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The Planthopper Genus *Prokelisia* (Homoptera: Delphacidae): Morphology of Female Genitalia and Copulatory Behavior

SUSAN E. HEADY[1] AND STEPHEN W. WILSON[2]

ABSTRACT: The female genitalia of the five species of the planthopper genus *Prokelisia* are described and illustrated and a key for identification is provided. Form of the valvifers of the 8th abdominal segment and shape and dentition of the median gonapophyses of the 9th abdominal segment are used to separate species. Copulation in two of the species is described.

The Nearctic delphacid genus *Prokelisia* consists of five species distinguished by characteristics of the male genitalia and frons (Wilson, 1982). Females have been difficult to identify because some individuals are intermediate in critical diagnostic features of the frons and no genitalic features were found that distinguished them (Wilson, 1982; pers. obs.). Morphometric analysis of frons length and width proved useful in separating most females and nymphs of two species (Denno et al., 1987).

Prokelisia planthoppers have been the focus of extensive ecological research (summarized by Denno et al., 1987), with emphasis on two sibling species using the same host plant (Wilson, 1982; Denno et al., 1987). No other North American planthopper taxon has received more ecological attention. Recent studies of the acoustic signaling and copulatory behavior of the sibling species *P. dolus* Wilson and *P. marginata* (Van Duzee) (Heady, unpublished data) resulted in accurate species assignment of females and discovery of a diagnostic character of the female genitalia. Once a reliable feature of females was available females could be accurately identified and examined for other genitalic characters.

Female genitalic characters have not been used extensively in planthopper systematics. This is due to the apparent lack of distinguishing features in some taxa (e.g., *Myndus*; Kramer, 1979), insufficient examination or availability of specimens that can be associated reliably with males, and the paucity of detailed morphological descriptions. Female genitalia and form of the pregenital sternite have been illustrated, but rarely described, for some issid, flatid, and nogodinid taxa (Doering, 1932, 1938; Doering and Shepherd, 1946; Kramer, 1976). Female genitalia have also been used in separating species of some delphacid taxa (e.g., Ossiannilsson, 1978) such as *Nilaparvata* (Okada, 1977): their morphology has been detailed by Müller (1942) and Asche (1985). Useful characters include the structure of the valvifer of the 8th abdominal segment (=first valvifer or lateral lobe [Ossiannilsson, 1978]), the shape and dentition of the median gonapophyses of the 9th abdominal segment (=second valvula or saw [Ossiannilsson, 1978]), the shape of the lateral gonapophyses of the 9th abdominal segment (=third valvulae or saw case [Ossiannilsson, 1978]), and the shape of the genital scale or atrium plate (Ossiannilsson, 1978; Remane, pers. comm.).

[1] Department of Entomology, Ohio Agricultural Research & Development Center, The Ohio State University, Wooster, Ohio 44691.

[2] Department of Biology, Central Missouri State University, Warrensburg, Missouri 64093.

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This study consists of description of the female genitalia of the species of *Prokelisia,* a key for identification of females, and notes on the positioning and coupling of male and female genitalia during copulation.

Materials and Methods

Specimens used for description had the following collecting data (SWW = S. W. Wilson collection, SEH = S. E. Heady collection; others are listed in Acknowledgments):

P. carolae Wilson—CANADA: BC: 149 m l., Cariboo, 29 May 1959, coll. G. G. E. Scudder (1 specimen, SWW collection).

P. crocea (Van Duzee)—IA: Story Co., Ames, 9 August 1926 (1 specimen, ISU collection); LA: St. Tammany Parrish, 23 June 1948, coll. E. L. Todd (1 specimen, SEH collection); NJ: Ocean Co., Tuckerton, 7 July 1976, coll. E. E. Grissell (3 specimens, SEH collection), 28 May 1987, coll. Denno and Wilson (8 specimens, SWW collection).

P. dolus—CA: Ventura Co., Pt. Mugu, 8 May 1982, coll. Nogano and Hogue, ex. *Spartina foliosa* (6 specimens, SWW collection); FL: Hillsborough Co., 15 mi SE Tampa, 15 May 1988, coll. Denno and Roderick (6 specimens, SEH collection); NJ: Ocean Co., Tuckerton, 28 May 1987, coll. Denno and Wilson (2 specimens, SWW collection; 20 lab reared specimens, SEH collection).

P. marginata (Van Duzee)—FL: Franklin Co., Alligator Point, 22 March 1975, coll. G. B. Marshall (2 specimens, SWW collection), Hillsborough Co., 15 mi SE Tampa, 15 May 1988, coll. Denno and Roderick (5 specimens, SEH collection); NJ: Middlesex Co., Cheesequake State Park, 27 May 1980, coll. Wilson (2 specimens, SWW collection).

P. salina (Ball)—CANADA: BC: Osoyoos, 25 July 1963, coll. G. G. E. Scudder (1 specimen, SEH collection); USA: AZ: Cochise Co., 1 mi S. Portal, 20 June 1985, 4800 ft at light, coll. J. H. Davidson, J. M. Davidson, M. A. Cazier (1 specimen, SWW collection); CA: Contra Costa Co., Albany Hill, 12 November 1950, coll. C. H. Spitzer (1 specimen, UC collection), San Bernardino Co., Chino, 1 July 1908, coll. E. D. Ball (1 specimen, Flock collection), San Diego Co., San Diego, 16 June 1908 (1 specimen, Flock collection), Tulare Co., Exeter, 23 August 1936 (1 specimen, UC collection); CO: Prowers Co., Lamar, 23 September 1927, coll. W. Carter, 18 July 1901 (1 specimen for each date, Flock collection), 20 August 1936, coll. M. B. Jackson, Paramorphotype, *Prokelisoidea frontalis* (Crawford), B. T. McDermott (1 specimen, KU collection), Grand Junction, 9 August 1905 (1 specimen, Flock collection); IL: Lake Co., Zion, 13 August 1937, Ross and Burke (1 specimen, SEH collection); KS: Reno Co., Medora, 24 June 1936, coll. D. R. Lindsay, Paramorphotype, *Prokelisoidea frontalis* (Crawford) B. T. McDermott (1 specimen, KU collection).

Specimens used for descriptions and illustration were pinned or preserved in 70% isopropyl alcohol. The abdomens of these were removed and cleared in 10% cold KOH overnight, immersed in water, stained with Gage's Stain (Barbosa, 1974:45), immersed in water, then placed in glycerol. Specimens used for scanning electron micrography (ISI-40 SEM) were platinum coated alive or as dried, pinned specimens.

Observations of copulation in *P. dolus* and *P. marginata* were based on laboratory reared specimens maintained on potted *Spartina alterniflora* Lois. Details

of rearing conditions are given by Denno et al. (1987). Copulating pairs on leaves were observed through a 10× hand lens. Each leaf bearing a copulating pair was immersed in a vial of 70% ethyl alcohol. *P. dolus* pairs remained in copula; however, all *P. marginata* uncoupled upon immersion. Micrographs, as described above, were made from the *P. dolus* specimens. Additionally, observations of male genitalic movements were facilitated by placing an individual under a dissecting microscope ventral side up and lightly anesthetizing the planthopper with carbon dioxide.

Results and Discussion

DESCRIPTIONS OF FEMALE GENITALIA: Terminology used in descriptions of the female genitalia follows Asche (1985). The genitalia of *P. crocea* are described in detail; only salient features are mentioned for the remaining species. The valvifer of segment 8 of each of the *Prokelisia* species is distinct and consistent despite variations in body size or wing form. The difference in shape of the anterior end of the valvifer is a reliable species specific feature. However, the appearance of this and the degree of curvature on the medial margin of the valvifer not only varies slightly among specimens but also can appear markedly different depending on whether the valvifers and lateral gonapophyses of segment 9 meet along the ventral midline (as in Figs. 6C, 7) or are separated (as in Fig. 6A, B, D). During copulation the valvifers separate laterally and the male inserts the aedeagus between them (Fig. 8A, C). In live non-copulating planthoppers and pinned specimens the valvifers are not separated on the ventral midline (Fig. 7). Clearing a specimen causes the abdomen to swell and results in separation of the valvifers and lateral gonapophyses (Figs. 1, 6). Because *P. dolus* and *P. marginata* are so similar, specimens representing extremes in variability were selected for illustration (Figs. 5F, G; 6C, D).

P. crocea (Figs. 1–3, 5A–C, 7A): Tergite 9 (="pygofer") oriented anteroventrally (see Asche, 1985), elongate, longitudinally concave in ventral midline. Anal tube and anal style subcylindrical. Genital scale and/or atrium plate apparently absent. Valvifers of segment 8 (=first valvifer) each covering ca. ⅓ of tergite 9 anterolaterally (Fig. 1); elongate; because parts of genitalia are moveable anteromedial margins may meet; medial margins at anterior end of valvifers broadly rounded; remainder of medial margin concave, greatest point of inflection at ⅓ to ½ distance from anterior end. Lateral gonapophyses of segment 9 (=third valvulae) elongate, may meet along medial margins; concave on dorsomedial aspect for most of length; broadly rounded posteriorly (Fig. 2); in ventral view, anterior margin rounded, connected on dorsal aspect to median gonapophyses of segment 9 (=second valvulae) by valvifer of segment 9 (=second valvifer) (Fig. 5A–C). In lateral view, median gonapophyses of segment 9 saber-shaped, with ca. 20–25 strong teeth on dorsal margin in distal ½, apex strongly angled posterodorsally (Fig. 5A). Gonapophyses of segment 8 (=first valvulae) slender, nearly acute posteriorly (Figs. 1, 2); with highly sclerotized rod-like anterior and interior rami extending length of each gonapophysis (Fig. 3); each gonapophysis connected at base to valvifer of segment 8 and apodeme of tergite 9 (Figs. 3, 4).

P. carolae (Figs. 5D, 6A, 7B): In ventral view, tergite 9 wider than that of *P. crocea*. Valvifers of segment 8 each with medial margin at anterior end broadly rounded; remainder of medial margin less strongly curved than that of *P. crocea*

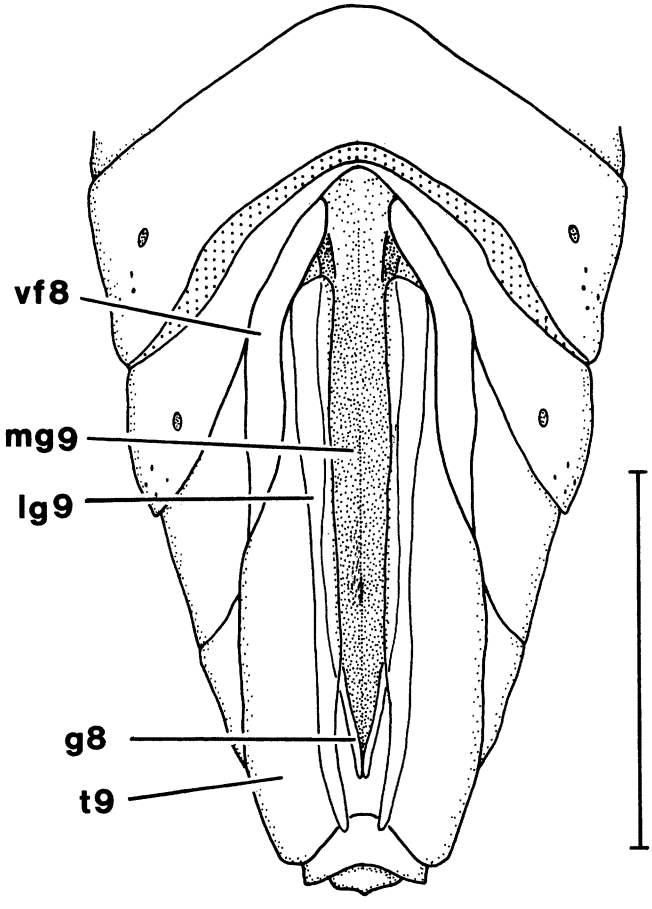

Fig. 1. *Prokelisia crocea* female genitalia, ventral view; from New Jersey. g8—gonapophyses of the 8th abdominal segment, lg9—lateral gonapophyses of the 9th abdominal segment, mg9—median gonapophysis of the 9th abdominal segment, t9—9th abdominal tergite, vf8—valvifer of the 8th abdominal segment. Scale = 1.0 mm.

and without well defined point of inflection ⅓ to ½ distance from anterior end (Fig. 6A). In lateral view, median gonapophyses of segment 9 with 25 strong teeth on dorsal margin in distal ½, apex slightly narrower than that of *P. crocea* and almost truncate (Fig. 5D).

P. salina (Figs. 5E, 6B, 7C): In ventral view, tergite 9 narrow. Valvifers of segment 8 each with medial margin at anterior end broadly rounded; remainder of medial margin with greatest point of inflection at ¼ to ⅓ distance from anterior end (Fig. 6B). In lateral view, median gonapophyses of segment 9 slender, sinuate in apical ⅓ of ventral margin; with ca. 14–17 strong teeth on dorsal margin in distal ½, apex narrow and almost truncate (Fig. 5E).

P. dolus (Figs. 5F, 6C, 7D): In ventral view, tergite 9 narrow. Valvifers of segment 8 each with medial margin at anterior end straight to slightly concave; remainder of medial margin strongly curved with well-defined greatest point of inflection at ¼ to ⅓ distance from anterior end (Fig. 6C). In lateral view, median

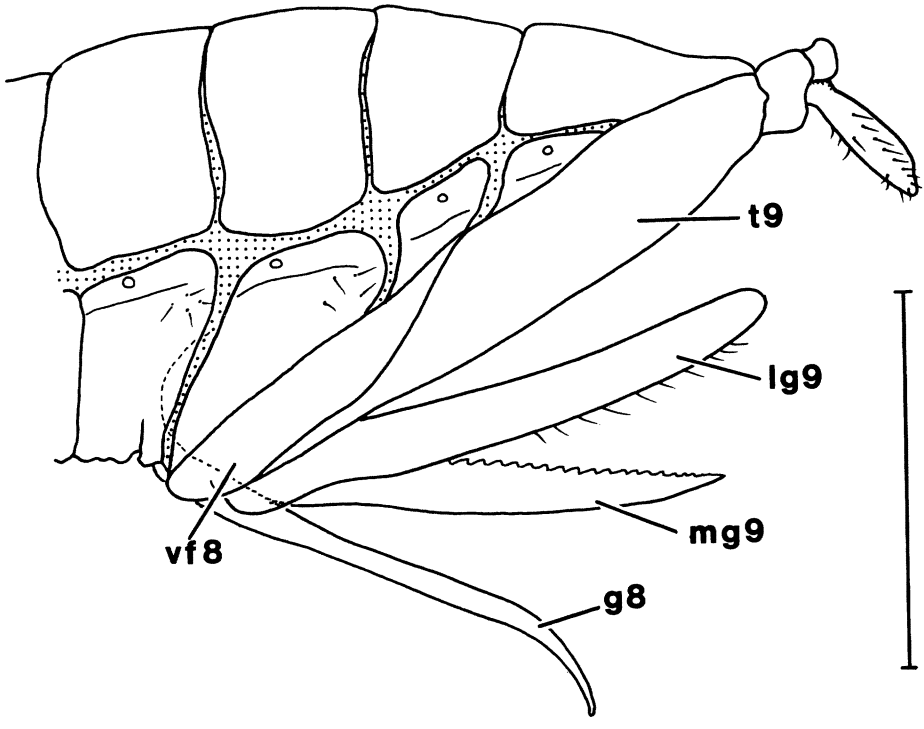

Fig. 2. *Prokelisia crocea* female genitalia, left lateral view; from Iowa. Symbols as in Fig. 1. Scale = 1.0 mm.

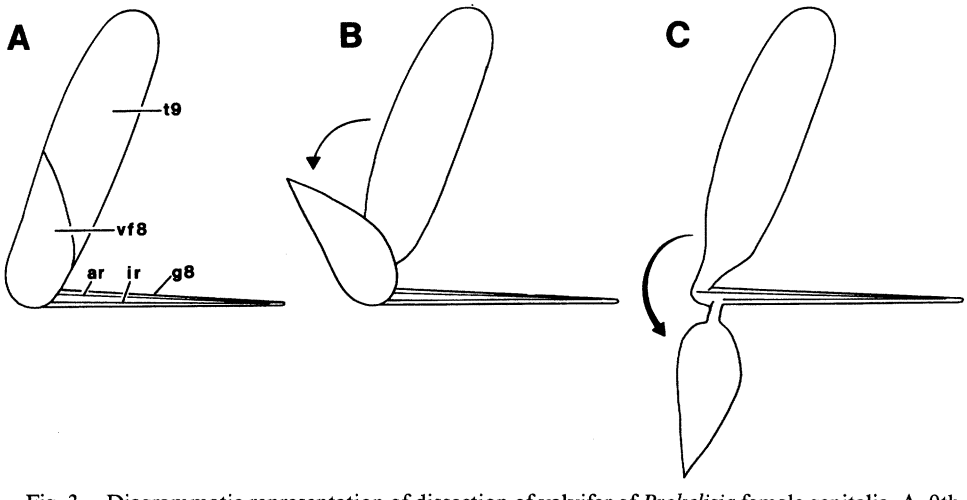

Fig. 3. Diagrammatic representation of dissection of valvifer of *Prokelisia* female genitalia. A. 9th tergite, valvifer, and gonapophysis, left lateral view. B. Valvifer moved anteroventrally. C. Valvifer moved ventrolaterally. ar—anterior ramus, g8—gonapophyses of the 8th abdominal segment, ir—interior ramus, t9—9th abdominal tergite, vf8—valvifer of the 8th abdominal segment.

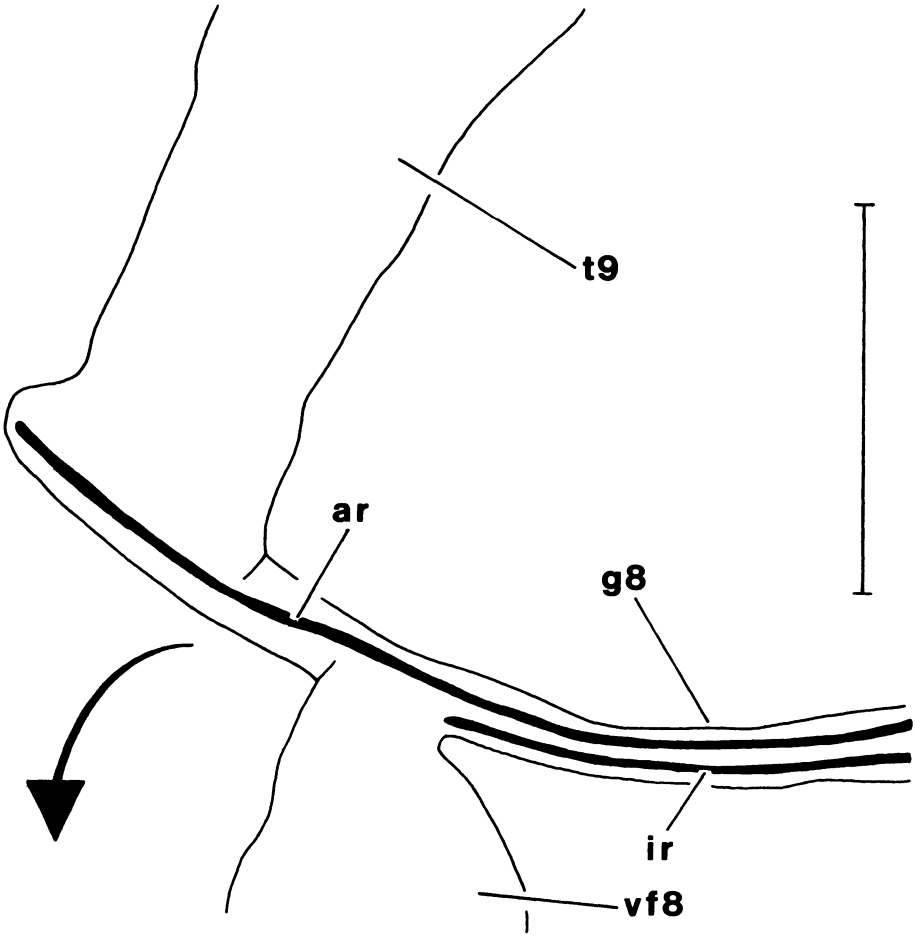

Fig. 4. *Prokelisia crocea* base of gonapophysis of 8th abdominal segment; from Iowa. Orientation and symbols as in Fig. 3. Scale = 0.25 mm.

gonapophyses of segment 9 with ca. 32 small teeth on dorsal margin in distal ½, toothed region widest in apical ¼, apex acute (Fig. 5F).

P. marginata (Figs. 5G, 6D, 7E): In ventral view, tergite 9 narrow. Valvifers of segment 8 each with medial margin at anterior end broadly rounded; remainder of medial margin weakly curved with poorly-defined greatest point of inflection at ¼ to ⅓ distance from anterior end (Fig. 6D). In lateral view, median gonapophyses of segment 9 with ca. 39–51 small teeth on dorsal margin in distal ½, toothed region widest in apical ⅓, apex acute (Fig. 5G).

Key to the Species of Female *Prokelisia*

1. Lateral margins of frons markedly convex and widest at or below basal ⅓; with brown longitudinal markings (Wilson, 1982:535); median gonapophyses of segment 9 with more than 30 small teeth (Fig. 5F, G); coastal salt marshes on *Spartina alterniflora* Lois. or *S. foliosa* Trin. . . . 2

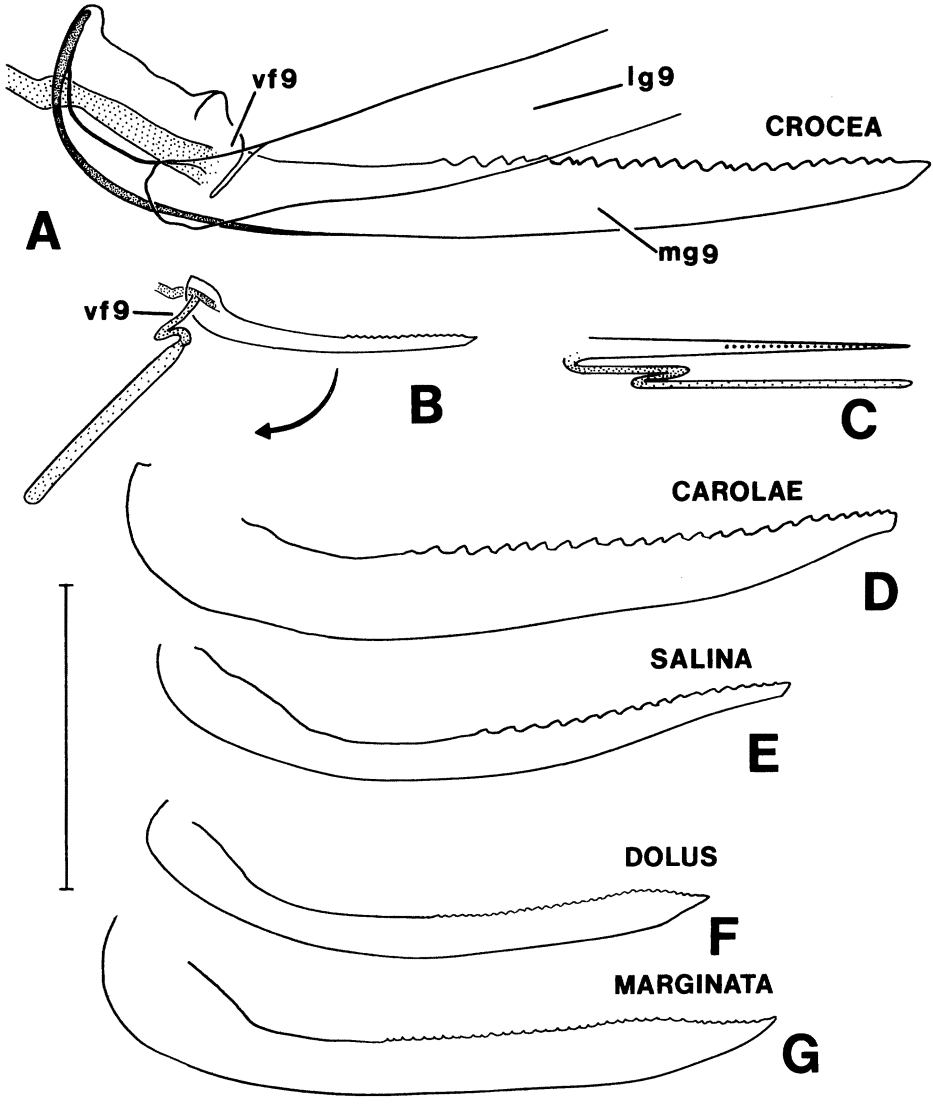

Fig. 5. Ovipositors of *Prokelisia* spp. A. *P. crocea* from Iowa, lg9—lateral gonapophysis of the 9th abdominal segment, mg9—median gonapophysis of the 9th abdominal segment, vf9—valvifer of the 9th abdominal segment. B. Diagrammatic left lateral view of attachment of left lateral and median gonapophyses and valvifer; left lateral gonapophysis pulled anteroventrally to reveal hidden basal connection with valvifer of the 8th abdominal segment. C. Diagrammatic dorsal view of median and left lateral gonapophyses and valvifer. D–G. Median gonapophyses. D. *P. carolae* from British Columbia. E. *P. salina* from Grand Junction, Colorado. F. *P. dolus* from New Jersey. G. *P. marginata* from Cheesequake, New Jersey. Scale (A, D–G) = 0.5 mm.

– Lateral margins of frons subparallel, if slightly convex then widest above basal ⅓; markings variable (Wilson, 1982:535); median gonapophyses of segment 9 with fewer than 30 strong teeth (Fig. 5A, D, E); freshwater marshes or upland habitats 3

2. Valvifers of segment 8 each with medial margin at anterior end straight

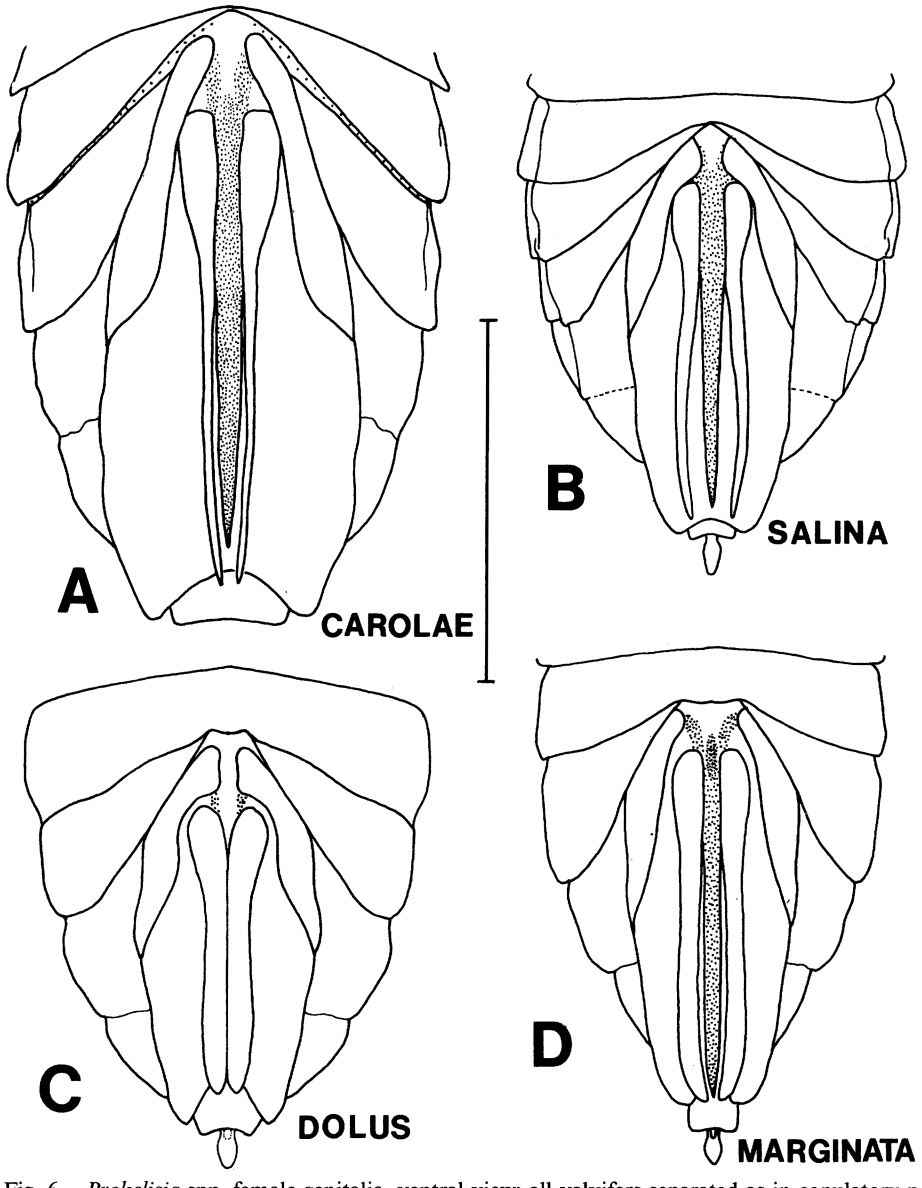

Fig. 6. *Prokelisia* spp. female genitalia, ventral view; all valvifers separated as in copulatory position. A. *P. carolae* from British Columbia. B. *P. salina* from Grand Junction, Colorado. C. *P. dolus* brachypter from New Jersey. D. *P. marginata* brachypter from Alligator Point, Florida. Scale = 1.0 mm.

to slightly concave (Figs. 6C, 7D); median gonapophyses of segment 9 with ca. 30–35 small teeth (Fig. 5F) ..... *P. dolus* Wilson

– Valvifers of segment 8 each with medial margin at anterior end broadly rounded (Figs. 6D, 7E); median gonapophyses of segment 9 with more than 35 small teeth (Fig. 5G) ..... *P. marginata* (Van Duzee)

3. Valvifers of segment 8 with medial margins strongly concave and with

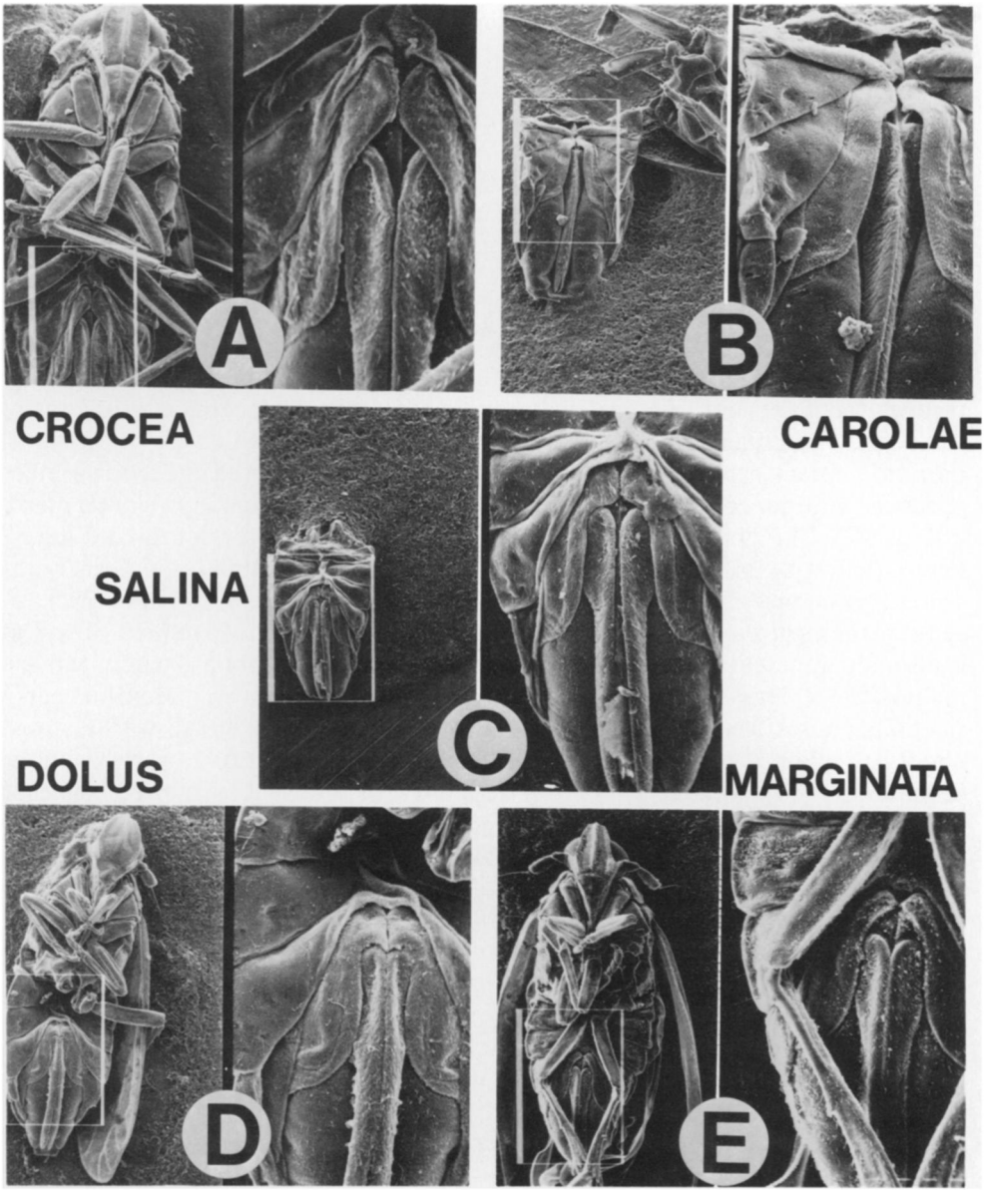

Fig. 7. Scanning electron micrographs of *Prokelisia* spp. females, ventral view; left = ×30, right = ×90; all valvifers not separated as in non-copulatory position. A. *P. crocea* from New Jersey. B. *P. carolae* from British Columbia. C. *P. salina* from Illinois. D. *P. dolus* brachypter from Florida. E. *P. marginata* brachypter from New Jersey.

greatest point of inflection ¼ to ⅓ distance from anterior end (Fig. 6B, 7C); median gonapophyses of segment 9 with fewer than 20 teeth (Fig. 5E) ..... *P. salina* (Ball)

– Valvifers of segment 8 with medial margins weakly to moderately concave and with greatest point of inflection ⅓ to ½ distance from anterior end

(Figs. 1, 6A, 7A, B); median gonapophyses of segment 9 with more than 20 teeth (Fig. 5A, D) 4

4. Valvifers of segment 8 with medial margins moderately concave and with greatest point of inflection well-defined (Figs. 1, 7A); widely distributed in eastern U.S. to Rocky Mts., on *Spartina pectinata* Link .... *P. crocea* (Van Duzee)

– Valvifers of segment 8 with medial margins weakly concave and with greatest point of inflection poorly defined (Figs. 5A, 7B); British Columbia to California ..... *P. carolae* Wilson

Copulatory Behavior

Mate attraction is facilitated by production of tymbal vibrations transmitted through the plant substrate (Heady, unpublished data). After attraction of a male to a female, the male moves parallel to her and his styles, which are in constant motion, contact her valvifers (Fig. 8A). The styles are placed posterior to the produced anterior end of the valvifer and anterior to the gonapophyses of segment 8 (Fig. 8C). The dorsoventrally articulated styles move continuously and alternately (left style moves dorsally as right style moves ventrally and then both switch directions). The movement of styles is apparent during coupling prior to aedeagus insertion and also upon completion of copulation. Movement of styles is also apparent when males are lightly anesthetized with carbon dioxide. Movement of the styles is not observable during copulation; however, abdominal contractions are visible. The styles of the male may act as "titillators" with a stimulatory function and act as an internal courtship device prior to insemination (Eberhard, 1985). After styles are inserted, then the aedeagus is inserted between the valvifers into the female's genital aperture (Fig. 8B, C). No other structures of the male's abdomen touch the female's abdomen during copulation. After insemination, the aedeagus and styles are withdrawn simultaneously.

Interspecific encounters between *P. dolus* and *P. marginata* are likely because these species are sympatric and synchronic on the same host plant (Denno et al., 1987). Several behavioral and morphological features of these planthoppers appear to serve as means of reproductively isolating these species. Both species, on average, respond to conspecifics but discriminate against heterospecifics by not calling (Heady, unpublished data). If a male does attempt genitalic connection with a heterospecific female (or an unreceptive conspecific female) he can be rejected. Females may reject by walking away, kicking the male away, or pressing the abdomen to the substratum. *P. dolus* and *P. marginata* heterospecific pairs never copulated, despite numerous attempts (Heady, unpublished data). If a male were able to force copulation with a heterospecific female, differences in genitalic morphology might serve to prevent successful copulation. Thus, specificity in genitalia may be a last resort during courtship if calling individuals fail to discriminate or if heterospecific males force themselves on females.

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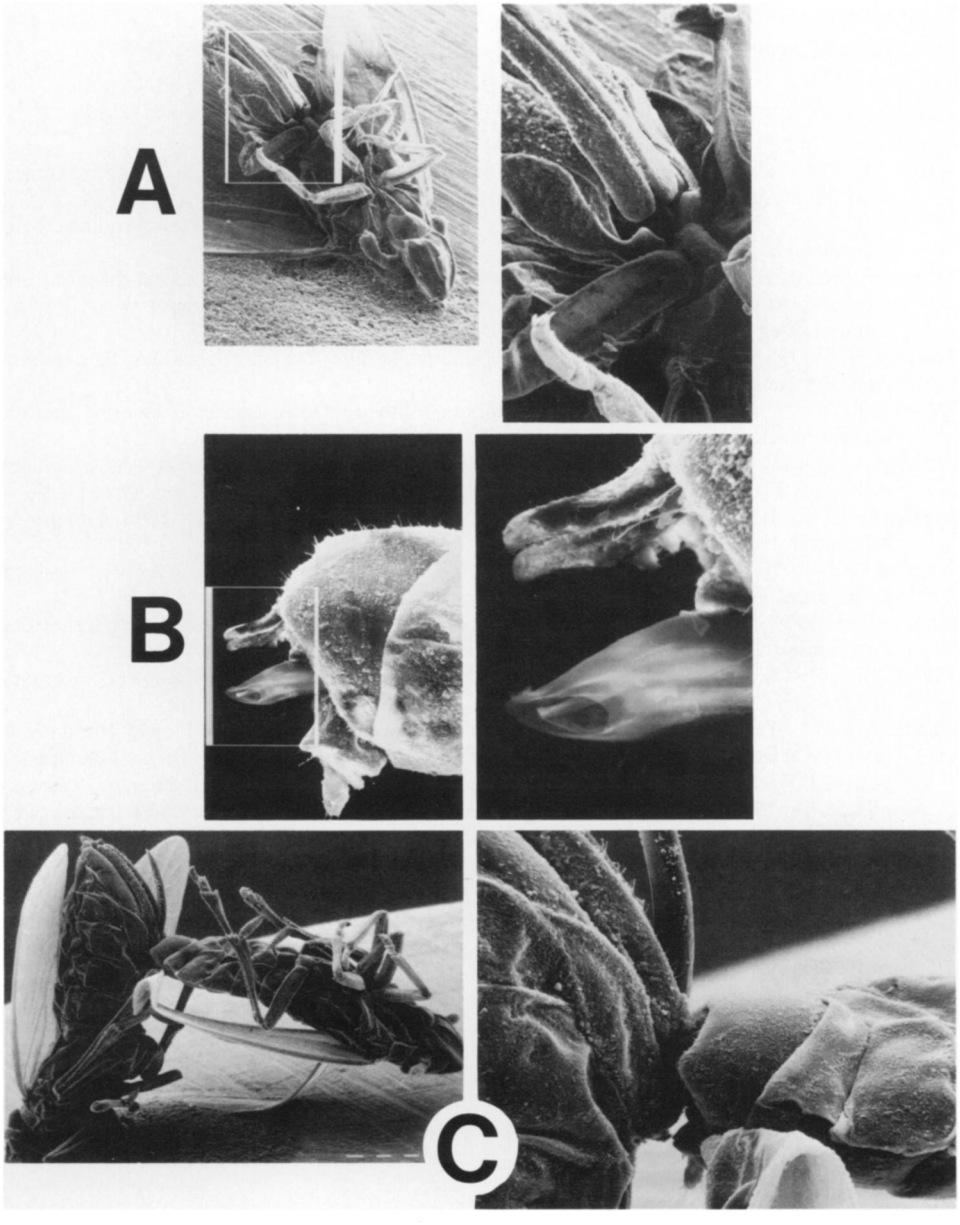

Fig. 8. Scanning electron micrographs of *Prokelisia dolus* (from New Jersey) copulation. A. Female with valvifers separated, left = ×30, right = ×90. B. Male genitalia, right lateral view (ventral aspect on top); left = ×146, right = ×438. C. Male and female in copula; left = ×30, right = ×112.

ifornia; T. J. Henry, National Museum of Natural History, Washington, D.C.; R. E. Lewis, Iowa State University, Ames; and G. G. E. Scudder, University of British Columbia, Vancouver. We thank M. Asche, H. Hoch, and R. Remane, Philipps Universität, Marburg, West Germany, for discussions and L. R. Nault and the Department of Entomology, The Ohio State University, Wooster, for providing research facilities and equipment. Research support was provided by

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