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ACOUSTIC SIGNALS IN THE HOMOPTERA: Behavior, Taxonomy, and Evolution

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INTRODUCTION

The use of acoustic signals in communication, both within and between species, occurs widely in the Insecta (2, 35, 36). The loud airborne sounds of many groups of Orthoptera and of the large cicadas among the Homoptera are well known (1). In these groups, where communication may take place between individuals at distances very much greater than their own body length, tympanal acoustic receptors are well developed (50, 66).

Some small insects are known to produce low intensity sounds. Many more possess structures that appear to be sound-producing mechanisms, but which have never been properly investigated (26, 35, 36). In recent years considerable advances have been made in our knowledge and understanding of the use of sound signals by small insects. For example, in species of *Drosophila*, and probably also in many other small winged insects, very close range, pulsed signals between individuals of the same species are produced by low frequency wing vibrations. These may only be detected by other individuals, when in very close proximity to the signaller, by the use of a displacement receptor—in *Drosophila* the lightly balanced antennal arista (7).

In order to communicate over longer distances small insects, because of the purely physical limitations of their size, would have to use very high frequency, or ultrasonic, sounds (49, 50). However, high frequency sounds are not suitable for communication in structurally complicated habitats dominated by plants (50). An alternative that has received much attention recently is the use

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of low frequency vibrations transmitted through a dense substrate (6, 51). This is now well known in some small leafhoppers and planthoppers (15, 37, 38, 40, 41, 78, 83) and also in some plant bugs (32, 33), in all of which the signals are transmitted through the plant substrate. An airborne component of the signals produced by these insects can be detected by the use of a suitable microphone, and this has been measured at between 25 and 35 dB at a distance of only 1 cm from the emitter. It is estimated that such sound levels would be sufficient to stimulate the most sensitive known insect ears over no more than a few centimeters, but the vibrational components in the plant substrate may be detected over distances of at least 1 to 2 m (51, 83). All species so far tested have been shown to respond only to the substrate-transmitted element of the sound emission (33, 37, 38, 65, 78). Little is known of the mechanisms involved in either production or reception of such vibratory signals, but it seems likely that, in plants, meaningful signals are carried by "bending waves" that are detected by insects normal to the plant surface (51). In this review the terms "sound" and "acoustic signals" are used to refer to both aerial- and substrate-transmitted vibrations.

In the Insecta the most common method of sound production is the frictional mechanism of stridulation. One specialized part of the body, the scraper, is brought sharply into contact with another specialized part, the file, which generally has a series of upstanding ridges or pegs and is thus set into vibration. This is especially well known in the Orthoptera, but examples occur in most other orders (26). The other well-known method of sound production in insects is the tymbal mechanism, in which a specialized area of cuticle (the tymbal) is alternately distorted and relaxed by an underlying tymbal muscle. This results in a series of clicks or discrete sound pulses, which may be variably damped. Until recently the tymbal mechanism was generally thought to be restricted to the Hemiptera, where it is best known and remarkably elaborated in the Cicadidae (Homoptera), but it is also well developed in various groups of Pentatomorpha (Heteroptera) (32, 33, 48). A similar mechanism is now known in some tiger moths (8, 36).

The present review is concerned with sound production and acoustic behavior in the Homoptera, and its taxonomic and evolutionary significance with respect to speciation.

The relatively conservative classification of Woodward, Evans & Eastop (87) for families and superfamilies of Homoptera will be followed. The Homoptera is generally regarded as a suborder of the Hemiptera and includes not only the larger cicadas (Cicadidae) but many generally smaller leafhoppers (Cicadellidae), tree hoppers (Membracidae), froghoppers (Cercopidae), and planthoppers (Delphacidae). These families, together with some smaller ones, are usually grouped together in the series Auchenorrhyncha. All remaining families of Homoptera, which include many very specialized insects such as the Aphidoidea, Coccoidea, and Aleyrodoidea, are grouped together to form the series Sternorrhyncha. Few records of sound production are available for the Sternorrhyncha. Aphids of the genus *Toxoptera* possess a frictional mechanism of sound production. Stridulation in these species may have an antipredator function (48). Of the remaining Sternorrhyncha only some species of Psyllidae have been recorded as producing sounds, probably by means of wing vibration (57). Nothing is known of the significance of such sounds. Here, I am concerned only with species of Auchenorrhyncha. All of these, as indeed all known Homoptera, are plant feeders and thus live their lives in intimate contact with their host plants, which not only provide food but also form the substrate on which they live.

There has been considerable controversy and confusion over the terminology used for insect acoustic signals (2, 35, 36, 47, 94), and no system that is generally applicable to all groups is available. In addition, it is often useful to describe signals, the functions of which are not fully understood, so that functional terminology may be difficult to use. I have therefore followed the general usage of previous students of Homopteran acoustic behavior. The system of Alexander (2) seems generally most useful.

ACOUSTIC SIGNALS AND SOUND PRODUCTION

The songs of Auchenorrhyncha may be divided conveniently into the loud calls of the generally larger Cicadidae and the quiet, low intensity calls of the remaining, generally smaller, leafhoppers, planthoppers, and related forms. It is unfortunate that no modern studies seem to have been made on the acoustic emissions of the larger, essentially tropical Fulgoroidea. In 1818 Kirby & Spence (46) wrote that "The great lantern fly (*Fulgora lanternaria* L.) from its noise in the evening—nearly resembling the noise of a cymbal, or razor grinder when at work—is called Scare-sleep by the Dutch in Guiana." However, Westwood (85) believed the sound to be due to a cicada. This is a fascinating and open field for research.

Loud Airborne Signals of Cicadidae

The often very loud sounds or songs of cicadas were first mentioned in the classical writings of Homer and were studied in some detail by Aristotle (54). The morphology of the tymbal mechanism was first clarified in the eighteenth century by Réaumur and has since been further elaborated by other workers (27, 54). Only with the advent of electronic methods of recording and analysis was it possible to study adequately the physiology of sound production and tymbal function (34, 60, 61, 64, 70, 72, 89, 94, 95). The following account of the tymbal mechanism is based primarily on the works of Pringle (60, 61) and Young (89, 90, 91, 94, 95).

THE TYMBAL MECHANISM The sound-producing mechanism of a typical male cicada consists of a pair of thin cuticular membranes, the tymbals, situated dorsolaterally one on each side of the first abdominal segment. Each tymbal membrane is strengthened by a series of sclerotized ribs, which are typically oriented dorsoventrally (Figure 1). The precise number and arrangement of the ribs varies greatly between species but is usually species specific. The tymbal is distorted or buckled by a large tymbal muscle, the apodeme of which is attached dorsally to the inner face of the tymbal. The basal insertion of the tymbal muscle is placed midventrally on a characteristic internal skeletal structure, usually known as the "chitinous V" (54, 60, 61). Contraction of this muscle results in a buckling of the tymbal membrane. Subsequent relaxation of the muscle results in the natural return of the membrane to its position of rest. In addition to the tymbal muscle, another tensor muscle is situated anterior to the tymbal, so that on contraction the curvature of the tymbal is increased, resulting in changes in elastic and acoustic properties of the membrane. Also associated with the tensor muscle are three complex groups of chordotonal sensilla (91), some of which on occasions have been wrongly identified as elastic ligaments (60). Within the first abdominal segment and immediately below the tymbals is a pair of air sacs. These derive from the tracheal system and vary greatly in size in different species. Together with the tymbals, they form the functional sound-producing unit.

Ventral to the tymbals on each side are situated the tympanic membranes with which are associated groups of chordotonal sensilla and which together form the acoustic receptors. Ventrally, a short detensor muscle functions to bend the rim and relax tension in the tympanum. In the living animal this muscle is contracted during singing. It thus probably functions to avoid self-inflicted damage caused by the high intensity of the tymbal sounds (60). In female cicadas fully developed tympanal organs are present, but tymbals are not.

In addition to the tymbal mechanism itself, two other structures may affect the calls produced by male cicadas. Often the tymbal membrane is partly concealed by a forward projecting fold of cuticle on each side of the abdomen. The size and development of these tymbal covers are characteristic for different genera and higher categories of cicadas. Also a similar rigid cuticular fold, the operculum (one on each side of the body), projects backwards ventrally, from the metathorax and extends back under the abdomen. The shape and size of these opercula vary greatly in different genera, but they are always closely adpressed to the ventral surface of the abdomen when at rest. During singing, the abdomen may be raised to increase the gap between the opercula and the abdomen (89).

CALL STRUCTURE The songs of cicadas consist of trains of pulses or clicks produced by rhythmic contraction of the tymbal muscles (34, 59, 60, 88, 90). In some species the two tymbals may operate in synchrony, though probably in most they regularly alternate (59, 60, 89, 94). Each contraction and relaxation of a tymbal may result in two separate pulses of sound: an in-click and an out-click. The in- and out-clicks may vary greatly in amplitude, depending on the form of buckling of the tymbal (60). Also, contraction of the tymbal tensor muscle may change the amplitude, especially of the in-click, and thus may change the pulse structure of a call.

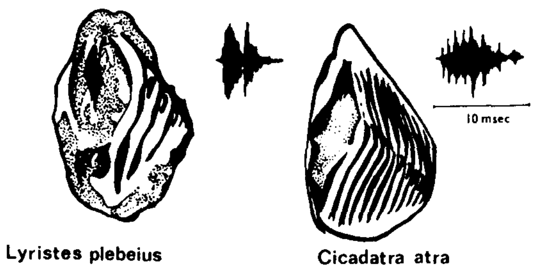

Figure 1 Diagrammatic views of right male tymbals and oscillograph records (to same scale) of single cycles of tymbal activity in the cicadas *Lyristes plebeius* and *Cicadatra atra*. After Popov (59).

Pringle (60) originally suggested from his studies of *Platypleura* species in Sri Lanka that cicada tymbal muscles were myogenic: that is, they respond to their own previous cycles of contraction without the intervention of separate motor nervous stimulation, in the same way as insect indirect flight muscles. Such a system would explain the very high rates of pulse repetition frequency found in the calls of many species. However, other workers have shown that the tymbal muscles of other cicadas are not myogenic but are neurogenic, requiring separate nervous stimulation between each cycle of contraction (59, 89). Recent reinvestigation (45) has confirmed a myogenic (asynchronous) tymbal muscle in *Platypleura capitata*, as originally suggested by Pringle (60). However, it now seems that most species of cicadas have neurogenic (or synchronous) tymbal muscles (89, 94). In such insects, pulse repetition frequencies may be increased by the buckling properties of the tymbal (59, 64).

In many cicadas, including *Cicada* and *Lyristes* species, the tymbal consists of a large, sclerotized distal area and a few lightly sclerotized ribs proximally (Figure 1). In such species, contraction and relaxation of the tymbal muscle result in two separate sound pulses—thought to be due to a single in-click and a single out-click (60). In other cicadas, such as species of *Cicadatra* and *Tibicina*, the tymbal has a smaller, sclerotized distal region and a highly developed proximal region with a number of strongly sclerotized ribs (Figure 1). When the tymbal muscle contracts in these species, a series of discrete and rapidly reproduced pulses are produced by the successive contractions of different ribs. Up to six separate sound pulses have been recorded from one contraction of a tymbal muscle in *Cicadatra atra* (59). In *Magicicada cassini* ten to twelve pulses may result from a single muscle contraction (64). Thus in species in which such mechanisms operate, rapid rates of pulse repetition may be achieved that mimic true myogenic systems. The assumption that the two pulses of sound produced by a single cycle of tymbal action in many cicadas are necessarily due to separate in- and out-clicks has been questioned (72). It is suggested that, at least in *Cystosoma saundersii*, the typical two pulses both result from the inward buckling phase: the first by buckling of rib 1 and the second by the combined buckling of ribs 2–4. The out-click is strongly damped and results in no clearly recognizable sound pulse. This may be more generally true also of other species.

Cicada calls are often of high intensity and have been recorded as audible to the human ear over distances of at least a mile in tropical forests (54). The high intensity of such signals is very largely due to the paired abdominal air sacs, which in any particular species are tuned to resonate at or near to the natural frequency of vibration of the tymbal (60). The basic sound frequency of cicada calls is thus primarily due to a combination of tymbal structure and air sac resonance. Most species have characteristic sound frequencies between 4 and 7 kHz (60), but in at least one remarkable species from Australia, *Cystosoma saundersii*, the sound frequency is concentrated at and below 1 kHz (88, 89). This insect is known as the bladder cicada because of the greatly enlarged abdomen, which includes the large air sacs necessary to resonate at such a low frequency. The auditory receptors of cicadas are tuned to the carrier frequency of their own species calls (93). The closely related *Magicicada septendecim* and *M. cassini* have very different peaks of sensitivity corresponding to the different carrier frequencies of their calls (70).

Cicada calls consist generally of modulated trains of pulses that are determined by patterning of motor input to the tymbal mechanisms. In addition, in many species a secondary modulation is imposed on the call by vertical movements of the abdomen (89), which result in opening and closing of the cavity formed between the thoracic opercula and the abdomen. This superimposed secondary modulation is well illustrated in the European *Lyristes plebeius* (22).

Another factor that may lead to distinct differences in the calls of cicadas is the nature of the tuning of the resonant air sacs. In most species where complex pulses of sound are produced, the air sacs are broadly tuned over a wide range of frequencies. Here, discrete pulses are clearly audible and the resonance of the air sacs is strongly damped (60). In some other species the air sacs are narrowly tuned to the natural frequency of the tymbal, and damping is low. The result is that the calls consist of coherent pulses modulated at the natural frequency of the tymbal. Such pure tone calls have now been identified in at least three species (53, 92, 94). A comparison of the calls of two closely related species of *Magicicada* showed that in *M. cassini* the song consists of discrete and complex pulses of sound corresponding to the buckling of individual tymbal ribs. However, in *M. septendecim* the call is a modulated pure tone, not divided into pulses, at a peak frequency of 1.3 kHz (95). Superficially, the tymbal structure of the two species is similar, but in *M. septendecim* the tymbal ribs are less rigid so that the buckling of each may be coupled to the phase of oscillation of the abdominal air sacs. The morphologically similar structures of these two species result in very different sound emissions.

Thus a combination of tymbal structure, resonant air sacs, and abdominal movements is responsible for the amazing varieties of calls that have been described for different cicada species (Figure 2). Despite the dominance of the tymbal mechanism among cicadas, frictional mechanisms are also known in several unrelated species. Most involve alary-thoracic systems of stridulation and "wing-clapping" (10, 11, 24), though no detailed analyses of recorded calls are known to me.

Leafhoppers (Cicadellidae), Planthoppers (Delphacidae), and Other Smaller Auchenorrhyncha

Until the 1940s it was widely believed that among the Auchenorrhyncha only the Cicadidae were capable of sound production; indeed, early classifications

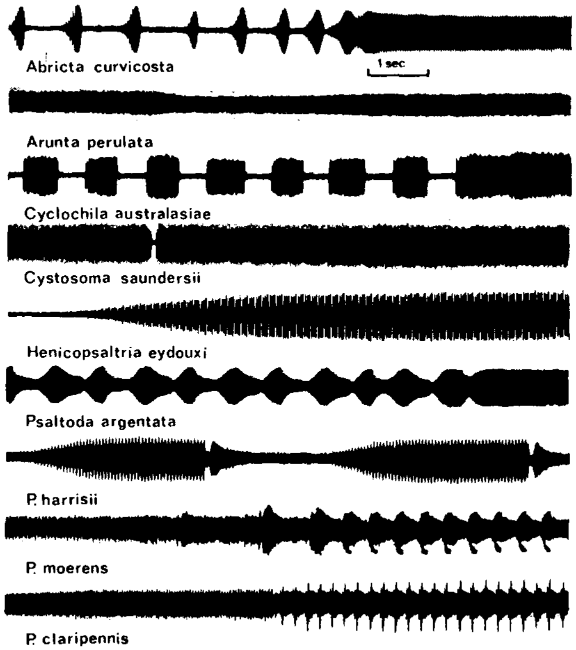

Figure 2 Oscillograms (all to same scale) of male calling songs of nine species of cicadas from Australia. After Young (90) and Young & Josephson (94).

separated the cicadas from other families on this basis. Ossiannilsson (55, 56) was the first to demonstrate unequivocally that species from a wide range of families, including the Delphacidae of the Fulgoroidea, the Cercopidae of the Cercopoidea, and the Cicadellidae and Membracidae of the Cicadelloidea, possess mechanisms similar in structure to the tymbal systems of the Cicadidae (Cicadoidea). Also, using simple techniques of recording and analysis, he was able to demonstrate that many species produce low intensity acoustic signals.

Since these pioneering publications, few other studies on the mechanisms of sound production in any of these insects have been published (68, 73), though more authors have recorded and analyzed the calls of different species (59, 16–21, 37–43, 52, 65, 67, 69, 75–84). Thus the following account of the mechanism is largely based on the findings of Ossiannilsson (56).

SOUND-PRODUCING MECHANISM In males of all species examined, a mechanism exists that is morphologically similar to that of the cicada tymbal. In many species, specialized and often striated areas of cuticle that are located dorsolaterally on either side of the first abdominal segment have been identified as tymbals. Internally, a pair of muscles [termed I advm$_{\text{I}}$ (56)] were identified as homologous to the tymbal muscles of cicadas. Other specialized muscles associated with the mechanism were found attached to large internal skeletal phragmata or apodemes associated with the metathorax and the first two segments of the abdomen. The development of these apodemes differs in different genera, and detailed features may often be diagnostic of species. Species of Delphacidae lack an obvious tymbal but possess similar musculature and the homologue of a tymbal muscle. Ossiannilsson suggested that vibration of the tymbal muscle would produce energy for sound production. Several other dorsoventral muscles are associated with the mechanism, and Ossiannilsson suggested that they modify the sound-producing properties of the tymbal, in the same manner as does the tymbal tensor muscle of cicadas (60). Unlike the cicadas, the females of most species studied have a similar, but less specialized, sound-producing mechanism. Also unlike the larger cicadas, none of the smaller species possess tuned air sacs, so that the whole system is highly damped. Detailed physiological investigations have yet to be made and would certainly be difficult with such small insects.

ACOUSTIC SIGNALS AND MEDIUM OF TRANSMISSION Studies following the early work of Ossiannilsson mostly assumed that calls are transmitted primarily through air and attempted to record them using sensitive microphones enclosed in elaborate soundproof chambers. Ossiannilsson himself suggested that the calls of small Auchenorrhyncha might be transmitted via the substrate, but this was not conclusively demonstrated until Ichikawa and his colleagues published a series of elegant studies on *Nilaparvata lugens*, the brown planthhopper (37–41). Using a gramophone crystal cartridge as a transducer, signals from a virgin female planthopper were detected in the rice plant on which the insect was resting. Virgin males were shown to respond to these vibratory signals by producing their own signals only when they were on a surface acoustically continuous with that from which the female was calling. This was usually either on the same plant or on a separate plant that was in physical contact with the one on which the female was calling. Playbacks of recorded calls have shown that both males and females detect the sounds as substrate-transmitted signals (16–18, 37, 38, 40, 41). Studies of other species have confirmed the importance of acoustic signals transmitted through the substrate, which is normally part of a host plant. No unequivocal demonstration of the significance of aerial signals in these insects is known to me.

Calls of leafhoppers and planthoppers usually consist of trains of pulses, sometimes in complex groups, with characteristic patterns of amplitude modulation and reproduced at consistent rates of repetition (9, 15–21, 37–43, 75–82). Thus they frequently resemble calls of cicadas in oscillograph analyses (Figure 3).

In females of some species where either there is no obvious tymbal mechanism or it is greatly reduced, sound production is accompanied by obvious dorsoventral vibrations of the whole abdomen (17, 37, 40); normally, however, this never results in contact with, and percussion of, the substrate. The vibrations appear to be transmitted to the plant through the tarsi and also sometimes through the inserted feeding stylets. The discrete damped pulses of sound so produced may perhaps indicate that some, as yet unidentified, click mechanism may be involved.

Male calls are usually much more complicated than those of females of the same species. In most species, pulses are grouped into complex, species-specific temporal patterns. Few measurements have been made, but pulse

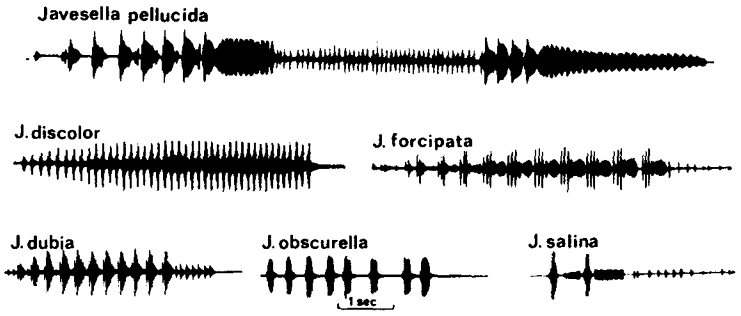

Figure 3 Oscillograms (all to same scale) of male calling songs of six species of *Javesella* from Europe. After de Vrijer (84).

repetition frequencies up to 220 per sec have been recorded for *Oncopsis avellanae* (Cicadellidae) (20, 21).

Little information is available about sound production in leafhoppers and planthoppers, but it is assumed that the tymbal mechanism is responsible for the production of the patterned calls and that these are transferred to the substrate through the legs. Even less is known about the reception of the signals by other individuals. Many groups of chordotonal sensilla are known to exist in the legs and bodies of insects. Any of these might function as specialized substrate-vibration detectors.

ACOUSTIC BEHAVIOR

Sound signals, like all other types of animal signals, may function in a variety of behavioral contexts. Different authors have devised a variety of classifications applicable to insect acoustic signals (2, 35, 36, 48). Most of these depend on a detailed understanding of the behavior of the species being studied, and this is lacking for most Homoptera. It should also be remembered that however dominant acoustic signalling may be in the behavior of any species, it is unlikely to be the only system that is important for a full understanding of complex behavior patterns. Thus, other signalling systems must also be considered.

Alexander (2) published one of the most useful classifications of known or suspected functions of acoustic signals in arthropods. He divided acoustic signals into nine categories, the last two of which were primarily concerned with eusocial species and are therefore of little significance when considering the Homoptera. Most authors have also clearly differentiated between interspecific (extraspecific) and intraspecific signals. The acoustic behavior of Homoptera is considered here under the following simplified series of categories, after Alexander (2): (*a*) disturbance and alarm, (*b*) calling (pair forming and aggregation), (*c*) aggression, (*d*) courtship and copulation.

Disturbance and Alarm

The category of disturbance and alarm includes acoustic signals that act in an interspecific context and generally are thought to have a predator-repelling function. In general, sound signals with such a function are relatively nonspecific emissions. Most cicadas when disturbed or handled produce characteristic and loud sounds that are widely thought to deter predators, though little conclusive evidence is available. Males of the North American cicada *Diceroprocta apache* were more readily preyed upon by the grasshopper mouse, *Onchomys torridus*, when experimentally silenced than when able to produce their normal disturbance or alarm call (74). Also it has been suggested that the very high sound levels of chorusing cicadas may have, in part, an antipredator function. Males of two or three species of *Magicidada* frequently form dense chorusing aggregations in North America. Field observations suggest that predatory birds avoid areas of highest sound intensity, thus contributing to the selective value of such chorusing behavior (71).

Among the smaller Auchenorrhyncha many species have been recorded as producing disturbance sounds or "calls of distress" (56), though no experimental studies have been made with predators.

Calling

Calling behavior includes pair forming and aggregation. It is surprising that despite the attention given to the calls themselves and to the mechanisms of sound production in cicadas, few conclusive field studies on the function of male songs have been published. In the case of the 17-yr cicadas, *Magicicada septendecim* and *M. cassini*, calling males were caged on small trees in the field and males and females were found to be attracted to the calls of their own species but not to those of the other (3, 4). The calling songs of these species resulted in aggregation of chorusing males, to which females were attracted for mating. Males of the Australian cicada *Cystosoma saundersii* also aggregate in chorusing groups on small bushes (23). Experimental male choruses with manipulated densities about twelve times greater than usually found naturally were established in the field. Greater numbers of both males and females were found to be attracted to the louder and denser choruses. Many other cicada species do not show the same aggregative responses and therefore do not form chorusing groups. In these species, females appear to be attracted to the vicinity of individual singing males (1, 22).

In the smaller Auchenorrhyncha, calls of males of most species appear to have the function of pair forming and bringing the sexes together, though it is not always clear over what distance they function (6, 49, 51, 65). In addition, in many species of Delphacidae and Cicadellidae, where adequate studies have been made, females also produce acoustic signals that alternate with those of the male and serve to bring the sexes into close proximity (5, 9, 15–19, 37–43, 65) (Figure 4).

In the acoustic repertoires of cicadas, leafhoppers, and planthoppers, the signals that may be categorized as calling songs generally show the greatest specificity and differentiation between species.

In addition to the specificity of the signals themselves, calling insects may use characteristic sites in their habitats from which to call. For many smaller species the host plant provides the major environmental feature, so that substrate-transmitted signals are probably normally confined in nature to the host plants of a particular species. No field-recording studies of leafhoppers or planthoppers are known to me. The larger cicadas are usually polyphagous, and individual adults may feed on a wide variety of plants. Characteristic physical

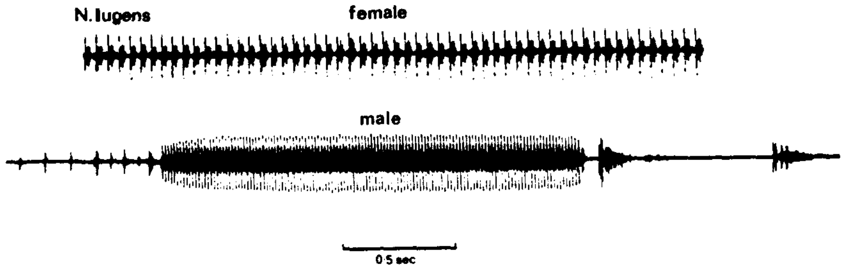

Figure 4 Oscillograms (to same scale) of male and female calling signals of brown planthopper, *Nilaparvata lugens*, from the Philippines. From Claridge et al (16), with permission from the Linnean Society of London.

sites, such as particular parts of trees or plants (22) or even rocks and stones (28), may be species diagnostic.

Aggression

Aggressive behavior involves signals that have the function of establishing dominance and of spacing out singing insects. Such signals have been widely studied in the Orthoptera but are less well known in the Homoptera. Among the non-chorusing Cicadidae, singing males of many species appear to space themselves out (1), and aggressive interactions have been observed between individuals in the field (22). Even in the aggregating species *Cystosoma saundersii*, repulsion between males, when in close proximity, has been noted. Playback of male calling songs to calling males in the field showed that at high sound intensities the insects would stop calling and move away. However, active aggression was not observed (23).

Among the smaller Auchenorrhyncha, various workers have identified distinct calls produced in male-male interactions (20, 39, 56). Males of *Nilaparvata lugens* kept together for several days after the adult ecdysis showed aggressive behavior towards each other and produced distinctive calls that differed from the normal calling song (39). However, in no species is the significance, if any, of such behavior understood.

Courtship and Copulation

Courtship and copulatory behavior involves signals with a variety of potential functions, particularly timing of insemination, facilitation of insemination, and pair maintenance (2). Among the Homoptera little is known of such close range signals. Some authors have classified calls as courtship signals when they are probably better categorized as calling signals (20). However, there is probably no sharp division between the two categories in many smaller species. True courtship calls have been recorded for the leafhopper *Amrasca devastans* (65).

Males of both *Magicicada septendecim* and *M. cassini* each produce two distinct and different courtship calls when in close proximity to females (3, 4). Though the exact function of these calls is uncertain, they undoubtedly play a role in successful copulation. In *Cystosoma saundersii*, females fly to male choruses and alight within 0.5 m of a singing male. They then seem to produce a pheromone that is dispersed by wing flicking. The male approaches and mating may take place, apparently without any courtship song (23). The possible role of pheromones has not been investigated in other cicadas, but there is no evidence that chemical signals are important among leafhoppers (65). Similarly, visual signals are probably important at close range in many cicadas (1, 3) and have been clearly demonstrated in the leafhopper *Amrasca devastans* (65).

TAXONOMY AND EVOLUTION

Here I am concerned not with higher classification and phylogeny but rather with species problems and the role of acoustic signals in speciation. The Auchenorrhyncha are abundant herbivores in most terrestrial environments. Many show great host-plant specificity, and species identification may be very difficult because of relatively slight morphological differences. Many species are important pests and vectors of plant diseases, so that a precise understanding of the specific status and genetic interrelationships between populations may be very important.

Species Problems

Most insects reproduce bisexually and have specific behavior mechanisms that serve to bring together males and females of the same species for mating, i.e. species recognition signals (58). In addition they prevent or reduce the possibilities of interspecific matings, resulting in species isolation. Several authors have emphasized the need to study the role of such pair-forming signals for our recognition of biological species (2, 3, 14, 15, 21). In the Auchenorrhyncha, it is clear that both in the large cicadas and in the smaller leafhoppers and planthoppers, pair-forming signals are principally acoustic.

In morphological descriptions of species of cicadas, the detailed structure of the tymbal and its sclerotized ribs is now usually given (e.g. 25, 29). Similarly, leafhopper and planthopper species are increasingly separated by taxonomists on the basis of detailed differences of the internal apodemes associated with the sound-producing mechanism. However, the significance of apodeme differences between closely related species is not understood, and no attempt has been made to correlate such structures with call characteristics. Indeed, at present, no group is sufficiently well known for such an attempt to be made.

CICADIDAE As long ago as 1929, Myers (54) remarked that "Every cicada with which we are familiar may be recognized with certainty by its song." Recent studies confirm this for sympatric species (59, 60, 88, 90), though allopatric species may not be so clearly differentiated in calls (28). The classic studies of Alexander & Moore (3, 4) on the periodical cicadas of North America showed, largely on the basis of song differences, that the complex consisted of three 13-yr species and three 17-yr species, where previously only one or two had been recognized. Similarly, the calls of species of *Cicada* in Portugal have been helpful in identifying biological species (12). A series of studies on the amazingly diverse cicada fauna of New Zealand have used analyses of acoustic signals (24, 25, 28–30). One of the largest and most abundant of New Zealand species, *Melampsalta cingulata,* consists of two very similar sibling species separated by call structure and aspects of their ecology (24).

The major features of the tymbal and associated features of the sound-producing system, together with the structure of the calls themselves, have been used as characters in the classification of cicadas (11, 30, 54). However, there appears to be no correlation between the physiology of the mechanism employed and the classification within the family (89). Even between very closely related species the nature of the calls may be fundamentally different (95).

DELPHACIDAE Among planthoppers, early studies showed clear differences in sound patterns between related species (56, 75), and detailed analyses of acoustic signals have been used recently to clarify specific status in several genera. In *Muellerianella,* Booij (9) studied populations from different parts of northern and western Europe. On the basis of acoustic analyses, hybridization experiments, and morphological studies, three distinct, but closely related species, were recognized. Similarly, in an as yet largely unpublished study, Vrijer (84) has demonstrated clear acoustic differences between the European species of *Javesella* (Figure 3). Also, Strübing & Hasse (82) have described acoustic differences between *J. pellucida* and the allopatric *J. azorica.* Males and females of each of the three common planthopper pests of rice in Japan, *Nilaparvata lugens, Laodelphax striatellus,* and *Sogatella furcifera,* have very distinct calls that serve to prevent interspecific matings (41). Populations that are attributed morphologically to *N. lugens* and that feed and reproduce on the grass *Leersia hexandra* differ significantly in the pulse repetition frequencies of calls of both sexes from those of sympatric populations that feed on rice (*Oryza* species) and its cultivars in the Philippines (18) (Figure 5). These differences are responsible for the lack of hybridization between the populations in the field. The two host-associated populations must therefore be regarded as distinct sibling species.

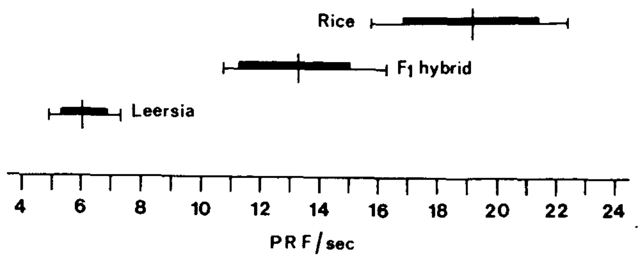

Figure 5 Pulse repetition frequencies (PRF) per second for female calling signals of two species of *Nilaparvata,* morphologically attributable to *N. lugens,* associated with rice and *Leersia hexandra* from the Philippines (Luzon) and F_1 hybrids between them. Vertical lines represent population means; thick horizontal lines, one standard deviation on either side of the means; and thin horizontal lines, the total range of individual means for each sample. After Claridge et al (18).

CICADELLIDAE Following the pioneering studies of Ossiannilsson (55, 56), in which many leafhopper calls were described, several authors have used acoustic signals in studies of difficult genera. In an outstanding series of studies, Strübing and her colleagues used acoustic data to clarify species problems in the very difficult genus *Euscelis* (76, 77, 79–81, 83). Similar studies have been valuable in the genus *Empoasca* (69) and have clearly separated sibling species of *Macrosteles* (62) and of *Oncopsis* (20, 21). Measures of pulse repetition frequencies of male calls of *Oncopsis* have been used in attempts to quantify interspecific differences and to assess variation within populations and species (21). The vectors of tungro virus disease of rice in tropical Asia, *Nephotettix virescens* and *N. nigropictus,* pose some difficulties in identification. In many areas, morphologically intermediate individuals occur commonly in field samples. These have been regarded as naturally occurring, interspecific hybrids (63). The calls of each species are quite distinct (15, 42, 43, 96). Calls of laboratory-produced hybrids are variable and intermediate between the parental species (Figure 6) (15, 96). Recordings of field-captured "intermediates" are not of the hybrid type but belong either to one or the other species (96). There is no evidence for true field hybridization between the species, but clearly some of the morphological characters previously used to separate them are not truly diagnostic.

Speciation

Biological species are characterized by distinct species recognition signals (58), which in addition may function as species-isolating mechanisms. Thus the process of speciation essentially consists of the evolution of distinct species recognition signals in different populations of what was previously one species. Such divergence of signals must be sufficient to reduce the possibilities of hybridization between the new species. In this review I shall not discuss current

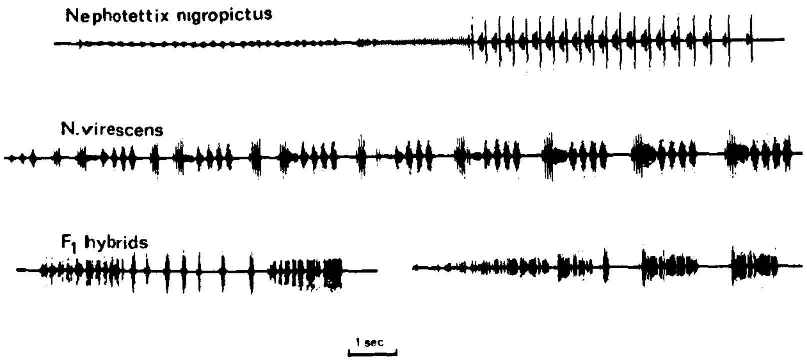

Figure 6 Oscillograms (to same scale) of parts of male calls of *Nephotettix nigropictus* and *N. virescens*, and two different individual hybrids between them. From Claridge (15), with permission of the Commonwealth Institute of Entomology.

controversies concerning the nature of speciation and the necessity, or otherwise, of an allopatric phase in the process (16–18, 22a, 31, 44, 58, 86). However, a major obstacle to the advancement of speciation theory at present is the paucity of experimental evidence for the evolution of species-isolating mechanisms. As established above, in the Homoptera Auchenorrhyncha, acoustic signals play a dominant and often all important role in pair formation and in species recognition. Acoustic signals have a particular practical advantage in studies of variation, since they are easily recorded and quantified from oscillographic analyses (15).

Few studies have been made of acoustic species-recognition signals, either in terms of individual variation within populations or of geographical variation between allopatric populations. It is well established that at any one locality the calls of sympatric cicadas are very distinct. Detailed analyses have not been made, but superficial comparisons of calls of populations of *Lyristes plebeius* and *Cicada orni* from southern France with those from parts of southern USSR showed no indication of obvious geographical variation (22). Further studies are required.

The smaller Auchenorrhyncha are more amenable to experimentation than cicadas, because many species are easily reared in the laboratory. Booij has investigated variation in the calls of two species of *Muellerianella, M. fairmairei* and *M. brevipennis,* in western Europe (9). Significant differences in some quantitative characters of the calls were found between populations of the same species. Claridge et al (16, 19) studied variation in male calls of populations of *Nilaparvata lugens* from nineteen different localities throughout southern and southeast Asia and northern Australasia. The pulse repetition frequency of male calls was measured under standard conditions for samples from each population, and significant differences were found between many of them. In particular, populations from northern Australia have higher pulse repetition frequencies than those from other regions (Figure 7). Difficulties were found in hybridizing insects from Australia with those from other regions, such as the Philippines. Males that were successful in such inter-population crosses were found, when recorded, to have pulse repetition frequencies significantly different from the mean of their own population in the direction of the mean for male calls from the population from which the female was derived (17). Successful crosses resulted in apparently normal F_1 and F_2 hybrids with no obvious reduction in fertility or sex ratio abnormalities. Thus the populations differ primarily in quantitative characteristics of male calls, which appear to be important in sexual communication. Recordings of F_1 and F_2 hybrid male calls gave intermediate pulse repetition frequencies, thus demonstrating a high degree of heritability in the call differences and suggesting a polygenic system of inheritance (16). Similarly, there is some geographical variation of calls in the green leafhoppers *Nephotettix virescens* and *N. nigropictus* in different parts of Asia (96). Thus it may be concluded that there is evidence for the evolutionary divergence of species recognition calls in allopatric populations of small Auchenorrhyncha, where suitable investigations have been made.

Sympatric host-associated populations, which are morphologically attributable to *N. lugens* in the Philippines, are separate biological species, which differ in pulse repetition frequencies of male and female calls (see above). Playback of prerecorded male and female calls to males and females of each population showed that each responded significantly more often to its own call than to that of the other, thus further demonstrating the communicative function of differences in pulse repetition frequency. Laboratory crosses between the

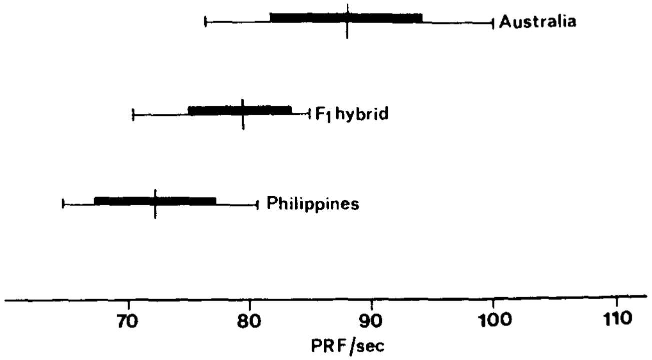

Figure 7 Pulse repetition frequencies (PRF) per second for male calls of the brown planthopper, *N. lugens*, from rice, populations from Australia (Queensland) and the Philippines (Luzon), and F_1 hybrids between them. Conventions as in Figure 5. After Claridge et al (16).

two populations showed little obvious reduction in fertility of F_1 or F_2 hybrids, but calls of both male and female hybrids were intermediate in pulse repetition frequencies between the two parentals (18) (Figure 5).

From these results it is clear that geographical variation in acoustic signals does occur and that divergence in such signals between populations may take place in advance of other obvious genetic differentiation. It is not possible to decide by what speciation process the two host-associated sibling species, presently both called *N. lugens,* arose. However, there is no evidence to warrant the tempting assumption that a sympatric process was responsible.

In the current controversies about the significance of sympatric diversification of host-specific populations of insect herbivores and parasites, the Auchenorrhyncha provide a particularly good group for investigation. If true sympatric host races exist as intermediate stages in sympatric speciation, it should be possible to detect them in this group, because of the relative ease with which acoustic recognition signals may be analyzed.

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