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The planthopper genus *Prokelisia*: Exoskeletal morphology of the tymbals (Hemiptera: Auchenorrhyncha: Fulgoromorpha: Delphacidae)

With 2 Tables and 2 Figures

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Abstract. The exoskeletal morphology of the structures associated with the production of vibrations used for communication via the substrate was described and illustrated for the males of each of four species of *Prokelisia*. Morphometric comparisons of the second abdominal sternite and its apodemes of *P. crocea* (VAN DUZEE), *P. dolus* WILSON, *P. marginata* (VAN DUZEE), and *P. salina* (BALL) resulted in significant differences among these structures suggesting divergence in the development of different species recognition signals during the evolution of these planthoppers.

Introduction

The vibrational signals of planthoppers are produced by the rapid movement of abdominal exoskeletal structures collectively referred to as tymbals (OSSIANNILSSON 1949, MITOMI et al. 1984). As part of their courtship behavior, males produce a call which is detected via substrate vibrations by a female (ICHIKAWA & ISHII 1974, ICHIKAWA 1976) who responds with a simpler call. These species-specific calls have been shown to be crucial for maintaining prezygotic isolation (HEADY & DENNO 1991, GILLHAM & DE VRIJER 1995) and the recognition of sibling species complexes in planthoppers has been supported based on analyses of the calls (CLARIDGE 1985, HEADY & DENNO 1991). The vibrational signals of a number of species of planthoppers have been examined including species in the delphacid genera *Chloriona* (GILLHAM & DE VRIJER 1995), *Dicranotropis* (STRÜBING & ROLLENHAGEN 1988), *Javesella* (DE VRIJER 1984, 1986), *Megamelus* (OSSIANNILSSON 1949), *Muellerianella* (BOOIJ 1982, DROSOPOULOS 1985), *Nilaparvata* (CLARIDGE et al. 1985a, b, 1988; CLARIDGE & MORGAN 1993; BUTLIN 1993), *Prokelisia* (HEADY 1993, HEADY & DENNO 1991), *Ribautodelphax* (DEN BIEMAN 1986, 1988; DE WINTER 1992, 1995; DE WINTER & ROLLENHAGEN 1990), and *Struebingianella* (STRÜBING & ROLLENHAGEN 1988), the flatid genus *Ormenaria* (MOORE 1961), and cixiids in the genera *Cixius* (OSSIANNILSSON 1949) and *Oliarus* (HOCH & HOWARTH 1993). Differences in calls likely result from differences in tymbal exoskeletal morphology, muscular morphology, and/or neuromuscular physiology. The obvious anatomical differences in the tymbals of the species so far examined suggest that, in some instances, structural differences may be related to differences in calls. Although the calls of a number of planthopper species have been detailed, there has been no systematic examination of tymbal morphology in any taxon.

Planthopper tymbals ("Singapparat" or "drumming organs" of ASCHE [1985] and OSSIANNILSSON [1949]) consist of exoskeletal modifications of the metapostnotum, and the tergites and sternites of the

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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. Sexual dimorphism in tymbal morphology was considered by ASCHE (1985) as one of the synapomorphies uniting the kelisiine through delphacine delphacids. And, the structure of the generally elongate apodemes of the second abdominal sternite was a synapomorphy of the plesiodelphacine and delphacine delphacids (ASCHE 1985). The second abdominal sternite is connected to other tymbal exoskeletal elements on each side by three ventral longitudinal muscles and a lateral intersegmental muscle in *N. lugens* (MITOMI et al. 1984).

The Nearctic planthopper genus *Prokelisia* has been the model for numerous studies in systematics, ecology, and behavior. This genus includes five species: *P. carolae* WILSON, *P. crocea* (VAN DUZEE), *P. dolus* WILSON, *P. marginata* (VAN DUZEE), and *P. salina* (BALL) (WILSON 1982; HEADY & WILSON 1990). Three of the five species are sympatric over a portion of their ranges and two, *P. dolus* and *P. marginata*, are not only sympatric but also occur on the same host plant, *Spartina alterniflora* LOIS in eastern North America and *Spartina foliosa* TRINIUS along the Pacific coast of North America. *P. crocea* feeds on *S. pectinata* LINK (HOLDER & WILSON 1992) and *P. salina* is thought to feed on *S. gracilis* TRINIUS. The host of *P. carolae* is unknown.

The species-specific vibrational signals of *P. dolus* and *P. marginata* have been characterized by HEADY & DENNO (1991). Since these species-specific calls are crucial for mate recognition and successful courtship, it might be expected that the morphology of the call producing structures would differ. The focus of our study was to determine if there are differences in tymbal exoskeletal morphology among species of *Prokelisia*.

Materials and Methods

The exoskeletal morphology of the tymbals of *P. crocea, P. dolus, P. marginata*, and *P. salina* were examined; specimens of *P. carolae* were not available for study. Ten males of *P. crocea, P. dolus*, and *P. marginata* and three males of *P. salina* were dissected. Specimens used for dissection were placed in 10% potassium hydroxide for twenty-four hours, then washed for ten minutes in distilled water; the specimens were then examined, and stored, in glycerol. If after clearing the tymbal morphology was difficult to discern, the specimen was stained with lignin. Illustrations were made using a camera lucida. 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 of males were structurally dissimilar and were the focus of description, illustration, and morphometric analyses. Specimens were oriented so that the apodemes of the second abdominal sternite were visible in caudal view (Fig. 1).

Measurements of the apodemes of the second abdominal sternite were made using an ocular micrometer and included 1) the distance between the apodeme bases, 2) the length of the apodemes from base to tip, 3) the distance between the tips of the apodemes, 4) the width of the abdominal sternite, 5) the height of the middle of the abdominal sternite, and 6) the height of the abdominal sternite under the apodemes (see Fig. 1A). Morphometric differences in tymbal measurements were analyzed using analysis of variance and multiple analysis of variance. Females of each species lacked development of the apodemes of the second abdominal sternite, thus, they were not subject to analyses (Fig. 2). Collecting data for the specimens examined are provided in the following. *P. crocea*: USA: Missouri: Pettis Co., Paintbrush Prairie, ca 15 km S. Sedalia, 6 July 1990, coll. S. Wilson (10 males, 1 female). *P. dolus*: USA: Alabama: Dauphin Island, 8 December 1990, coll. S. Wilson (4 males); Louisiana: Piaquemines Parish, Rt. 23 near Boothville, 7 Dec 1990, coll. S. Wilson (6 males, 1 female). *P. marginata*: USA: New Jersey, Ocean County, Tuckerton, 28 May 1987, coll. S. Wilson (10 males, 1 female). *P. salina*:

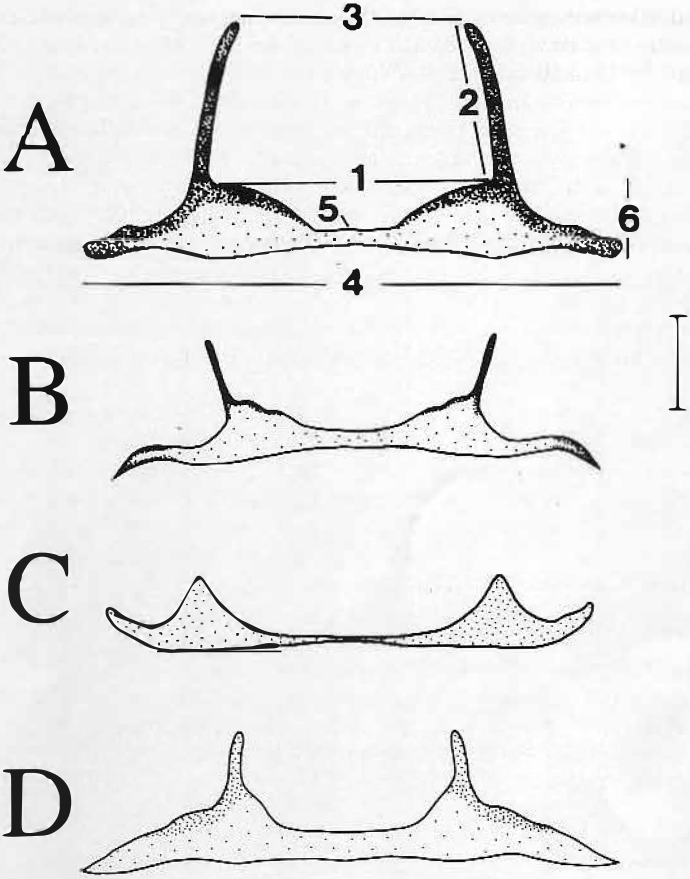

Fig. 1: Caudal view of second abdominal sternites of the males of four *Prokelisia* species (see text for explanation of measurements). A: *P. crocea*; B: *P. dolus*; C: *P. marginata*; D: *P. salina*. Scale = 0.1 mm.

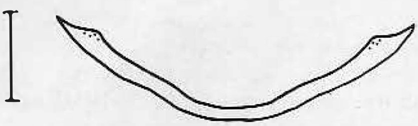

Fig. 2: Caudal view of the second abdominal sternite of a *Prokelisia crocea* female. Scale = 0.1 mm.

USA: Arizona: Cochise County, 1.5 km S. Portal, 23 June 1965, coll. J. H. Davidson, J. M. Davidson, M. A. Cazier (1 male); Florida: Franklin County, 16 km NE Eastpoint, 12 May 1975 (1 male); Wyoming: Carbon County, Saratoga Lake, 11 July 1995, coll. S. Wilson (1 male, 1 female).

Results

P. crocea (Figs. 1A, 2; Table 1) – Tymbal second abdominal sternite apodemes darker than abdominal sternite, moderately slender, elongate; length greater than $^2/_3$ distance between bases of apodemes; apices rounded, converging slightly. Abdominal sternite convex between apodeme bases, narrowing abruptly in middle. Portion of abdominal sternite extending laterally from base of apodeme weakly concave on dorsal aspect, apex rounded.

Table 1: Mean (± standard deviation) tymbal measurements (mm) of four *Prokelisia* species.

Measurement	*P. crocea* (N = 10) Mean ± SD	*P. marginata* (N = 10) Mean ± SD	*P. dolus* (N = 10) Mean ± SD	*P. salina* (N = 3) Mean ± SD
1. Distance between apodeme bases	0.30 ± 0.028	0.26 ± 0.017	0.25 ± 0.025	0.267 ± 0.0382
2. Apodeme length	0.24 ± 0.041	0.05 ± 0.014	0.09 ± 0.024	0.075 ± 0.0000
3. Distance between apodeme tips	0.32 ± 0.077	0.27 ± 0.024	0.28 ± 0.026	0.300 ± 0.0433
4. Width of abdominal sternum	0.58 ± 0.039	0.48 ± 0.037	0.48 ± 0.041	0.558 ± 0.0144
5. Height of abdominal sternum in middle	0.06 ± 0.013	0.02 ± 0.002	0.03 ± 0.008	0.050 ± 0.0000
6. Height of abdominal sternum under apodeme	0.09 ± 0.013	0.04 ± 0.012	0.07 ± 0.013	0.075 ± 0.0000

Table 2: Analysis of variance of tymbal measurements of four *Prokelisia* species (df = 3,29; $p < 0.05$).

Measurement	F[a]
1. Distance between apodeme bases	9.30*
2. Apodeme length	92.37*
3. Distance between apodeme tips	1.76
4. Width of abdominal sternum	15.46*
5. Height of abdominal sternum in middle	43.67*
6. Height of abdominal sternum under apodeme	25.82*

[a]* = significant

P. dolus (Fig. 1B; Table 1) – Tymbal second abdominal sternite apodemes darker than abdominal sternite, very slender, elongate; length ca. $^1/_3$ distance between bases of apodemes; apices rounded, diverging. Abdominal sternite sinuate between apodeme bases, gradually narrowing in middle. Portion of abdominal sternite extending laterally from base of apodeme strongly concave on dorsal aspect, apex acuminate.

P. marginata (Fig. 1C; Table 1) – Tymbal second abdominal sternite apodemes concolorous with abdominal sternite, broadly triangular, short; length less than $^1/_4$ distance between bases of apodemes. Abdominal sternite broadly concave between apodeme bases, very narrow in middle. Portion of abdominal sternite extending laterally from base of apodeme strongly convex on dorsal aspect, apex rounded.

P. salina (Fig. 1D; Table 1) – Tymbal second abdominal sternite apodemes slightly darker than abdominal sternite, elongate; length less than $^1/_3$ distance between bases of apodemes. Abdominal sternite slightly convex on median aspects of apodeme bases, very slightly concave in middle. Portion of abdominal sternite extending laterally from base of apodeme weakly convex on dorsal aspect, apex acuminate.

Morphometric analysis of tymbal measurements – The mean (± standard deviation) measurements (mm) of the second abdominal sternite of the four *Prokelisia* species are presented in Table 1. Multiple analysis of variance (MANOVA) conducted on all measurements for all four species was significant, indicating that the species did indeed differ in tymbal morphometric features ($F = 218.44$; df = 23,174; $p < 0.05$). Analysis of variance (ANOVA) comparisons among the four species for each of the six measurements showed that five of the six measurements of *Prokelisia* were significantly different (Table 2).

Discussion

The second abdominal sternites of the four species differed from one another especially in the shape and length of the apodemes (Fig. 1, Tables 1, 2). *P. crocea* had the broadest sternum, which is reflective of its overall larger body size (WILSON 1982), but its apodemes were also the most elongate and thickest of the four species (Fig. 1A). The general shape of the second abdominal sternite of *P. salina* was most similar to that of *P. crocea* but the apodemes were distinctly shorter (Fig. 1D). The second abdominal sternite of *P. dolus* was similar in shape to those of *P. crocea* and *P. salina* but the apodemes were relatively short and very slender (Fig. 1B). The shape of the second abdominal sternum of *P. marginata* was very different from those of the other three species – the short, broad apodemes were triangular in shape (Fig. 1C). The greatest differences in apodeme shapes were between *P. marginata* and *P. dolus* which co-occur on the same host plant and which produce distinctly different mating calls used for species recognition (HEADY & DENNO 1991). If morphological differences in tymbal structures are reflective of differences in the calls produced then divergence in the development of different species recognition signals is likely to have occurred during the evolution of these planthoppers. The significant differences in both morphology and signals between *P. marginata* and *P. dolus* suggest character displacement in both morphology and behavior.

Recently, several sibling species complexes of delphacids have been discovered (BOOIJ 1982, CLARIDGE 1985a, DEN BIEMAN 1986, DROSOPOULOS 1985). Recognition of the species in these complexes has relied on differences in the vibrational signals and host plant affinities. Most delphacids are decidedly monophagous with few well documented polyphagous species (WILSON et al. 1994); however, many poorly studied species have been recorded from more than one host plant species. Examination of tymbal morphology in these species might prove useful in recognizing some sibling species complexes.

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