PROBLEMS IN IDENTIFICATION OF SPECIES OF LEAFHOPPERS AND PLANTHOPPERS

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ABSTRACT

The problem of determining whether differences between individuals and between populations are intraspecific is discussed, based on examples from the European fauna. Different types of character, including coloration, genitalia and apodemes are considered, as are also the effects of parasitism, teneral condition, seasonal variation and geographical variation on these. Several tests for application to doubtful cases are proposed.

INTRODUCTION

Nowadays the definition of an animal species is almost universally based on a biological concept, e.g. that of Mayr (1940):-

"groups of actually or potentially breeding natural populations which are reproductively isolated from other such groups."

The problem of the field zoologist is to recognise species when he rarely has the opportunity to study genetics within a population and to perform interbreeding experiments between populations. As a rule closely related sibling species differ widely in certain aspects of their biology and this is why taxonomic and biological aspects of any field situation are very much interconnected. I plan to discuss some situations which I have met in the British leafhopper and planthopper fauna in order to illustrate ways in which these problems may be approached.

CHARACTERS

External characters

For this purpose, I am broadly dividing characters into four groups, i.e. external, male genitalia, male sternal apodemes and female genitalia. I use the term "external characters" for all aspects of coloration, as well as for morphology of the head, thorax, wings and legs. Early taxonomists relied largely upon these for recognition of species.

Male genitalia

In the past hundred years we have come to rely on male genitalia for species recognition in Auchenorhyncha. In some groups this is a very valuable criterion, and a genus like Edwardsiana, rightly honouring James Edwards for his extensive pioneering work on their aedeagi, could not be identified in any other manner.

Male sternal apodemes

Rather more than thirty years ago, Dr. Frey Ossiannilsson published the booklet "Insect Drummers" (1949), in which he described the drumming calls of the smaller Auchenorhyncha and figured the apodemes of the muscles in the base of the abdomen used in their production. In a subsequent publication (Ossiannilsson, 1951) he showed that these gave valuable criteria for separating male Macrosteles species. Subsequently they have been applied in some genera where the male genitalia are too simplified to be taxonomically useful, e.g. Zygina (Günthart, 1974) and Alebra (Le Quesne, 1977).

Female genitalia

Both the last-mentioned characters apply only to males and it is pertinent to ask if there are similarly useful characters for females. The form of the seventh abdominal sternum is often valuable at a generic level, but rarely gives good specific characters. In Delphacids the first gonocoxae are often useful, while the length and shape of the gonoplac (otherwise known as the ovipositor sheath) is presumably related to oviposition behaviour, e.g. in Oncopsis, where the latter has been studied by Claridge and Reynolds (1972). The pattern of teeth on the second gonopophyses (the inner parts of the ovipositor) have proved useful in some genera, e.g. Macropsis (Wagner, 1950).

COMPLICATING FACTORS IN SPECIES RECOGNITION

Having briefly mentioned the main types of taxonomic character at our disposal, we come to the fundamental question - how far can we rely on them for species recognition. This is where it is necessary to consider how far the above-mentioned characters are good criteria of a species.

Normal variation limits within a population

The first question we have to ask is the extent of normal variation within a single population of a species. For instance, the common European froghopper, Philaenus spumarius is very variable in colour pattern and Linnaeus described several colour morphs as separate species. A number of authors have looked at this problem, but it has only been studied in depth recently by Dr. Halkka in Finland, who has bred it out and studied the genetics (Halkka, Halkka, Raatikainen and Hovinen, 1973; Halkka, Raatikainen and Vilbaste, 1976; etc.). Selective pressures differ in the various colour-morphs so that the proportions in different populations are not always the same and a case of industrial melanism has recently been studied by workers at Cardiff (Lees, 1981; Dent, 1981).

The species Oncopsis flavicollis, found commonly on Betula, shows a colour polymorphism in the females, while the males are much more uniform in colour. Again, the different morphs were described as separate species by early workers like Curtis. This case also has been studied for a number of years at Cardiff by Claridge and co-workers (Claridge and Nixon, 1981) and studies are still continuing.

However, male genitalia are not as invariant as many workers at first hoped. The species Edwardsiana crataegi, which is common on hawthorn, apple and some related trees and bushes shows considerable variation in male genitalia, causing China (1943) to consider that two species were involved. However, studies on British and Channel Island populations have led me and others to realise that the forms coexist in a single population. There appears to be a distinct correlation between the length of the upper appendage and its direction in side view.

Effects of parasitism or other pathological states

There are three groups of parasites of Auchenorhyncha reported from Europe and all are widespread in Britain. Larvae of small wasps of the family Dryinidae feed at first inside the bodies of leafhoppers, but later form sacs attached externally to the body. In some cases the sacs appear while the host is still a nymph, and the latter does not reach maturity, but in leafhoppers of the subfamily Typhlocybinae, these sacs are often seen attached to the base of the abdomen of the adult host. This parasitism may cause more or less severe reduction of the male genitalia and invariably causes severe damage to the sternal apodemes. In cases where there is a difference of coloration between the sexes, e.g. in the genus Alebra, parasitised males may exhibit a female type of colour-pattern.

Diptera of the family Pipunculidae remain within the host throughout their larval stages and their presence in adult Auchenorhyncha is usually manifested by a swollen and misshapen appearance of the abdomen. They too can cause reduction of the male genitalia and of the sternal apodemes.

The third group of parasites attacking Auchenorhyncha are the Strepsiptera. The female parasite does not leave the host after becoming adult, but may be seen looking like a black bead partially embedded in the host's exoskeleton. While still larval, Strepsiptera again cause the host's body to become distended and misshapen. In the British fauna, these parasites were thought until recently to confine their attacks on Auchenorhyncha to the Delphacid planthoppers, but recently Waloff (1981) has described a new species from the primitive leafhopper Ulopa reticulata and Crowson (1976) has reported stylopized Eupelix cuspidata.

Parasitism by Strepsiptera also affects normal development of the genital organs and moreover often causes sex-associated differences in coloration. It was customary to regard many parasitised forms as intersexes, but Kathirithamby (1974, 1977, 1979) regards many of them rather as forms in which nymphal characteristics have been retained. This appears particularly to be the case in some abnormal Eupteryx, in which no obvious signs of parasitism could be found.

Effects of teneral condition

Teneral specimens can generally be recognised by their rather shiny and soft appearance in life, and the tendency of dried specimens

to collapse on keeping. The coloration of such specimens may well be atypical - for example, dark markings may take some hours to develop after ecdysis and in at least one case, the Typhlocybine leafhopper Kybos populi, teneral forms show an attractive red colour that disappears in more mature specimens. Günthart (1979) has recently shown that the examples which Edwards described as Zygina pruni were in fact teneral specimens of Zygina flammigera.

In another paper, Günthart (1977) has pointed out that the sternal apodemes take two to three days to reach full development: thus use of these characters on teneral specimens could lead to fallacious results.

Phenotypic variation

There are a number of cases where the ecological circumstances can affect the individual and I will refer to these as phenotypic variation. The effect of crowding, for example, on locust development is well known to all entomologists, but it is only in recent years that Mochida (1973) has shown that nymphal densities of the Delphacid planthopper Javesella pellucida determine the proportion of macropterous individuals to appear in the population.

An observation which I discussed in a paper published seventeen years ago (Le Quesne, 1965) is still not satisfactorily explained and probably is in this category. Populations of the froghopper Neophilaenus lineatus on the grass Molinia caerulea, which grows under acid, peaty conditions, contain a substantial proportion of dark forms, while those from other grasses consist entirely of pale forms. Is some chemical present in the Molinia which causes expression of the dark phenotype? Or do we have in reality two species, only distinguishable by the fact that one has a colour dimorphism?

Effects of seasonal variation

The most striking effects of seasonal variation are with the male genitalia in the Euscelis genus of leafhoppers, which has been investigated in detail by Prof. H.J. Müller (1954, 1957). Euscelis incisus is normally bivoltine in most of Europe: the spring generation is somewhat smaller and darker than the summer generation and the male has a narrow aedeagus, without appendages. On the other hand, the summer generation has a much broader aedeagus with long recurved hooked appendages. The biological purpose of this difference is not clear, but Müller showed that the switch could be produced artificially in the laboratory by alteration of the day-length.

In the case of Euscelis lineolatus, which is normally univoltine with a simple aedeagus at the latitude of Britain, forms occur in southern Europe with even more strongly developed appendages than in the summer form of incisus. Müller showed experimentally in this case that these forms were only produced at temperatures above 27°C.

Another interesting case of seasonal variation, again without an obvious purpose, is the reversible colour change in some Zygina specie

of leafhopper, described in detail by Vidano (1961) for Z. suavis (= rhamnicola). Specimens of this species taken in the autumn are relatively lightly marked with red, while during hibernation and immediately afterwards, the red colour is much more extensive. However, later in the spring, much of the red coloration vanishes again.

I realise that many of the participants in this meeting are studying tropical situations, where seasonal influences are less likely to be important, but nevertheless these examples are worth bearing in mind.

Effects of geographical variation

In some ways the biological species concept is most difficult to apply to geographically separated populations. Here we must note Mayr's phrase "potentially breeding natural populations". For this test, we must either try experimental crosses or make assumptions. If one can find a gradual cline rather than sharp steps in a character, the presumption that we have geographical variation seems the most likely. For example, Wagner (1955) found a smooth cline in the form of the aedeagus of the froghopper Philaenus spumarius from northern to southern Europe. Similarly, Woodroffe and I (Le Quesne and Woodroffe, 1976) found that series of the Typhlocybine leafhopper Eupteryx stachydearum from localities between latitudes 57° and 49° in Britain and the Channel Isles showed a similar gradation in the form of the male aedeagus. There seems in fact a general tendency towards stronger development of aedeagus appendages as one goes further south in Europe. Since higher temperatures and increased day-length in Euscelis have similar effects, as mentioned earlier, it seems possible that there is a general tendency towards stronger development of the aedeagal appendages as the climate becomes warmer: use of photoperiod to distinguish between seasons could be a method evolved secondarily towards this end.

It will be more difficult to distinguish a stepped cline and geographically non-overlapping species. Woodroffe and I (loc. cit.) described a case where we believe that there is a stepped cline in Europe from north-west to south-east in the leafhopper Agallia laevis. In this case, specimens from Jersey, Channel Islands, were the same as specimens described by Ribaut from France, while specimens from Cornwall, in the south-west of England, were quite distinct. A third form was originally described by Zakhvatkin from the eastern Mediterranean area. These forms could well represent incipient new species.

TESTS FOR RECOGNITION OF SPECIES

There are a number of tests which can be applied to particular cases of the problem of whether different forms constitute distinct species. Some are listed below.

Do the different forms occur within a single population?

Forms occurring apparently within a single population may represen coexisting species or variation within a single species. Species co-existing within the same habitat will have developed behavioural differences, as well as morphological differences, leading to the next three questions.

Are there behavioural differences, especially in the drumming calls?

When problems arise that could suggest the coexistence of sibling species, premating isolating mechanisms are likely to be involved, and the drumming calls are well worth studying, if one is equipped to do so. For example, one may mention the work of Claridge and Howse (1968) on Oncopsis and of Strübing (1970, 1976, 1978) on Euscelis species.

Are intermediate forms found?

In cases where morphological differences apparently occur within a population, it is well worth examining a series of specimens to see if intermediate forms occur or if the specimens can all be subdivided into distinct groups. In some polymorphisms, the majority of specimens may fall into one or other of the distinct forms, which are probably selected for in nature, but the occasional intermediate form can normally be found if enough specimens are examined.

Are mating pairs of differing forms found in nature?

Pairs of individuals found mating obviously will have no premating isolating mechanisms and therefore are likely to be of the same species, especially if more than one mixed couple is found. This was the reason that I felt sure that the populations of Neophilaenus lineatus on Molinia which I mentioned earlier contained only a single species.

Are differences associated with visible signs of parasitism or defective reproductive organs?

As mentioned earlier, parasitisation can cause incomplete development of the reproductive organs. An example is parasitised Edwardsiana rosae, which sometimes have aedeagi with the appendages partly fused, figured by Ribaut (1936) as aberr. manca.

Could they be seasonal forms of the same species?

Replacement of one form by another at different times of the year should act as a clue to this type of relationship, which can only be proven in the final analysis by study of captive populations.

CONCLUSION

Taxonomic, ethological and ecological studies form an integrated pattern, each aspect helping to clarify the other two. I have dealt entirely with the problem of deciding whether a particular form is a good species or not: there remains, of course, the thorny problem of deciding what is the correct name of the taxon in accordance with the

International Code of Zoological Nomenclature. The unfortunate fact that different authors in applying the Code may have given a number of names to a well-recognised insect has caused some ecologists to look askance at the work of the taxonomist, but in fact the two studies, as well as that of the ethologist, are inseparable.

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DISCUSSION

In connection with the variation in the aedeagus of Philaenus spumarius in Europe, I have examined specimens from North America taken at such diverse latitudes as James Bay and California and not found a similar variation on this continent, suggesting that the effect is not merely one of temperature. The diversity seems to represent subspecies in Europe, the central European one of which is the dominant form in both eastern and western North America (Hamilton, 1979).

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