Proc. 6th Auchen. Meeting, Turin, Italy, 7-11 Sept. 1987, 233-243.

SPECIES, SPECIATION AND ACOUSTIC SIGNALS IN AUCHENORRHYNCHA

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ABSTRACT

The biological species is the most useful concept for sexually reproducing organisms. Acoustic signals are used dominantly as specific mate recognition signals, or ethological isolating mechanims, by Auchenorrhynha. Analyses of calls allow determination of biological status for host-associated, and geographically isolated, populations. The few detailed studies available give support to theories of allopatric speciation, but little to sympatric ones.

KEY WORDS

Biological species, Specific mate recognition systems, isolating mechanisms, Nilaparvata lugens, Nephotettix.

INTRODUCTION

The identification of leafhoppers and planthoppers has always caused major problems. Indeed it was these problems that provided the major stimulus for the first of these Auchenorrhyncha meetings held in Cardiff in 1973. The use of genitalic characters in the early years of this century made possible the recognition of many more species than before. In recent years a further revolution , at least for some genera, has been established by the study of internal abdominal and thoracic apodemes. These structures, associated with the sound producing mechanism, have provided many new characters and thus allowed further separation at the species level.

Because of the need to understand the genetic status of so many species of Auchenorrhyncha of economic and ecological importance, many workers around the world are now undertaking biotaxonomic (or biosytematic) studies on different genera or species groups (see other papers in this volume). These studies aim to establish the status of populations associated with different host plants in the same and different geographical regions (for further discussion on methodology see Claridge & Morgan, 1987).

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SPECIES CONCEPTS

The biological species, as first fully elaborated by Ernst Mayr (1942, 1963), Cain (1954) and others, is now widely accepted as the most useful species concept for sexually reproducing organisms. Among the Auchenorrhyncha sexual reproduction is usual. Indeed the first definite record of a parthenogenetic planthopper was only recently published (den Biemen & de Vrijer, 1987), though pseudogamy may be more common but has been little studied (Booij & Guldenmore, 1984; Drosopoulos, 1977). Probably the best definition of the biological species is - "Species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (Mayr, 1942). In this emphasis is placed on reproductive isolation in the field. Thus the only criterion for determining species status is that of interbreeding under natural conditions.

Few workers have had difficulty in accepting this concept in theory. However, in practice there may be many difficulties. First, it may not be possible to observe reproductive behaviour for many groups of organisms. Usually, taxonomists have only dead samples on which to work so that a basic morphological approach to species is inevitable. Nevertheless there are surely few taxonomists who do not believe that the morphological differences which they use to separate species do not reflect genetic differentiation and reproductive isolation.

A second and more fundamental problem in using the biological species concept is that of determining the status of populations which do not meet in the field. The major problem is that posed by populations isolated from each other in space - often termed geographical isolation. (It should be noted that the same difficulties arise for populations isolated in time, but these will not be considered here.) The test of natural reproductive isolation is obviously not possible for such forms. In this context the well known terms allopatric and sympatric are often used, but may cause great difficulties. Particularly for smaller animals it is not easy to decide when forms are truly sympatric - that is have the possibility of meeting in breeding condition in nature. Very small spatial barriers may be adequate to achieve allopatry. Certainly the phrase geographical isolation may be very misleading with its implication of large scale spatial separation.

A major consequence of the acceptance of the biological species was the development of the concept of species isolating mechanisms as major species characteristics (Dobzhansky, 1937; Mayr 1963; etc.). These "mechanisms" consist of any attributes of species which reduce the chances of interspecific hybridisation. This category of species differences is therefore very mixed and includes both pre- and postmating barriers.

In recent years major criticisms have been made of the biological species by Hugh Paterson (eg. 1978, 1981, 1985). Paterson prefers to refer to the biological concept as the isolation concept and contrasts it with his own recognition concept. His criticisms have been taken up also by others, including Vrba (1985) and Eldridge (1985). Paterson objects to the concept of "isolating mechanisms" with the implication that the variety of species characters included in the category have evolved under the pressure of natural selection to achieve isolation *per se*. By contrast his recognition concept lays emphasis on the signals which constitute the specific mate recognition systems (SMRS) of a species. He stresses that such signals do not depend for their existence on pressures from other species, but are internal characteristics.

This is not the place to elaborate further on this interesting controversy, but it should be noted that in practice the premating ethological isolating mechanisms of Mayr correspond closely to the SMRS of Paterson. Indeed authors who have been interested in the biological species have often emphasised the importance of differences in courtship and sexual behaviour for establishing species status (eg. Alexander, 1967; Claridge, 1965). In recent biotaxonomic studies on Auchenorrhyncha particular attention has been paid to the acoustic signals used widely in premating behaviour by these insects.

ACOUSTIC SIGNALS AND SPECIES PROBLEMS

One of the major developments in Auchenorrhyncha research in recent years has been the increasing interst in acoustic behaviour. Some of the earliest classifications of the group were based on the behaviour of sound production and divided the series into two very unequal subgroups - on the one hand the singing cicadas, and on the other the supposedly non-singing leafhoppers, planthoppers, etc.(see Claridge, 1985b). All this was changed when Frej Ossiannilsson (1949) published his classic study and showed the fallacy of such a dichotomy. In a wide-ranging review of representative species from all major north european familes, he showed that they all possessed a sound producing apparatus, resembling to varying degrees the cicada tymbal. Even more significantly he was able to record for the first time the very quiet sounds produced by males, and often also females, of many species. Ossiannilsson's study is still the basis for all modern work. Recent authors have been able to take advantage of newer electronic techniques of recording and analysis, but no one has again attempted such a wide-ranging survey. It is clear that most, if not all, families of Auchenorrhyncha use acoustic signals in communication and that for all, except Cicadidae, low intensity substrate transmitted signals are dominant (for reviews see Claridge, 1985a,b). Such signals may be used in different biological contexts, but they dominate in courtship and mating interactions and therefore function in species recognition.

Indeed some workers have been able to use play-back techniques to release appropriate behaviour in insects of the opposite sex (eg. Claridge et al., 1985b; de Vrijer 1984).

Analyses of acoustic signals have now been used to clarify species limits, often revealing the existence of previously unsuspected sibling species, in several genera of leafhoppers - Euscelis (many papers by Strübing and colleagues, for summary see Strübing, 1983), Oncopsis Claridge & Nixon, 1986), and planthoppers - Nilaparvata (summary in Claridge & Morgan, 1987)(figures 1 & 2), Muellerianella (Booij, 1982), Javesella (de Vrijer, 1984,1986), and Ribautodelphax (den Biemen, 1986). There is no doubt that these techniques will have to be used more widely to establish species status for many other groups of economically important species.

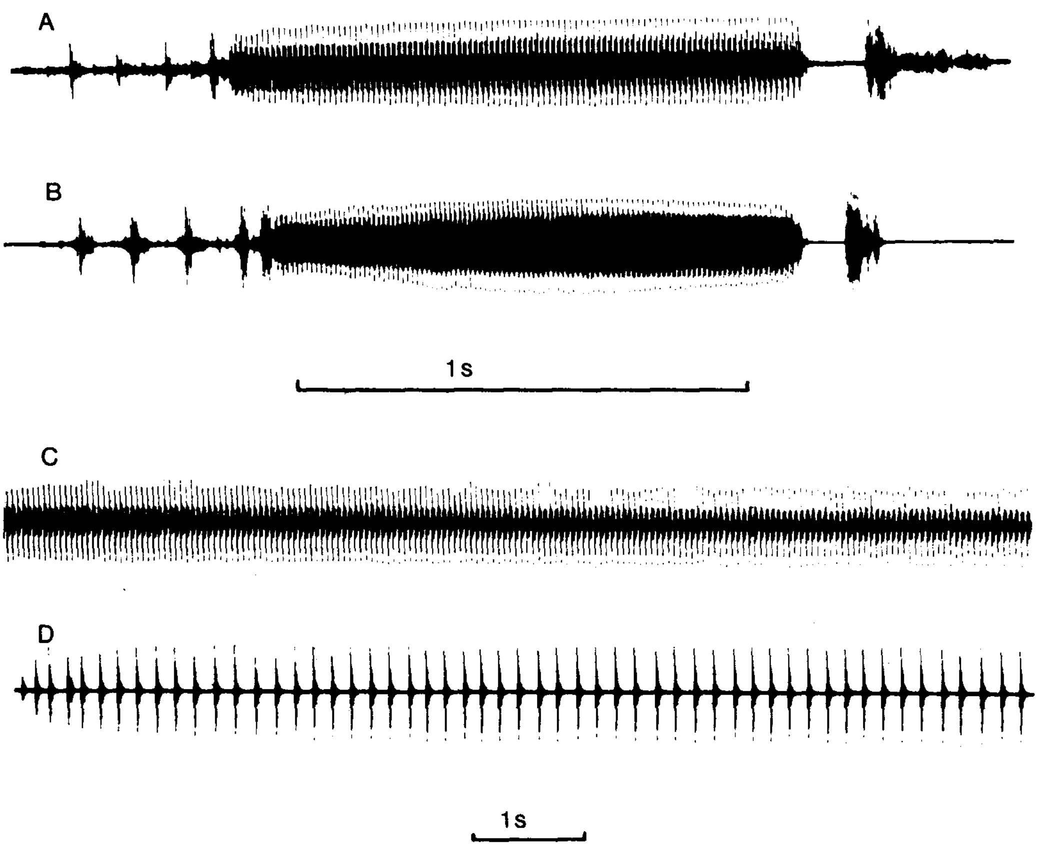

Fig. 1 - Oscillograms of typical signals of males (A&B) and females (C&D) of Nilaparvata lugens from rice-feeding (A&C) and Leersia-feeding populations (B&D) from Philippines. Time marks 1 sec. (after Claridge et al., 1985b)

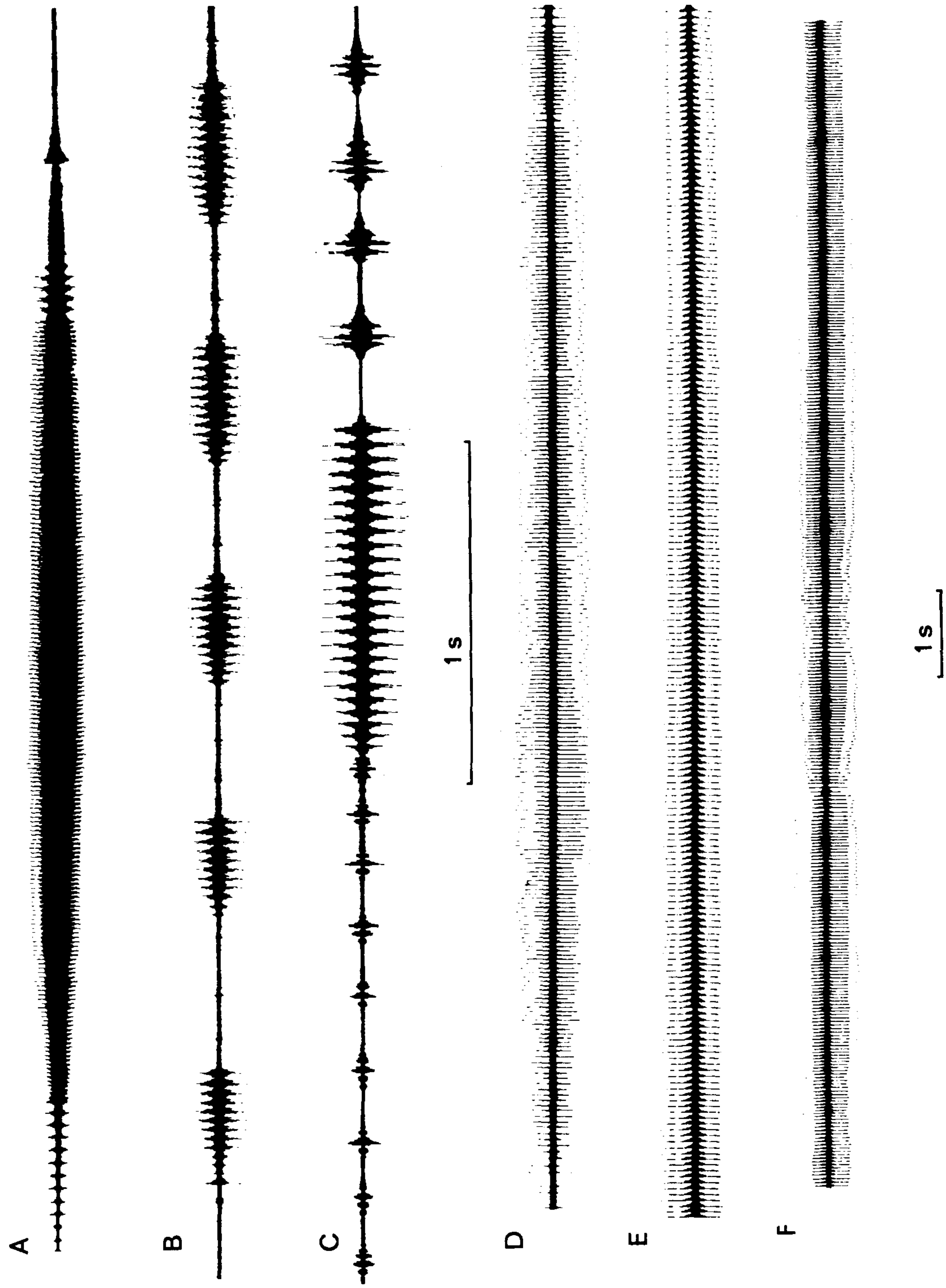

Fig. 2 - Oscillograms of male (A-C) and female (D-F) calls of N. bakeri from Philippines (A&D), N. muiri from Japan (B&E) and N. maeander from Nigeria (C&F). Time marks 1 sec. (after Claridge & Morgan, 1987)

Reliable differences in acoustic signals may be used in taxonomy for species discrimination, but it does not necessarily follow that such differences are themselves important in specific mate recognition. This can only be shown by experiment. In the brown planthopper of rice, Nilaparvata lugens (Stål), both males and females produce calls consisting of distinct temporal patterns of pulses during premating behaviour (figure 1). Receptive males respond to calling females by replying with their own call and moving rapidly about on the host plant until contact is made (Claridge et al. 1984, 1985a). Of the variables which have been studied, rates at which pulses are produced, or pulse repetition frequency (PRF), seems to be critical for successful recognition (Claridge et al. 1984). Indeed populations of the as yet unnamed sibling species very closely related to N. lugens, but found on the weed grass Leersia hexandra, differ most obviously from the rice-feeding species in differences of PRF of both male and female calls (figure 1).

Problems of possible field hybridisation between species may also be resolved by acoustic studies. For example there has been some controversy concerning possible hybridisation between the two species of green leafhoppers, Nephotettix virescens (Dist.) and N. nigropictus (Stal) - vectors of important virus diseases of rice in tropical Asia. In some field populations morphologically intermediate individuals are often found. Ramakrishnan & Ghauri (1979) first suggested that such individuals might be natural hybrids between the two species. The male calls of these two species are very distinct (figure 3). Yusof (1982) bred some definite species hybrids in the laboratory and recorded their calls. These were very variable between individuals and showed a breakdown of the complex parental patterns with generally intermediate characteristics (figure 3). Thus it is possible to identify true hybrids by acoustic analysis. Of the many morphological intermediates from field populations which have been recorded, all show the distinct calls of one or other species. No natural hybrids have been identified on this basis. It thus seems clear that some of the morphological characters which are frequently used to discriminate these two species are not completely diagnostic of the true biological species.

SPECIATION

The very large numbers of sympatric species of insect herbivores and parasitoids which are found in most terrestrial communities has led many workers, including Darwin himself, to doubt that processes of allopatric speciation are adequate to explain their existence. In recent years similar ideas have been argued strongly by many workers, most notably Guy Bush (eg. 1975). Bush advocates the sympatric evolution of host races and the subsequent complete separation of the races as species by adaptation to

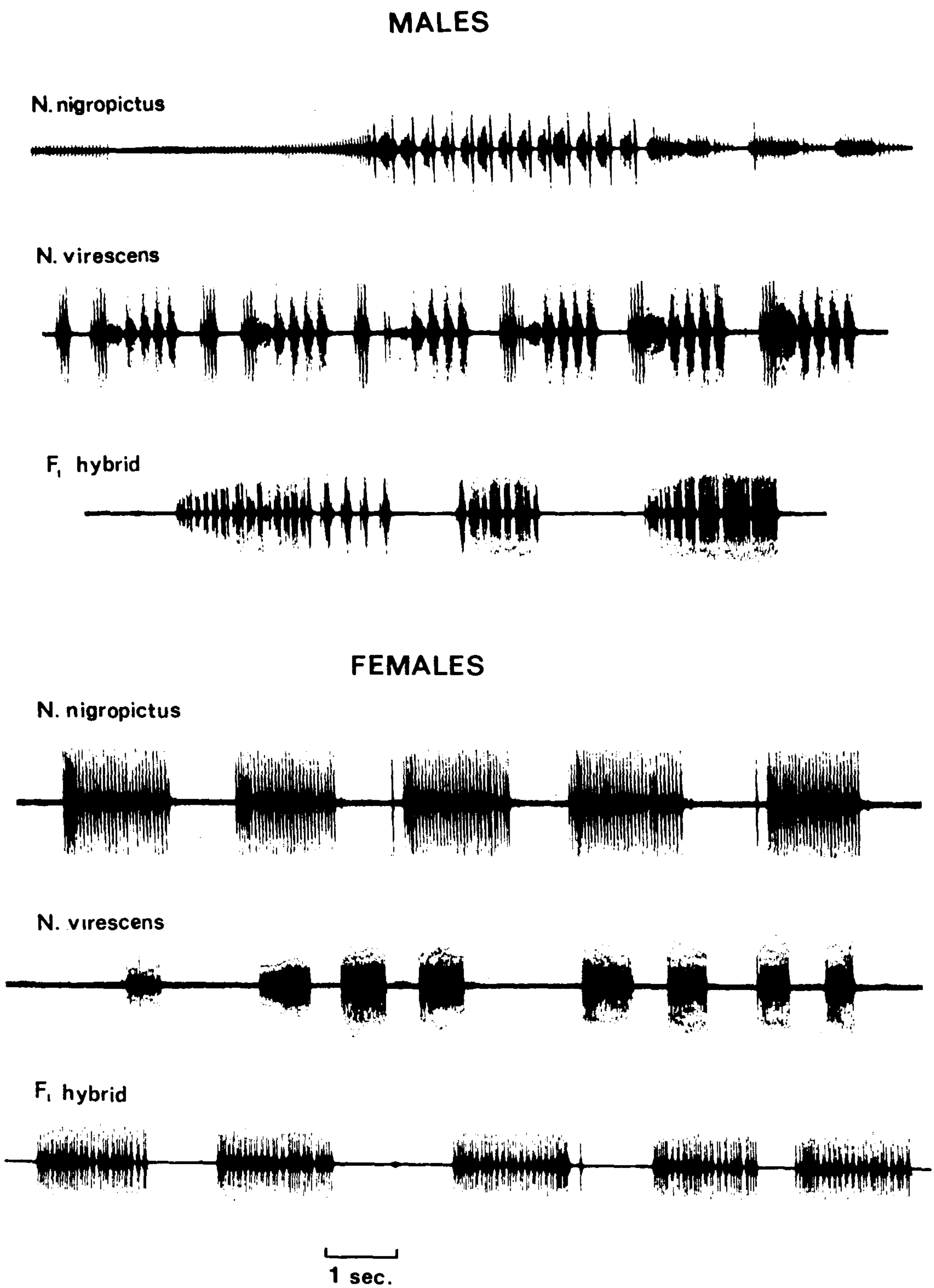

Fig. 3 - Oscillograms of male and female calls of Nephotettix virescens and N. nigropictus, and of laboratory hybrids between them. (after Claridge, 1985b).

new hosts. Others have argued strongly that formidable genetic problems exist for any such hypotheses (eg. Futuyma & Mayer, 1980). Nevertheless such ideas are widely accepted by ecologists (eg Price, 1980; Strong, et al. 1984).

A major argument against the hypotheses of Bush is that no definite examples of sympatric host races in sexually reproducing species have been found. Most supposed host races, on detailed examination, have been shown to be groups of sibling species (review in Claridge, 1988). Examples among the Auchenorrhyncha are provided by the treehoppers of the Enchenopa binotata complex in North America (Wood & Guttman, 1983), and our own studies on leafhoppers of the Oncopsis flavicollis group in Britain (Claridge & Nixon, 1986).

In discussions on speciation little attention is usually given to the evolution of premating isolation (sensu Mayr) or specific mate recognition (sensu Paterson). Clearly such evolution is critical to the origin of new species. Paterson (1985) argues that geographically isolated populations may diverge only very slowly in essential characters of the SMRS, because such features are strongly buffered against change by stablising selection. However, others, including West-Eberhard (1983), suggest on the contrary that sexual selection may be expected to produce rapid divergence of such signals in isolated populations. Several studies on Auchenorrhyncha show variation in acoustic call characteristics in geographically separated populations. For example, Booij (1982) described differences in several variables of the calls of the two planthopper species, Muellerianella fairmairei and M. brevipennis, from different parts of Europe. Similarly there is evidence of geographical variation in calls of the leafhoppers, Nephotettix virescens and N. nigropictus, in Asia (Yusof, 1982; and in Claridge, 1985b). However, the biological significance of the variation in these two examples is unknown.

In Nilaparvata lugens, significant differences in PRF of male calls have been described for populations from different parts of Asia and Australasia (Claridge et al., 1985a). As outlined above, this character is known to be a major element of the SMRS for this species. Indeed difficulties in laboratory hybridisation experiments between some populations were correlated with the degree of differentiation in male call PRF of the parental types. Thus, this species provides clear evidence of rapid allopatric evolution of SMRS characters which could lead to complete speciation. It is interesting that the very closely related sibling species associated with Leersia hexandra differs from sympatric rice-feeding populations primarily in PRF characteristics of male and female calls.

It is unfortunate that as yet there are no further comparable data on other Auchenorrhyncha. These insects provide outstandingly good material for testing some of the current controversies in speciation theory. I urge others to take up these exciting problems.

ACKNOWLEDGMENTS

I thank my colleagues in Cardiff for their help over the years on the various projects cited here. Particularly I thank John Morgan and my wife, Clare, for assisting in the preparation of this manuscript. I am grateful also for longstanding financial support for research on rice-associated problems to the Tropical Development and Research Institute, London, and for work on British leafhoppers to the Natural Environment Research Council.

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