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Tymbal Morphology and Co-occurrence of *Spartina* Sap-feeding Insects (Hemiptera: Auchenorrhyncha)

Stephen W. Wilson[1]

Abstract

The exoskeletal morphology of the structures associated with the production of substrate vibrations used for communication was examined for members of three guilds of sap-feeding insects on the cordgrasses *Spartina alterniflora* Loisel, *S. patens* (Aiton) Muhl., and *S. pectinata* Link (Poaceae: Chloridoidea). Measurements of the second abdominal sternite and its apodemes, the "tymbal," were made for the males of 14 species of planthoppers and 2 species of leafhoppers (Hemiptera: Auchenorrhyncha: Caliscelidae, Cicadellidae, Delphacidae, Derbidae). Morphometric comparisons revealed significant differences among the insect species on each of the cordgrass species. If tymbal morphology reflects definitive features of the vibrational signals then coexistence by the members of each sap-feeding guild is likely fostered by partitioning the "substrate resource." Tymbal morphology may be a valuable tool for determining the presence of sibling species and for providing insights regarding behavior, ecology, and evolution of these insects.

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The sap-feeding insects of three species in the grass genus *Spartina* (Poaceae: Chloridoidea), *S. alterniflora* Loisel, *S. patens* (Aiton) Muhl., and *S. pectinata* Link, have been the focus of extensive ecological and behavioral studies (e.g., Heady and Wilson 1990, Holder 1990, Heady and Denno 1991, Holder and Wilson 1992, Denno and Peterson 2000). Each of these *Spartina* species harbors a guild of monophagous or oligophagous sap-feeding planthoppers and leafhoppers (Hemiptera: Auchenorrhyncha) – four species on *S. alterniflora*, ten species on *S. patens*, and five species on *S. pectinata* (Table 1). Species of *Spartina* also harbor other sap-feeding hemipterans such as aphids and scale insects (Sternorrhyncha: Aphididae, Coccoidea), and seed bugs (*Ischnodemus* spp., Blissidae) and stink bugs (*Rhytidolomia saucia* (Say), Pentatomidae) (Johnson and Knapp 1996). As well, there are generalist leafhoppers (Cicadellidae) that occasionally feed on these grasses (Whitcomb et al. 1987). Coexistence of seven of the sap-feeding insects on *S. patens* apparently results from differences among the species in microhabitat occupancy, phenology, and body size (Denno 1980).

Substrate-borne vibrational signals can serve several functions including species recognition and mate location, recruitment to feeding locations, and predator avoidance (Cocroft and McNett 2006, Virant-Doberlet et al. 2006, Hill 2009). These signals are employed by numerous leafhopper, treehopper, and planthopper species (Cocroft 1999, Drosopolous and Claridge 2006, Zezlina and Virant-Doberlet 2007), and a cicada species (Claridge et al. 1999). During courtship, signals are produced by males then detected by females, which typically respond with a simpler signal (Ichikawa and Ishii 1974, Ichikawa 1976). The signals aid in locating potential mates, are species-specific, and serve to maintain prezygotic reproductive isolation (Inoue 1982, Heady and Denno 1991,

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Table 1. The sap-feeding Auchenorrhyncha guilds of three species of *Spartina* (Denno 1977, 1980; Holder 1990).

Taxon	*S. alterniflora*	*S. patens*	*S. pectinata*
Caliscelidae			
Aphelonema	-	*simplex* Uhler	*simplex* Uhler
Delphacidae			
Delphacodes	*penedetecta* Beamer	*detecta* (Van Duzee)	-
Megamelus	n. sp.	*lobatus* Beamer	*metzaria* Crawford
Neomegamelanus	-	*spartini* (Osborn) *elongatus* (Ball)	-
Prokelisia	*dolus* Wilson *marginata* (Van Duzee)	-	*crocea* (Van Duzee)
Tumidagena	-	*minuta* McDermott *terminalis* (Metcalf)	-
Derbidae			
Anotia	-	-	*fitchi* (Van Duzee)
Cicadellidae			
Amplicephalus	-	*simplex* (Van Duzee)	-
Destria	-	*bisignata* (Sanders & DeLong)	-
Neohecalus	-	*lineatus* (Uhler)	*lineatus* (Uhler)

Gillham and de Vrijer 1995, Langellotto and Denno 2001). Reproductive isolation has been documented for sibling species of *Enchenopa, Nilaparvata,* and *Ribautodelphax* all of which are monophagous on different host plants (Claridge 1985a,b; de Winter and Rollenhagen 1990; Claridge and deVrijer 1994; Hunt 1994; Rodriguez et al. 2004) or sibling species of *Prokelisia* which occur on the same host species (Heady and Denno 1991).

The vibrational signals are produced by rapid movements of the entire abdomen or by movement of internal abdominal exoskeletal structures collectively referred to as tymbals (Ossiannilsson 1949, Mitomi et al. 1984). The structures responsible for producing signals have not been determined in some taxa (e.g., flatid planthoppers). In delphacid planthoppers, signals are produced by tymbals ("Singapparat" or "drumming organs" of Asche (1985) and Ossiannilsson 1949) which consist of exoskeletal modifications of the metapostnotum and the tergites and sternites of the first and second abdominal segments. The morphology of these exoskeletal tymbal elements and their associated muscles have been described and illustrated for *Dicranotropis hamata* (Boheman) and briefly described for 25 additional species of delphacids, one cixiid, and one issid by Ossiannilsson (1949). Detailed descriptions and illustrations of the exoskeletal morphology and anatomy of the muscles of *Nilaparvata lugens* (Stål) were made by Mitomi et al. (1984). The exoskeletal morphology and mechanism for

sound production in *N. lugens* was described by Zhang et al. (1988). The tymbals of 36 species of delphacids were illustrated by Asche (1985) who used major structural differences in the tymbals in his phylogenetic analysis of the family.

Differences in the vibrational signals likely result from differences in tymbal exoskeleton morphology, muscular morphology, and/or neuromuscular physiology. Tymbal morphology differed significantly in four out of five species of *Prokelisia* with the greatest differences in tymbal structures between *Prokelisia marginata* (Van Duzee) and *Prokelisia dolus* Wilson, which share the same host plant, *Spartina alterniflora* (Miller and Wilson, 1999) (Table 1). These two species of *Prokelisia* produce species specific vibrational signals that serve to prevent hybridization (Heady and Denno 1991). Several species of sap-feeders that each produce vibrational signals critical for reproduction occupy the same *Spartina* host plants (Table 1). Interference in courtship behavior would be possible among species producing vibrational signals at the same time unless there are significant differences in those signals. As tymbal morphology and signal production are possibly linked, I compared the morphology of species occurring on each of the three *Spartina* species to determine if there are significant structural differences among them.

Materials and Methods

The exoskeletal morphology of the tymbals of 14 species of planthoppers and 2 species of leafhoppers was examined. Specimens were obtained from collections at the University of Central Missouri and the University of Maryland. Specimens were collected in the following localities: *Delphacodes penedetecta* Beamer, *D. detecta* (Van Duzee), *Megamelus* n. sp., *M. lobatus* Beamer, *Neomegamelanus elongatus* (Ball), *N. spartini* (Osborn), *Prokelisia dolus, P. marginata, Tumidagena minuta* McDermott, *T. terminalis* (Metcalf), and *Amplicephalus simplex* (Uhler) in Ocean Co., New Jersey; *Neohecalus lineatus* (Uhler) in Ocean Co., New Jersey and Pettis Co., Missouri; *Anotia fitchi* (Van Duzee) in Johnson Co., Missouri; *Megamelus metzaria* Crawford and *P. crocea* (Van Duzee, in Johnson Co. and Pettis Co., Missouri; *Aphelonema simplex* Uhler in Pettis Co, Missouri, and Hancock Co. and Tuscola Co., Michigan; *P. dolus* in Piaquemines Parish, Louisiana and Dauphin Island, Alabama. The abdomens of four males and one female of each species were removed and cleared in 10% potassium hydroxide for ca. 24 h, washed for 10 min in water, then placed in glycerol for examination. If tymbal morphology was difficult to discern after clearing, the specimen was stained with lignin. After examination, each abdomen was placed in a glycerol filled genitalia vial and pinned under the specimen from which it came.

There were no obvious differences among males of the different species in the morphology of the tymbal elements of the metapostnotum and first abdominal sternite. The apodemes of the second abdominal sternite were dissimilar and were the focus of description, illustration, and morphometric analyses. Females had no discernible development of any structures thus were not described, illustrated, nor measured.

Specimens were oriented so that the apodemes of the second abdominal sternite were visible in caudal view. Measurements of the apodemes were made using an ocular micrometer and included: 1) distance between the apodeme bases, 2) length of the apodemes from base to apex, 3) distance between apices of the apodemes, 4) width of the abdominal sternite, 5) depth of the middle of the abdominal sternite, and 6) depth of the abdominal sternite under the apodemes (see Miller and Wilson 1999). Morphometric differences were analyzed using one way analysis of variance (ANOVA) for each species inhabiting the same host plant. For those morphometric features found to be significantly different, pairwise comparisons of species were conducted using Tukey's Honestly Significant Difference test (Roscoe 1975).

Results

Descriptions of the tymbals of the sap-feeding guild of *Spartina alterniflora.*

Delphacodes penedetecta (Fig. 1A, Table 2). The tymbal apodemes were slender, elongate, darker than the abdominal sternum, rounded at the apices and converged toward the apices. The abdominal sternum narrowed slightly between the apodemes and the portion extending laterally from the base of each apodeme was short and sinuate on the dorsal aspect and rounded laterally.

Megamelus n. sp. (Fig. 1B, Table 2). The tymbal apodemes were slender, elongate, darker than the abdominal sternum, rounded at the apices, and sub-parallel to each other. The abdominal sternum narrowed slightly between the apodemes and the portion extending laterally from the base of each apodeme was sinuate on the dorsal aspect and rounded laterally.

Prokelisia dolus (Fig. 1C, Table 2). The tymbal apodemes were very slender, elongate, darker than the abdominal sternum, rounded at the apices, and diverged from the bases to the apices. The abdominal sternum narrowed between the apodemes and the portion extending lateral from the base of each apodeme was sinuate on the dorsal aspect and tapered laterally.

Prokelisia marginata (Fig. 1D, Table 2). The tymbal apodemes were broad and subtriangular and rounded at the apices. The position of the apodemes did not diverge towards the apices. The abdominal sternum was extremely narrow between the apodemes and the portion extending laterally from the base of the apodemes was relatively short, concave on the dorsal aspect and rounded laterally.

Descriptions of the tymbals of the sap-feeding guild of *Spartina patens.*

Delphacodes detecta (Fig. 2B, Table 3). The tymbal apodemes were moderately slender, elongate, darker than the abdominal sternum, rounded and slightly hooked at the apices and subparallel to each other. The abdominal
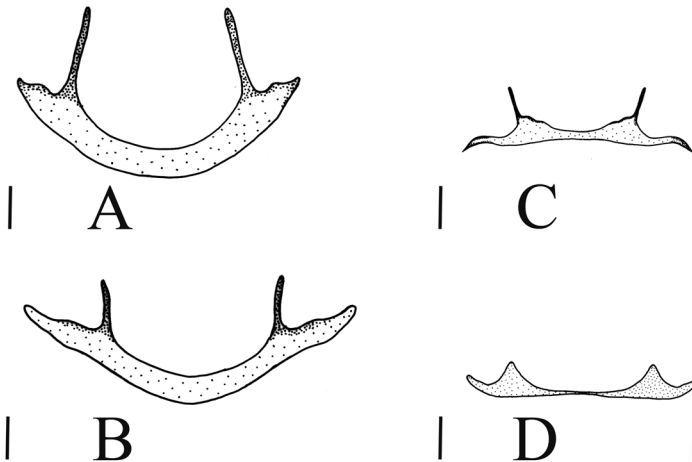

Figure. 1. Caudal view of second abdominal sternites of *Spartina alterniflora* sap-feeders. A. *Delphacodes penedetecta.* B. *Megamelus* n. sp. C. *Prokelisia dolus* D. *P. marginata.* Scales = 0.1 mm.

Table 2. Mean (± standard deviation) tymbal measurements (mm) and analysis of variance for four sap-feeders on *Spartina alterniflora* (df = 3, 15; P < 0.05).

	Apodeme				Sternum	
	bases	length	apices	width	mid depth	ap depth
Dp	0.35 ± 0.013	0.24 ± 0.014	0.34 ± 0.031	0.61 ± 0.059	0.06 ± 0.015	0.08 ± 0.023
Mn	0.36 ± 0.011	0.17 ± 0.019	0.37 ± 0.015	0.70 ± 0.012	0.05 ± 0.016	0.05 ± 0.018
Pd	0.23 ± 0.024	0.09 ± 0.037	0.29 ± 0.025	0.48 ± 0.051	0.03 ± 0.013	0.06 ± 0.013
Pm	0.26 ± 0.013	0.06 ± 0.013	0.27 ± 0.024	0.47 ± 0.037	0.02 ± 0.003	0.04 ± 0.013
F	75.145*	50.890*	14.132*	27.378*	6.961*	3.374*

Dp = D. penedetecta, Mn = Megamelus n. sp., Pd = Prokelisia dolus, Pm = Prokelisia marginata.
* = significant at P < 0.05.

sternum narrowed slightly between the apodemes and the portion extending laterally from the base of each apodeme was short and sinuate on the dorsal aspect and rounded laterally.

Megamelus lobatus (Fig. 2C, Table 3). The tymbal apodemes were slender, elongate, darker than the abdominal sternum, rounded at the apices, and diverged toward the apices. The abdominal sternum narrowed slightly between the apodemes and the portion extending laterally from the base of each apodeme was sinuate on the dorsal aspect and broadly rounded laterally.

Neomegamelanus spartini (Fig. 2E, Table 3). The tymbal apodemes were slender, elongate, darker than the abdominal sternum, rounded at the apices, and diverged slightly toward the apices. The abdominal sternum narrowed slightly between the apodemes and the portion extending laterally from the base of each apodeme was sinuate on the dorsal aspect and rounded laterally.

Neomegamelanus elongatus (Fig. 2F, Table 3). The tymbal apodemes were slender, longer than those of *N. spartini*, darker than the abdominal sternum, rounded at the apices, and subparallel to each other. The abdominal sternum narrowed significantly between the apodemes and the portion extending laterally from the base of each apodeme was convex on the dorsal aspect and rounded laterally.

Tumidagena minuta (Fig. 2G, Table 3). The tymbal apodemes were slender, very elongate, darker than the abdominal sternum, rounded at the apices, and curved slightly toward each other. The abdominal sternum narrowed strongly between the apodemes and the portion extending laterally from the base of each apodeme was concave on the dorsal aspect and rounded laterally.

Tumidagena terminalis (Fig. 2H, Table 3). The tymbal apodemes were slender, very elongate, darker than the abdominal sternum, rounded at the apices, subparallel and the apices curved sharply toward each other. The abdominal sternum narrowed slightly between the apodemes and the portion extending laterally from the base of each apodeme was sinuate on the dorsal aspect and rounded laterally.

Aphelonema simplex (Fig. 2D, Table 3). The tymbal apodemes of specimens found on *S. patens* and *S. pectinata* were very similar and were represented by strongly swollen darkend areas on the dorsal aspect of the abdominal sternum. The abdominal sternum narrowed slightly between the apodemes and the portion extending laterally from the base of each apodeme was broadly concave on the dorsal aspect and rounded laterally.

Amplicephalus simplex (Fig. 2A, Table 3). The tymbal apodemes appeared to be represented by small swollen areas near the middle of the abdominal sternum on the dorsal aspect. The abdominal sternum narrowed strongly between the apodemes and the portion extending laterally from the base of each apodeme was broadly concave on the dorsal aspect and bifurcate laterally.

Neohecalus lineatus. See Descriptions of the tymbals of the sap-feeding guild of *Spartina pectinata*, below.

Descriptions of the tymbals of the sap-feeding guild of *Spartina pectinata*.

Anotia fitchi. The male and female specimens examined did not appear to possess tymbals.

Megamelus metzaria (Fig. 3A, Table 4). The tymbal apodemes were slender, elongate, darker than the abdominal sternum, subparallel and rounded and slightly hooked at the apices. The abdominal sternum narrowed slightly between the apodemes and the portion extending laterally from the base of each apodeme was convex on the dorsal aspect and rounded laterally.
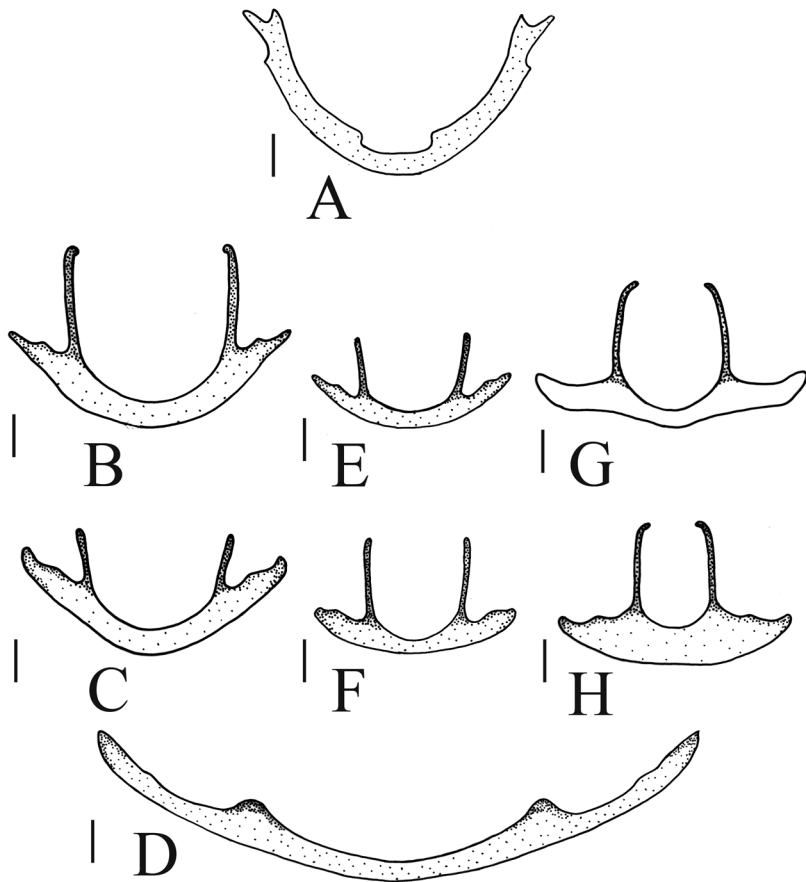
Figure 2. Caudal view of second abdominal sternites of *Spartina patens* sap-feeders. A. *Amplicephalus simplex* B. *Delphacodes detecta*. C. *Megamelus lobatus*. D. *Aphelonema simplex*. E. *Neomegamelanus spartini*. F. *N. elongatus*. G. *Tumidagena minuta*. H. *T. terminalis*. Scales = 0.1 mm.

Prokelisia crocea (Fig. 3B, Table 4). The tymbal apodemes were slender, very elongate, darker than the abdominal sternum, rounded at the apices, and converged toward the apices. The abdominal sternum narrowed strongly between the apodemes and the portion extending laterally from the base of each apodeme was sinuate on the dorsal aspect and rounded laterally.

Neohecalus lineatus (Fig. 3C, Table 4). The tymbal apodemes of specimens found on *Spartina patens* were represented by slightly swollen areas on the dorsal aspect of the abdominal sternum. The abdominal sternum narrowed between the apodemes and the portion extending dorsolaterally from the base of the apodemes was broadly concave on the dorsal aspect and narrowed apically. The tymbal apodemes from specimens found on *Spartina pectinata* were similar to those from *Spartina patens*, however, the apodemes were slightly longer.

Table 3. Mean (± standard deviation) tymbal measurements (mm) and analysis of variance for nine sap-feeders on *Spartina patens* (df = 8, 36; $P < 0.05$).

	Apodeme			Sternum		
	bases	length	apices	width	mid depth	ap depth
Dd	0.37 ± 0.025	0.27 ± 0.033	0.41 ± 0.085	0.65 ± 0.053	0.05 ± 0.018	0.07 ± 0.009
Ml	0.33 ± 0.022	0.21 ± 0.023	0.38 ± 0.036	0.62 ± 0.027	0.05 ± 0.011	0.06 ± 0.015
Ns	0.18 ± 0.006	0.14 ± 0.009	0.19 ± 0.006	0.52 ± 0.014	0.04 ± 0.001	0.05 ± 0.013
Ne	0.21 ± 0.017	0.18 ± 0.008	0.24 ± 0.030	0.42 ± 0.025	0.04 ± 0.000	0.06 ± 0.000
Tm	0.14 ± 0.019	0.15 ± 0.020	0.14 ± 0.019	0.46 ± 0.047	0.02 ± 0.009	0.07 ± 0.007
Tt	0.24 ± 0.012	0.23 ± 0.023	0.14 ± 0.036	0.50 ± 0.006	0.07 ± 0.005	0.07 ± 0.006
Aps	0.78 ± 0.013	0.04 ± 0.000	0.78 ± 0.013	1.24 ± 0.030	0.08 ± 0.000	0.08 ± 0.000
Ams	0.15 ± 0.003	0.04 ± 0.000	0.15 ± 0.003	0.75 ± 0.014	0.07 ± 0.006	0.07 ± 0.007
Nl	0.25 ± 0.016	0.03 ± 0.007	0.25 ± 0.016	0.83 ± 0.016	0.06 ± 0.017	0.07 ± 0.007
F	597.213*	103.765*	26.916*	20.718*	8.030*	1.704

Dd = *D. detecta*, Ml = *M. lobatus*, Ns = *N. spartini*, Ne = *N. elongatus*, Tm = *T. minuta*, Tt = *T. terminalis*, Aps = *Aphelonema simplex*, Ams = *Amplicephalus simplex*, Nl = *N. lineatus*.
* = significant at $P < 0.05$.

Morphometric analyses of tymbals. Analyses of the six features associated with the tymbals for the sap-feeders found on *S. alterniflora, S. patens,* and *S. pectinata* resulted in significant differences among the species on each host. All six features, distance between the apodeme bases, apodeme length, distances between the apodeme apices and sternum width, depth at the middle, and depth under the apodeme bases, were significantly different among the four species from *S. alterniflora* (Table 2). All features, except depth under the apodeme bases, were significantly different among the nine species from *S. patens* (Table 3). Four features, except sternum width and depth under the apodeme bases, were significantly different among the four species from *S. pectinata* (Table 4).

The Hutchinsonian ratio of 1.2:1 to 1.4 :1 has been used as a comparative measure of body size, mass, or length of feeding structures that would allow coexistence among species with similar niches (Hutchinson 1959, Brown 1975, Denno 1980). Comparison of the ratios of the dry body mass of *S. patens* sapfeeders was used by Denno (1980) to examine niche differentiation among those species. Following Denno (1980), I compared the apodeme lengths of the species on each of the *Spartina* species. Every one of the species on *S. alterniflora* differed from the closest species in apodeme length by a ratio ≥ 1.3:1 (Table 5, Fig. 4). Among the *S. patens* fauna, *D. detecta* differed from *M. lobatus* and all others with shorter apodeme lengths, *T. terminalis* differed from *N. elongatus* and all others with shorter apodeme lengths, *M. lobatus* differed from *T. minuta* and all others with shorter apodeme lengths, *N. elongatus* differed from *N. spartini* and the others with shorter apodeme lengths, and *T. minuta* and *N. spartini* differed from *Am. simplex* and *Ap. simplex* (Table 6, Fig. 5). Among the *S. pectinata* fauna the two delphacids, *P. crocea* and *M. metzaria* had apodeme lengths ≥ 1.3:1 compared to those of *Ap. simplex* and *N. lineatus* (Fig. 6).

Discussion

Niche differentiation via resource partitioning has been suggested as a result of competition among similar organisms for resources which can include food, nutrients, space, and mates. Numerous studies of vertebrate and invertebrate animals and plants indicate that physical and behavioral attributes of potentially competing species serve to aid in allowing coexistence. This differentiation can
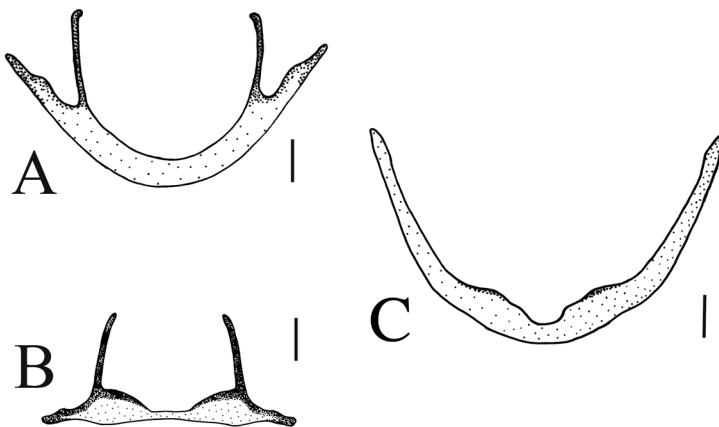

Figure 3. Caudal view of second abdominal sternites of *Spartina pectinata* sap-feeders. A. *Megamelus metzaria.* B. *Prokelisia crocea.* C. *Neohecalus lineatus.* Scales = 0.1 mm.

Table 4. Mean (± standard deviation) tymbal measurements (mm) and analysis of variance for four sap-feeders on *Spartina pectinata* (df = 3, 15; $P < 0.05$).

	Apodeme				Sternum	
	bases	length	apices	width	mid depth	ap depth
Mm	0.40 ± 0.024	0.22 ± 0.012	0.46 ± 0.026	0.74 ± 0.011	0.07 ± 0.005	0.07 ± 0.003
Pc	0.29 ± 0.014	0.27 ± 0.059	0.28 ± 0.094	0.58 ± 0.035	0.07 ± 0.013	0.08 ± 0.013
Aps	0.78 ± 0.013	0.04 ± 0.000	0.78 ± 0.013	1.24 ± 0.030	0.08 ± 0.001	0.08 ± 0.000
Nl	0.25 ± 0.016	0.03 ± 0.007	0.25 ± 0.016	0.83 ± 0.016	0.06 ± 0.017	0.07 ± 0.007
F	790.888*	65.760*	94.840*	509.880*	1.255	1.913

Mm = M. metzaria, Pc = P. crocea, Aps = Aphelonema simplex, Nl = Neohecalus lineatus.
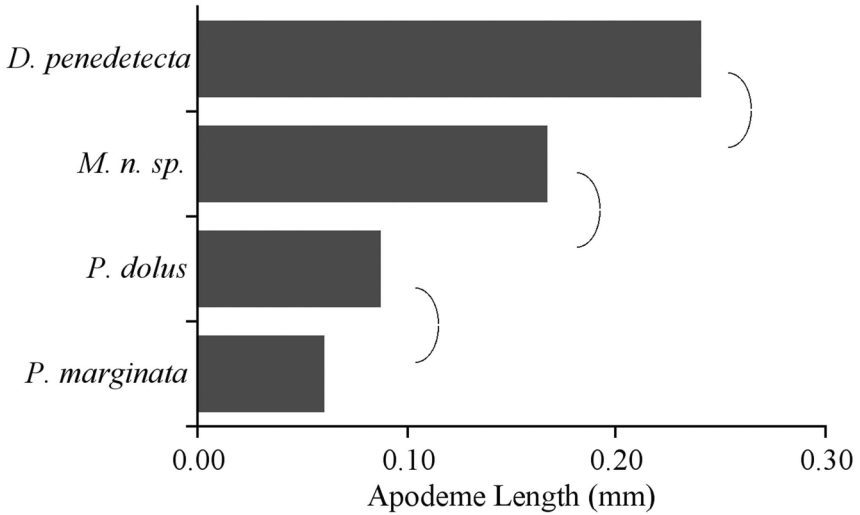* = significant at $P < 0.05$.

Figure 4. Mean tymbal apodeme lengths (mm) of *Spartina alterniflora* sap feeders. Arcs represent Hutchinsonian ratios ≥ 1.3.
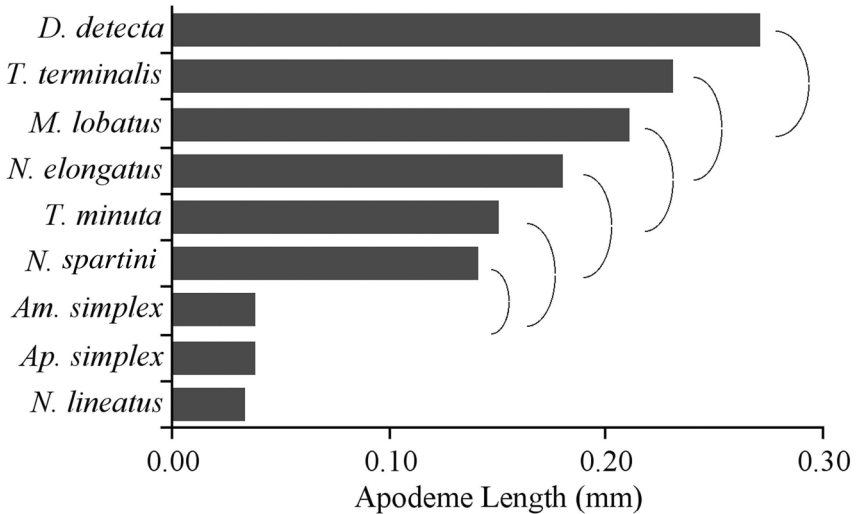

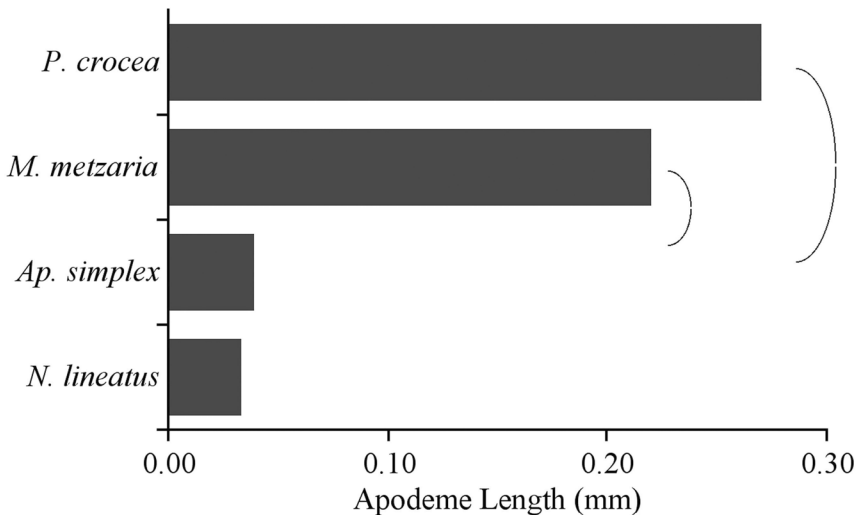Figure 5. Mean tymbal apodeme lengths (mm) of *Spartina patens* sap feeders. Arcs represent Hutchinsonian ratios ≥ 1.3.

Figure 6. Mean tymbal apodeme lengths (mm) of *Spartina pectinata* sap feeders. Arcs represent Hutchinsonian ratios ≥ 1.3.

include the partitioning of airborne sounds (Gogala and Riede 1995, Riede and Kroker 1995, Sueur 2002).

Niche differentiation among the well-studied sap-feeding guild of leaf-hoppers and planthoppers on *S. patens* centered on the stratum of the plant occupied by each species, elevation of the marsh where the hosts of each species occurred, and body size of the insects (Denno 1980). There was little difference in phenology among the species in each stratum suggesting that most of the species are likely to be reproducing during the same time of the season. Thus, it is possible that several species produce substrate-borne vibrational signals on the same plants at the same time.

In the leafhopper *Graminella nigrifrons* (Forbes), the reactions of con-specifics to vibrational signals included alternation of signals which likely resulted from inhibition upon detecting a signal (Hunt and Morton 2001). In the treehopper *Ennya chrysura* (Fairmaire), adults can produce "jamming" signals that serve to interfere with the courtship of other individuals (Miranda 2006). Artificially produced disruptive vibrational signals have been used to interfere with mating in the leafhopper *Scaphoideus titanus* Ball (Eriksson et al. 2012). A cacophony of similar signals produced by a variety of species on a plant could potentially reduce reproductive success.

Of the guilds of sap-feeding insects examined here, *S. patens* harbors the greatest number of species, possibly because the habitat in which this grass occurs suffers from less disturbance than that of *S. alterniflora* (Denno and Roderick 1990). Five of the six analyzed morphometric features were significantly different among the species and the Hutchinsonian ratios for apodeme lengths were ≥ 1.3:1 for each of the species except *T. minuta* and *N. spartini,* which occupy different strata of their host plant, and *Am. simplex* and *Ap. simplex,* which differ in their ability to colonize new hosts, and *N. lineatus,* which is rarely collected (Denno 1980).

The five species from *S. alterniflora* differed in four of the analyzed features and the Hutchinsonian ratios of apodeme lengths were ≥ 1.3:1 for all species combinations. This grass is often subject to more disturbance and is more

Table 5. Pairwise comparisons of mean tymbal measurements (mm) using Tukey's Honestly Significant Difference (*q* values) for four sap-feeders on *Spartina alterniflora* (df = 12).

| | Apodeme | | | Sternum | | |
	bases	length	apices	width	mid depth	ap depth
Dp - Mn	12.92*	16.14*	5.90*	21.82*	6.02*	4.33*
Dp - Pd	16.07*	12.89*	4.37*	23.24*	4.45*	2.87
Dp - Pm	0.69	6.65*	2.20	5.30*	2.12	3.13
Mn - Pd	3.14	3.25	1.52	1.52	1.57	1.46
Mn - Pm	13.61*	9.49*	8.09*	27.12*	3.89	1.20
Pd - Pm	16.76*	6.24*	6.57*	28.64*	2.32	0.26

Dp = D. penedetecta, Mn = Megamelus n. sp., *Pd = Prokelisia dolus, Pm = Prokelisia marginata.*
* = significant at *P* < 0.05.

Table 6. Pairwise comparisons of mean tymbal measurements (mm) using Tukey's Honestly Significant Difference (q values) for nine sap-feeders on *Spartina patens* (df = 12).

	Apodeme	Sternum				
	bases	length	apices	width	mid depth	ap depth
Dd - Ml	5.37*	6.79*	2.14	2.31	0.10	2.13
Dd - Ns	23.19*	14.07*	12.80*	9.19*	3.19	4.32
Dd - Ne	20.11*	9.62*	9.96*	15.98*	3.33	1.73
Dd - Tm	28.60*	13.21*	15.26*	12.67*	7.50*	0.86
Dd - Tt	16.81*	3.57	15.24*	10.68*	2.73	0.29
Dd - Aps	50.42*	26.05*	20.43*	39.17*	4.24	1.73
Dd - Ams	27.75*	26.05*	14.87*	6.57*	2.98	0.86
Dd - Nl	14.86*	26.77*	9.05*	12.05*	1.34	0.58
Ml - Ns	17.82*	7.28*	10.65*	6.87*	3.29	2.19
Ml - Ne	14.74*	2.83	7.81*	13.66*	3.44	0.40
Ml - Tm	23.24*	6.42*	13.11*	10.36*	7.60*	3.00
Ml - Tt	11.44*	3.22	13.09*	8.36*	2.63	2.42
Ml - Aps	55.78*	19.26*	22.58*	41.48*	4.14	3.86
Ml - Ams	22.39*	19.26*	12.73*	8.88*	2.88	3.00
Ml - Nl	9.50*	19.98*	6.91*	14.37*	1.24	2.71
Ns - Ne	3.08	4.45	2.84	6.79*	0.14	2.59
Ns - Tm	5.41*	0.86	2.46	3.49	4.31	5.18*
Ns - Tt	6.38*	10.50*	2.44	1.49	5.92*	4.61
Ns - Aps	73.61*	11.99*	33.23*	48.35*	7.44*	6.05*
Ns - Ams	4.56	11.99*	2.08	15.76*	6.17*	5.18*
Ns - Nl	8.33*	12.70*	3.75	21.24*	4.53	4.90
Ne - Tm	8.50*	3.60	5.30*	3.30	4.17	2.59
Ne - Tt	3.30	6.05*	5.28*	5.30*	6.06*	2.02
Ne - Aps	70.53*	16.44*	30.39*	55.14*	7.58*	3.46
Ne - Ams	7.65*	16.44*	4.92*	22.55*	6.32*	2.59
Ne - Nl	5.24*	17.15*	0.91	28.03*	4.67	2.30
Tm - Tt	11.80*	9.65*	0.02	1.99	10.23*	0.58

Table 6. Continued.

	Apodeme	Sternum				
	bases	length	apices	width	mid depth	ap depth
Tm - Aps	79.02*	12.84*	35.69*	51.84*	11.75*	0.86
Tm - Ams	0.85	12.84*	0.38	19.24*	10.48*	0.00
Tm - Nl	13.74*	13.56*	6.20**	24.73*	8.84*	0.29
Tt - Aps	67.23*	22.49*	35.67*	49.85*	1.52	1.44
Tt - Ams	10.95*	22.49*	0.36	17.25*	0.25	0.58
Tt - Nl	1.94	23.20*	6.18*	22.73*	1.39	0.29
Aps - Ams	78.17*	0.00	35.31*	32.60*	1.26	0.86
Aps - Nl	65.28*	0.71	29.48*	27.11*	2.91	1.15
Ams - Nl	12.89*	0.71	5.82*	5.48*	1.64	0.29

Dd = D. detecta, Ml = M. lobatus, Ns = N. spartini, Ne = N. elongatus, Tm = T. minuta, Tt = T. terminalis, Aps = Aphelonema simplex, Ams = Amplicephalus simplex, Nl = N. lineatus.
* = significant at *P* < 0.05.

variable in height than *S. patens*. The congeners, *P. dolus* and *P. marginata* exhibited the greatest amount of difference in tymbal structure compared to other members of the genus (Miller and Wilson 1996).

The four species from *S. pectinata* differed in only two of the analyzed features; Hutchinsonian ratios of apodeme lengths were $\geq$ 1.3:1 for the two delphacids, *P. crocea* and *M. metzaria* versus the caliscelid *Ap. simplex* and the cicadellid *N. lineatus*. This tallgrass prairie species is found in much smaller patches than the other *Spartina* species and is likely fed upon by more species of itinerant generalist leafhoppers (Holder 1990, Wilson et al. 1993). Further, *P. crocea* is abundant throughout the growing season in the upper portions of this relatively tall grass whereas *M. metzaria* is found at the base of the plants and is only commonly collected in the early fall (Holder and Wilson 1992). The caliscelid *Ap. simplex* and leafhopper *N. lineatus* are usually very rare. At one location, Blue Lick Natural Area, Pettis County, Missouri, both *N. lineatus* and *M. metzaria* were enormously abundant and *P. crocea* was absent (Wilson, personal observation).

Host plants provide resources for sap-feeding insects that include nutrition, water, oviposition sites, and a substrate for communication via vibrational signals. The partitioning of resources has been shown to allow coexistence of potentially competing species (Schoener 1974, McClure and Price 1975, Denno 1980). The partitioning of food resources has been related to differences in the morphology of structures associated with feeding, such as beak size in finches (Grant and Grant 2006) and proboscis length in bumblebees (Pyke 1982). Tymbal morphology likely affects the vibrational signals used to recognize conspecifics. If so, then the occurrence of several species on the same host could result in a cacophony of signals unless the "substrate resource" is partitioned in some manner. Tymbal morphology could be indicative of reproductive isolation among species and may be useful for determining sibling species as well as providing insights about behavior, ecology, and evolution in guilds of sap-feeding insects that communicate via substrate vibrations.

Acknowledgments

Literature Cited

Asche, M. 1985. Zur Phylogenie der Delphacidae (Homoptera: Cicadina: Fulgoromorpha). Marburger Entomologische Publikationen 2(1): 1–910.

Brown, J. H. 1975. Geographical ecology of desert rodents, pp. 315–341. *In:* M. L. Cody and J. M. Diamond (eds.) Ecology and evolution of communities. Belknap Press, Cambridge, Massachusetts.

Claridge, M. F. 1985a. Acoustic signals in the Homoptera: behavior, taxonomy and evolution. Annual Review of Entomology 30: 297–317.

Claridge, M. F. 1985b. Acoustic behavior of leafhoppers and planthoppers: species problems and speculation, pp. 103–125. *In:* L. R. Nault and J. G. Rodriquez (eds.). The leafhoppers and planthoppers. Wiley, New York.

Claridge, M. F., and P. W. F. de Vrijer. 1994. Reproductive behavior: the role of acoustic signals in species recognition and speciation, pp. 216–233. *In*: R. F. Denno and T. J. Perfect (eds.). Planthoppers: Their ecology and management. Chapman & Hall, Inc., New York.

Claridge, M. F., J. C. Morgan, and M. A. Moulds. 1999. Substrate-transmitted acoustic signals of the primitive cicada *Tettigarcta crinita* Distant (Hemiptera Cicadoidea, Tettigarctidae). Journal of Natural History 33: 1831–1834.

Cocroft, R. B. 1999. Offspring-parent communication in a subsocial treehopper (Hemiptera: Membracidae: *Umbonia crassicornis*). Behaviour 136: 1–21.

Cocroft, R. B., and G. D. McNett. 2006. Vibratory communication in treehoppers (Hemiptera: Membracidae), pp. 305–317. *In*: S. Drosopoulos and M. F. Claridge (eds.). Insect sounds and communication. CRC Taylor & Francis, New York. 532 p.

de Winter, A. J., and T. Rollenhagen. 1990. The importance of male and female acoustic behaviour for reproductive isolation in *Ribautodelphax* planthoppers (Homoptera: Delphacidae). Biological Journal of the Linnean Society 40: 191–206.

Denno, R. F. 1977. Comparison of the assemblages of sap-feeding insects (Homoptera-Hemiptera) inhabiting two structurally different salt marsh grasses in the genus *Spartina*. Environmental Entomology 6: 359–371.

Denno, R. F. 1980. Ecotope differentiation in a guild of sap-feeding insects on the salt marsh grass, *Spartina patens*. Ecology 61: 702–714.

Denno, R. F., and M. A. Peterson. 2000. Caught between the devil and the deep blue sea, mobile planthoppers elude natural enemies and deteriorating host plants. American Entomologist 46: 95–109.

Denno, R. F., and G. K. Roderick. 1990. Population biology of planthoppers. Annual Review of Entomology 35: 489–520.

Drosopoulos, S., and M. F. Claridge (eds.). 2006. Insect sounds and communication. CRC Taylor & Francis, New York. 532 p.

Eriksson, A., G. Anfora, A. Lucchi, F. Lanzo, M. Virant-Doberlet, and V. Mazzoni. 2012. Exploitation of insect vibrational signals reveals a new method of pest management. PloS ONE 7(3): 1–5.

Gillham, M. C., and P. W. F. de Vrijer. 1995. Patterns of variation in the acoustic calling signals of *Chloriona* planthoppers (Homoptera: Delphacidae) coexisting on the common reed *Phragmites australis*. Biological Journal of the Linnean Society 54: 245–269.

Gogala, M., and K. Riede. 1995. Time sharing of song activity by cicadas in Temengor forest reserve, Hulu Perak and in Sabah, Malaysia. Malayan Nature Journal 48: 297–305.

Grant, P. R,. and B. Grant. 2006. Evolution of character displacement in Darwin's finches. Science 313: 224–226.

Heady, S. E., and R. F. Denno. 1991. Reproductive isolation in *Prokelisia* planthoppers (Homoptera: Delphacidae): acoustic differentiation and hybridization failure. Journal of Insect Behavior 4: 367–90

Heady, S. E., and S. W. Wilson. 1990. The planthopper genus *Prokelisia* (Homoptera: Delphacidae): morphology of female genitalia and copulatory behavior. Journal of the Kansas Entomological Society 63: 267–278.

Hill, P. S. M. 2009. How do animals use substrate-borne vibrations as an information source? Naturwissenschaften 96: 1355–1371.

Holder, M.D. 1990. The sap-feeding insect guild of prairie cordgrass, *Spartina pectinata*. unpubl. Masters Thesis, Central Missouri State University, Warrensburg.

Holder, M. D., and S. W. Wilson. 1992. Life history and descriptions of the immature stages of the planthopper *Prokelisia crocea* (Van Duzee) (Homoptera: Delphacidae). Journal of the New York Entomological Society 100: 491–497

Hunt, R. E. 1994. Vibrational signals associated with mating behavior of the treehopper, *Enchenopa binotata*). Journal of the New York Entomological Society 102: 266–270.

Hunt, R. E., and T. L. Morton. 2001. Regulation of chorusing in the vibrational communication system of the leafhopper *Graminella nigrifrons*. American Zoologist 41: 1222–1228.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? American Naturalist 93: 145–159.

Ichikawa, T. 1976. Mutual communication by substrate vibration in the mating behavior of planthoppers (Homoptera: Delphacidae). Applied Entomology and Zoology 11: 8–23.

Ichikawa, T., and S. Ishii. 1974. Mating signals of the brown planthopper, *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae): vibration of the substrate. Applied Entomology and Zoology 9: 196–198.

Inoue, H. 1982. Species-specific calling sounds as a reproductive isolating mechanism in *Nephotettix* spp. (Hemiptera: Cicadellidae). Applied Entomology and Zoology 17: 253–262.

Johnson, S. R., and A. K. Knapp. 1996. Impact of *Ischnodemus falicus* infestation on growth and gas exchange of *Spartina pectinata* in a northeastern Kansas tallgrass prairie. Environmental Entomology 25: 1122–1127.

Langellotto, G. A., and R. F. Denno. 2001. Benefits of dispersal in patchy environments: mate location by males of a wing-dimorphic insect. Ecology 82: 1870–1878.

McClure, M. S., and P. W. Price. 1975. Competition among sympatric *Erythroneura* leafhoppers (Homoptera: Cicadellidae) on American sycamore. Ecology 56: 1388–1397.

Miller, A., and S. W. Wilson. 1999. The planthopper genus *Prokelisia* (Homoptera: Delphacidae): Exoskeletal morphology of the tymbals. Reichenbachia 33: 37–42.

Miranda, X. 2006. Substrate-borne signal repertoire and courtship jamming by adults of *Ennya chrysura* (Hemiptera: Membracidae). Annals of the Entomological Society of America 99: 374–386.

Mitomi, M., T. Ichikawa, and H. Okamoto. 1984. Morphology and vibration-producing organ in adult rice brown planthopper *Nilaparvata lugens* (Homoptera: Delphacidae). Applied Entomology and Zoology 19: 407–17.

Ossiannilsson, F. 1949. Insect drummers. A study on the morphology and function of the sound-producing organ of Swedish Homoptera Auchenorrhyncha with notes of their sound production. Opuscula Entomologica Supplement 10: 1–145.

Pyke, G. H. 1982. Local geographic distributions of bumblebees near Crested Butte, Colorado: competition and community structure. Ecology 63: 555–573.

Riede, K., and A. Kroker. 1995. Bioacoustics and niche differentiation in two cicada species from Bornean lowland forest. Zoologischer Anzeiger 234: 43–51.

Rodriguez, R. L., L. Sullivan, and R. B. Cocroft. 2004. Vibrational communication and reproductive isolation in the *Enchenopa binotata* species complex of treehoppers. Evolution 58: 571–578.

Roscoe, J. T. 1975. Fundamental research statistics for the behavioral sciences (2nd ed.). Holt, Rinehart and Winston, Inc., New York. 483 pp.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185: 27–39.

Sueur, J. 2002. Cicada acoustic communication: potential sound partitioning in a multispecies community from Mexico (Hemiptera: Cicadomorpha: Cicadidae). Biological Journal of the Linnean Society 75: 379–394.

Virant-Doberlet, M., A.Cokl, and M. Zorovic. 2006. Use of substrate vibrations for orientation: from behaviour to physiology, pp. 81–97. *In*: S. Drosopoulos and M. F. Claridge (eds.). Insect sounds and communication. CRC Taylor & Francis, New York. 532 p.

Whitcomb, R. F., J. Kramer, J. E. Coan, and A. L. Hicks. 1987. Ecology and evolution of leafhopper-grass host relationships in North American grasslands. *In* K. F. Harris (ed.), Current topics in vector research 4: 121–178.

Wilson, S. W., J. L. Smith, and P. D. Calvert. 1993. Planthoppers of a Missouri tall-grass prairie (Homoptera: Fulgoroidea). Journal of the Kansas Entomological Society 66: 75–80.

Zezlina, I., and M. Virant-Doberlet. 2007. Vibrational communication of *Metcalfa pruinosa* (Hemiptera: Fulgoroidea: Flatidae). Annals of the Entomological Society of Amererica 100: 73–82.

Zhang, Z. T., W. Z. Korg, J. L. Gao, and T. H. Shao. 1988. Acoustic signal-producing organ of brown planthopper (BPH). International Rice Research Newsletter 13: 38–39.