

WHAT DO WE REALLY KNOW ABOUT HOST SELECTION IN AUCHENORRHYNCHA?

PROF.DR. R.H. COBBEN¹⁾

ABSTRACT

This survey deals with various aspects of the relations between Auchenorrhyncha and their hosts. It is concluded that the present knowledge of these relations is poor and refers mainly to only two of the more than thirty families known.

Research on olfactory host recognition has only just made its start. A provisional inventory of olfactory sense organs of the antenna and the labium revealed interesting patterns of evolutionary diversification, but about the actual function of these structures nothing is known. The literature on feeding behaviour is shortly discussed.

About the experimental analysis of host selection and host suitability a few critical remarks are made. Various aspects of variability and polymorphism in host relations are briefly touched upon. With respect to discussions on coexistence, polyphagy and cryptic species, the importance of multifaceted biotaxonomic research is stressed.

Finally, it is discussed that evolutionary significant patterns and changes in host relations can only be studied by modern phylogenetic analysis, both of the Auchenorrhyncha and their hosts.

INTRODUCTION

Mike Wilson, in a foreword to reports on two Auchenorrhyncha meetings in Tymbal (1986), concluded: "In general, our knowledge of host plants in Auchenorrhyncha is well behind that of other Hemiptera, especially Sternorrhyncha". Indeed, the answer to the question chosen as the title of this paper, will be at the end of the present survey: 'Precious little'.

The subject of host selection is very wide and its many aspects can be studied by a wide variety of biological disciplines such as physiology, ethology, ecology, and evolutionary biology. I will try to summarize what is known and, more in particular, to indicate what is not known about the various aspects of host selection in Auchenorrhyncha. In the literature dealing with host relationships, most of the discussions refer to Auchenorrhyncha of the northern hemisphere and mostly to representatives of the families Cicadellidae and Delphacidae (generally called leafhoppers and planthoppers, respectively). However, there are more than thirty families of Auchenorrhyncha (Strümpel, 1983), with species predominantly in the tropics, for which virtually nothing is

1) Lab. of Entomology, Agricultural University, Wageningen, the Netherlands.

know about host relations. Because of limits of space, this survey is far from complete. My only hope here is to stimulate further research.

DISTANT LOCALIZATION OF HOSTS

Knowledge of the first phase in the sequence of behavioral responses of phytophagous insects to (the series of) plant stimuli has been critically reviewed by Visser (1986). Changes in search and locomotion patterns of an insect when approaching food resources, have been analysed in only a few species outside Hemiptera. As regards Auchenorrhyncha, I am aware of only two experimental studies dealing with host recognition at short distance. These refer to 3 planthopper species on rice (Obata et al., 1981) and 2 *Empoasca* leafhoppers on host and non-host dicotyledons (Saxena & Saxena, 1974, 1975). For the planthoppers, mixtures of volatile compounds of rice, and not single components seem to be responsible for attraction and since antennectomized planthoppers showed no response, the antennae are involved in olfaction.

The results with one of the two *Empoasca* spp. (*E. devastans*, a cotton pest) revealed the following sequence of perceptions from the surrounding of the host: colour of host (maximum distance 360 cm), moist background (180 cm), water vapour and odour of host (1 cm). Unfortunately, no detailed observations were described of the locomotory activities of the individual hoppers during host searching.

The role of vision and olfaction during long-distance orientation of Auchenorrhyncha is entirely unknown. The fact that many species are attracted to light and yellow traps indicates the importance of vision, but whether and how vision works during flight in detecting special vegetations remains unsolved. With very few exceptions, adult Auchenorrhyncha are equipped with highly developed compound eyes. The same is true for the larval stages, including the first (in contrast to many Heteroptera). One may wonder why, since a single plant generally suffices for the complete development of a larva. I guess that an important function of the eyes is to enable quick recognition of physically disturbing factors, such as predators and large herbivores. An ultimate escape act by jumping or flying would dislodge the insect from its host, and searching behaviour for the same or a new host plant would be necessary. Can Auchenorrhyncha perceive and evaluate blends of odours of plant communities? Can they subsequently discriminate between odour components at a closer distance of certain associations of plant species? What are the signal odours? Or is the whole process of host finding from a distance just by chance, trial and error?

SENSE ORGANS FOR OLFACTION

Antenna

The antenna is presumably the one appendage of Homoptera bearing sensilla for olfaction. Since olfactory tests on what kind of airborne signals the antennae of Auchenorrhyncha may perceive, have never been reported, a comparative inventory of types and distribution of sensilla would be worthwhile for two purposes. (1) The study of evolution of sense organs through the major taxa, which may bear some relation to gross alterations in categories of host selection; (2) Selection of the proper taxa for sensory, physiological and histological studies.

Only a few studies have been devoted to the olfactory structures of auchenorrhynchous antennae. Hansen (1900) compared distributions and gross structures of sense organs by visual optics in representatives of quite a number of families. In recent times, scanning electron microscopy (SEM) and transmission electron microscopy (TEM) have concentrated on various groups of Fulgoromorpha (Lewis & Marshall, 1970; Marshall &

Lewis, 1971) and on Tettigometridae (Bourgoin, 1985).

A cursory SEM analysis of most families (pers. obs.) reveals three striking interrelated trends in antennal evolution: gradual reduction of segments, resulting ultimately in only three segments (scapus, pedicellus, flagellum); progressive reduction of setosity; concentration and elaboration of specialized sensilla. For these tendencies the two major groups of cicadines prove quite distinct.

Cicadomorpha. The three-segment condition is clearly realized only in Cercopidae and, less distinct, in Membracidae and Aetalionidae. In Cicadellidae, more than 3 segments occur, in varying numbers (7-4), whereas Cicadidae retained the more primitive condition with 7 undifferentiated segments. Segment 3 and 4 of the antennae of the latter family, the song cicadas, bear many papillate porous sensilla, which may serve for olfaction (as dealt with in more detail by U. Klein, this volume). In the 4 remaining cicadomorphous families, the sensilla are lenticular and less numerous; they occur in the families with more than 3 segments on the segments 4-7. Through complete fusion of the terminal segments these placodoid sensilla became clustered in Cercopidae on the widened base of the third segment forming the flagellum; they range in number from 7 (Philaenus, Thomaspis) through 10 (Aphrophora) to about 26 in Cercopis. Another peculiarity of the cercopid antenna is constituted by 1-3 (according to genera) spinous sensilla (very long in Thomaspis) at the base of the flagellar constriction, and these are probably also odour receptors.

Fulgoromorpha. The sensory equipment of Fulgoromorpha which contains some 20 families, evolved in a quite different way. All representatives studied have the advanced 3-segmented condition. In contrast to Cicadomorpha, it is the bulbous second segment (pedicel), which harbours a rather elaborate system of sense organs. Perhaps the most primitive condition is found in Tettigometridae, a family which I have reason to believe is an ancient branch of Fulgoromorpha. Besides 4 other types of small sensilla the pedicel in this family contains a set of large typically placodoid sensilla, the numbers of which range in classes according to subfamilies from 35 up till 200 (Bourgoin, 1985). Of interest are 6 very minute sensilla, probably mechanoreceptors, inserted within the porous body of each placodoid sensillum. A wide variety of plaque-like sense organs occurs in representatives of other fulgoromorphous families (Marshall & Lewis, 1971). These plaques can be thought to be derived from typical placodoid sensilla (flat plates of porous cuticle) by crinkling of the edges and transformation of the lentiform porous cuticle into folds, ridges or finger-like processes, the whole system being surrounded by cuticular denticles. The climax in this anagenetic series of transformations seems to be reached in fulgorids like Pyrops candelaria (Lewis & Marshall, 1970) and Fulgora laternaria (pers. obs.), where the entire second segment is densely covered with highly elaborate plaque organs. One wonders what kind of forces related to host selection have led to such bizarre olfactory organs. Fulgoromorpha are further characterized by the presence of an elaborate sense organ of unknown function, situated at the base of the flagellum, which I propose to call the Bourgoin organ, in honour of its discoverer (Bourgoin, 1985). The limited number of taxa studied suggests also independent anagenetic progress in number, arrangement and complexity of antennal sense organs within single families. Future studies should be extended to other taxonomic groups and should also cover ontogenetic changes. In some delphacids and issids I have studied, the sensilla of the second segment develop de novo after the first instar, increasing in number towards the adult stage. The Bourgoin organ is already present in the first instar, although structured differently from that of the adult.

Labium.

Fulgoromorpha. In contrast to Cicadomorpha, Fulgoromorpha possess a large sensillum in a cavity on each side of the labium, close to the labial apex (incorrectly termed 'labial palpi' (Sogawa, 1977)). It has been described for Nilaparvata lugens (Sogawa, 1977) as a multilobed structure with two major and 8-10 minor porous branches. Two possible functions have been suggested for them, olfaction or hygroreception (Foster et al., 1983). From cursory SEM of this sensillum in representatives of various families, I conclude that it most probably serves olfaction while the insect is making contact with the plant surface. Just after arrival on a potential host, the planthopper perhaps senses the odour layer of the plant surface in advance of the decision whether to probe or not. Careful observation of behaviour during the exploring phase before probing, and comparison of such behaviour in cicadellids, which lack the preapical sensilla would be interesting. The morphological variability of this sense organ is considerable and partly parallels the evolution of the antennal sensilla. In its simplest form, it is a large spherical sensillum placodeum, as in some tettigometrids, issids and a flatid that I have studied; in the dictyopharid Dictyophara europaea, it is slit-like. The sensillum is probably secondarily lost in the trunk-feeding fulgorid Fulgora lateraria. In Cixiidae, the olfactory organ consists of an elongated cavity harbouring an adpressed, long tooth-like sensillum, pointing anteriorly. Of interest is the amount of variation in Delphacidae. It now seems clear that the cladogram of subfamilies runs from the most primitive Asiracinae, through Kelisiinae, Stenocraninae towards the most evolved and species-rich Delphacinae (Asche, 1985). The corresponding evolution of the preapical labial sense organ appears in the respective subfamilies as follows. In Asiraca clavicornis In Kelisia brucki the organ is bilobed, each lobe consisting of 4-5 extending branches. The sensillum is less antler-like in Stenocranus major; the short secondary branches do not project from the surrounding cavity. The sense organ as described for Nilaparvata (Sogawa, 1977) may prove to be representative for Delphacinae when more samples have been studied.

FEEDING

Elements of cicadine feeding behaviour such as probing, salivation, and actual ingestion have been excellently reviewed for cicadellids and delphacids by Backus (1985) and specifically for the brown rice planthopper (Nilaparvata lugens) by Sogawa (1982). Therefore a brief resumé will suffice here. Behavioral and physiological studies have been confined to very few species of the two families; so it is too early for generalizations.

Chemosensory tarsal sensilla are supposed to be absent in the one planthopper and the one leafhopper species studied (Backus, 1985), but scrutiny should be extended to more species and families. Sensilla of the labial apex harbour both mechanoreceptors and chemoreceptors in Nilaparvata. The sensillar equipment of the delphacid rostrum seems rather poor in comparison with conditions in other families. Cursory SEM reveals a great diversity of numbers and types of sensilla between and within cicadellids and delphacids, of which few have been studied, though they merit more thorough study. The same applies to the proprio-mechanoreceptors of the stylets, since Backus (1985) reported considerable differences between the leafhopper and the planthopper species studied by her. Finally, the precibarial sensilla should be mentioned, which have long been presumed to function as gustatory organs in Hemiptera. Backus & McLean (1985) first presented experimental

evidence that these sensilla indeed function as taste receptors and play a decisive role in ultimate acceptance of a host. What the sensilla actually detect is still a mystery.

Subjects discussed in the review on N. lugens (Sogawa, 1982) are: structure and function of mouthparts, salivation, excretion, probing and sucking stimulants, effects of feeding, and resistance of host varieties. Only fragmentary information on these subjects is available for some cicadellids, but there are virtually no data for the many other families. Selection of special plant tissues for feeding is known only for a few families: mesophyll by typhlocybinae cicadellids, phloem by delphacids and the majority of cicadellids, xylem by larvae of cicadids, cercopids and some cicadellids in both larval and adult stages; mixed phloem-xylem feeding is employed by some cicadellids. The extreme dilution of xylem fluid has been associated with the long developmental time of periodical cicadas (White & Strehl, 1978). However, xylem-feeding froghoppers and cicadellids show quite normal developmental cycles. Porrect cephalic swelling should be indicative of xylem feeding. If so, one wonders whether the excessively elongated heads in various fulgoroïd families and in some cicadellids are associated with this type of feeding. In Delphacidae, a parallel is found in Dictyophorodelphax, which feed on Euphorbia in Hawaii (Zimmerman, 1948), and have the alimentary canal entering far into the cephalic prolongation (Kershaw, 1913).

HOST SELECTION AND HOST SUITABILITY

Most of the literature concerning experiments on host relations of pest species deals with forced rearing on single plant specimens or parts of them (e.g. Agarval & Krishnananda, 1976; Cordero & Newson, 1962). These studies discuss host suitability for survival, growth, reproduction and oviposition. Such experiments are useful for screening potential virus vectors of Cicadina, but they prevent the insects from making a choice. In the field, the delphacid, Struebingianella lugubrina, for example, is found in the Netherlands, almost exclusively on Glyceria maxima. Nevertheless, entire larval development was successful on 11 other grasses in laboratory rearings (Boeve, unpubl.).

The earliest experiment on host selection was performed by Nuorteva (1952) with the froghopper Aphrophora alni. He tested 4 plant species arranged in a single row and replaced successively the most favoured plant species by another one. Eight plant species were tested in this way and ultimately arranged according to decreasing attractiveness for the froghoppers. The validity of the conclusions drawn from this experiment may be questioned. A more reliable method of analysing host choice has been developed by de Vrijer for Javesella spp. (unpublished) and den Bieman (1987) for Ribautodelphax spp. Series of potential host grasses are arranged in such a way that the ultimate distribution of the insects on the plants is maximally attributable to free choice. The same method is appropriate to assess host suitability for growth, reproduction and oviposition. In this way, one can assess that most species of Javesella and all taxa studied of Ribautodelphax tend more to monophagy or restricted oligophagy than formerly assumed. Occasionally, in such experiments, significant preference was observed for plant species that were not field hosts. This demonstrates that experimental conditions may influence the attractiveness of plants in an unnatural way. Besides that, the host suitability of a plant species may also be subject to natural variability in consequence of ecological, seasonal, genetical, and geographic variation.

HOST SPECIALIZATION, HOST ALTERNATION, POLYMORPHISM, FIELD HOST RELATIONS.

Host specialization

The following survey is restricted to the two large delphacid and cicadellid families in W. Europe (including Scandinavia, excluding Spain and Portugal) for two reasons: they are better known, and I have some personal acquaintance with them. The compendium is based on regional compilations (Le Quesne, 1960, 1969; Ossiannilsson, 1978, 1981, 1983; Ribaut 1936, 1952), various local surveys (e.g. Vidano & Arzone, 1976; Waloff & Solomon, 1973; Whittaker, 1969), and unpublished data, in particular on delphacids by den Bieman. Data are summarized by feeding class. Arbitrarily, I define the following categories: monophagous (1 host plant species), oligophagous sensu stricto (2 - 4 species of one plant genus), oligophagous sensu lato (2-4 host plant species belonging to different, not necessarily related genera), polyphagous (5 or more host plant species). The summary of data is presented in Table 1.

Table 1. Distribution of feeding types among different families of planthoppers and leafhoppers. (see text for further explanation)

	Total nr. of spp.	Unknown	Categories of host specialization ¹⁾			
			Monophagous	Oligophagous 's.s.'	Oligophagous 's.l.'	Polyphagous
Delphacidae	137	35	45 (44%) 9 (9%)?	14 (14%)	25 (25%) 3 (3%)?	5 (5%) 1 (1%)?
			-----		-----	
			67%		33%	
Cicadellidae (excl. Typhl.)	381	213	53 (32%) 11 (7%)?	45 (27%) 10 (6%)?	15 (9%) 16 (10%)?	6 (4%) 12 (7%)?
			-----		-----	
			71%		29%	
Typhlocybinae	173	29	30 (21%) 9 (6%)?	31 (22%) 4 (3%)?	48 (33%) 9 (6%)?	8 (6%) 5 (4%)?
			-----		-----	
			51%		49%	

1) Questionmarks indicate uncertainty about the category assigned

The host choice of more than half of the cicadellids (excluding Typhlocybinae) is not exactly known. This high figure refers mostly to species of low mixed vegetation. Our knowledge of food-plant relations is more complete for delphacids (26% unknown) and for typhlocybines (16% unknown). For the feeding classes of the better known species, monophagy prevails in Delphacidae and Cicadellidae, but not in Typhlocybinae. Verified polyphagy exists in less than 6% of the three major taxa considered. If the classes 'monophagy' and 'oligophagy s.s.' are combined and compared with the sum of the other two classes (Table 1), a clear preponderance of host specialization is seen in the first two taxa, but much less so in Typhlocybinae. Additional accurate field and laboratory observations are necessary to prove such generalizations about field host specialization.

An earlier conclusion from field studies of the cicadine fauna of acidic and calcareous grasslands (Morris, 1971; Waloff & Solomon, 1973),

indicating that the architecture of the plant communities in general is more important than the plant species themselves seems questionable in view of Table 1. I will deal later with supposed differences in feeding classes between inhabitants of trees and of low vegetation.

Host alternation

Although rare in Cicadina, some striking examples of alternation of hosts are known. In its simplest form, the phenomenon represents a temporal change of hosts for aestivation or hibernation. Several species of Empoasca and Zygina fly to conifers for hibernation. Since they remain active in flight and even puncture conifer needles at low temperatures, I assume that they undergo considerable physiological change. Shifts in feeding substrate during ontogeny occur in some cicadellids (e.g. Allygus spp., larvae on grasses, adults on trees), cixiids and cicadids (larvae subterranean, adults on various trees). The multivoltine membracid Centrotus cornutus utilizes three levels in Italy at altitude 1300 m (Arzone, 1971): larvae on a herbaceous plant, feeding and ovipositing adults each on a different woody plant; data from other parts of Europe indicate other plant relations and cycles (person. observ.). Distinct alternation of hosts for oviposition and feeding, associated with alternating generations, occurs in some typhlocybines. The eggs of Edwardsiana rosae hibernate in young stems of Rosa, whereas the eggs of the following generation are laid into the mid-ribs of the leaves of Rosa, but also of other plants (Claridge & Wilson, 1978). Ficocymba ficaria spends 2 generations on Ficus carica as summer host and one generation on Lonicera spp. in winter (Vidano, 1960). Cyclic change of hosts for oviposition but not for feeding occurs in Muellerianella fairmairei; this species sticks to Holcus for feeding and oviposition during summer, but requires Juncus for oviposition of the hibernating eggs (Drosopoulos, 1977).

Polymorphism

In an intricate experimental study, Müller (1987) demonstrated that the so-called balanced colour polymorphism of Mocydia crocea is associated with polymorphism in host preference. This cicadellid lives on grasses in the Onobrychido-Brometum in Europe. It exhibits 6 larval morphs, differing in colour pigmentation. Survival of larvae on 22 grass species revealed different spectra corresponding with the 6 classes of colour morphs. This means, for instance, that one particular morph grows optimally on several host species, whereas none of the grasses tested is optimum food for another colour morph. Müller suggested that this ecophysiological polymorphism is of primary significance for the species and the associated colour phenotypes have secondary differential survival values, as in the well known example of adult polymorphism in Philaenus spumarius (Halka et al., 1976, and many other papers). It would be interesting to know whether the differential survival value of M. crocea on different hosts is associated with differential host selection. Intraspecific variation in nutritional utilization may occur in other species with larval colour polymorphism (such as spp. of Evacanthus, Allygus, Elymana, Cicadula, and some typhlocybines). One wonders whether such nutritional polymorphism occurs also in species not having phenotypic markers; experimental analysis of such examples would be very difficult.

COMMUNITIES OF CICADINES AND HOSTS

Are feeding types different on trees and low vegetation?

It has been argued (Claridge & Wilson, 1976, 1978) that most tree-associated leafhoppers in W. Europe, especially Typhlocybinae, have a

more restricted host range than species living in low vegetation, such as grasslands. The larger three-dimensional space and permanence of trees favours greater host-plant specificity in tree-feeding species. In order to test this hypothesis, I divided the various host categories of leafhoppers (Table 1) according to trees and low vegetation. The results are summarized in Table 2. These preliminary data on host specialization in typhlocybines give little support for the assumption that life on trees has induced more restriction in food selection than in species living in low vegetation, (although the category 'monophagous' for trees is twice as high as for low vegetation). The figures for the remaining cicadellids at first sight seem to confirm the presumption that species living on trees are much more restrictive in food choice than those from low vegetations. However, the 97% of the two categories with strong food restriction refers to 66 species, of which 45 belong to the genera Idiocerus and Macropsis. Of the latter genus, 7 species are confined to low vegetation and they are all monophagous or oligophagous in the narrow sense. Thus, the evolutionary history of species as reflected in their taxonomic relations, may have had a major and perhaps dominant impact on host bonds.

Table 2. Distribution of feeding types among leafhoppers of trees and low vegetation. (see text for further explanation)

		Categories of host specialization ^{1) 2)}			
		Monophagous	Oligophagous 's.s.'	Oligophagous 's.l.'	Polyphagous
Typhlocybinae	Low vegetation	14 + 5?	31 + 3?	36 + 3?	5 + 3?
		-----		-----	
		53		47	
	Trees	31 + 10?	12	31 + 4?	8 + 4?
	-----		-----		
		53		47	
Cicadellidae (excl. Typhl.)	Low vegetation	28 + 8?	10 + 9?	14 + 14?	7 + 10?
		-----		-----	
		55		45	
	Trees	40 + 2?	50 + 5?	1 + 1?	1?
	-----		-----		
		97		3	

1) Numbers in percentages

2) Questionmarks indicate uncertainty about category assigned

Coexistence of closely related species.

The study of Ross (1957) on the coexistence of Erythroneura species on Platanus occidentalis has often been referred to in literature as an exception to the rule of competitive exclusion. However, later authors (McClure & Price, 1975) have experimentally demonstrated competition between these species on sycamore. Further studies are needed to show whether and how coexistence may depend on different strategies of resource utilization. Two Eupteryx species coexisting on stinging nettle, exclude each other at all developmental stages according to shaded or exposed sites (Stiling, 1980). Other interesting taxa worth experimental study on the exclusion principle are the delphacid Chloriona species on Phragmites (most often 2, sometimes even 5 species are found together, den Bieman, unpublished) and the large complexes of Idiocerus leafhoppers on Salix and Populus. Also of interest for further studies in this field are spittlebugs, since larvae belonging to different species occur frequently within a single spittle mass (Halka et al., 1977).

The analysis of patterns reviewed in this chapter refers to representatives of only two families. The phenomena discussed are largely

unknown for the many remaining families particularly from subtropical and tropical faunas.

CRYPTIC SPECIES AND EVOLUTIONARY ASPECTS

Speciation.

While compiling the data on host specialization (Table 1) I came across more than 10 species of cicadellids in W. Europe revealing distinct geographic variation in host relations. Many other vicarious subspecies and very closely related species provide evidence for allopatric divergence. On the other hand, very closely related, but biologically different species often occur together on similar or closely related hosts in sympatric situations. Much more detailed research is needed before accepting sympatric speciation as the most plausible speciation model in such cases, as for example claimed for complexes of typhlocybinae Erythroneura spp. in USA by Ross (..). The hypothesis of sympatric speciation in the membracid Enchenopa binotata complex through shifts in host choice has been strongly advocated by Wood & Guttman (1983). It seems to me that the six characters which have been interpreted in favour of such a mode of speciation could equally well be used to support spatial diversification.

Claridge & Wilson (1976) referred to unpublished data of Adams, who found significant morphometric differences between Alnetoidea alneti populations (Typhlocybinae) from 4 different tree species, which possibly represent genetically isolated species. According to these authors, it might be possible that so-called polyphagous species on trees are groups of 'extreme' sibling species; this would strengthen their arguments about the preponderance of specificity in arboricolous leafhoppers in contrast to species living in low vegetation. An interesting example of cryptic species is found in the complex of 'Oncopsis flavicollis' leafhoppers on birches in S. Britain (Claridge & Nixon, 1986); such studies demonstrate the enormous importance of modern multifaceted biotaxonomic research.

Phylogeny and radiation.

Another way to gain insight into past speciation patterns associated with shifts of hosts is by modern phylogenetic analysis. Ross (1974, and earlier work) was the first applying the cladistic method to various groups of cicadellids and superimposed host relations on the respective cladograms. For instance, he analysed a monophyletic subgroup of Erythroneura comprising more than 300 spp. in N. America. The reconstruction led to the inference that the ancestral host genus was Quercus and that many clades of this group of Erythroneura radiated independently from Quercus to other host genera. It seems to me that more careful cladistic analysis is needed to warrant the conclusions drawn. In a study by Nault (1985) detailed cladistic analysis of morphological, biochemical and behavioral data proved to be crucial in reconstructing the phylogeny of pathogens transmitting Dalbulus leafhoppers on Tripsacum and Zea species. I support the plea of that author that such approach should be applied to other economically important complexes of species, but I would like to add that comparable investigations on related groups of non-pest species are also needed.

Such studies should be extended as well to selected taxa of the more than 30 remaining families of which we know virtually nothing. Special attention should be focused, before it is too late, to the most spectacular examples of trophic radiation on oceanic islands. As for other insect groups, the Hawaiian hemipteran fauna provides an excellent subject for the study of this fascinating aspect of evolutionary biology. The explosive radiation of Delphacidae on Hawaii has long been known

(Zimmerman, 1948). The few gramminicolous forms occurring there, are well known immigrants and notorious pests. Though on the continents delphacids are almost entirely associated with grasses and other monocotyledons, all endemic Hawaiian taxa (134 species, 7 genera known in 1948) live on a variety of ferns and dicotyledons (mostly trees), the majority being monophagous. A Modern taxonomic analysis of this fauna would be an exciting challenge.

ACKNOWLEDGEMENTS

I thank my colleagues C.F.M. den Bieman, P.W.F. de Vrijer and A.J. de Winter for their help in the preparation of this paper.

J.C. Rigg, Centrum voor landbouwpublikaties en landbouwdocumentaties, kindly corrected the English text.

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