

Acoustic Signals, Species and Speciation in Auchenorrhyncha: A Historical Review

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Males of Cicadidae have been known since classical times to produce loud noises. These are usually species specific and function in mate finding and courtship. It is little more than fifty years since we first recognised that all other families of Auchenorrhyncha have the potential to produce sounds, albeit of very low intensity, by a diversity of tymbal-like mechanisms (Ossiannilsson, 1949). Frej Ossiannilsson had the simplest of technologies available both to record and analyse any low intensity sounds that he heard, but he did demonstrate that all species studied have an apparent mechanism to produce acoustic signals, and he heard and recorded many. We now know that smaller hoppers communicate primarily by transmitting acoustic signals through the substrate on which they live – generally parts of living green plants (Claridge, 1985). Recent digital systems both of recording and analysis are revolutionising acoustic studies on these insects.

Some form of the biological species concept (Mayr, 1942) is most useful for analysing diversity in most groups of insects. Such species are characterised by more or less complete reproductive isolation between them, maintained by species isolating barriers (Coyn and Orr, 2004). Of these, pre-mating barriers are of the greatest evolutionary significance and are more or less equivalent to the specific mate recognition systems of Paterson (1985). In all known groups of Auchenorrhyncha these are characterised by signals that are primarily acoustic and therefore relatively easy to record and to manipulate. Also it is then possible to play back prerecorded signals in experimental procedures. The classic studies by Alexander and Moore (1962) on the periodical cicadas of USA, *Magicicada*, first showed the presence of more biological species than had been previously recognised of those well studied insects and play-back experiments demonstrated the isolating functions of specific male calls. Many other cicada species have since been recognised mainly on a basis of song differences. Since the discovery that substrate transmitted vibratory signals are produced by other Auchenorrhyncha, similar increased diversity of species has been shown in most families. Also play-back experiments have shown the isolating function of acoustic signals in some well studied examples (Claridge, 1985).

A major revolution in thinking about species and speciation over the past twenty years has been a result of the development of molecular genetic technologies. For example it is now possible to study gene flow in natural populations at very fine levels. Such studies clearly show that many distinct sympatric biological species do show low levels of genetic exchange without losing the integrity by which we recognise them. Mallet (1995), with some other geneticists, has suggested that this level of gene flow is incompatible with the biological species concept and therefore has advocated yet another new species concept – the genotypic cluster concept. What the new data really show is the significance of natural selection in maintaining species characters despite low levels of hybridisation and thus gene flow. Reproductive isolation need not be absolute in order to maintain co-existing biological species.

Theories of allopatric speciation, which require at least some period of spatial or geographic isolation of incipient species populations, have dominated evolutionary thinking since mid 20thC. Contrary ideas of sympatric speciation where there is no requirement for such spatial isolation (Bush, 1975) are equally old and now widely supported. The relatively new realization that natural selection may maintain distinct species in the face of gene flow may resolve these old controversies? There is strong evidence of both apparent sympatric host race formation (Wood, 1993) and also of geographical variation in pre-mating acoustic isolating barriers (Claridge, 1993) among Auchenorrhyncha. These insects provide excellent material to pursue these ideas.

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An Ancient Symbiont of Auchenorrhyncha from the Bacterial Phylum *Bacteroidetes*

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Several insect groups have obligate, vertically transmitted bacterial symbionts that provision hosts with nutrients limiting in the diet (Buchner 1965). Some of these bacteria have been shown to descend from ancient infections of ancestral hosts. Many groups within the Auchenorrhyncha including representatives of Cicadidae, several subfamilies of Cicadellidae, Membracidae, Cercopoidea, and Fulgoroidea are hosts to a distinct clade of bacterial symbionts, which inhabit specialized bacteriomes of their hosts (Moran et al., in press). This newly described symbiont lineage belongs to the phylum Bacteroidetes. It corresponds to the “a-symbiont” of Mueller (1962), Buchner (1965) and other authors, although some confusion is associated with that designation in the literature. Among previously studied bacteria, this new taxon is most closely related to the genus *Blattabacterium* consisting of symbionts of cockroaches. Analyses of 16S rRNA genes indicate that the phylogeny of the Bacteroidetes symbiont is completely congruent with the phylogeny of insect hosts as currently resolved, based on published studies. Certain groups, such as Delphacidae and Flatidae and some leafhoppers, lack the symbiont, probably due to secondary loss, as first proposed by Mueller (1962). Two species of Peloridiidae (Coleorrhyncha) were found to lack this symbiont taxon, although other bacterial sequences, probably representing symbionts, were obtained.

The distribution and phylogenetics of this symbiont taxon are most readily interpreted as supporting the ancient acquisition of a symbiont by a shared ancestor of these insects. Thus, the results are consistent with a monophyletic Auchenorrhyncha. Alternative interpretations of current evidence are that some or all Fulgoroidea acquired a closely related symbiont independently or that a single colonization occurred in the ancestor of all Hemiptera followed by loss of the symbiont in the hemipteran sister group of Fulgoroidea. As visualized in a species of spittlebug (Cercopidae), the symbionts have extraordinarily large cells with elongate shape, often more than 50 microns in length; *in situ* hybridizations verified that these correspond to the phylum Bacteroidetes. All of the host insects also harbor at least one additional obligate symbiont, the phylogenetic affiliation of which varies among insect host groups. For example, in most Cicadellinae the second symbiont is *Baumannia cicadellicola*, a member of the *Gammaproteobacteria* (Moran et al. 2003).

Limited genomic sequencing of this symbiont from *Homalodisca coagulata* indicate that it has a small genome and retains a number of pathways for the biosynthesis of essential amino acids (N. A. Moran, DongYing Wu, J. Eisen, unpublished data). Thus, this symbiont is mostly likely involved in host nutrition and may have been an important element in the evolution of the sap-feeding lifestyles of auchenorrhynchan groups.

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