MORPHOLOGY OF THE DIGESTIVE AND REPRODUCTIVE SYSTEMS OF *DALBULUS MAIDIS* AND *GRAMINELLA NIGRIFRONS* (HOMOPTERA: CICADELLIDAE)

JAMES H. TSAI AND JOAN L. PERRIER
Fort Lauderdale Research and Education Center, University of Florida, IFAS
3205 College Avenue, Fort Lauderdale, FL 33314

ABSTRACT

The corn leafhopper, *Dalbulus maidis* (DeLong and Wolcott) (Homoptera: Cicadellidae) is the principal vector of maize rayado fino marafivirus, corn stunt spiroplasma and maize bushy stunt phytoplasma in tropical and subtropical areas of the Western Hemisphere. The black-faced leafhopper, *Graminella nigrifrons* (Fobes) (Homoptera: Cicadellidae) is the principal vector of maize chlorotic dwarf waikavirus in North America. The morphology of their digestive and reproductive systems was studied by light microscopy, and illustrations were made to aid in dissection and injection of pathogenic inoculum for various vector-pathogen relation studies. In both species, two salivary glands, located one on each side of the head, extend into the mesothorax. Each gland consists of principal and accessory glands. The former contains an anterior lobe and posterior lobe. Two types of acini are present in the anterior lobe, whereas the posterior lobe has four acini. The accessory glands of *D. maidis* and *G. nigrifrons* are very similar rod to elbow-shaped structures. The esophagus of both species is a narrow tube originating from the pharynx and extending to the anterior midgut below the filter chamber. The anterior midgut is a large sac-like structure extending from the metathorax through the entire length of the abdomen, and then ascends backward to the anterior of the midgut to form the filter chamber. The filter chamber of *D. maidis* has a more complex structure than that of *G. nigrifrons*. There are two pairs of Malpighian tubules in both species. The central tubule is formed from a pair of fused tubules within the filter chamber; the other tubules extend along the front of the hindgut. In *G. nigrifrons* the three tubules run parallel to each other along the top of the posterior midgut. In *D. maidis*, the central tubule and one tubule from the other pair run along the interior of the deep loop of the posterior midgut; the other tubule runs along the exterior of the loop. The ovaries of both species contain six ovarioles. Each ovariole consists of a terminal filament, a germarium, developing oocytes and eggs within follicles and a pedicle. The ovarioles contain six follicles. In *G. nigrifrons* each ovariole usually contains only one egg within the last follicle whereas the ovarioles of *D. maidis* often contain two eggs. The ovarioles open into the lateral oviduct, common oviduct and the vagina. The spermathecae open into the common oviduct. A collaterial gland and accessory glands are present. The male of both species has two lateral testes each with six follicles. A pair of accessory glands arise at the posterior of each seminal vesicle and open into the lateral ejaculatory duct.

Key Words: Internal morphology, anatomy, leafhopper, maize, corn stunt spiroplasma, maize rayado fino marafivirus, maize bushy stunt phytoplasma, maize chlorotic dwarf waikavirus

RESUMEN

Dalbulus maidis (DeLong y Wolcott) (Homoptera: Cicadellidae) es el principal vector del marafivirus del rayado fino del maiz, del espiroplasma de la atrofia del maiz y del fitoplasma de la atrofia ramificada del maiz en áreas tropicales y subtropicales del Hemisferio Occidental. *Graminella nigrifrons* (Fobes) (Homoptera: Cicadellidae) es el vector principal del waikavirus del enanismo clorótico del maiz en Norteamérica. La morfología de sus sitemas digestivo y reproductivo fue estudiada mediante microsco-

pía de luz. Fueron hechas ilustraciones para ayudar la disección y la inyección de inóculo patogénico para estudios sobre la relación vector-patógeno. En ambas especies, dos glándulas salivales, localizadas a cada lado de la cabeza, se extienden en el mesotórax. Cada glándula consiste de glandulas principales y accesorias. La últimas contienen un lóbulo anterior y un lóbulo posterior. Dos tipos de acini están presentes en el lobulo anterior, mientras que el lóbulo posterior tiene cuatro acini. Las glándulas accesorias de *D. maidis* y *G. nigrifrons* son muy similares a bastones o a estructuras en forma de codo. El esófago de ambas especies es un tubo estrecho que se origina en la faringe y se extiende hacia la parte anterior del intestino medio, bajo la cámara filtrante. La parte anterior del intestino medio es una estructura en forma de bolsa que se extiende a todo lo largo del abdomen, a partir del metatórax y asciende hacia la parte anterior del intestino medio para formar la cámara filtrante. La cámara filtrante de *D. maidis* tiene una estructura más compleja que la de *G. nigrifrons*. Hay dos pares de túbulos de Malpighi en ambas especies. El túbulo central está formado de un par de túbulos fundidos dentro de la cámara filtrante; los otros túbulos se extienden a lo largo del intestino posterior. En *G. nigirifrons* los tres túbulos corren paralelos a lo largo de la cima del intestino medio. En *D. maidis* el túbulo central y un túbulo del otro par corren a lo largo del interior de la curvatura de la parte posterior del intestino medio; el otro túbulo corre a lo largo del exterior de la curvatura. Los ovarios de ambas especies contienen seis ovariolas. Cada ovariola consisite de un filamento terminal, el germario, que desarrolla los oocitos y los huevos dentro de los folículos, y un pedúnculo. Las ovariolas contienen seis folículos. En *G. nigrifrons* cada ovariola usualmente contiene sólo un huevo dentro del último folículo mientras que las ovariolas de *D. maidis* a menudo conienen dos huevos. Las ovariolas se abren en el oviducto lateral, el oviducto común y la vagina. La espermateca se abre dentro del oviducto común. Una glándula colateral y una accesoria están presentes. El macho de ambas especies tiene dos testículos, cada uno con seis folículos. Un par de glándulas accesorias se alza en la parte posterior de cada vesícula seminal y se abre en el conducto eyaculatorio lateral.

Maize (*Zea mays* L.) is the world's most widely grown crop. An average of 380 million tons are produced annually on 120 million ha in 53 countries in almost all tropical areas of the world, including tropical highlands over 3000 m in altitude and temperate areas as far north as the 65th latitude. Because different ecological conditions exist between the temperate areas and the tropics, disease agents and their insect vectors also differ. To date, three important maize pathogens, maize rayado fino marafivirus, corn stunt spiroplasma (*Spiroplasma kunkelii*) and maize bushy stunt phytoplasma are known to be persistently transmitted by the corn leafhopper, *Dalbulus maidis* (DeLong & Wolcott), the principal leafhopper vector in hot and humid tropics as well as in the southern US (Chen & Liao 1975, Davis & Whorley 1973, Gamez 1973, Nault & Bradfute 1979, Tsai & Falk 1988). This vector is found abundantly from the southern US to Argentina (Nault 1980). In temperate areas, maize chlorotic dwarf waikavirus is most prevalent and is transmitted semipersistently by the blackfaced leafhopper, *Graminella nigrifrons* (Forbes) (Nault et al. 1973).

Because of the economic importance of these diseases in the Western Hemisphere, maize pathogens and their vectors have been the subject of many studies. However, only a few studies on the location of maize pathogens in various organs and tissues of Auchenorrhynchous vectors have been conducted using electron microscopy and serological techniques (Ammar 1985, 1987, Ammar & Nault 1985, 1991, Ammar et al. 1994, Childress & Harris 1989, Falk et al. 1988, Herold & Munz 1965, Falk & Tsai 1984, 1985, Nault & Gordon 1988). These studies involved dissections of insects to assay for virus presence in different organs. Because it is difficult to perform these dis-

sections with accuracy, a guide to the internal morphology was needed. The information on internal structures of the vectors of maize pathogens is scarce (Ammar 1985, 1986, 1987, Ammar & Nault 1991, Backus 1985, Childress & Harris 1989, Tsai & Perrier 1993). Accordingly, we initiated this detailed study of the internal morphology of *D. maidis* and *G. nigrifrons* for the purpose of facilitating the study of the fate of maize pathogens in their vectors.

Materials and Methods

Dalbulus maidis was reared in the laboratory on corn, *Zea mays* L. (var. Saccharata "Guardian"). *Graminella nigrifrons* (Forbes) was reared on a combination of oats (*Avena sativa* L.) and sweet corn in a growth room at 24±1°C and constant photoperiod of 12:12 (L:D). Approximately 300 adults of both sexes from both species were dissected. Insects were placed in a freezer at 0°C for periods of one to two h, then were dissected in a solution of 60 parts deionized water to 1 part safranin red 1%. The organs removed were left in the solution for 60 min, then were rinsed and observed with a dissecting microscope and a compound microscope at magnifications from 10× to 400×. When stains were not used, the organs were placed on a black background in order to observe delicate structures. Observations of other fine structures (the salivary glands, the filter chamber and its internal structure, the ovarioles, and various other glands) were performed on cold-anesthetized insects kept at 7.6°C. The dissections were performed in stain solutions of 120 parts Clarke's solution to 1 part neutral red 0.01% (Sogawa 1965) or 120 parts Clarke's solution to 1 part methelyne blue chloride 0.01%. Some of the finer details could be observed within the salivary glands by using these stains together.

Results and Discussion

Digestive System

Salivary glands. The salivary glands of *G. nigrifrons* and *D. maidis*, which are present on each side of the thorax and head (Sg in Figs. 1 and 3), consist of principal and accessory glands (Pg, Ag in Figs. 5 and 6). The principal gland contains an anterior lobe and a posterior lobe (Al, Pl in Figs. 5 and 6). Two types of acini, or follicles were observed in the anterior lobe, along with a small spherical appendage (I, and Sa in Fig. 5; I, II and Sa in Fig. 6). The posterior lobe contains four acini (III-VI in Figs. 5 and 6). The I and II cells and the spherical appendage open anteriorly into the principal salivary duct (I, II, Psd in Figs. 5 and 6); the III through VI cells open posteriorly into the same duct (Fig. 6; III-VI, Psd). At this juncture the accessory duct (Asd in Fig. 6) joins the principal salivary duct. The two principal ducts unite to form the common salivary duct (Sd in Fig 6) which extends into the head to the salivary syringe which in turn opens into the salivary canal in the stylets (Ammar 1985, Backus 1985, Sogawa 1965). In contrast, in *Hecalus lefroyi* Dist., these two principal ducts open separately into the salivary syringe (Saxena 1955).

Sogawa (1965) states that the anterior lobe of Cicadellidae usually contain two distinctly different types of bi-nucleate cells; the number, size and shape vary from species to species. We confirm this conclusion for these two species. The anterior lobe of *D. maidis* (Al in Fig. 6) is large and translucent. The distal region, which contains the I-cells (I in Fig. 6), consists of two to four large ovoid cells with large nuclei. A small spherical appendage also arises from this region (Sa in Fig. 6). The I-cells emerge from the center of the II-cells (II in Fig 6). This proximal area usually contains six smaller cells arranged concentrically. The cytoplasm appears denser than that of the I-cells and the nuclei are smaller. Both the I- and II-acini are often smaller than those illus-

trated (I, II in Figs. 5 and 6). The anterior lobe of *G. nigrifrons* differs from that of *D. maidis* in that it usually contains only one acinus type (II in Fig. 5). This acinus is a tri-lobed group of cells containing one or two cells per lobe (II in Fig. 5)). The spherical appendage arises from this structure (Sa in Fig. 5). Rarely, another group of cells, similar to the I-acinus of *D. maidis*, has been observed.

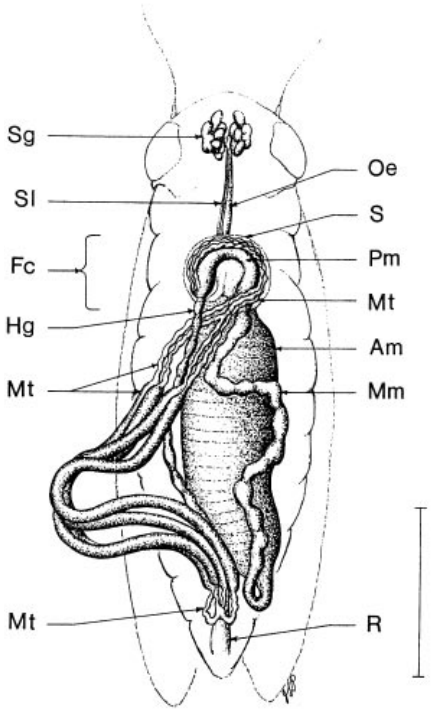
The posterior lobe of the Cicadellidae described by Sogawa (1965) contains acini III through VI. These bi-nucleate cells are all arranged concentrically. There are six III-type cells and varying numbers of IV-, V- and VI-type cells. Both *D. maidis* and *G. nigrifrons* have similar posterior lobes (Pl in Figs. 5 and 6). The III-, IV-, and V-type cells are all six in number. The VI-acinus contains three cells.

The III-type cells in *D. maidis* are large, translucent, and teardrop-shaped, and are separate from one another. Their nuclei are large and pronounced (III in Fig. 6). The rosette shaped IV-acinus is the most noticeable in the salivary gland (IV in Fig. 6); the cytoplasm is dense and the large nuclei are faint. Approximately 70% of the IV-acini observed had this amorphous, swollen shape. Other IV-type cells were more defined and separate from each other. The insects with the more defined IV-cells had anterior lobes that were reduced in size. The six V-type cells of *D. maidis* are much smaller than the IV-type cells with smaller nuclei (V in Fig. 6). This acinus again varies in shape ranging from amorphous to well-defined teardrop-shaped cells. The VI-acinus, situated at the center of the V-acini (IV in Fig. 6) is small, also tear drop-shaped and contains three indistinct cells.

The posterior lobe of *G. nigrifrons* is similar to that of *D. maidis* (Pl in Fig. 5). The III-type cells show no significant variation (III in Fig. 5). The IV-acinus, however, is much less pronounced than that of *D. maidis* (IV in Fig. 5). Its shape similarly ranges from amorphous to well-defined cells. Approximately 50% of the *G. nigrifrons* observed had well defined IV-type cells. Occasionally these cells had a hardened, shrunken appearance. The only noticeable difference between the V and VI-acini of the two insects was the smaller size of the V-type cells of *G. nigrifrons* (V in Fig. 5).

The accessory glands of *D. maidis* and *G. nigrifrons* are very similar (Ag in Figs. 5 and 6) and range from rod- to elbow-shaped. The size of the gland and the length of the accessory salivary duct (Asg in Figs. 5 and 6) vary within species. The variation in numbers and morphology of acini could be due to the age of the insect or to physiological factors. Because numerous fat bodies fill the head and surround the salivary glands, it is sometimes difficult to separate the smaller and more translucent acini from the fat bodies. In *Nephotettix cincticeps* Uhler, the principal gland has at least five lobes and five cell types (I-V) (Nasu 1965) whereas only four lobes and four cell types were reported in the principal gland of *Empoasca fabae* (Harris) (Berlin & Hibbs 1963). Gil-Fernandez & Black (1965) reported that *Agallia constricta* (Van Duzee) had four lobes and five acini in its principal gland. As many as 21 acini have been observed in the principal gland of *Cicadula sexnotata* (Fallen) [=*Macrosteles quadrilineatus* (Stal)] (Dobroscky 1931).

Foregut. Backus (1985) described the ciberial and esophageal regions of the mouthparts of several leafhoppers. The foregut begins at the bases of the mandibular and maxillary stylets with the precibarium. Fluid passes from the stylets to the precibarium then into the cibarium (or sucking pump) and then to the esophagus. In both *D. maidis* and *G. nigrifrons* the esophagus is a narrow tube that originates posteriorly to the pharynx above the tentorial bar (Nault & Ammar, 1989); it continues posteriorly until it enters the anterior midgut just below the filter chamber (E, Amg, Fc in Figs. 1, 2, 3, and 4). Traversing parallel to the esophagus is a slender strand of cells which is probably a suspensory ligament (Ammar 1985) (Sl in Figs. 1, 2, 3, and 4). This strand originates near the esophageal valve (Ammar 1985) on the anterior midgut and follows the esophagus into the head.



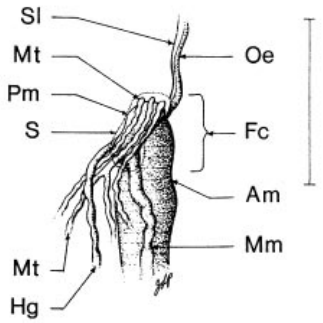


Fig. 1. *G. nigrifrons*. Dorsal view of digestive system of adult female. Sg, salivary gland; Oe, esophagus; Sl, suspensory ligament; Fc, filter chamber; S, filter chamber sheath, Mt, Malpighian tubules; Am, anterior midgut; Mm, mid-midgut; Pm, posterior midgut; Hg, hindgut; R, rectum. Vertical bar=1.0mm

Fig. 2. *G. nigrifrons*. Lateral right view of filter chamber. Oe, esophagus; Sl, suspensory ligament; Fc, filter chamber; S, filter chamber sheath; Mt, Malpighian tubules; Am; anterior midgut; Mm, mid midgut; Pm, posterior midgut; Hg, hindgut; Vertical bar=1.0 mm.

Midgut and Filter Chamber. Ingested fluid passes through the esophagus into the anterior midgut. In both *D. maidis* and *G. nigrifrons* the anterior midgut is large and sac-like (Am in Figs. 1 and 3), surrounded by a translucent muscular sheath composed of circular fibers (Snodgrass 1935, Goodchild 1966). The anterior midgut extends from the metathorax, nearly the entire length of the abdomen, and then constricts sharply to become the mid-midgut (Am, Mm in Figs. 1 and 3). The mid-midgut then ascends, returning to the anterior-most portion of the anterior midgut (Figs. 1 and 3: Mm); at this point it swells slightly to form the posterior midgut and the beginning of the filter chamber (Pm, Fc in Figs. 1 and 3).

In *G. nigrifrons* the posterior midgut forms a simple loop surrounding the top of the anterior midgut (Pm, Fc in Figs. 1 and 2) where these two opposing ends of the midgut appear to fuse (Bharadwaj et al. 1966). At the distal end of the loop, where it exits the filter chamber, the posterior midgut constricts to form the hindgut (Hg in Fig. 1). There appears to be a circular band of muscles at this junction, which is probably the pyloric sphincter (Ammar 1985). This point marks the end of the filter cham-

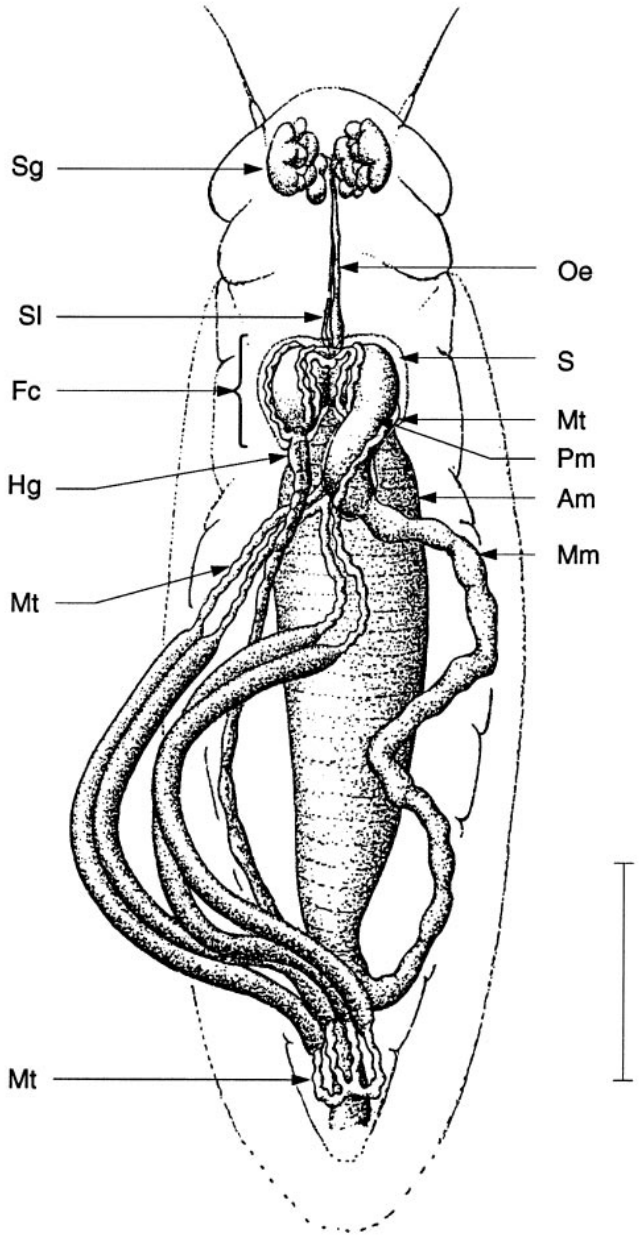


Fig. 3. *D. maidis.* Dorsal view of digestive system of adult female. Sg, salivary gland; Oe, esophagus; Sl, suspensory ligament; Fc, filter chamber; S filter chamber sheath, Mt, Malpighian tubules; Am, anterior midgut; Mm, mid-midgut; Pm, posterior midgut; Hg, hindgut; R, rectum. Vertical bar=1.0mm

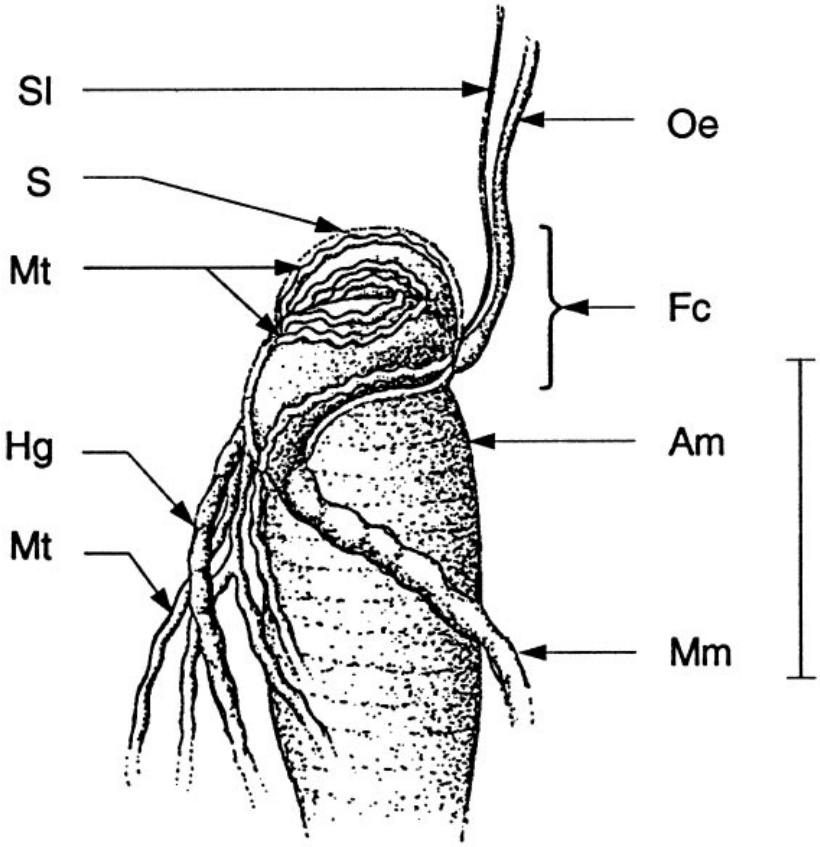


Fig. 4. *D. maidis*. Lateral right view of filter chamber. Oe, esophagus; Sl, suspensory ligament; Fc, filter chamber; S, filter chamber sheath; Mt, Malpighian tubules; Am; anterior midgut; Mm, mid-midgut; Hg, hindgut; Vertical bar=1.0 mm.

ber (Fc in Fig. 1). A common sheath surrounds the filter chamber, enclosing the top of the anterior midgut, the posterior midgut and the origins and proximal ends of the Malpighian tubules (S, Am, Pm, Mt in Figs. 1 and 2). The gross morphology and sheath formation of the filter chamber are similar to those of *M. quadrilineatus* (Dobroscky 1931), *Eugnathodus indica* Pruthi and *Nephotettix apicalis* Fabr. (Saxena 1955), *Euscelidius variegatus* (Khm.) and *Euscelis plebejus* (Fall) (Munk 1967) and *A. constricta* (Bharadwaj et al. 1966). However, mesophyll feeding leafhoppers, such as *E. fabae*, do not have a filter chamber (Berlin & Hibbs 1963).

The filter chamber of *D. maidis* is more complex than that of *G. nigrifrons*. The posterior midgut forms a deeper loop which covers the entire top of the anterior midgut (Fc, Pm, Am in Figs. 3 and 4). The sheath covering this area appears to be formed in sections, permitting fat bodies to attach themselves to the folds in the posterior midgut and to the anterior midgut around the periphery of the filter chamber.

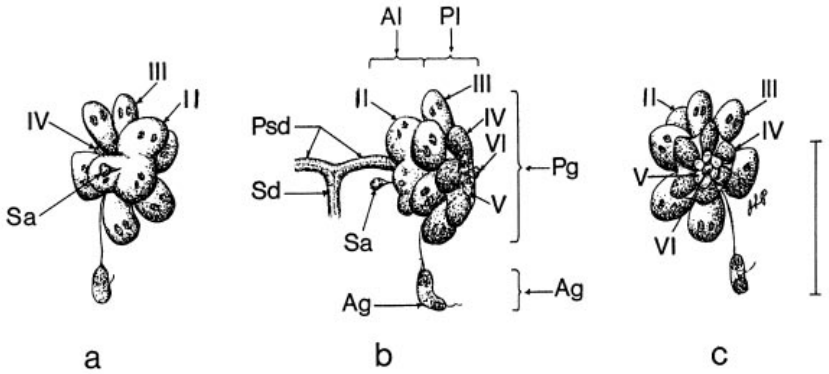


Fig. 5. *G. nigrifrons.* Detail of salivary glands. a, anterior; b, laterial; c, posterior; Pg, principal gland; Ag, accessory gland; Al, anterior lobe; Pl, posterior lobe; II-VI, acini in principal gland; Sa, spherical appendage; Psd, principal salivary duct; Sd, salivary duct. Vertical bar=0.25 mm.

Malpighian tubules. In both *D. maidis* and *G. nigrifrons* the Malpighian tubules arise within the filter chamber from the posterior end of the posterior midgut (Pm, Mt in Figs. 1 and 3). What appear to be three tubules loop back through the filter chamber along the posterior midgut to emerge near the beginning of the chamber, or the anterior end of the posterior midgut (Pm, Mt in Figs. 1 and 3).

There are two pairs of Malpighian tubules. The central tubule is comprised of one pair which is fused for the length of the filter chamber. Once this tubule emerges from the filter chamber, it divides into two ureters. (Mt in Figs. 1, 2, 3, and 4). One ureter extends behind the hindgut along with one tubule from the other pair (Mt, Hg in Figs. 1, 2, 3, and 4); the other ureter and tubule extend in front of the hindgut. Four Malpighian tubules were also found in *M. quadrilineatus* (Dobroscky 1931) and *E. indica* and *N. apicalis* (Saxena 1955) as well as *E. fabae* (Berlin & Hibbs 1963).

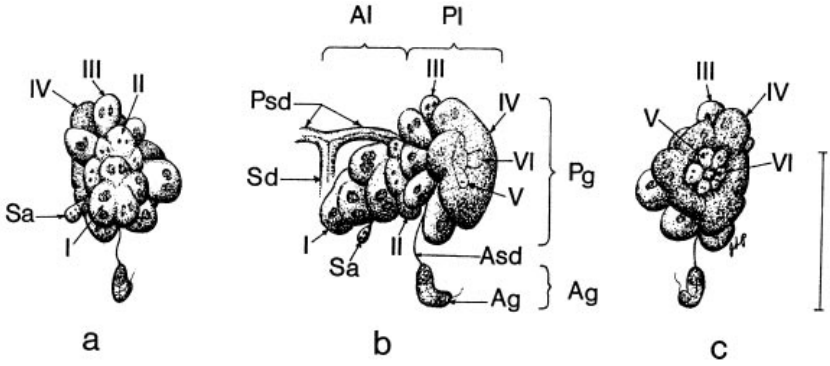


Fig. 6. *D. maidis.* Detail of salivary glands. a, anterior; b, lateral; c, posterior; Pg, principal gland; Ag, accessory gland; Al, anterior lobe; Pl, posterior lobe; I-VI, acini in principal gland; Sa, spherical appendage; Psd, principal salivary duct; Asd, accessory salivary duct; Sd, salivary duct. Vertical bar=0.25mm.

In *G. nigrifrons*, the three tubules run parallel to each other along the top of the posterior midgut (Mt, Pm in Figs. 1 and 2); the central tubule is the fused pair. In *D. maidis*, the central tubule (the pair) and one tubule from the other pair run along the interior of the deep loop of the posterior midgut (Mt, Pm in Figs. 3 and 4); the other tubule runs along the exterior of the loop (Mt in Figs. 3 and 4).

In both species, the Malpighian tubules appear translucent and lobulate for the proximal third of their length after which they swell to become opaque and tubular (Mt in Figs. 1 and 3). The four tubules extend toward the anus where they constrict to become lobulate again. At this point the four tubules fuse and become loosely attached to the rectum by means of fibrous ligaments. (Mt in Figs. 1 and 3).

Hindgut. In both *D. maidis* and *G. nigrifrons*, the hindgut arises from the posterior midgut at the boundary of the filter chamber. (Hg, Pm, Fc in Figs. 1 and 3). It extends downward toward the anus where the hindgut swells to become the rectum (Hg, R in Figs. 1 and 3). The hindgut passes in between the Malpighian tubules (Hg, Mt in Figs. 1 and 3).

Reproductive System

Female. The reproductive systems of *D. maidis* and *G. nigrifrons* are similar to each other in most respects. The ovaries of both species contain six ovarioles (O, Ol in Figs. 7 and 8). Each ovariole consists of a terminal filament, a germarium, developing oocytes and eggs within follicles, and a pedicle (Tf, G, F, and P in Figs. 8b and c). The ovarioles of both *D. maidis* and *G. nigrifrons* contain six follicles, the smallest of these is closest to the germarium, the largest opens into the pedicle. The major difference between the reproductive systems of the two species was observed within the ovariole. In mature *G. nigrifrons*, each ovariole usually contains only one egg within the last follicle (F in Fig. 9b). The follicle before the last is usually small, about one quarter the size of the egg. The ovarioles of *D. maidis* often contain two eggs, one partially in the last follicle and partially in the pedicle, the other in the previous follicle. When there is only one egg, the follicle before the last is large, at least one half the size of the egg (F, P in Fig. 9c). This could be one of the reasons that *D. maidis* is more prolific than *G. nigrifrons* (Tsai 1988, unpublished).

Each ovariole ends anteriorly with a terminal filament which unites with those of the other ovarioles to form a suspensory ligament (Sl in Figs. 7 and 8). These in turn appear to attach with the ligaments of the other ovary to form a median ligament which attaches dorsally to the body wall (Snodgrass 1935) at the roof of the second thoracic segment. Posteriorly, the pedicle of each ovariole opens into the calyx of the ovary (P, C in Figs. 7 and 8). These in turn open into the lateral oviducts, which join to form the common oviduct (Lo, Co in Figs. 7 and 8). The common oviduct bends very sharply toward the vagina (Co, V in Figs. 7 and 8). At the point where it opens into the vagina, the common oviduct is joined by the globular- to teardrop-shaped spermatheca (Co, S, V in Figs. 7 and 8). Two types of glands are also present: a colleterial gland and accessory glands (Cg, Ag in Figs. 7, 8 and 8a). These glands, along with the vagina are attached to the opening of the ovipositor (OP in Figs. 7 and 8). The large tubular colleterial gland, which often attaches itself to the neck and body of spermatheca, varies in length and can extend into the thorax (Cg, S in Figs. 7 and 8). The small, translucent, tubular accessory glands appear to originate from within the vaginal wall as a single gland which branches into two ducts. These ducts seem to extend through the vaginal wall (V, Ag in Figs. 7, 8 and 9a). A similar female reproductive system was described for *A. constricta* (Gil-Fernandez & Black 1965) and *M. fascifron* (Becker 1979). However, an average of ten ovarioles on each side of the ovary was observed for *N. cincticeps* (Nasu 1965).

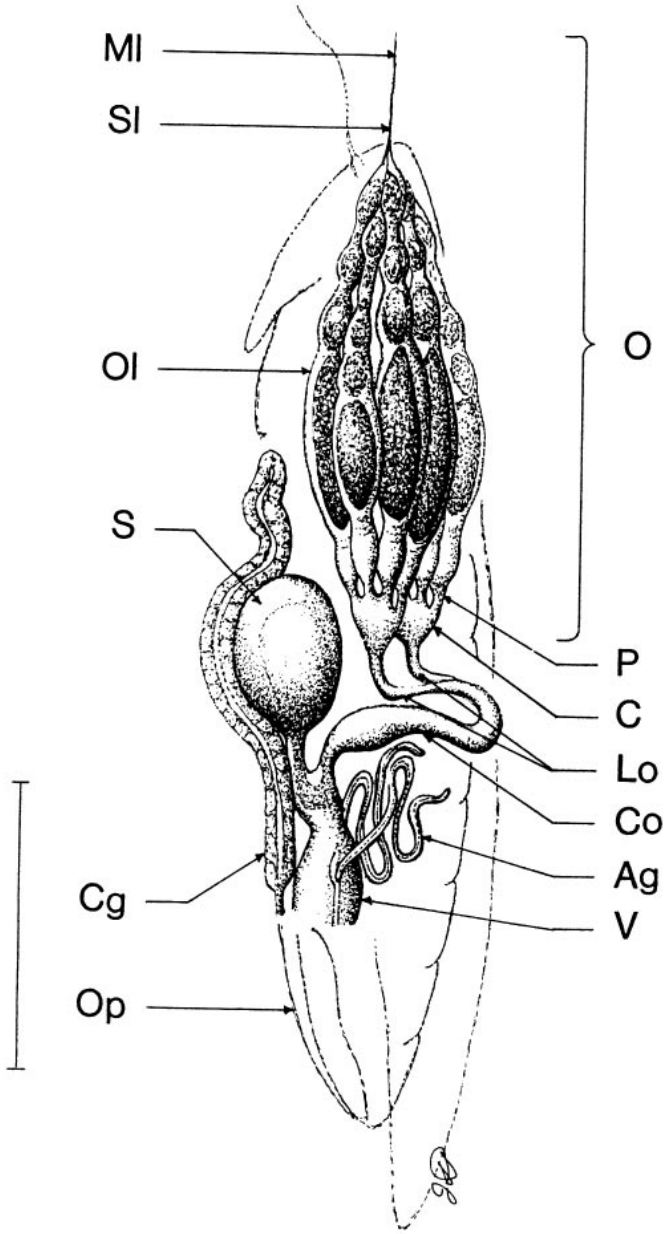


Fig. 7. *G. nigrifrons.* Female reproductive system. Lateral view. O, ovary; Ol ovariole; Sl, suspensory ligament; Ml, median ligament; P, pedicle; C, calyx; Lo, lateral oviduct; Co, common oviduct; S, spermatheca; Cg, colleterial gland; Ag accessory gland; V, vagina; Op, ovipositor. Vertical bar=1.0 mm.

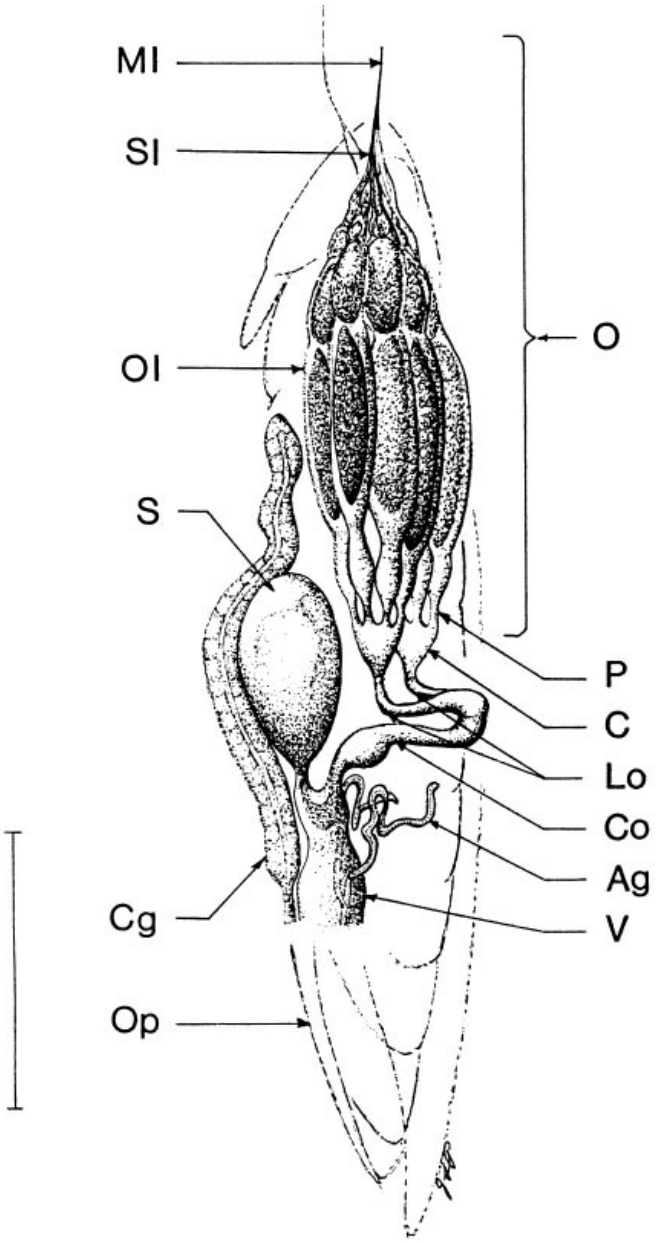


Fig. 8. *D. maidis*. Female reproductive system. Lateral view. O, ovary; Ol, ovariole; Sl, suspensory ligament; Ml, median ligament; P, pedicle; C, calyx; Lo, lateral oviduct; Co, common oviduct; S, spermatheca; Cg, colleterial gland; Ag accessory gland; V, vagina; Op, ovipositor. Vertical bar=1.0 mm.

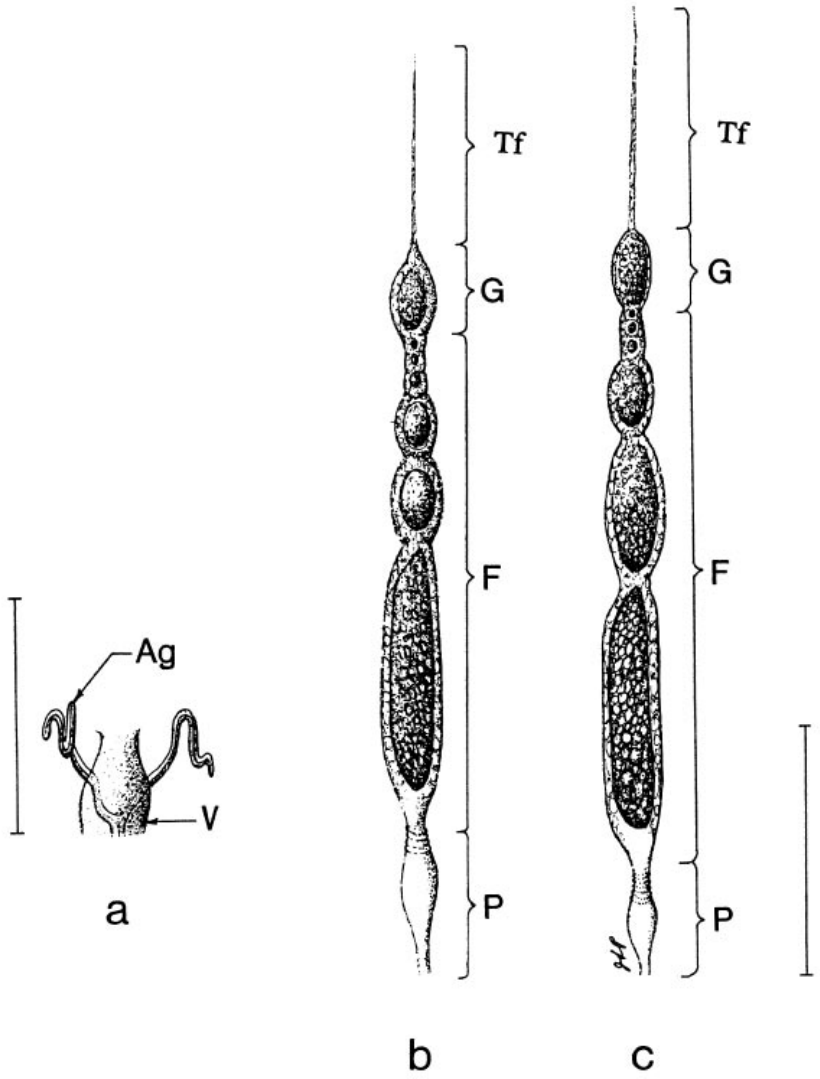


Fig. 9a. *D. maidis* and *G. nigrifrons* female. Ventral view. V, vagina; Ag, accessory gland. Vertical bar=1.0 mm.

Fig. 9b. *G. nigrifrons* detail of ovariole.

Fig. 9c. *D. maidis* detail of ovariole. Tf, terminal filament; G, germarium; F, follicles; P, pedicle. Vertical bar=0.5 mm.

Male. Both *D. maidis* and *G. nigrifrons* have two lateral testes situated ventrally at the junction of the abdomen and the thorax (T in Figs. 10 and 11a). The testes, which contain six follicles each, are often surrounded by fat bodies. The ovoid follicles join at the base of the testes to open into the very narrow vas deferens (T, Vd in Figs.

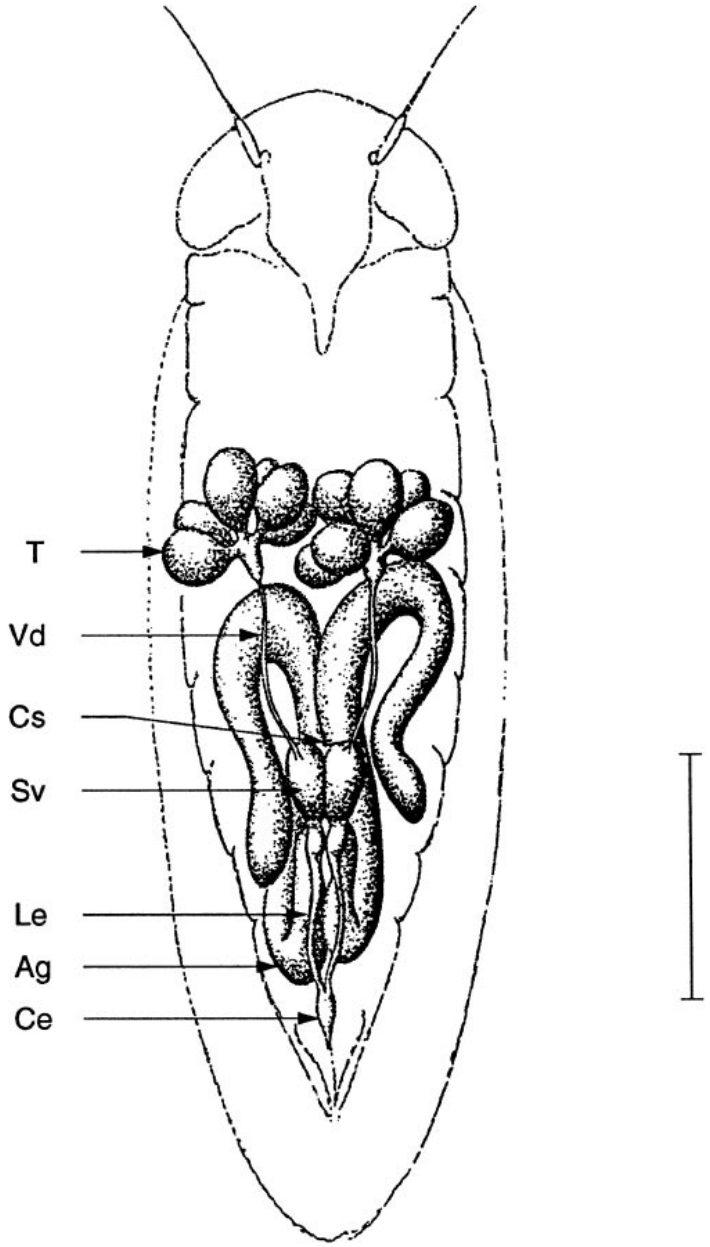


Fig. 10. *G. nigrifrons.* Male reproductive system. Ventral view. T, testes; Vd, vas deferens; Sv, seminal vesicle; Cs, common sheath; Le, lateral ejaculatory duct; Ce, common ejaculatory duct; Ag, accessory gland. Vertical bar=1.0 mm.

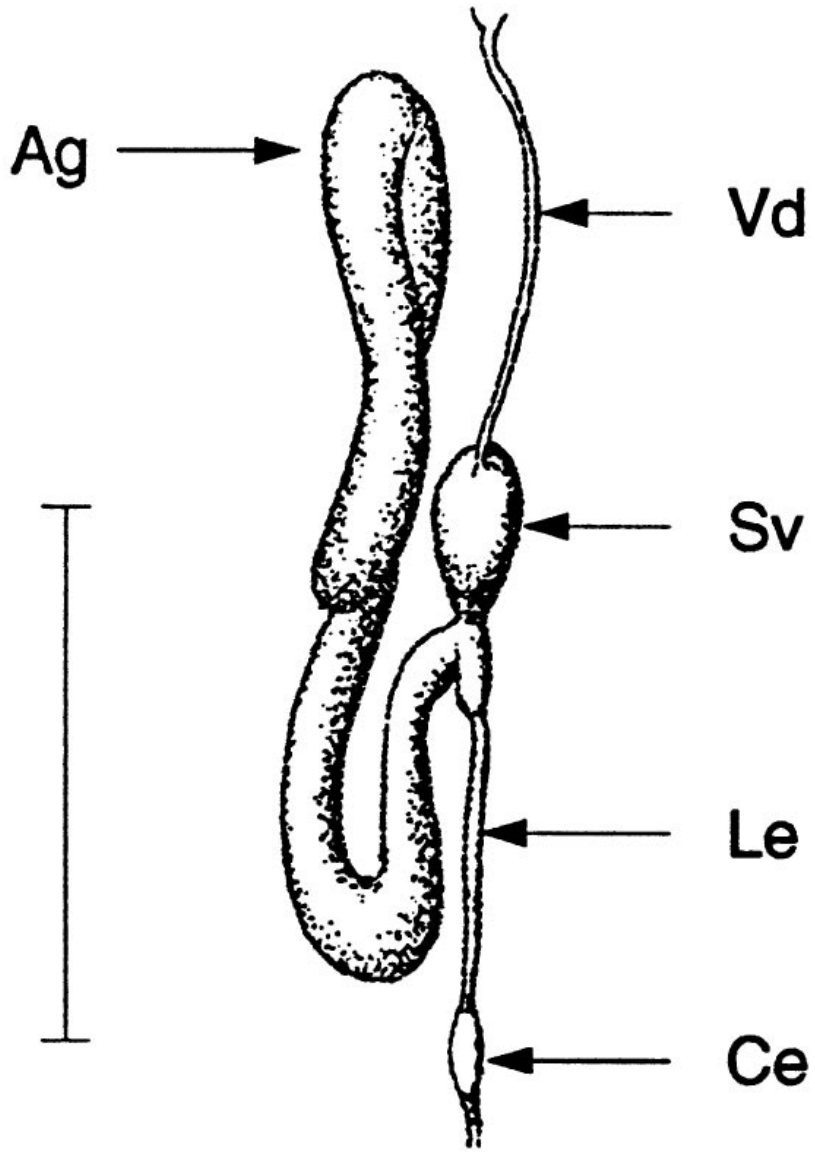


Fig. 11. *D. maidis.* Male reproductive system. Lateral view. Vd, vas deferens; Sv, seminal vesicle; Le, lateral ejaculatory duct; Ce, common ejaculatory duct; Ag, accessory gland. Vertical bar=1.0 mm.

10, and 11) which in turn opens into the egg-shaped seminal vesicle (Vd, Sv in Figs. 10, and 11). The seminal vesicle constricts to form the lateral ejaculatory duct which joins the bladder-shaped common ejaculatory duct (Sv, El, Ce in Figs. 10, and 11). The two lateral seminal vesicles are joined together by a common sheath (Sv in Figs. 10 and 11). An accessory gland arises at the posterior of each seminal vesicle and opens into the lateral ejaculatory duct (Ag, Sv, Le in Figs. 10, and 11). These accessory glands are long, tubular, and of uniform diam. Similar observations were made on the male organs of *A. constricta* by Gil-Fernandez & Black (1965) and *M. quadrilineatus* (Becker 1979). The organs of both male and female reproductive systems vary in size according to the age of the insect.

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