such a condition is to be found in a family which has reticulate venation (Aetalionidae). This development is of interest because of its recurrence in widely separated groups from Permian times until the present day.

Geographical Isolation

The importance of geographical isolation as a factor enabling speciation to take place is well established, likewise the fact that the degree of evolutionary divergence of a group of organisms in any area may be a measure of its period of isolation.

The three major regions where the greatest evolutionary development of leafhoppers occurred during Tertiary times are Australia, the Neotropical Region and Madagascar. That is to say, there are to be found in these three areas far more endemic groups above the level of genera than else-

where. The only other parts of the world with high category endemic groups, and they are comparatively few in number, are in the Afro-oriental region, the Eremian Sub-region of the Palaearctic Region, western North America and the Philippine Islands.

Australia

In Australia there is a single endemic family of leafhoppers (Eurymelidae), and among representatives of the Cicadellidae two endemic sub-families (Tartessinae and Austroagalloidinae), of which the former extends tenuously into the Oriental Region, and four endemic tribes (Stenocotini, Thymbrini, Trocnadini and Reuterellini). The remaining representatives of the leafhopper fauna have an Antarctic distribution (South Africa, Australia, New Zealand and probably southern South America), a trans-tropical distribution (Australia, Oriental Region, Tropical Africa and to a less extent Tropical America), or are cosmopolitan.

It is unusual for a family to be confined to a single geographical area and the Eurymelidae is the only family of leafhoppers, with the exception of two relict ones in South America, to have such a restricted distribution. Its only extension is into New Guinea, whence a few species have been recorded, though only one is particularly distinctive, and New Caledonia, whence a single species is known.

Because of their limited distribution and the fact that some representatives seem to be in a state of active speciation, the Eurymelidae are a particularly favourable group for a study of evolutionary change. It is possible that they received an evolutionary stimulus as a result of the change of climate which took place in Australia during the Pleistocene because of the effect this change had on eucalypt speciation, on which trees most eurymelids feed.

Eurymelids, of which there are thirty-two genera and approximately one hundred species, are ant-attended, gregarious insects; adults and nymphs cluster together on the branches, and in one group, on the roots of trees.

The following levels of evolutionary divergence can be recognized:

(i) Local populations which differ from each other slightly in colour-pattern and have as well minor differences in size and in the shape of the various parts of the male genitalia (for example, species in the genera *Anipo* Evans and *Katipo* Evans).

(ii) Populations, possibly of polymorphic species, which differ from each other in size and have constant colour-pattern differences, but lack genitalia differences (to be found among the *Eurymela fenestrata* Le P. and *S.* complex).

(iii) Species which differ from other species in the same genus in size and in constant colour and minor structural features.

(iv) Genera, between which there may be no greater differences than between species, and which have acquired generic status merely as a result of the passage of time and the occurrence of secondary speciation (for example, the genera *Ipoella* Evans and *Ipoidea* Evans).

(v) Monotypic genera which have acquired distinctiveness as the re-

sult of the acquirement of some unusual structural modification (*Eurymelita* Evans, *Cornutipo* Evans).

(vi) Groups of genera, which are linked together by the presence, or absence, of adaptive features associated with a specialized environment.

The above categories and their sequence conforms with the concept of speciation as a gradual and continuous process. Beyond the fact that most species of the Eurymelidae have representation in every Australian State, little information is available concerning their distribution, except that some are known to be restricted to a particular climatic environment. Even less has been recorded about the extent of their food-plant relationships although it is known that some of the more stable and generalized forms feed on plants, such as *Casuarina* and on representatives of the Proteaceae, which antedate in origin the radiation of *Eucalyptus*.

South America

In the Neotropical Region there occur representatives of three relict families of leafhoppers, two of which are endemic in the sense that they now lack representation elsewhere (Biturritidae and Nicomiidae) while one is represented by a single genus in tropical America and another in Asia (Aetalionidae).

None of these families is comparable with the Eurymelidae from an evolutionary point of view since they comprise essentially Mesozoic insects which have remained comparatively stable during the Tertiary.

There are, as well, in tropical South America eight endemic groups of sub-family or Tribal status, all of which have undergone extensive evolutionary change during the Tertiary (Neocoelidiinae, Gyponini, Membracinae, Hoplophorinae, Hyphinoinae, Darninae, Smiliinae, Tragopiini). Some of these now have representation also in the Nearctic Region.

Two of the sub-families mentioned above belong to the family Cicadellidae and the rest to the Membracidae, and the latter, because of their bizarre appearance, are comparatively well-known insects.

Although the Membracidae are of world-wide occurrence and the most generalized forms are to be found in the Oriental Region, Africa and Australia, it is only in the Neotropical Region that they underwent startling evolutionary changes during the Tertiary. These changes, so far as external morphology is concerned, are related more particularly to the shape of the pronotum and the venation of the forewing.

There has been much discussion as to the adaptive significance of the varied shapes of prothorax which are to be found among Membracids. Some closely resemble plant spines and even ants, and doubtless in these instances their perfection may have been associated with selection. Others, and these are probably in the majority, are almost certainly neutral characters of doubtful adaptive significance. The plasticity in membracids of that part of the genetic system which determines pronotum shape is foreshadowed, or at least paralleled, in other groups of leafhoppers (e.g. Macropsini, Ulopiini, Ledrini) although in these the system is more rigidly controlled.

Madagascar

In Madagascar, as in Australia and the Neotropical Region, stable relict forms of leafhoppers occur (e.g. *Paulianiana dracula* Evans); an endemic tribe of which the evolutionary development parallels that of a related tribe in Australia (Platyjassini in Madagascar, Reuterellini in Australia); a group of genera which would merit tribal differentiation if it were not for the fact that their derivation is known (*Eryapus* spp. derived from *Acostemma* Signoret (Krisnini)); genera in which prolific normal speciation has occurred (e.g. *Poecilocardia* Metcalf with twenty-seven species in Madagascar and seven in Africa) and a genus comprising seventeen species in which seemingly 'explosive' speciation has taken place (*Coloborrhis* Germar).

The last mentioned occurrence, which has recently been described elsewhere (Evans, 1959), is of unusual interest and merits discussion.

Before describing some of the differences which separate *Coloborrhis* spp. it is necessary to mention the nature of the differences which separate species in other leafhopper genera. These are principally as follows: changes in colour-pattern accompanied by slight differences in the male genitalia but not by significant ones of size or proportions (e.g. *Poecilocardia* spp.); minor changes in size, proportions, colour-pattern, and male genitalia (e.g. *Macropsis* spp.); major changes in size and colour-pattern and slight ones in the shape of the various parts of the male genitalia, but no change in proportions (e.g. *Tartessus* spp., *Eurymeloides* spp.); progressive changes in size and proportions unaccompanied by ones of colour (e.g. *Cephalelus* spp.); slight, if any, changes in size, shape, proportions or colour, but differences in the male genital armature (e.g. *Balclutha* spp.).

Speciation in the Genus Coloborrhis

There is a group of small leafhoppers comprising a tribe, the Ulopini, which usually retain a structural feature in their heads (known as the maxillary suture) which has been lost in most leafhoppers since, at least, as early as Permian times. These insects range in size from between 2.5 and 5 mm. in length and they are frequently dimorphic (forms occurring either with, or without, hind wings).

On the basis solely of comparative morphology I have suggested (Evans, 1947) that the Ulopini may lie at the base of one of the lines of descent of present-day leafhoppers. Most ulopids live in concealed situations and are relatively inactive, but species in two genera in particular (*Moonia* Distant and *Coloborrhis*) are active arboreal insects and are known only in the fully winged form. The former genus has representation in India, and the latter, which may well be derived from *Moonia*, in Africa and Madagascar.

In the whole of Africa there is but a single species of *Coloborrhis* (*C. corticina* Germar) which is of widespread distribution, occurring both in the tropics and in temperate regions. This species also occurs in Madagascar and it is presumed that there it is of adventitious origin and is the form from which all the other sixteen species may have been derived. Its

principal characteristics are as follows: in length it ranges from 3.5-4.4 mm., and the head is in two planes consisting of a ventral face and a vertical crown. The latter is in alignment with the pronotum which is anteriorly declivous and posteriorly somewhat raised and rounded and in alignment with the scutellum. The forewings have reticulate venation and the tibiae of all three pairs of legs are flattened.

The following are among the divergent characteristics which occur among the sixteen derived species: an appreciable increase in size range (3.5-7.6 mm.); a variously shaped head which may be in three, instead of in two planes, and of which the crown may be short and narrow, long, wide and spatulate, or may bear raised prominences. The pronotum may be flat, evenly rounded, humped posteriorly, have small, or large, paired, rounded, or conical humps, or an apically forked median elevation. The scutellum may be flat, convex, raised into a prominence or consist of a vertical sail-like process. In the forewing the venation may be slightly or profusely reticulate, the anal veins may be separate or form a Y vein and vein Cu1 may be sharply bent proximally. The tibiae may be quadrilateral in section and parallel-sided, or flattened and if flattened, parallel-sided or oval in outline.

These many and varied developments, which are very considerably greater in magnitude than differences between any other species known to me, would seem to represent an explosive release of genetic potentialities. Among the aberrant characteristics found among the various species, each of which could equally well be regarded as belonging to a monotypic genus, are some known elsewhere only among Palaeozoic and Mesozoic leafhoppers, some found elsewhere only in relict groups not now represented in Madagascar and Africa, and some not found elsewhere among other genera of the Ulopiini but only in genera in representatives of subfamilies and tribes of later derivation.

Before discussing possible factors associated with the speciation of *Coloborrhis*, mention needs to be made of its seemingly different nature from the production of aberrant forms associated with the isolation of small populations on oceanic islands. On the island of St Helena there are two aberrant endemic genera of leafhoppers (*Stonasla* Buchanan White and *Nehela* Buchanan White, Agalliinae), while on Juan Fernandez an endemic genus (*Evansiola* China) comprises species, some of which are aberrant to the extent of being grotesque (e.g. *E. kuscheli* China).

While in both the two islands mentioned and in Madagascar, the original populations may have been derived from small initial numbers of insects, opportunities for ecological radiation will have been considerably less in the former than in the latter.

Sewall Wright (1937) has argued that in small populations the accidental loss of genes may in certain circumstances be a more successful evolutionary process than selection. Mayr (1954) too has discussed other mechanisms that might operate in peripheral populations, as follows:

The genetic composition of a population which is one of a series of large contiguous populations of a widespread species is continuously

affected by the immigration of genes derived from distant or adjacent populations. In such a population there will be a selective premium on genes which do well in a great variety of genetic backgrounds and which are thus adapted to cope with a continuous inflow of alien genes. The selective value of many genes will change drastically in the altered genetic background of a newly-founded peripherally isolated population. This will lead to a rapid change of gene frequencies simultaneously at many loci assisted by the selective effects of the change in the physical and biotic environment of the isolated area. Furthermore, a different set of genes is apt to be superior in such an area in which gene flow does not interfere with selection by the local environment. The period of genetic re-organization and relaxed selection pressure is not only a period permitting rapid evolutionary change but also offers an otherwise unavailable opportunity for a drastic ecological change of a somewhat unbalanced genetic system.

Mention has been made of the occurrence in the Neotropical Region of three relict families. One of these, the *Biturritidae* (originally Lampropoteridae), comprises ten genera. The various species in these genera, some of which are monotypic, show a degree of divergence from each other which is similar in range and in nature to those which separate the several species of *Coloborrhis* (Evans, 1948).

Both the *Biturritidae* and *Ulopinæ* will have had their origin during Mesozoic times and it is suggested as a possibility that several of the groups of present-day leafhoppers, which will have become differentiated during the Tertiary, may have owed the inception of their discontinuities to explosive speciation similar in nature to that which is recorded above.

Sympatric Speciation

The concept of sympatric speciation is, at the present time, almost universally discredited and any mention of it, even as a possibility, might seem to have no place in a contribution purporting to be scientific. This is especially so when, as is the case in the present instance, a suggestion is made which is unsupported by experimental evidence.

Nevertheless, in my opinion, it is possible that sympatric speciation may take place within a particular group of leafhoppers, the *Typhlocybinae*, and the reason for this opinion is because among these insects discontinuities between populations of an ecological and ethological nature would seem to be more readily capable of achievement than isolation of a geographical nature.

*Typhlocybid*s, which are of world-wide distribution and are particularly well represented in the Holarctic region, range in length from 2-4 mm. The group comprises some one hundred genera, several of which contain many hundreds of distinct species.

These leafhoppers differ greatly in the extent to which they are restricted in their feeding requirements. Some feed, mate and breed only on a single species of plant or on a limited range of related plants. Others have wider feeding habits. The mere fact that related species have different

ranges of food plants implies an ability, on occasion, to become accommodated to a new diet.

Mention has already been made of the songs of Homoptera and it may be of significance that typhlocybrids have unusually large apodemes for the support of their tymbal muscles, and hence presumably are particularly 'vocal'. It is accordingly suggested that an isolating factor which may have enabled the formation of large numbers of sympatric species might be the synchronization of the acquisition of a new call note with that of a new food plant.

The reason it is suggested that it is improbable that geographical isolation has been the principal factor enabling prolific speciation to take place among typhlocybrids is because their small size and swarming habits make them particularly liable to transport in the upper air and hence to rapid and wide dispersal.

Conclusions

A consideration of some of the evolutionary changes undergone by certain Homoptera supports in general the concept that speciation is a gradual and continuous process which is predominantly allopatric and that the origin of the higher categories is the result of the extrapolation of normal speciation.

At the same time it would seem that this explanation is insufficient to explain all the observed facts of the evolutionary development of leafhoppers.

It may be suggested in addition (i) that evolutionary changes occurred more rapidly during Palaeozoic than subsequently, (ii) that while geographical isolation is often a stimulus to speciation (with different effects depending not only on the size of the initially isolated population, but also on the size of the land area involved) it is not an essential enabling requirement and that sympatric speciation may also take place; and finally (iii) that the steps which have given rise to some of the higher categories of leafhoppers may have been initiated by abrupt and not by gradual evolutionary changes.

REFERENCES

- Evans, J. W. (1947), *Trans. R. ent. Soc. Lond.*, 97: 39.
 ——— (1948), *Trans. R. ent. Soc. Lond.*, 99: 497.
 ——— (1957), *Trans. R. ent. Soc. Lond.*, 109: 275.
 ——— (1959), *Mem. Inst. Sci. Madagascar*, E, 11: 31.
 Huxley, J. S., ed. (1940) *The New Systematics* (Oxford).
 Mayr, E. (1942), *Systematics and the Origin of Species* (New York).
 ——— (1954), *Change of Genetic Environment and Evolution, Evolution as a Process* (London).
 Pringle, J. W. S. (1957), *Proc. Linn. Soc. Lond.*, 167: 146.
 Sewertzoff, R. N. (1931), *Morphologische Gesetzmässigkeiten der Evolution* (Jena).
 Wright, S. (1937), *Proc. nat. Acad. Soc.*, 23: 307.