Overview of the Phylogeny, Taxonomy and Diversity of the Leafhopper (Hemiptera: Auchenorrhyncha: Cicadomorpha: Membracoidea:Cicadellidae) Vectors of Plant Pathogens

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ABSTRACT

Comprising~20,000 described species, leafhoppers (Cicadellidae) are the largest family of sap-sucking herbivores and comprise the largest number of known vectors of plant pathogens of any insect family. Although recent studies of tropical faunas indicate that the vast majority of extant species remain to be discovered, availability of new cybertaxonomic tools is enabling newly trained taxonomists to increase the rate of species discovery. Phylogenetic relationships among leafhoppers remain largely unexplored, but recent published phylogenies based on morphological and molecular data have begun to elucidate the phylogenetic status and relationships of previously recognized tribes and subfamilies. As a result of such studies, several changes to the higher classification have been proposed, including changes to the concepts of subfamilies Cicadellinae, Delocephalinae and Megophthalminae, the groups comprising the majority of known vector species. Taking newly available phylogenetic information into account may help focus the ongoing search for competent vectors on the groups most closely related to known vector species. New molecular phylogenetic and functional genomic tools and techniques may facilitate more rapid and extensive surveys of the microbiota associated with non-pest leafhoppers and promote more comprehensive approaches to the study of the evolution of leafhopper-pathogen-plant associations.

Keywords: Homoptera, phylogeny, taxonomy, evolution, endosymbiont, bacteria, Mollicutes, virus, *Xylella*

INTRODUCTION

Leafhoppers (Cicadellidae) are the largest family of the insect order Hemiptera and

the most diverse family of sap-sucking herbivores. They are distributed worldwide, from tropical rainforests to arctic tundra and from sea level to >4,000 meters elevation and may be found feeding on nearly all major groups of vascular plants. Beginning with their first appearance during the lower Cretaceous [35], the evolution of leafhoppers has been closely tied with that of their vascular plant hosts and, as is becoming increasingly clear, various endosymbiotic and pathogenic microbes [9, 43, 55, 64]. Unfortunately, the vast majority of leafhopper species are known only from a few museum specimens, often from a single locality. Little is known of the ecology of most species, including their feeding preferences and competence as potential vectors of plant pathogens. Host plant data are available for less than 10% of known species and many of the available records represent incidental collections that have not been confirmed by detailed study of feeding behavior. Although basic knowledge of leafhopper taxonomy and ecology is increasing steadily, ecological data for most species will remain scarce for the foreseeable future. Thus, strategies are needed that allow predictions about ecological characteristics to be made based on data available for the few species that have been studied in detail and their inferred relationships to other, less well studied species. Only about 1% of known leafhopper species have been shown to be capable of transmitting plant pathogens but this probably reflects the still very poor state of knowledge of leafhopper-host plant-pathogen associations. The number of species that are actual or potential vectors is likely to be much larger than the ~200 currently documented. Indeed, vectors have not yet been identified for the great majority of plant pathogens thought to require an insect vector. Nevertheless, the fact that competent vectors are clustered among a few taxonomic groups suggests that at least some of the traits associated with vector competence are phylogenetically conservative. Phylogenetic analysis therefore represents a tool for discovery of new or potential leafhopper vectors. Some evolutionarily conservative traits, such as preferential feeding on particular vascular fluids (phloem vs. xylem) and associated morphological modifications allow predictions to be made regarding the competence of various leafhopper species as vectors for particular kinds of pathogens. An improved understanding of leafhopper phylogeny may facilitate the development of models that predict disease outbreaks based on the presence and abundance of particular leafhopper species and higher taxa in agroecosystems. In this paper, I summarize current knowledge of the phylogeny and biodiversity of leafhoppers, review recent changes to the higher classification, examine the distribution of known vectors and the pathogens

vectored among leafhopper lineages, and discuss the implications of recent phylogenetic results for the study of pathogen-vector associations. Detailed lists of leafhopper species known to be vectors and their associated pathogens have been published by Nielson [57], Maramorosch and Harris [51], Harris [39], Redak *et al*. [59], Weintraub and Beanland[69],Weintraub[68] and Ammar *et al*. [2], but new vector species continue to be discovered [1].

Known diversity

The number of valid, described species of Cicadellidae presently stands at ~20,000. These species are included in ~2,400 currently valid genera. Over the past 60 years, cicadellid taxonomists have described an average of 201 new species per year (Fig. 1). Discovery and description of new species increased steadily in the post-WWII period and reached its peak in the 1970s and early 80s but fell precipitously thereafter due to the retirement of nearly all of the most prolific leafhopper taxonomists, mostly in the USA and Europe (Blocker, DeLong, Freytag, Knight, Kramer, Linnavuori, Nielson, Oman and Young). Unfortunately, these individuals were not replaced by new leafhopper experts and, although a few of them trained graduate students, almost none of the students succeeded in obtaining employment as taxonomists. Following a lull during the 1990s, leafhopper species discovery has increased slowly but steadily over the past decade and again exceeded the 60-year average for species described per year in 2010 and 2011, the most recent years for which complete data are available. Three major factors account for this recent trend and suggest that leafhopper species discovery will continue to increase dramatically in the coming decades.

First, thanks to recent increases in support for basic science in several countries, especially Brazil and China, newly invigorated cicadellid systematics research programs have emerged and many new students are being trained in leafhopper taxonomy. Indeed, two large laboratories in China have accounted for 133 (54%) of the 247 papers published on leafhopper taxonomy over the past 5 years. If such training programs can be sustained and if even a few of the trainees are able to obtain full-time employment as systematists, then we may be on the verge of a new golden age of leafhopper systematics.

Second, recent bioinventory projects in previously undersampled biodiversity hotspots worldwide have yielded enormous numbers of new specimens, many representing new species and higher taxa. Some such projects have employed

previously underutilized sampling methods such as insecticidal fogging of forest canopies and vacuuming in grasslands. Study of such samples indicates that 90% or more of the tropical species of Cicadellidae remain unnamed [20, 41]. Recent taxonomic revisionary studies based on this newly collected material [11, 12, 15, 17, 18, 19, 49, 50] have increased numbers of species in previously known tropical genera by 50-94% in addition to erecting many new genera. Because large backlogs of samples from the tropics remain unstudied and vast areas remain unsampled, the species represented in these recent studies probably represent only a small fraction of global leafhopper biodiversity.

Finally, increased adoption of cybertaxonomic methods that streamline the process of describing species and publishing revisionary studies will likely accelerate species discovery as well as facilitate efficient storage and retrieval of large amounts of taxonomic information via relational databases and web applications [17, 26, 71]. The availability of such labor saving tools and a well-trained workforce of early-career scientists should provide the momentum needed to complete the task of documenting the world leafhopper fauna. Indeed, the tremendous diversity of the world fauna demands that new more efficient approaches to species discovery and synthesis be applied by leafhopper systematists. If taxonomists continue to describe species at present rates, barring a dramatic increase in the number of active leafhopper taxonomists, several more centuries of work will be required to completely document the extant world fauna. Given present rates of habitat fragmentation and destruction, many leafhopper species are undoubtedly being driven to extinction each year, most without our even being aware of their existence.

Leafhopper phylogeny

Knowledge of phylogenetic relationships of leafhoppers has improved substantially over the past 20 years but remains highly incomplete. The vast majority of leafhopper taxa have never been included in an explicit phylogenetic analysis. Most published phylogenetic studies have focused on relationships among major lineages [12, 23, 24, 25, 29, 34, 47, 62, 76, 77] rather than among species within a single genus [10, 21, 22, 66] and some of the latter have been based on intuitive assessments of character evolution rather than explicit cladistic analysis [33, 36, 70]. DNA sequence data, representing only a handful of gene regions, have been incorporated into only a few species-level phylogenetic analyses of Cicadellidae [21, 22, 29]. Such molecular data are crucial for species-level

phylogenetics of leafhoppers because the morphological differences among species within a single genus are often subtle, shape-based, and difficult to encode in a character matrix.

Phylogenetic analyses based on morphological and molecular data strongly support the monophyly of superfamily Membracoidea[6, 23, 34], the group comprising leafhoppers and treehoppers. However, current best estimates of the phylogeny of this group (Fig. 2a) indicate that the family Cicadellidae is paraphyletic with respect to a lineage comprising the three recognized families of treehoppers (Aetalionidae, Melizoderidae and Membracidae). The treehopper lineage is derived from within a lineage of leafhoppers mostly comprising species with short crowns and facial ocelli, including Idiocerinae,Macropsinae and Megophthalminae (sensulato, including Agalliini), which include many vectors of phloem-borne plant pathogenic viruses and phytoplasmas.

Another major lineage recovered with strong branch support by combined analysis of morphological and molecular data includes Deltocephalinae (sensulato), the concept of which was recently expanded [77, 78] to include ten other groups treated as separate subfamilies in the most recent published world catalogue (Table 1), plus a few tribes previously included in other subfamilies [58].

The same analysis supported Young's [72] restricted definition of the sharpshooter subfamily Cicadellinae, but indicated a close relationship between this group and three other subfamilies, Evacanthinae, Mileewinae, and Typhlocybinae. A more detailed analysis of relationships within Cicadellinae based on morphological and molecular data and including nearly all genera of Proconiini and representatives of all genus groups of Cicadellini recognized by Young [62, 72, 73, 74] indicates that neither of the two tribes recognized by Young is monophyletic. The *Oncometopia* genus group, included by Young in Proconiini, was recovered as a distinct lineage separate from other proconiines and Cicadellini was paraphyletic with respect to both groups [62].

Recent and ongoing analyses have begun to explore finer-scale relationships within a few other cicadellid lineages (subfamilies) identified by the broader prior analyses [7, 12, 76, 77] but, because of the high diversity of the group, many aspects of membracoid phylogeny remain poorly studied. Comprehensive morphology-based phylogenetic analyses of relationships among genera within tribes have so far been performed for only five of the 130 tribes of leafhoppers [47, 52, 62, 75]. Other genus-level analyses of leafhoppers have sampled primarily within the faunas of particular regions and/or are not comprehensive [7, 12, 16, 29, 32, 44, 46, 48]. Species-level phylogenetic relationships have

been explored within only a few genera [5, 10, 18, 21, 22, 36, 49, 63, 66].

Recent changes in the higher classification of Cicadellidae

Although many aspects of the phylogeny of leafhoppers and related membracoids remain poorly resolved, strong support for certain groupings of genera in published phylogenies has prompted several recent changes in the higher classification of leafhoppers. In the most recent comprehensive world leafhopper checklist, Oman *et al*. [58] proposed a provisional higher classification that recognized 40 subfamilies and 121 tribes of Cicadellidae (Table 1). This classification retained many of the elements proposed by Evans [28] in his comprehensive review of the world fauna, but also included nine subfamilies and 47 tribes described more recently as a result of improved knowledge of tropical faunas. Subsequent to the 1985 cut-off date for Oman *et al.* [58], an additional new subfamily and 11 new tribes have been proposed [31, 78]. To better reflect hypothesized phylogenetic relationships, substantial reductions in the number of subfamilies have been proposed recently [13, 14, 77], so only 25 cicadellid subfamilies are recognized currently (Table 1).

Among the major changes to the classification proposed recently are the synonymy of ten groups recognized as separate subfamilies by Oman *et al.* [58] with Deltocephalinae and the transfer of some tribes previously placed in other subfamilies (Cicadellinae, Nirvaninae, Nioniinae) to Deltocephalinae [77]. Other proposed changes include the treatment of Agalliini as a tribe of Megophthalminae rather than as a separate subfamily, and placement of Makilingiini and Tinteromini as tribes of Mileewinae rather than as separate subfamilies. Additional subfamily synonymies are likely to be proposed in the near future, given ongoing phylogenetic studies. For example, recent analyses [62]suggest that Phereurhininae and Signoretiinae are derived from within Cicadellidae (sensu Young) and that Idiocerinaeand Eurymelinaeare closely related with the former having apparently given rise to the latter [23, 48].

One change possibly warranted by the phylogenetic results that has, nevertheless, not been proposed is the treatment of Cicadellidae and Membracidae as synonyms (yielding "Membracidae, sensulato" because Membracidae is the older name), despite strong evidence that the former is paraphyletic with respect to the latter. Cicadellidae has been retained as a paraphyletic taxon because it is well defined morphologically, is a well known group among entomologists, and a strategy for reclassifying the families of Membracoidea so that each represents a monophyetic group and is not unnecessarily

confusing (e.g., resulting in a proliferation of small families or a lumping of well known groups) is not yet apparent.

Implications for the study of vector-pathogen associations

Biologists studying vector-pathogen associations have long recognized the need for phylogenetic information to inform research aimed at identifying the most likely vectors among the numerous leafhopper species usually present in agroecosystems. Until very recently, however, absence of explicit phylogenetic estimates has required that taxonomy serve as a surrogate. Published phylogenetic studies have shown that many traditionally recognized higher taxa (genera, tribes, subfamilies) are monophyletic groups (Table 1). Nevertheless, such studies have also shown that some previously recognized groups are para-or polyphyletic and this has important implications for the study of vector biology.

Examination of the current best estimate of the phylogeny of Cicadomorpha (Fig. 2a) indicates that plant pathogen vectors are distributed among several distantly related lineages of leafhoppers and treehoppers. This probably reflects the fact that searches for competent vectors have focused almost entirely on the small minority of species that occur in agroecosystems and feed on economically important plants. The widespread occurrence of known vectors among most of the major lineages of leafhoppers strongly suggests that more systematic surveys would reveal that many other members of these lineages, as well as members of related groups that have not yet been reported to include vectors, are capable of transmitting plant pathogens. Alternatively, the physiological traits associated with vector competence may be extremely labile evolutionarily, but this seems unlikely, given the complexity of such associations [2, 69].

The phylogenetic results (Fig. 2a) reveal that feeding preference (inferred for most groups based on mouthpart morphology) is conservative, but not without homoplasy. The outgroup Cicadoidea and Cercopoidea feed preferentially on xylem and some have been shown to be competent vectors of the xylem borne pathogen *Xylella fastidiosa* [59]. These two superfamilies comprise the sister group to Membracoidea. Myerslopiidae, a relict group of flightless, soil-dwelling membracoids, may also be xylem feeders, given their inflated faces, but feeding has never been observed in this group [37]. The branching sequence of the earliestdivergences in the lineage that includes Cicadellidae and the three treehopper families have not yet been resolved satisfactorily (Fig. 2a), but a most parsimonious reconstruction of feeding preference indicates that the derivation

of this lineage likely involved a shift from xylem to phloem feeding. Most major lineages of leafhoppers and treehoppers are thought to prefer to feed on phloem, the main exceptions being found in the lineage comprising Cicadellinae and Typhlocybinae. Cicadellinae sensustricto (sharpshooters) feed preferentially on xylem and Typhlocybinae (microleafhoppers) feed preferentially on mesophyll. The phylogeny revealed a close relationship between Cicadellinae and Evacanthinae. Several species of Cicadellinae are competent vectors of *Xylella fastidiosa* [59]and some members of the related Evacanthinae (tribe Pagaroniini: *Friscanus* and *Pagaronia*) have also been shown to be capable of transmitting this pathogen (Nielson 1968). Mileewinae[14]are relatively rare inhabitants of tropical forests not known to feed on economically important plants but, given their close relationship with Cicadellinae, they should be tested for competence as vectors of *Xylella*.

Detailed phylogenetic studies of Deltocephalinae, the group comprising the largest number of confirmed vector species, show that the subfamily as previously defined [58] is polyphyletic (Table 1). A substantial expansion of the concept of this subfamily was proposed recently and Deltocephalinae, in its present sense[78], is a well-supported monophyletic group. Known vectors of plant pathogenic mollicutes (phytoplasmas and spiroplasmas) and viruses are distributed among several major deltocephaline lineages including two early-diverging lineages (Acinopterini, Fieberiellini) and several more recently derived groups (e.g., Chiasmini, Deltocephalini, Macrostelini, Opsiini). The largest deltocephaline tribe, Athysanini, which includes numerous identified vectors, is highly polyphyletic, with various genera grouped together in distantly related lineages and several of these lineages include known vectors (Fig. 2b). The scattered distribution of known vectors across multiple lineages of deltocephalines suggests that many undiscovered vectors exist within this group. None of the groups currently included in Deltocephalinae that were previously placed in other subfamilies is known to include competent vector species, but failure to find vectors in these groups may have resulted in part from their not having been targeted in surveys of potential vectors because they were previously not included in one of the subfamilies known to include vector species.

Other groups of Membracoidea known to include smaller numbers of vectors of plant pathogens are Aphrodinae, Coelidiinae, Iassinae, Idiocerinae, Macropsinae, and Typhlocybinae. Aphrodinaeis sister to the lineage comprising Neocoelidiinae and Deltocephalinae. Given that both Aphrodinae and Deltocephalinae include vectors of

mollicutes and viruses, Neocoelidiinae should also be tested as potential vectors. The vast majority of neocoelidiines are restricted to the Neotropics but a few species occurring in temperate North America feed on Asteraceae and *Pinus*. Coelidiinae, a pantropical group most common in rainforests and only rarely present in agroecosystems, includes only one known vector species. Iassinae (sensulato) includes tribes Gyponini (=Scarinae) and Iassini, each of which includes one known phytoplasma vector species. These arboreal phloem feeders primarily inhabit tropical forests and savannas, and are uncommon in agroecosystems. Idiocerinae, Macropsinae, and Megophthalminae (=Agalliinae) are closely related members of a large lineage that also includes Membracidae and other treehoppers. Idiocerinae and Macropsinae are restricted to woody hosts, but many megophthalmines feed on herbaceous plants. Several members of these leafhopper subfamilies are vectors of mollicutes and/or viruses, but only one treehopper has, so far, been shown to transmit a plant pathogen (*Micrutalis malleifera*, a vector of pseudo-curly top virus [61]). Oak-feeding treehoppers have more recently been implicated via PCR screening as potential vectors of bacterial leaf scorch in oaks (*Quercus* spp.), caused by *Xylella fastidiosa*, but transmission tests have not been performed [79]. Like other members of the lineage including Idiocerinae and Megophthalminae, treehoppers are thought to feed preferentially on phloem sap, but these results indicate that they also, at least occasionally, ingest sufficient quantities of xylem to become infected with *Xylella*.

Although they are derived from within a large lineage that mostly includes the xylem-feeding sharpshooters and related groups, Typhlocybinae feed preferentially on mesophyll. However, a few species have been shown to be competent vectors of phloem borne pathogens, and this is consistent with observations of occasional phloem feeding in some species [30, 45].

Future research

Relatively few leafhopper species have been shown to be vectors of plant pathogens. These species are distributed among most of the major lineages of leafhoppers (Fig. 2), but known vectors are over-represented in the faunas of Europe, North America and Australia compared to other regions [53]. This undoubtedly reflects greater efforts to document pathogen/vector associations in the more economically developed parts of the world rather than any tendency of these regional faunas to be more efficient vectors. Greater efforts are needed in non-anthropogenic ecosystems, especially in the tropics, to

identify and characterize leafhopper-pathogen associations because some of these will ultimately spread to human-dominated landscapes asa result of anthropogenic habitat alterations and climate change. The vast majority of leafhopper species either do not feed on economically important plants and/or do not occur in large enough numbers to be considered pests. Previous work on leafhopper vectors and associated pathogens has focused primarily on species associated with crops and, to a much lesser extent, on weeds associated with crops [69].Nevertheless, vectors remain unknown for the vast majority of plant pathogens thought to require an insect vector[69]. More thorough and systematic screening would undoubtedly reveal that many, if not most, species of Cicadellidae harbor plant pathogens. Recent PCR screening has often shown this to be the case [1, 40] although only a minority of species that tested positive for pathogens in such PCR-based studies have been shown to be competent vectors. Available evidence also suggests that related pathogens tend to be associated with particular lineages of leafhopper vectors [42].

Recent molecular genomic and phylogenetic studies of leafhopper-associated bacteria have revealed that pathogens and endosymbionts are often closely related and indicate that the physiological and evolutionary mechanisms that facilitate associations between such microbes and leafhoppers are essentially the same [8, 9, 43, 55, 60]. Indeed infection of the leafhopper vector by a plant pathogen has often been shown to benefit the vector in various ways [33, 54] although negative and neutral effects have also been reported [3, 4]. In most well-studied plant pathogen- leafhopper vector associations, the leafhopper-associated pathogenic organisms require an insect vector to facilitate their spread and inhabit and multiply within cells of the insect vector, indicating a substantial degree of co-adaptation between pathogen and vector. In the most common circular, propagative associations, the pathogen must first travel from the gut to the salivary gland and traverse at least three intercellular barriers before it can be injected into the host plant by the feeding insect [69]. The complexity of such physiological co-adaptations suggests that, although the number of potential vectors is large, the number of actual vectors is much smaller.

A few well-studied model systems [56, 59] have provided tantalizing clues regarding the co-evolutionary processes involved in vector-pathogen-plant associations. More comprehensive studies are needed to elucidate the distributions of specific plant pathogens and vector competence across entire lineages of leafhoppers. Such knowledge will facilitate the development of more robust models for predicting the

vector potential of various leafhopper groups. Ultimately, it should also improve our understanding of the roles pathogenic and mutualistic microbes have played in the evolutionary diversification of leafhoppers, and vice versa.

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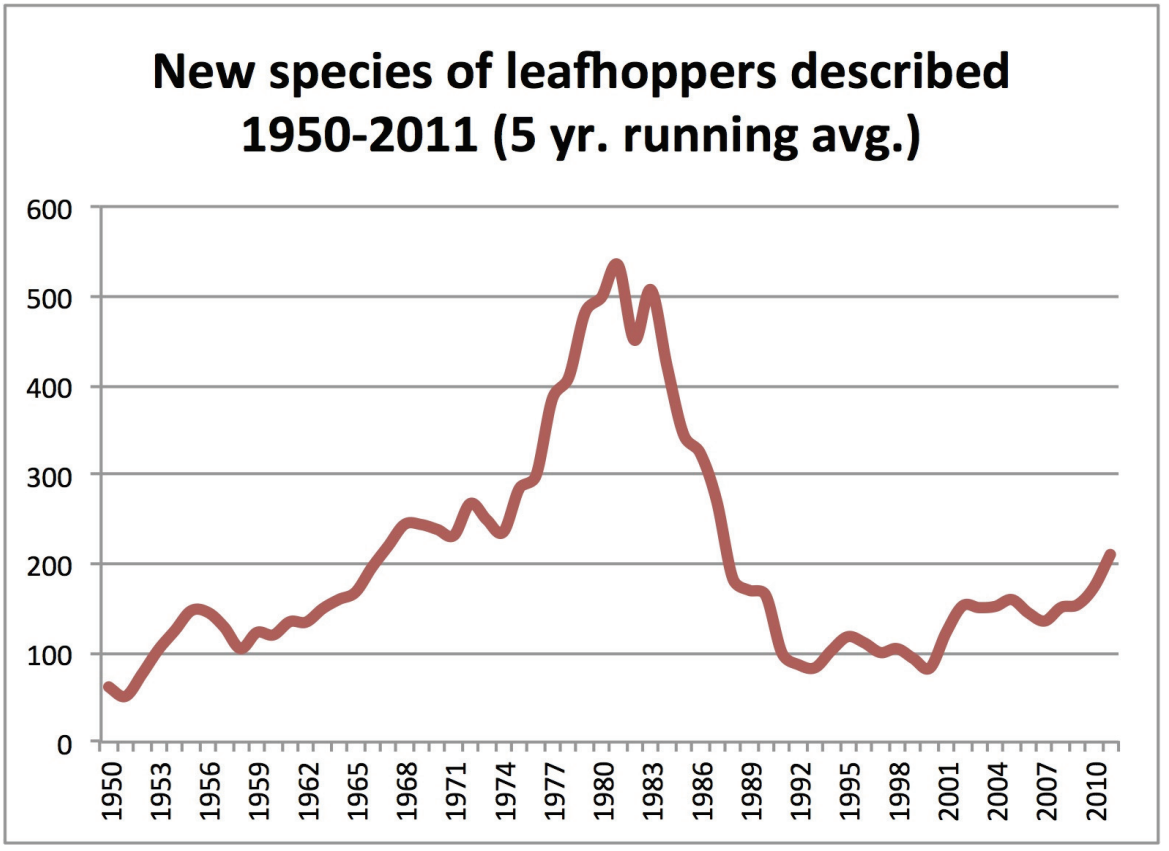


Fig. 1. Numbers of new leafhopper species described per year, 1950-2011, plotted as five-year running averages.

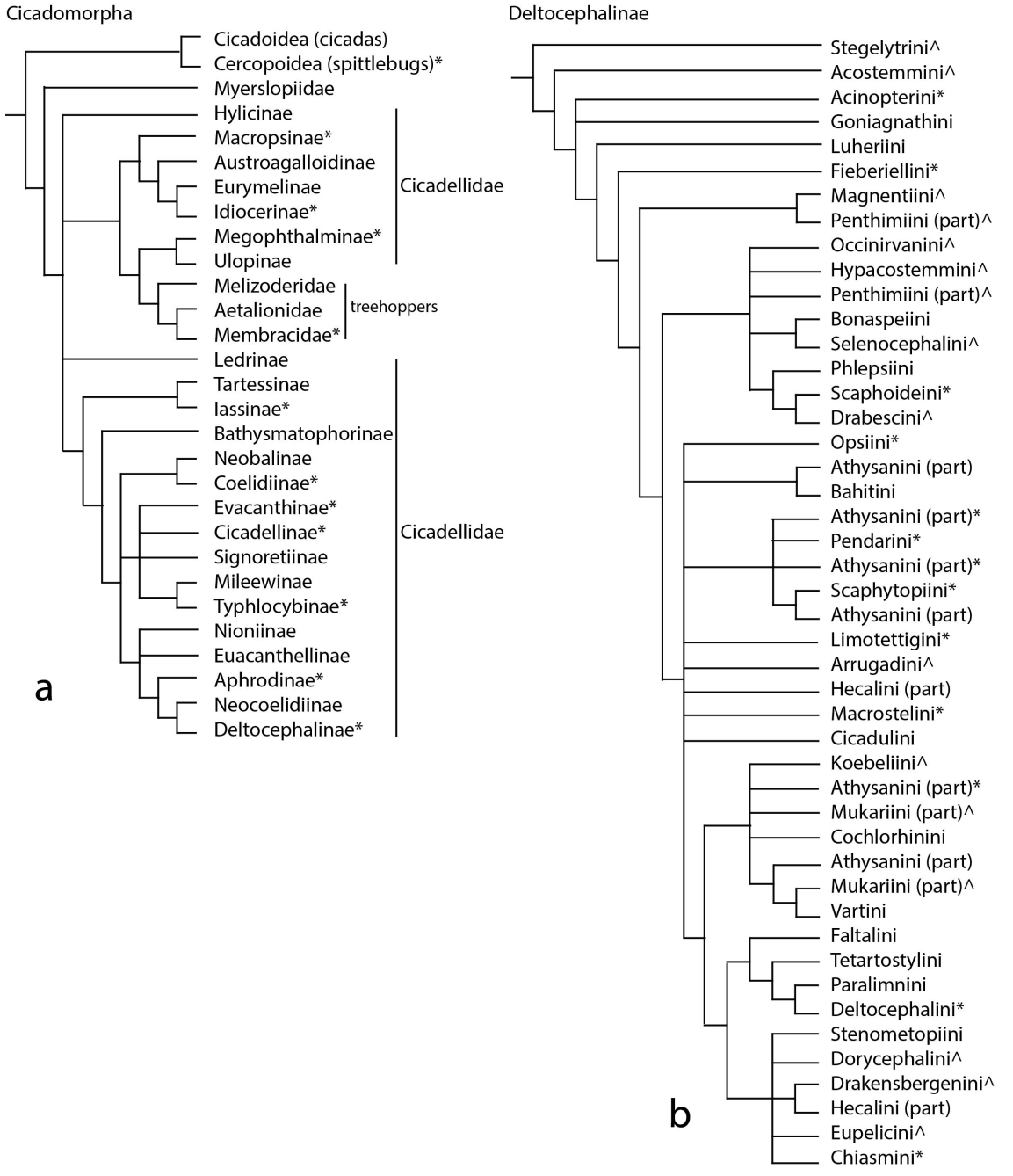


Fig. 2. Current best estimates of the phylogeny of Membracoidea (a) and Deltocephalinae (b) based on analyses of morphological and molecular data [24, 25,78]. Poorly supported branches are collapsed into polytomies. Groups previously included in other subfamilies but added to Deltocephalinae recently are marked with ^. Groups that include one or more confirmed vector species are marked with *.

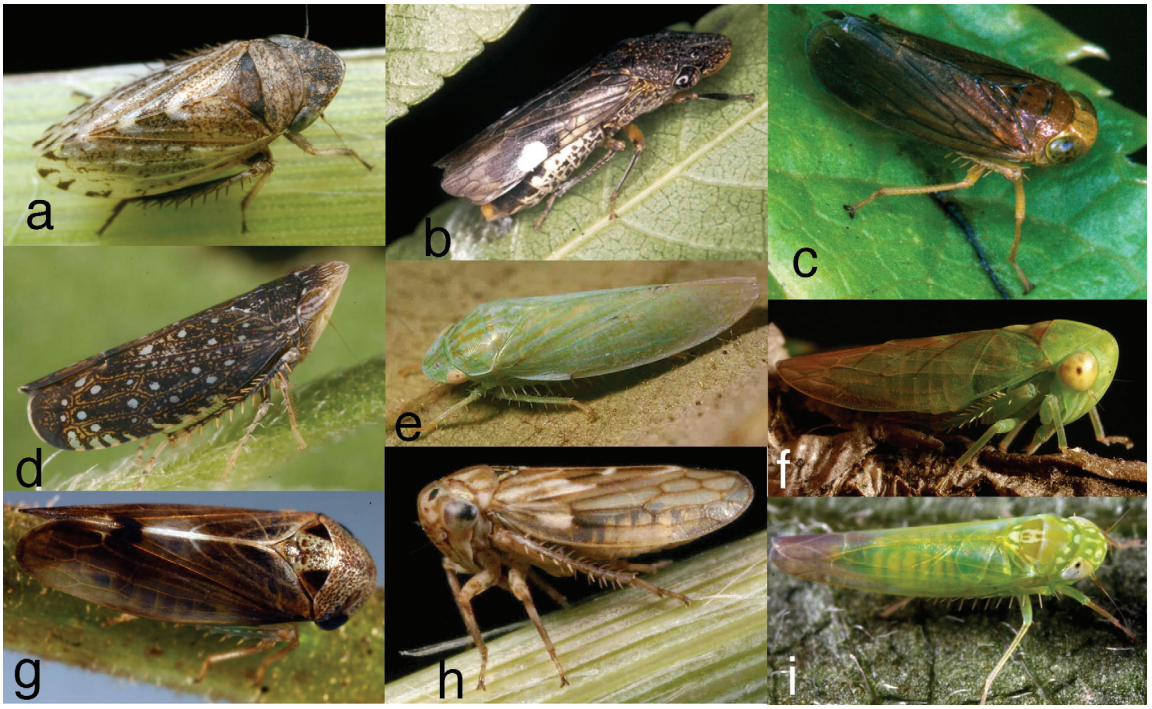


Fig.3. Representatives of the nine currently recognized leafhopper subfamilies known to include vectors of plant pathogens: a, *Anoscopusserratulae* (Aphrodinae); b, *Homalodisca vitripennis* (Cicadellinae); c, *Jikradia olitoria* (Coelidiinae); d, *Scaphytopius frontalis* (Deltocephalinae); e, *Gyponana* sp. (Iassinae); f, *Idiocerus* sp. (Idiocerinae); g, *Pediopsoides distinctus* (Macropsinae); h, *Ceratagallia agricola* (Megophthalminae); i, *Empoasca* sp. (Typhlocybinae).

Table 1. Subfamilies recognized by Oman *et al.* (1990), their current taxonomic and phylogenetic status. Feeding preferences are for most groups are inferred based on head morphology. Under vector status, presence in the group of confirmed vectors of *Xylella,* Mollicutes (phytoplasmas and spiroplasmas), and viruses are indicated by X, M, and V, respectively.

type genus	family-group sensu Oman *et al.* (1990)	current status	reference	feeding preference	vector status	phylogenetic status
Acostemma	Acostemminae	tribe of Deltocephalinae	77	phloem	?	monophyletic but relationships among genera unknown
Adelungia	Adelungiinae	tribe of Megophthalminae	13	phloem	?	phylogenetic status and relationships among genera unknown
Agallia	Agalliinae	tribe of Megophthalminae	37	phloem	M, V	probably paraphyletic ([32])
Aphrodes	Aphrodinae	subfamily (concept expanded)	38	phloem	M, V	monophyletic or paraphyletic with respect to Deltocephalinae
Arrugada	Arrugadinae	tribe of Deltocephalinae	77	phloem	?	monophyletic (monobasic)
Austroagalloides	Austroagalloidinae	subfamily	13	phloem	?	monophyletic (monobasic)
Bathysmatophorus	not included	subfamily	67	xylem	?	monophyletic but relationships among genera unknown
Bythonia	Bythoniinae	tribe of Iassinae	13	phloem	?	monophyletic (monobasic)
Cicadella	Cicadellinae	subfamily	13	xylem	X, M, V	paraphyletic with respect to Phereurhininae ([62])
Coelidia	Coelidiinae	subfamily	13	phloem	M	monophyletic but relationships among genera unknown
Deltocephalus	Deltocephalinae	subfamily (concept expanded)	77	phloem	M, V	monophyletic but many tribe and genus relationships unresolved
Drakensbergena	Drakensbergeninae	tribe of Deltocephalinae	77	phloem	?	monophyletic (monobasic)
Euacanthella	Euacanthellinae	subfamily (concept expanded)	37	phloem	?	monophyletic but relationships among genera unknown
Eupelix	Eupelicinae	tribe of Deltocephalinae	77	phloem	?	monophyletic
Eurymela	Eurymelinae	subfamily	13	phloem	?	monophyletic but relationships among genera unknown
Evacanthus	Evacanthini (Cicadellinae)	subfamily (concept expanded)	12	xylem	X	subfamily monophyletic but some tribes paraphyletic
Evansiola	Evansiolinae	tribe of Megophthalminae	37	phloem	?	monophyletic (monobasic)
Gypona	Gyponinae	tribe of Iassinae	13	phloem	M	monophyletic but relationships among genera unknown
Hylica	Hylicinae	subfamily	13	phloem	?	monophyletic but relationships among genera unknown
Iassus	Iassinae	subfamily (concept expanded)	13	phloem	M	monophyletic but relationships among genera unknown
Idiocerus	Idiocerinae	subfamily	13	phloem	M	paraphyletic with respect to Eurymelinae ([48])
Koebelia	Koebeliinae	tribe of Deltocephalinae	77	phloem	?	monophyletic but relationships among genera unknown
Ledra	Ledrinae	subfamily (concept narrowed)	44	phloem	?	monophyletic
Macropsis	Macropsinae	subfamily	13	phloem	M, V	monophyletic but relationships among genera unknown
Makilingia	Makilingiinae	tribe of Mileewinae	14	xylem	?	monophyletic (monobasic)
Megophthalmus	Megophthalminae	subfamily	13	phloem	M	possibly paraphyletic with respect to Ulopinae
Mileewa	Mileewini (Cicadellinae)	subfamily (concept expanded)	14	xylem	?	paraphyletic with respect to Typhlocybinae
Mukaria	Mukariinae	tribe of Deltocephalinae	77	phloem	?	monophyletic but relationships among genera unknown
Neobala	Neobalinae	subfamily	13	phloem	?	monophyletic but relationships among genera unknown
Neocoelidia	Neocoelidiinae	subfamily	52	phloem	?	monophyletic
Nionia	Nioniinae	subfamily (concept narrowed)	13	phloem	?	monophyletic but relationships among genera unknown
Nirvana	Nirvaninae	tribe of Evacanthinae	12	xylem	?	monophyletic but relationships among genera unknown

Paraboloponа	Paraboloponinae	tribe of Deltocephalinae	77	phloem	?	monophyletic but relationships among genera unknown
Penthimia	Penthimiinae	tribe of Deltocephalinae	77	phloem	?	polyphyletic
Phereurhinus	Phereurhininae	subfamily	13	xylem	?	monophyletic but relationships among genera unknown
Phlogis	Phlogisinae	tribe of Signoretiinae	65	xylem	?	monophyletic but relationships among genera unknown
Selenocephalus	Selenocephalinae	tribe of Deltocephalinae	77	phloem	?	polyphyletic
Signoretia	Signoretiinae	subfamily (concept expanded)	65	xylem	?	monophyletic but relationships among genera unknown
Stegelytra	Stegelytrinae	tribe of Deltocephalinae	77	phloem	?	monophyletic but relationships among genera unknown
Tartessus	Tartessinae	subfamily (concept expanded)	44	phloem	?	monophyletic but relationships among genera unknown
Tinteromus	not included	tribe of Mileewinae	14	xylem	?	newly described by Godoy & Webb ([31])
Typhlocyba	Typhlocybinae	subfamily	13	mesophyll	M	monophyletic but relationships among genera unknown
Ulopa	Ulopinae	subfamily	13	phloem	?	monophyletic but relationships among genera unknown
Xestocephalus	Xestocephalinae	tribe of Aphrodinae	13	phloem	?	monophyletic (monobasic)