THE LEAFHOPPERS AND PLANTHOPPERS

Edited by

L. R. NAULT
Department of Entomology
Ohio Agricultural Research and Development Center
The Ohio State University, Wooster

J. G. RODRIGUEZ
Department of Entomology
University of Kentucky, Lexington

A Wiley-Interscience Publication
JOHN WILEY & SONS
New York • Chichester • Brisbane • Toronto • Singapore

Library of Congress Cataloging in Publication Data:
Main entry under title:

The Leafhoppers and planthoppers.

Contributions to a symposium held in honor of Dwight M. DeLong at the 1983 meeting of the Entomological Society of America in Detroit, Mich.
"A Wiley-Interscience publication."
Includes bibliographies and index.
1. Leaf-hoppers—Congresses. 2. Planthoppers—Congresses. 3. Insect-plant relationships—Congresses. 4. DeLong, Dwight Moore, 1892-1984—Congresses. I. Nault, L. R. II. Rodriguez, J. G., 1920- III. DeLong, Dwight Moore, 1892-1984. IV. Entomological Society of America.
QL525.L43 1985 595.7'52 85-5383
ISBN 0-471-80611-0
Printed in the United States of America
10 9 8 7 6 5 4 3 2 1

6
Internal Morphology and Ultrastructure of Leafhoppers and Planthoppers

EL-DESOUKY AMMAR
Department of Economic Entomology, Faculty of Agriculture
Cairo University
Giza, Egypt

6.1 INTRODUCTION

During the course of studying two circulative plant pathogens *in situ* in their planthopper vectors (4, 5), the literature search on the anatomy and histology of Auchenorrhyncha, indicated a paucity of knowledge, particularly at the ultrastructural level, on such an economically important group of insects. In their 1969 review of Homopteran morphology, Forbes and MacCarthy (27) stated that "great gaps still exist in our knowledge of the morphology of vector insects." Now, after 16 years, this statement is still true. Although the literature is rich with reports on the occurrence and accumulation sites of several viruses and mollicutes in various organs of their auchenorrhynchan vectors (76, 78, 86), the majority of these reports did not include a description of the ultrastructure of these organs, particularly in non-viruliferous" or "non-inoculative" insects. This was probably done on the assumption that the ultrastructure of the tissues involved would be largely similar to that of comparable tissues in other insect groups. But this is not necessarily so, as indicated by ultrastructural studies on the salivary glands of aphids (61, 71) or leafhoppers and planthoppers (3). Clearly, a better knowledge of the ultrastructure of homopterans will help in understanding their roles as vectors or disease inducers, and also in improving our interpretation of results when looking for a disease agent *in situ* or for its cytopathological effect on the vector. As an

example, presumed mycoplasma-like organisms in the salivary syringe and saliva of *Macrosteles fascifrons* (Stål) (73) were interpreted later, after further ultrastructural studies, as vesicles containing salivary material (74).

Even on the light microscope level, some auchenorrhynchous groups, not necessarily the most economically important ones, have been better studied than others. For instance, although all known vector species in Fulgoroidea belong to Delphacidae and Cixiidae (33), most detailed anatomical studies in this superfamily dealt with a few representative species from other families, notably Fulgoridae and Flatidae (29, 40, 41), probably because of their larger size compared to Delphacidae. However, as will be seen from this chapter, remarkable differences in several systems exist not only between the two superfamilies Cicadoidea and Fulgoroidea, but also between families of each, and in the case of the large and diverse Cicadellidae, between subfamilies or tribes.

This review deals with most of the available literature on the internal anatomy, histology, and ultrastructure of Auchenorrhyncha. The systematics and species names follow those adopted by Nielson (66) and Harris (33). The relevance or involvement of some structures in transmission, assembly, or accumulation of plant viruses or mollicutes is briefly mentioned. Additionally, some previously unpublished observations and electron micrographs on several organs from two delphacids, *Peregrinus maidis* (Ashmead) and *Javesella pellucida* (Fab.), and some cicadellids, particularly *Graminella nigrifrons* (Forbes), are included. The techniques used in preparing these organs for electron microscopy were as described previously for *J. pellucida* (4), *P. maidis*, and other species (3, 5). It is hoped that this work will focus attention, and perhaps stimulate more research, on some aspects that have been poorly studied so far, in the anatomy, histology, and ultrastructure of leafhoppers and planthoppers.

6.2 ALIMENTARY CANAL AND ASSOCIATED STRUCTURES

As in the rest of the Homoptera, the alimentary canal in leafhopper and planthoppers consists of the food canal, formed by apposition of the maxillary stylets, the precibarium, described by Backus (Chapter 7), and the gut. The latter is divided into foregut, midgut, and hindgut (Figs. 6.1 and 6.2). The foregut and hindgut are of ectodermal origin, whereas the midgut is of endodermal origin (16).

6.2.1 Foregut

The foregut starts with the cibarium, more commonly called the *sucking*, *cibarial*, or *pharyngeal pump*. This pump, which forms the greater part of the pharynx, is a short elliptical sac situated within the head just above the tentorium. The cibarium is composed of a layer of epithelial cells, lined with

cuticular intima and surrounded by two layers of (inner) longitudinal and (outer) circular muscles (28, 75). In most Homoptera, there is a gustatory organ on the epipharynx near the beginning of the cibarium (27). In the leafhopper *Typhlocyba ulmi* (Linné), Willis (89) reported that the epipharynx bears in its midline a series of perforations just before passing into the dorsal wall of the cibarium. Above this perforated plate lies a mass of cells considered to form a gustatory organ. These cells are fairly compact and similar to those of the peripheral layers of nerve ganglia. An epipharyngeal gustatory organ, consisting of eight sensillum pores, and a hypopharyngeal gustatory organ consisting of four sensillum pores were reported in the aphid *Myzus persicae* (Sulzer) (72). More details on the gustatory organs in leafhoppers are found in Chapter 7.

Following the short pharynx, which turns caudad over the tentorial bar, and starting near the vertex of the head is the esophagus (27, 89). This is usually a narrow, thin-walled tube that extends posteriorly to the mesothorax, metathorax, or first abdominal segment. Its epithelium, composed of small, uninucleate, cuboid cells that secrete a cuticular intima, is surrounded only by circular muscles in several Cicadellidae (75); whereas in some Fugloroidea it is surrounded by two layers of diagonal muscles that cross each other almost at a right angle (41). Ultrastructure of the esophagus epithelium in the delphacid *P. maidis* reveals a very thin cuticular intima and numerous cell inclusions of various sizes and shapes, in which concentric layers of apparently mineralized material are found (Fig. 6.3a). These inclusions are similar to the mineralized spherites found in the epithelia of Malpighian tubules and midgut of the fulgorid *Pyrops candelaria* L. These spherites indicate a storage excretory function (20, 22). The occurrence of such spherites in the esophagus epithelium of *P. maidis* suggests that, at least in the Delphacidae, this organ may not be "purely passive" in conducting food to the midgut, as was generally assumed previously (23, 27).

The esophagus opens into the midgut by an "esophageal valve," which is poorly developed in Cercopidae and Membracidae (62), but is usually well-defined in other Auchenorrhyncha. In many Cicadellidae, this valve is formed by a circular fold of the esophageal epithelium, lined by cuticular intima, that projects into the lumen of the midgut (75). However, in *Phalix titan* Fennah (Fulgoroidea, Tettigometridae) the valve cells appear to resemble those of the midgut (29). Goodchild (30) indicated that since this valve is not concerned with the formation of a peritrophic membrane in Hemiptera, it must function mainly in preventing regurgitation of food.

6.2.2 Midgut and Filter Chamber

The midgut, or ventriculus, differs markedly between the two superfamilies Cicadoidea and Fugloroidea, and also between some families, subfamilies, or tribes within each. In xylem and phloem feeders of Cicadoidea, a "filter chamber" is formed. Its accepted function is that of disposing of surplus water

by passing it directly to the hindgut, leaving a more concentrated solution for the ventriculus (27). A gradient of increasingly complex filter chambers has been reported by Saxena (75) within the Cicadellidae, and by Forbes and MacCarthy (27) within the Auchenorrhyncha, with the most complex type being reported in Cercopidae, which must deal with very dilute xylem sap. In the cicadellid subfamily Typhlocybinae, for example, *Typhlocyba* and *Empoasca*, which are mostly mesophyll feeders, a true filter chamber is not formed (Fig. 6.1a). Instead, the posterior end of the midgut near the junction with the Malpighian tubules, is closely apposed to the slightly dilated anterior end of the midgut,and bound there by delicate strands of muscle. The apposed parts are not enclosed within any chamber or a common membrane (75). The epithelium of the tubular intestine at the point of contact is thin and vacuolated; pumping movements in this area have been reported (89).

In Cicadellidae, other than Typhlocybinae, a similar apposition of the two extremities of the midgut exists, but the two parts are enclosed within a "filter chamber" by a thin sheath. Here, the midgut has a clearly defined anterior sac, posterior to which a narrow tubular intestine passes toward the rear of the abdominal cavity. Then it returns to a point near the esophageal valve where, together with the proximal ends of the Malpighian tubules, it passes beneath the peritoneal covering of the anterior midgut sac that forms the wall of the filter chamber. In the subperitoneal space, the posterior end of the midgut may follow a sinuous course, before emerging from the filter chamber. In species of Balcluthini (75), Agallinae (12), Macrostelini (82), and Euscelini (63), this chamber is relatively short and the distal end of the midgut forms a simple loop within the chamber (Figs. 6.1 b and d). In other cicadellids the chamber is larger and the enclosed part of the posterior midgut is coiled (Fig. 6.1c), with maximum coiling being reported in the Tettigellinae and Hecalinae (75). In all Cicadellidae with a filter chamber, a suspensory ligament runs from the midgut sac and filter chamber to join the esophagus or pharynx. Kershaw (41) described briefly the alimentary canal in Membracidae. The posterior part of the esophagus, together with portions of the posterior midgut and proximal parts of the Malpighian tubules are twisted together, and the whole mass or knot is invested by a peritoneal membrane.

Generally, the epithelia of all parts concerned with the filter chamber have flattened cells (Fig. 6.1d), large nuclei, and weakly staining cytoplasm (30). The midgut wall is composed of an outer muscular layer, containing circular and sometimes longitudinal muscles, followed by an epithelial layer of columnar or cuboid cells, usually binucleate with a striated brush border (75). Ultrastructurally, this border is composed of closely packed, double or multimembraned, microvilli (21, 50, 82). Occasionally, at the base of the epithelial cells, under the basal lamina (basement membrane), smaller cells are found; these are termed *nidi*, *replacement*, or *regenerative* cells (21, 75, 81). Marshall and Cheung (51) reported that the filter chamber in some Cicadidae and Cercopidae has two cell types: large cuboid cells that secrete a mucoprotein, and extremely thin cells that have regular tubular invaginations of the basal

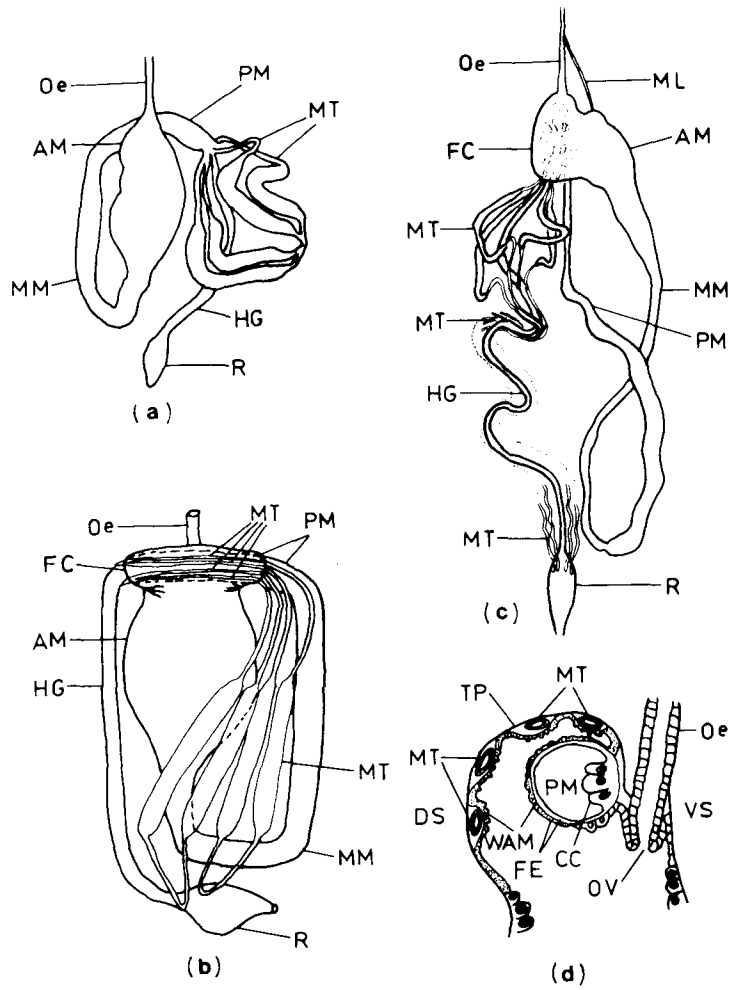

Fig. 6.1 Alimentary canal in leafhoppers (Cicadellidae). **(a)** *Empoasca;* **(b)** *Euscelis;* **(c)** *Tettigoniella;* **(d)** *Euscelis*, schematic sagital section in the filter chamber region. AM, anterior midgut; CC, columnar cells; DS, dorsal side; FC, filter chamber; FE, flatenned epithelium; HG, hindgut; ML, muscular ligament; MM, mid-midgut; MT, Malpighian tubule; Oe, esophagus; OV, esophageal valve; PM, posterior midgut; R, rectum; TP, tunica propria; VS, ventral side; WAM, wall of anterior midgut. [(a) redrawn from Saxena (75); (b) and (d) redrawn from Munk (63); (c) after Goodchild (30).]

plasma membrane. A thin cellular sheath and a thick muscle layer surround the filter chamber, whereas the filter chamber proper is lined by mucoprotein (secreted by the cuboid cells), which appears to bind potassium ions. These authors suggested that the Malpighian tubules produce a hypertonic fluid rich in potassium. This establishes an osmotic gradient from the anterior midgut to the filter chamber and then to the Malpighian tubules, so that water passes

almost directly to the hindgut and absorption of nutrients takes place in the more central regions of the midgut.

The alimentary canal of Fulgoroidea is contrasting in its simplicity, at least in gross morphology, to that of Cicadoidea (30). In Fulgoroidea the midgut is a narrow tube throughout its length and coiled into a knot-like cluster of loops from which the esophagus emerges anteriorly and the sac-like rectum posteriorly (Figs. 6.2a–d). However, a tubular or lobulate anterior diverticulum that opens into the anterior end of the midgut, extends forward alongside the esophagus into the thorax or head (30). In Delphacidae, this diverticulum is extended into the most anterior part of the head (Fig. 6.2c), whereas in *Oliarus* (Cixiidae) the diverticulum does not enter the head (Fig. 6.2d), but bends backward through the thorax reaching near the abdomen (41). In some Fulgoroidea, between the esophageal valve and the junction of the Malpighian tubules, the cluster of midgut loops is enclosed in a membranous sheath (Fig. 6.2a). In *Phalix* (Tettigometridae) this sheath is double layered; the inner cells being oenocyte-like, and the outer cells form a thin pavement epithelium (Fig. 6.2b). In *Pyrops tenebrosus* Fab. (Fulgoridae) the sheath is formed entirely of the pavement epithelium, but there is a continuous layer of oenocyte-like cells on the outer side of the midgut itself. Goodchild (29, 30) postulated that these oenocyte-like cells are able to resist the inflow of water to the blood, while the midgut cells absorb solutes from the ingesta. Thus, the contents of the intestine would become more dilute during passage along the midgut, leaving the sac-like rectum with little osmotic work to perform. However, there are cases in which the sheath is incomplete or absent, both as an enclosing membrane and on the outer surface of the midgut (29, 45, 62). Goodchild (30) suggested that the small Delphacidae, which apparently lack this sheath (Fig. 6.2c), are probably mesophyll feeders with no water-control problems. But, according to Waloff (87) and Sogawa (84), several delphacids (e.g., *Nilaparvata lugens* (Stål)) feed on the phloem. Thus, the problem of water balance in Delphacidae remains unsolved. In *Pyrilla perpusilla* Walker (Fulgoroidea, Lophopidae) a filter chamber, different from that of Cicadoidea, has been reported (58). In this species, the two extremities of the coiled midgut are twisted together like two threads of a rope, the epithelial cells of the coiled portions of midgut are thinner at the point of contact, and the coiled portions are surrounded by a cellular sheath. In some Sternorrhyncha, filtering mechanisms take the form of simple contact between parallel lengths of intestine, ensheathed by the peritoneal layer of the posterior midgut (in Aleyrodoidea and some Aphidoidea), or with the ends of the midgut twisted together (in Psylloidea) (30).

Another still debatable question is the function of the anterior diverticulum found in Fulgoroidea. Since it is usually filled with air bubbles, Licent (45) suggested that this diverticulum helps in reducing the insect's body weight, whereas Kershaw (41) suggested that it may serve as a food reservoir and to separate air from food before it passes to the midgut. However, Goodchild (30) indicated that air is commonly found in the alimentary canal of other plant-sucking Homoptera without apparent ill effect. He postulated that the diverticulum is a corollary of the ensheathed midgut in that it is used to inflate the thorax at the time of molting, a function the specialized midgut is no longer able to perform. In cells of the anterior diverticulum of *Gyarina nigritarsis* Karsch (Flatidae), accumulations of rod-like inclusions, particularly at the nymphal stage, were found by light microscopy. It was suggested that these inclusions are secreted by the above cells for subsequent utilization (31). No similar inclusions have been reported in other species, but the secretory activity of the anterior diverticulum has been suggested by several authors (29, 41, 62). Ultrastructure of the epithelial cells of this diverticulum in the delphacid *P. maidis* revealed abundant rough endoplasmic reticulum, extensive infoldings of the basal plasma membrane forming extracellular spaces, and presumptive, electron-dense, secretory vesicles (Fig. 6.3b). These cells are usually binucleate with apical microvilli lined by a thin multilayered membrane. However, in the midgut epithelium of *P. maidis* (Fig. 6.4a), microvilli are separated from the gut lumen by a much thicker (ca. 0.3 μm) multilayered membrane. A similar lining membrane has been found in the midgut of another delphacid, *J.*

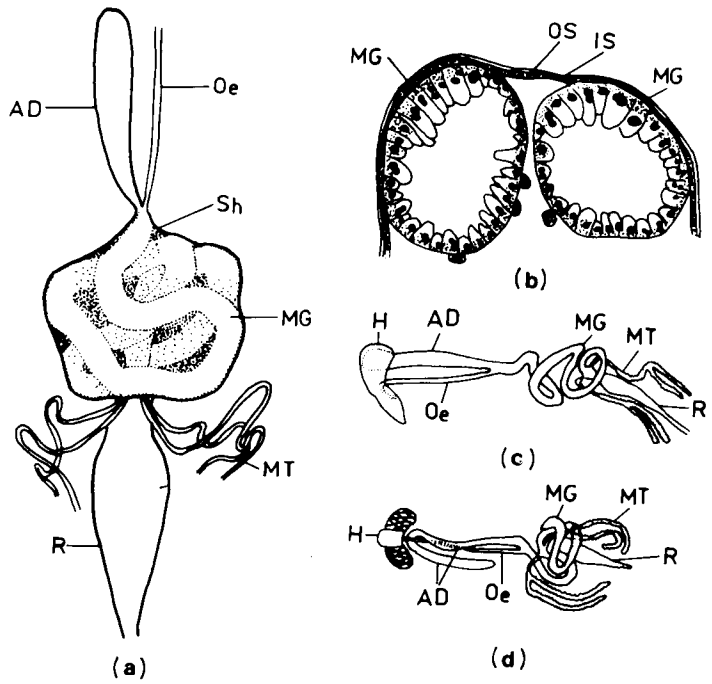

Fig. 6.2 Alimentary canal in planthoppers (Fulgoroidea). **(a)** *Pyrops*, Fulgoridae; **(b)** *Phalix*, Tettigometridae, cross section of part of ensheathed midgut; **(c)** *Perkinsiella*, Delphacidae; **(d)** *Oliarus*, Cixiidae. AD, anterior diverticulum; H, head; IS, inner layer of sheath; MG, midgut; MT, Malpighian tubule; Oe, esophagus; OS, outer layer of sheath; R, rectum; Sh, intestine sheath. [(a) and (b) after A. J. P. Goodchild (30) (c) and (d) redrawn from Kershaw (41).]

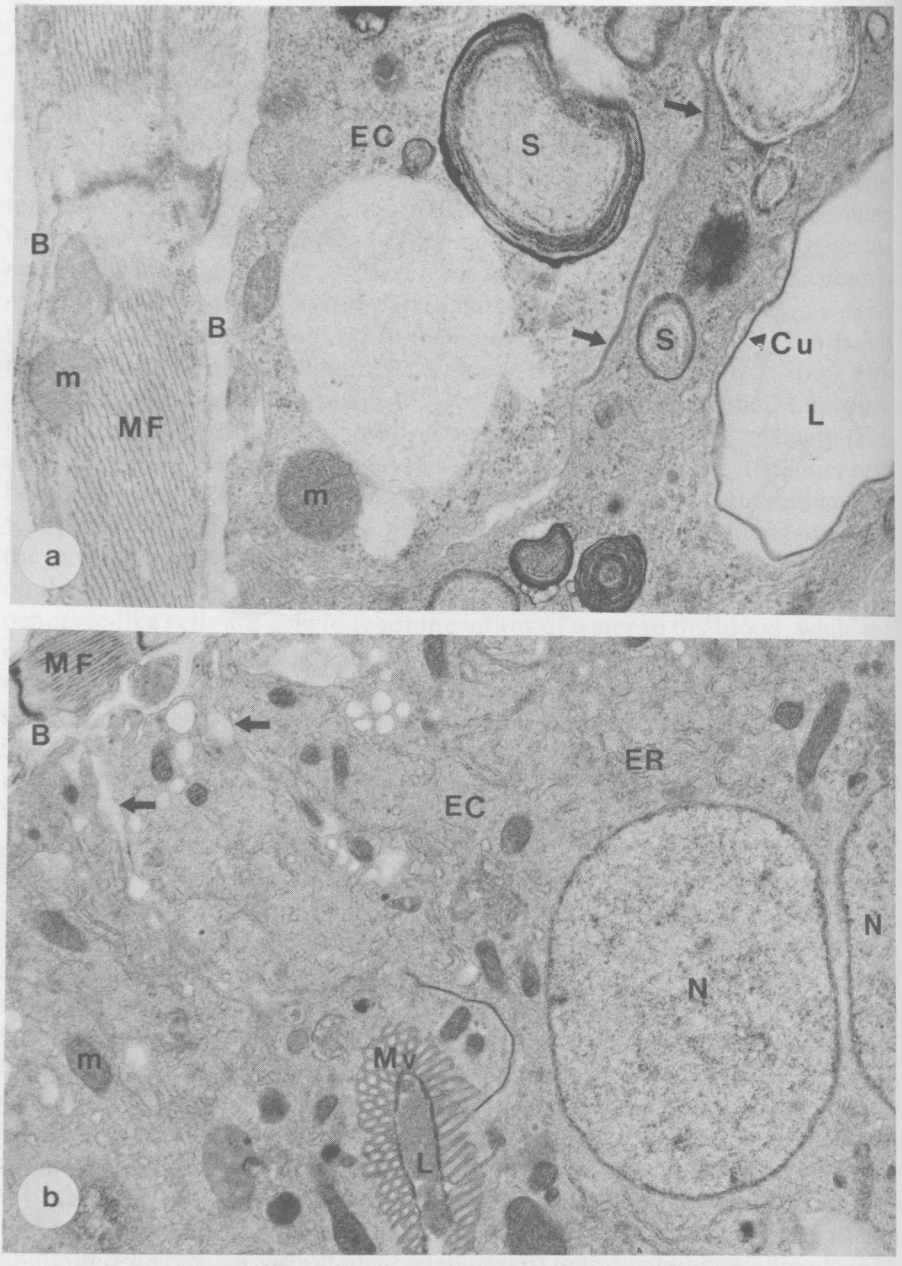

Fig. 6.3 **(a)** Esophageal wall in *Peregrinus maidis*. Epithelial cells (EC), lined with thin cuticular intima (Cu), contain multilaminated, apparently mineralized spherites (S); arrows indicate septate desmosomes at the junction between cells. 21,000x. **(b)** Anterior diverticulum in *P. maidis*. Binucleated epithelial cells (EC) with apical microvilli (Mv), rough endoplasmic reticulum (ER), and extracellular sinuses (arrows). 9000x. B, basal lamina; L, lumen; m, mitochondrion; MF, muscle fibers; N, nucleus.

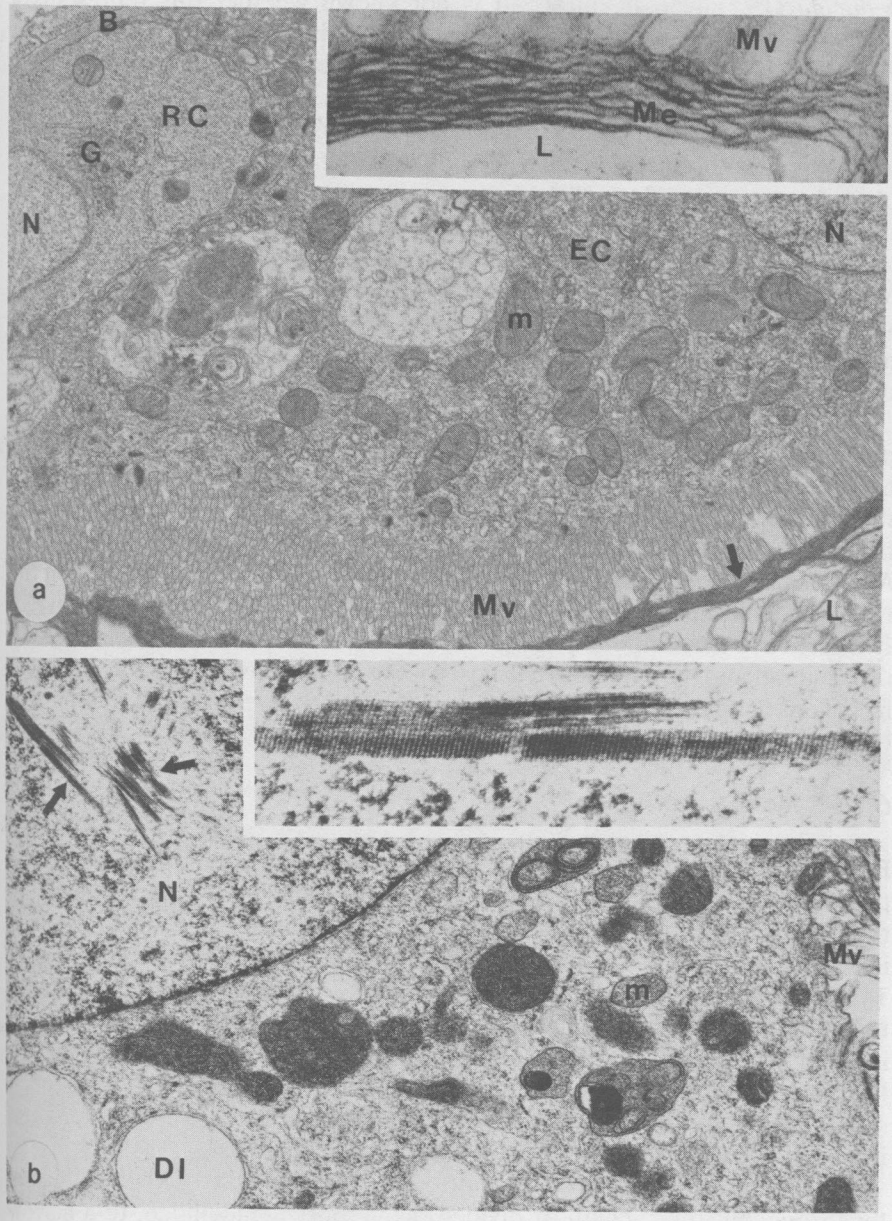

Fig. 6.4 **(a)** Midgut wall in *Peregrinus maidis*. Epithelial cells (EC), with apical microvilli (Mv), lined with a thick multilayered membrane (arrow); a smaller regenerative cell (RC) is seen at the base. 9000x. Inset: Details of the lining membrane (Me) and microvilli (Mv) in the midgut of *Javesella pellucida*. 20,000x. **(b)** Part of an epithelial cell in a Malpighian tubule of *P. maidis*. Note apical microvilli (Mv) and intranuclear paracrystalline inclusions (arrows), shown at higher magnification in the inset. 13,500x; inset, 60,000x. B, basal lamina; DI, probably dissolved inclusions; G, Golgi body; L, lumen; m, mitochondrion; N, nucleus.

pellucida (13, Fig. 6.4a, inset). It is not known whether this represents a peritrophic membrane, which is thought to be lacking in Hemiptera (30, 81). In *P. candelaria* (Fulgoridae) the midgut epithelial cells are separated from the lumen by an extensive plexiform surface coat, cytochemically defined as a PAS-positive acid mucopolysaccharide. It was suggested that this coat is particularly important as a site of enzymatic digestion and may possibly act also as a place for action binding (50). More recently, interesting ultrastructural and cytochemical differences between cells of the anterior, middle, and posterior parts of the midgut in *P. candelaria* have been reported by Cheung and Marshall (22). They suggested that the anterior midgut is ultrastructurally suited to enzyme synthesis and release and to the absorption of nutrients; the middle midgut for storage excretion; and the posterior midgut for the secretion of ions from the hemolymph to the gut lumen.

After being ingested with food by their vectors, circulative plant viruses are presumed to pass through the gut wall into the hemocoel. Many of these viruses have been reported to accumulate and perhaps multiply in the midgut cells of their vectors (76, 78). Additionally, rice dwarf virus was reported to pass through the microvilli of the third ventriculus (posterior midgut) in the vector *Nephotettix cincticeps* Uhler (64). Maize mosaic virus was found to bud on the nuclear membrane of regenerative cells in the midgut of infective *P. maidis* (5). In infective and non-infective individuals of the latter species, epithelial cells of the midgut and Malpighian tubules contained intranuclear paracrystalline inclusions of unknown nature (Fig. 6.4b), that might be confused with filamentous viruses or viral inclusions.

6.2.3 Malpighian Tubules

Four Malpighian tubules are reported in Auchenorrhyncha, opening near the posterior end of the midgut. In many species of Cicadellidae, two Malpighian tubules open separately and two are fused just before entering the midgut, but in some species all four tubules are fused at their proximal end (45, 75). In Typhlocybinae and Balcluthini, the distal ends of the four tubules are fused together, with the lumen being continuous across the junction (Fig. 6.1a), but in other Cicadellidae the distal ends of the tubules are separately attached to the rectum (Fig. 6.1c). In many Fulgoroidea, the four Malpighian tubules open separately into the midgut (30), while in Delphacidae the proximal regions fuse in pairs to form two ureters (Fig. 6.2).

Malpighian tubules may be lobulate or smoothly tubular, of a similar diameter throughout their length or divided, as in most Cicadellidae, to a narrow proximal part and a wider distal one. In cross sections, the first part, believed to be excretory, is composed of one layer of uninucleate epithelial brush-bordered cells around the lumen, with no surrounding muscle fibers. But the second part, the so-called glandular is composed of very large cells that almost occlude the lumen, surrounded by a thin layer of muscle fibers (75). Ultrastructure of the Malpighian tubules in the cicadellid *G. nigrifrons* (Fig. 6.5a), the

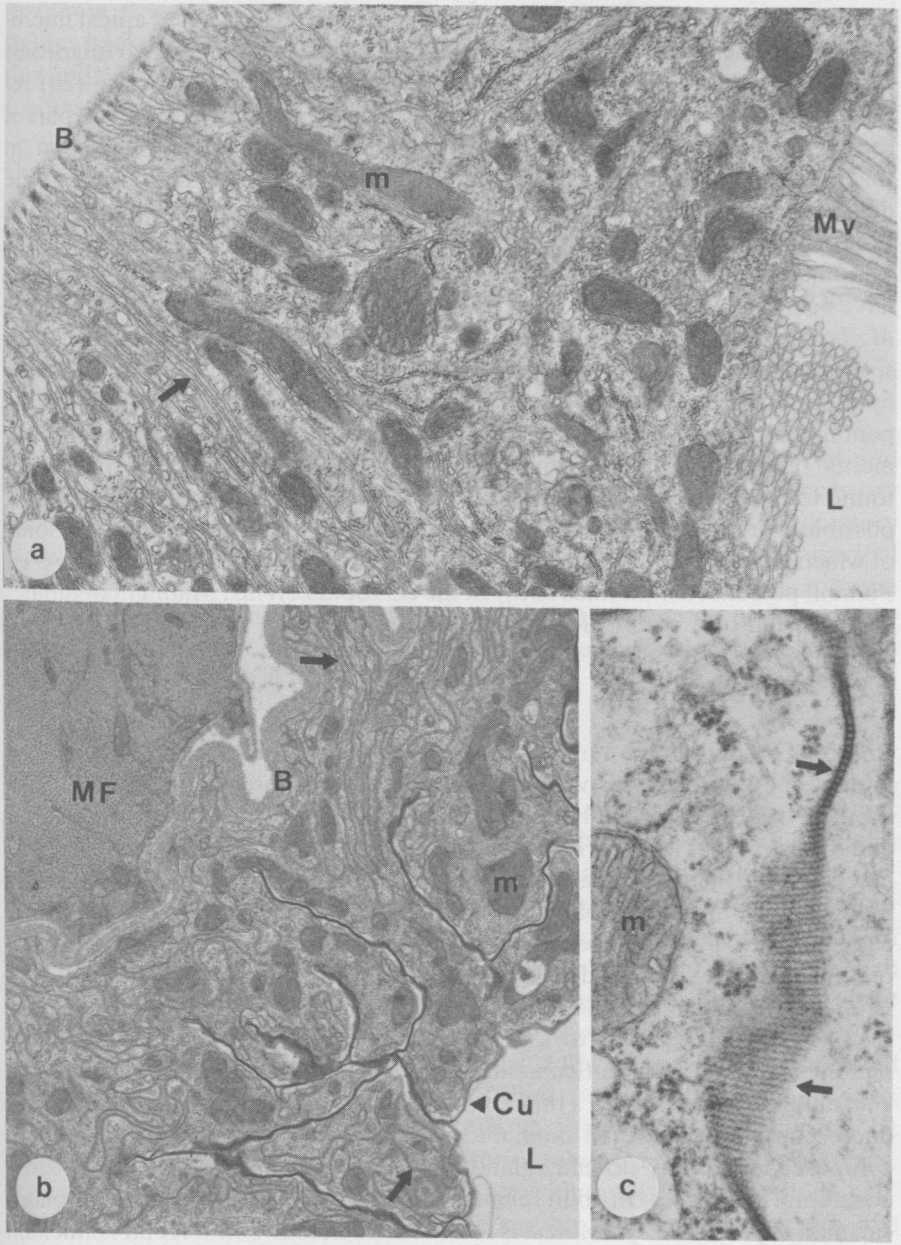

Fig. 6.5 **(a)** Malpighian-tubule epithelium of *Graminella nigrifrons*. Note apical microvilli (Mv), and deep extensive basal infoldings of plasma membrane (arrow), with associated long mitochondria (m); B, basal lamina. 14,000x. **(b)** Hindgut epithelium of *Peregrinus maidis*, lined with cuticular intima (Cu). Note extensive basal and apical infoldings of plasma membrane (arrows), and thick basal lamina (B). 9000x. **(c)** Details of a septate desmosome (arrows), commonly found at cell junctions of gut epithelium, in *P. maidis*. 45,000x. L, lumen; m, mitochondrion; MF, muscle fibers.

delphacid *P. maidis*, and the fulgorid *P. candelaria* (20) revealed apical microvilli and extensive basal infoldings of plasma membranes. In the two fulgoroids just mentioned, mineralized spherites are frequently found. Cheung (20) reported that in *P. candelaria* these spherites, which are found in the distal part of the Malpighian tubules, may develop from mitochondria. He suggested that, in this insect, secretion of ions, and mineral storage excretion may occur at the distal part, whereas resorption of solutes may occur at the proximal part of Malpighian tubules as well as in the rectum.

Some interesting structures in the Malpighian tubules of Auchenorrhyncha have been found by electron microscopy. In a certain region of these tubules in *M. fascifrons*, *N. cincticeps*, and some other leafhoppers, a bizarre-shaped secretory product, the brochosomes, has been reported (64, 81, 82). These are lipid- and protein-containing bodies consisting of hollow polyhedra, upon the pentagonal and hexagonal facets of which are constructed sculptured compartments. It is noteworthy that similar structures, of unknown function, have been found to cover the whole body surface of several leafhopper species (32). It is possible that brochosomes are excreted in the honeydew of leafhoppers, some of which have the habit of "grooming" themselves with their excrement (A. H. Purcell, personal communication). In the cercopid *Ptyelus*, Malpighian tubules are reported to secrete calcium carbonate in the form of a spiral shell (81).

6.2.4 Hindgut

In most Cicadellidae, a "pyloric valve" is found at the junction between the midgut and hindgut. This valve, situated behind the origin of the Malpighian tubules, is formed of a fold of uninucleate cells that project from the posterior end of the midgut into the lumen of the hindgut (75). The latter consists of an anterior long "ileum" and a posterior short "rectum" (Fig. 6.1). The wall of the hindgut is composed of barrel-shaped uninucleate epithelial cells, lined by cuticular intima. The ileum is surrounded by circular muscles whereas the rectum is usually surrounded by longitudinal and circular muscles (23, 75).

In Fulgoroidea the hindgut consists of an expanded thin walled sac-like rectum (Fig 6.2), similar to that of Heteroptera; the pyloric valve and the rectum are lined with cuticular intima (29). The rectal walls, dorsally and ventrally, are composed of a thin epithelial layer, described as *syncytial* by light microscopy, with scattered small nuclei. The lateral walls form the rectal pad, composed of larger, domed, gland-like cells, with large nuclei and dense cosinophil cytoplasm. In adult females, the "rectal organ," a large hemispherical mass of yeast-like symbiotes, is found between the ventral rectal epithelium and its peritoneal covering (29, 58). Ultrastructural studies on the rectal epithelium of *P. candelaria* (19) and *P. maidis* (Fig. 6.5b), revealed extensive basal and apical infoldings of plasma membranes. The lateral cell membranes take a sinuous course and include many septate desmosomes (Fig. 6.5c). The cuticular intima lining the rectum of *P. candelaria* is about 0.4 μm thick, whereas that of *P. maidis* is much thinner. Cheung (19) suggested that the rectum in *P. candelaria* is concerned with transport of water and/or essential solutes back to the hemolymph, as in many other insects (16). The extremely thin cuticle lining both the esophagus and the rectum in *P. maidis* has also been reported in Peloridiidae (Coleorrhyncha), which similarly possess no filter chamber (69). This may indicate that in such cases, these two parts of the alimentary canal may be involved in water or ion regulation. However, more extensive ultrastructural, cytochemical, and physiological studies are necessary for understanding the problem of osmoregulation in Fulgoroidea, particularly the Delphacidae, which includes the majority of vector species in this superfamily.

6.3 SALIVARY SYSTEM

The salivary glands in Homoptera are labial glands, lying in the head and thorax. On each side, typically, there is a principal gland and an accessory gland; both are composed of secretory and duct cells. The duct of the accessory gland unites with that of the principal gland (Fig. 6.6), then the two principal ducts usually unite to form a common salivary duct that discharges into the salivary pump or syringe. A short meatus connects this pump to the salivary canal, the posterior of the two canals formed by the apposition of the maxillae (56).

6.3.1 Salivary Glands and Ducts

Large anatomical differences exist between the salivary glands of various groups in Auchenorrhyncha (56, 68). In Typhlocybinae, the principal gland is composed of three to four lobes (11, 89). In another cicadellid subfamily, Hecalinae, the principal gland is subdivided into a small rosette-shaped cluster of about 15 "lobules" situated in the prothorax and an elongated cluster of about 45 lobules, which extends forward along the lateral margins of the head (75). Based on staining reactions, the three lobes of the principal gland of *Typhlocyba* did not seem to differ in structure or function (89). In Deltocephalinae and Tettigellinae, a histochemical study by Sogawa (83) indicated that the principal gland is composed of a bilobed compact mass, made up of six types of acini, or follicles, of secretory cells. In *N. cincticeps* the anterior lobe consists of cell types I and II, and the posterior lobe of cell types III–VI (Figs. 6.6a and c). All secretory cells are binucleate with ramifying intracellular canaliculi. In this insect, the accessory gland is composed of two parts, a proximal globular part and a distal tubular one. The wall of the principal duct is composed of a layer of epithelial cells, surrounding a lumen lined by chitinous intima. Sogawa (83) suggested that type IV cells of the principal gland produce digestive enzymes, type V cells secrete one of the sources of the salivary sheath, and that the tubular part of the accessory gland may absorb selectively certain non-protein solutes from the hemolymph. Five types of acini in the principal

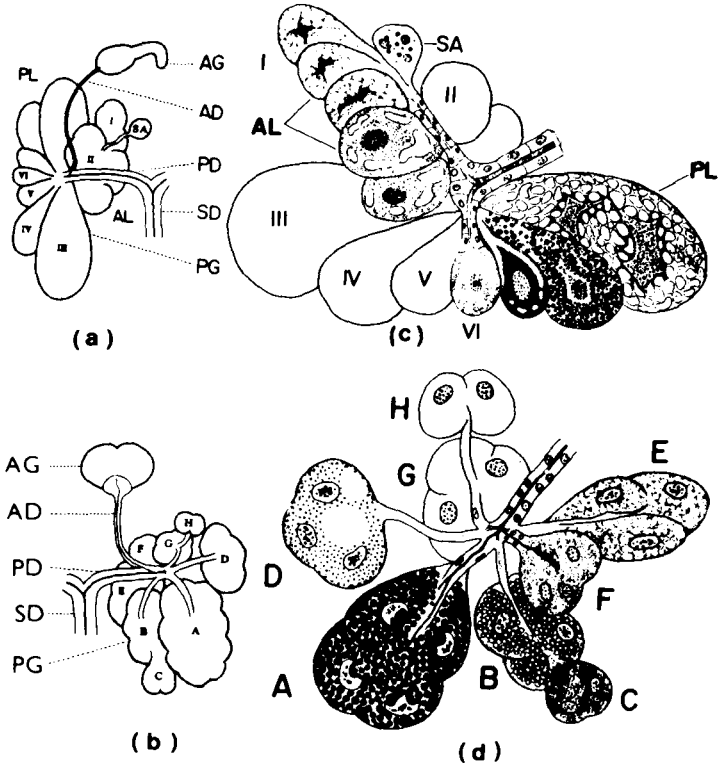

Fig. 6.6 Diagrams of the salivary glands and ducts in **(a)** Deltocephalinae (Cicadellidae) and **(b)** Delphacidae; and diagramatic sections of the principal salivary glands in **(c)** *Nephotettix cincticeps* (Cicadellidae), and **(d)** *Leodelphax striatellus* (Delphacidae). I–IV, acini types in Cicadellidae; A–H, acini types in Delphacidae; AD, accessory duct; AG, accessory gland; AL, anterior lobe; PD, principal duct; PG, principal gland; PL, posterior lobe; SA, small appendage; SD, salivary duct. [After Sogawa (83).]

salivary gland were distinguished in *M. fascifrons* (*Cicadula sexnotata*, 23) and in *Agallia constricta* Van Duzee (28), whereas only three types were detected in that of *Idiocerus atkinsoni* L. and *I. clypealis* L. (7). Little is known about the salivary glands of Cercopidae. Nuorteva (68) described briefly those of *Aphrophora* and *Philaenus*, indicating that the principal salivary gland is composed of a compact group of cells and a "crown" of sometimes tubular acini, corresponding respectively to the anterior and posterior lobes of that in Cicadellidae. In the cicada *Purana tigrina* Walk., the principal salivary gland consists of several digitate lobes, arranged in two sectors, cephallic and thoracic. All lobes of both sectors are reported to be similar in histology and staining reactions (49). The accessory gland in this insect is apparently unique, consisting of a very long convoluted, collapsible secretory tube which is more than 30 times longer and six times wider than the accessory salivary duct. Livingstone (49) suggested that this gland serves in secretion and storage of watery saliva.

In Fulgoroidea, Miles (55) reported 10 lobes in the gland of a flatid, without distinguishing an accessory gland. In several species of Delphacidae, Sogawa (83) and Balasubramanian and Davies (9) described nine to ten types of acini. Sogawa designated one of these as an accessory gland, and listed the number of cells in each type of acinus as varying between two and eight; whereas Balasubramanian and Davies listed two kinds of acini as unicellular, but these authors agree that all secretory cells are binucleate. Salivary secretions are apparently collected in intracellular vacuoles before passing into the narrow intercellular lumen of the duct system. Each acinus has its own ducteole, which connects the intercellular canaliculi and the principal salivary duct (Figs. 6.6b and d). Duct cells are generally much smaller than secretory cells, and their staining reaction is not as diverse as the latter (9). In *Laodelphax striatellus* (Fall.) and *N. lugens*, eight acini (designated A–H) in addition to an accessory gland are reported (83). On the basis of a histochemical study on the latter species, Sogawa (84) suggested that the salivary sheath is the product of two distinct secretions, a protein and probably an unsaturated lipid, which are formed in acinus A and acini G and H, respectively. Acinus E is thought to secrete a quinone, which functions as a tanning agent to enhance the coagulation of the proteinaceous secretion from acinus A during the process of stylet sheath formation. In addition to the sheath material, a diffusible or watery saliva, which probably contains digestive enzymes is also secreted by the salivary glands. α-Glucosidase, which hydrolyzes sucrose and trehalose, and β-glucosidase, which acts on phenolic glucosides, were detected in the salivary glands of *N. lugens*. However, more extensve studies on the salivary secretions and their sources have been reported on Heteroptera than on Homoptera, probably because the former have simpler salivary glands, at least morphologically (56).

Detailed ultrastructural studies on the salivary glands of Homoptera are also scanty, dealing mainly with aphids (61, 71). When examined by light microscopy, the salivary glands of *P. maidis* are similar to those of other delphacids described by Sogawa (83), in having eight acini (A–H) in the principal gland in addition to an accessory gland. However, Balasubramanian (8) reported only six types of acini in the principal salivary gland of *P. maidis*. Electron microscopy on this species (Ammar, unpublished) indicated that acini types B and C are similar, as are acini types G and H, whereas all other acini are different. Thus only six acinar types in the principal gland and one in the accessory gland are distinguishable. Each acinar type contains secretion granules or vesicles, different in electron opacity, internal structure, shape, or size from those of other types. Generally, extensive basal infoldings of the plasma membrane in secretory cells and apical infoldings of that in duct cells were observed. Ducteoles were lined with spiral cuticular intima. Muscle cells and myofibrils, supplied with small nerves and tracheoles, were found usually in the peripheral areas of the principal salivary glands of *P. maidis* (Fig. 6.7) and *M. fascifrons* (3). These muscle cells probably help, by contraction, in the discharge of secretory material from secretory cells to salivary ducteoles and ducts. In

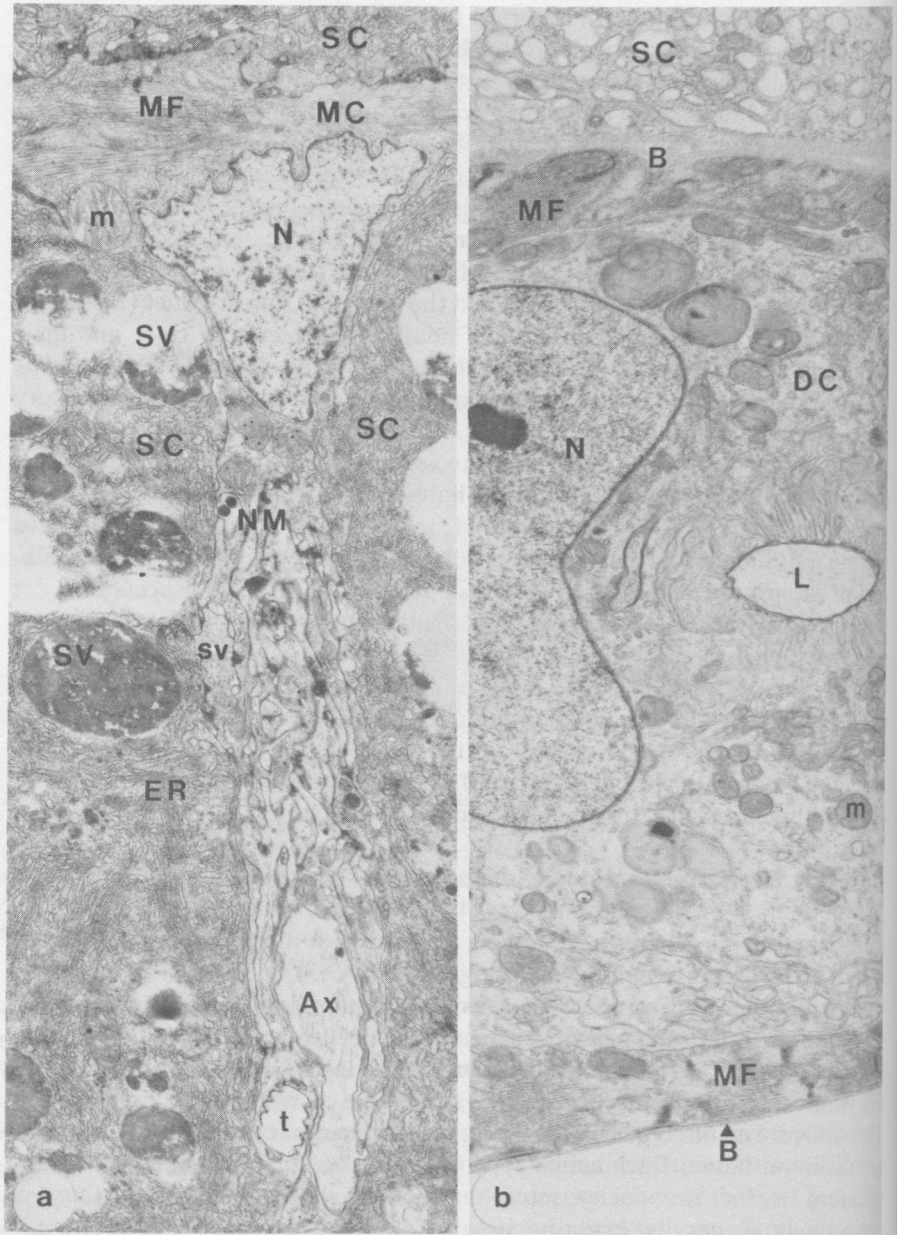

Fig. 6.7 Sections in the principal salivary gland of *Peregrinus maidis*. **(a)** Part of acinus A; secretory cells (SC) with extensive rough endoplasmic reticulum (ER) and full to empty secretion vesicles (SV); between these cells is a muscle cell (MC) containing nucleus (N), mitochondria (m), and myofilaments (MF). Ax, nerve axon; NM, neuromuscular junction; sv, synaptic vesicles; t, tracheole. 9000x. **(b)** Duct cells (DC) surrounding cuticule-lined lumen (L) of a salivary ducteole. Note striated myofibrils (MF) under the basal lamina (B) surrounding duct cells. m, mitochondrion; SC, secretory cell. 9000x; from Ammar (3).

unoccupied spaces (47). Colored whitish, pale yellow, or greenish, this fat or adipose tissue, with bi- or uninucleate cells, is well-supplied with tracheae and surrounded by many small cells that lack obvious accumulations of lipid (28). In aphids, such cells are apparently connective tissue cells (72). The fat tissue is more abundant in leafhopper nymphs and females than in males, usually decreasing with insect age (80). In the cicadellid *Colladonus montanus* Van Duzee (88), the fat tissue consists of urate cells, which surround the mycetomes, and trophocytes, which occur throughout the insect's body. Large accumulations of granule-laden trophocytes were found in nymphs, whereas in adults various stages of apparent depletion occurred. These stages involved utilization of granules or in some cases of entire cells, followed by the appearance of stellate nuclei, and increasing vacuolation. Littau (46) reported that glycogen, protein, and fat are stored in the fat-body cells in leafhoppers, and that the cytoplasm of these cells was richer in RNA in females than in males. Since the suspensor filaments of the ovarioles are in contact with fat tissue, it was suggested that the latter may provide a source of nourishment for the developing oocytes.

Ultrastructure of cells of fat tissue in the head of *P. maidis* (Fig. 6.8a) showed accumulations of large lipid droplets, masses of glycogen granules, in addition to numerous mitochondria, rough endoplasmic recticulum and irregular-shaped electron-dense vesicles. These vesicles look similar to the phagocytic inclusions reported in fat cells of *A. constricta* (77), and may be related to the cytolysomes found in the fat cells of other insects (81). Several reports suggested that fat tissues in leafhoppers and planthoppers are major sites for multiplication and accumulation of propagative plant viruses in their vectors (33, 76, 78).

6.5 MYCETOMES AND MYCETOCYTES

The mycetome is a special organ in the hemocoel composed of large mycetocyte cells, housing symbiotic organisms, and surrounded by an epithelium either free of symbiotes or harboring secondary symbiotes. Mycetocytes usually contain a large multilobate, reportedly polyploid, nucleus. They are thought to be derived from fat cells or leucocyte blood cells (27, 37, 44). Among Homoptera, only the Typhlocybinae appear to be without mycetocytes (27). In other Cicadellidae, mycetomes are paired organs, usually distinct on each side of the abdomen (14, 23). Two membrane bound, colorless to yellowish mycetomes are located in the first through third abdominal segments of *A. constricta*, attached to the integument by tracheae (28). In the earliest embryological stages of *Graphocephala coccinea* Forstier, the mycetome is a spherical unpaired organ, but later in development it is replaced by two lateral organs (39). In this and many other cicadellids more than one type of symbiotic organism has been reported (37, 44). The mycetocytes of the embryonic, postembryonic, and adult stages of *N. cincticeps* have been studied ultra-

aphids, a single myoepithelioid cell connecting both lobes of the principal salivary gland has been reported (71). Apparently, muscle cells have not been reported in the salivary glands of insects outside the Homoptera.

Circulative plant viruses and mollicutes are presumed to pass from the vector to the plant with the salivary secretions during feeding and salivation. Many of these disease agents have been reported in the salivary glands of their vectors (33, 48, 76, 78). Recently, maize mosaic virus was found in most acini of the principal and accessory salivary glands of infective *P. maidis*. Virus particles budded on nuclear, cytoplasmic, and plasma membranes of secretory cells, and were found in the cytoplasm, secretion vesicles, intracellular vacuoles, and in extracellular and intercellular spaces (5). Several workers reported the occurrence of virus-like particles in the salivary glands of leafhoppers and planthoppers that were not infective to plants (e.g., 4, 34, 79). Also, rickettsia-like bodies were found in cytoplasmic vacuoles of acini types III–V of non-infective *M. fascifrons* (74). Bacteroid symbiotes were reported in the cytoplasm and nuclei of secretory cells in the salivary glands of *N. cincticeps* (64). However, the nature of the relationship between the above organisms and their leafhopper or planthopper hosts clearly needs further investigation.

6.3.2 Salivary Pump

The salivary pump, or syringe, in Auchenorrhyncha has been described in detail in very few species. In *T. ulmi* (Typhlocybinae), this pump lies in, and toward the anterior end of, the chitinous hypopharynx (89). It consists of a chamber with anterior and lateral thick chitinous walls, but the posterior wall, or diaphragm is composed of a sheet of thin flexible chitin. Inserted on this diaphragm, and protruding into the pump chamber, is a thickened piston-like structure, the base of which is attached to two large flat muscles. The common salivary duct enters the pump chamber ventrally on a level with the tip of the piston with no valve in this afferent duct. A fine ejaculatory (or efferent) duct runs from the anterior end of the pump chamber to the tip of the hypopharynx lip. In *M. fascifrons* (Macrostelini) a somewhat more complex salivary pump has been described by Raine and Forbes (73). It consists of a piston in a closed cylinder, connected posteroventrally to an afferent duct from the salivary gland, and to an efferent duct to the stylets. The opening of the afferent duct is regulated by a flap valve, which allows the saliva to enter the pump and prevents it from flowing back. But in the above species the efferent canal is apparently not supplied with a valve like that reported in some Heteroptera.

6.4 FAT BODY

In Homoptera, the so-called fat body is a tissue of irregular masses of large cells or trophocytes, containing fat granules. The fat tissue is distributed in the hemocoel, mostly in the abdomen and head, where cell masses appear to fill

unoccupied spaces (47). Colored whitish, pale yellow, or greenish, this fat or adipose tissue, with bi- or uninucleate cells, is well-supplied with tracheae and surrounded by many small cells that lack obvious accumulations of lipid (28). In aphids, such cells are apparently connective tissue cells (72). The fat tissue is more abundant in leafhopper nymphs and females than in males, usually decreasing with insect age (80). In the cicadellid *Colladonus montanus* Van Duzee (88), the fat tissue consists of urate cells, which surround the mycetomes, and trophocytes, which occur throughout the insect's body. Large accumulations of granule-laden trophocytes were found in nymphs, whereas in adults various stages of apparent depletion occurred. These stages involved utilization of granules or in some cases of entire cells, followed by the appearance of stellate nuclei, and increasing vacuolation. Littau (46) reported that glycogen, protein, and fat are stored in the fat-body cells in leafhoppers, and that the cytoplasm of these cells was richer in RNA in females than in males. Since the suspensor filaments of the ovarioles are in contact with fat tissue, it was suggested that the latter may provide a source of nourishment for the developing oocytes.

Ultrastructure of cells of fat tissue in the head of *P. maidis* (Fig. 6.8a) showed accumulations of large lipid droplets, masses of glycogen granules, in addition to numerous mitochondria, rough endoplasmic recticulum and irregular-shaped electron-dense vesicles. These vesicles look similar to the phagocytic inclusions reported in fat cells of *A. constricta* (77), and may be related to the cytolysomes found in the fat cells of other insects (81). Several reports suggested that fat tissues in leafhoppers and planthoppers are major sites for multiplication and accumulation of propagative plant viruses in their vectors (33, 76, 78).

6.5 MYCETOMES AND MYCETOCYTES

The mycetome is a special organ in the hemocoel composed of large mycetocyte cells, housing symbiotic organisms, and surrounded by an epithelium either free of symbiotes or harboring secondary symbiotes. Mycetocytes usually contain a large multilobate, reportedly polyploid, nucleus. They are thought to be derived from fat cells or leucocyte blood cells (27, 37, 44). Among Homoptera, only the Typhlocybinae appear to be without mycetocytes (27). In other Cicadellidae, mycetomes are paired organs, usually distinct on each side of the abdomen (14, 23). Two membrane bound, colorless to yellowish mycetomes are located in the first through third abdominal segments of *A. constricta*, attached to the integument by tracheae (28). In the earliest embryological stages of *Graphocephala coccinea* Forstier, the mycetome is a spherical unpaired organ, but later in development it is replaced by two lateral organs (39). In this and many other cicadellids more than one type of symbiotic organism has been reported (37, 44). The mycetocytes of the embryonic, postembryonic, and adult stages of *N. cincticeps* have been studied ultra-

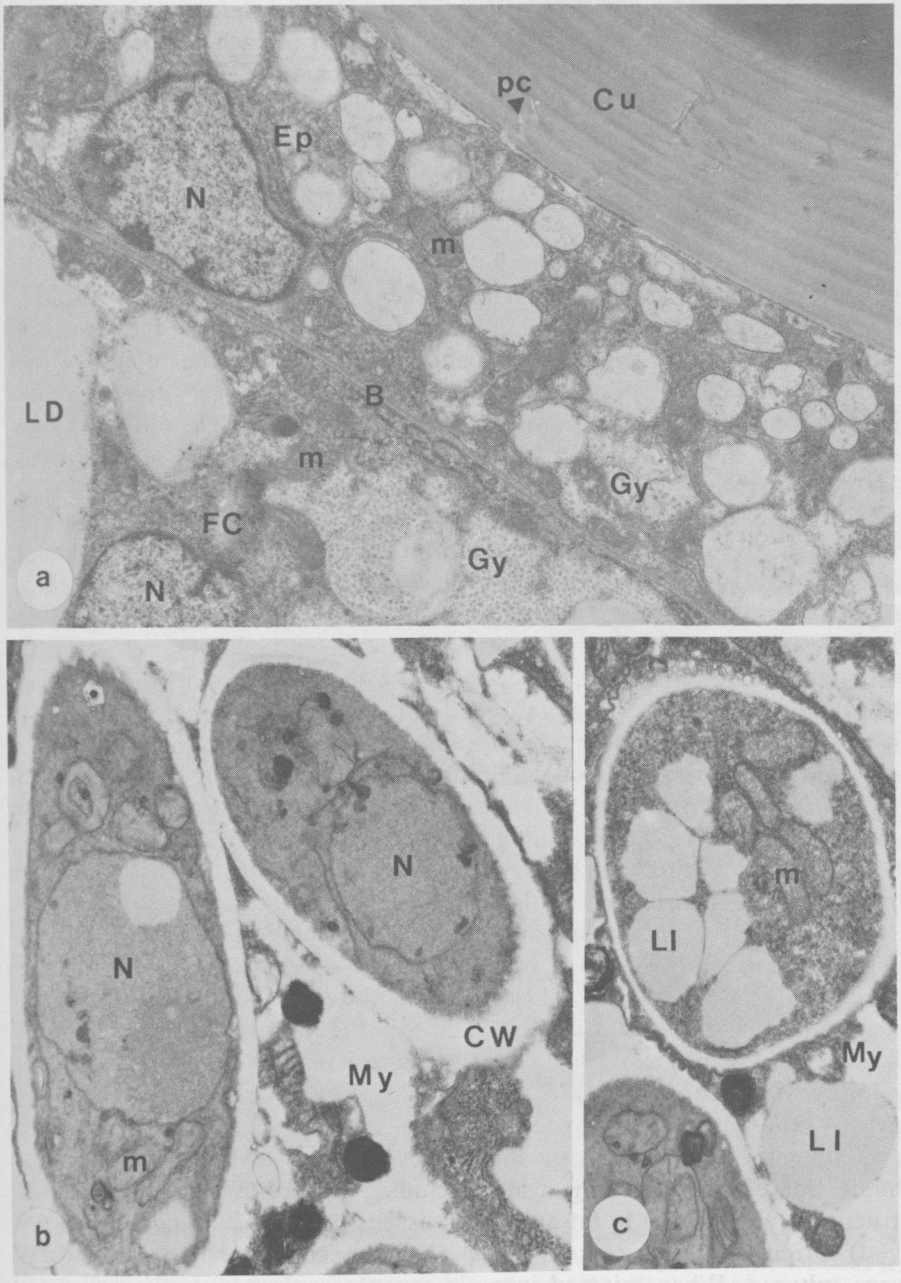

Fig. 6.8 **(a)** Epidermal (Ep) and fat (FC) cells, in the head of *Peregrinus maidis*. Note multilamellated cuticle (Cu) with pore canals (pc), large lipid droplets (LD) in fat cell, and glycogen granules (Gy) in both tissues. B, basal lamina; N, nucleus. 9000x. **(b)** and **(c)** Yeast-like symbiotes in the egg mycetome of *P. maidis*. Note enveloped nucleus (N), mitochondria (m), cell wall (CW), and lipid inclusions (LI) in these symbiotes, and similar inclusions in the mycetocyte (My). 14,000x.

structurally (64). In the embryo, before blastokinesis, L (electron lucent) and H (electron opaque) symbiotes are found together in each cell of the mycetome. At the blastokinetic stage, L and H symbiotes are found in separate cells, while smaller bacteroids are found between yolk bodies. In the nymphal and adult stages, the mycetome is divided into four distinct areas: an external monolayer of uniform cells, an intermediate (multilayered) area containing H symbiotes, an internal area containing L symbiotes, and a central area containing bacteroids.

In Fulgoroidea, females are reported to have an unpaired mycetome, the rectal organ, composed of a few large binucleate mycetocytes (14). In Derbidae, this organ is situated behind the pyloric valve, between the intestinal epithelium and the muscular layer, and protruding into the lumen of the hindgut. But in Meenoplidae, the ring-shaped rectal organ is situated within the pyloric valve, between the two walls of the intestinal fold. In addition to the rectal organ, found only in females, Buchner (14) described several other symbiote-containing organs found in both sexes in Fulgoridae, Cixiidae, Delphacidae, and some other fulgoroid families. Some workers reported that the rice delphacids *L. striatellus*, *N. lugens*, and *Sogatella furcifera* (Horv.) do not have a distinct mycetome, but harbor yeast-like symbiotes in the fat body (17, 67). However, Buchner (14) indicated that although symbiotic yeasts are commonly housed in fat body cells in Fulgoroidea, special f organs allied with yeasts are found. In Delphacidae, these are paired, very small, and easily overlooked tubular mycetomes situated in the vicinity of the gonads. Nevertheless, generally a well-defined mycetome ball is found in the eggs of leafhoppers and planthoppers, including Delphacidae (Figs. 6.8 b and c). From the eggs of *N. lugens*, two morphologically different yeast-like symbiotes were isolated, which had a common antigenicity with those isolated from *L. striatellus* and *S. furcifera* (65). In adult males and females of *N. lugens*, yeast-like symbiotes were reported only in the abdomen, never in the head or thorax (17). However, electron microscopy of the fat tissue in the head of adult *P. maidis* (Fig. 6.9a) revealed yeast-like organisms similar to those found in the egg mycetome (Figs. 6.8 b and c). These organisms possess a cell wall, a membrane bound nucleus, mitochondria, lipid, and electron-dense inclusions. Some of these organisms appeared to be in the process of budding or cleavage, as reported with other yeasts (17, 53). In the egg mycetome and adult fat tissue, mycetocytes contained lipid material; their large nuclei were irregularly shaped, sometimes to accommodate or partly engulf several of the yeast-like symbiotes. Some other microorganisms, including bacteroids and rickettsia-like structures, were found in fat and other tissues of adult *P. maidis* (Figs. 6.9 b–d). From laboratory-reared insects of this species, four bacterial isolates were cultured. When injected into old nymphs, only one of these isolates *(Staphylococcus scuiri)* proved pathogenic (Ammar, Nault, Styer, and Saif, unpublished).

An interesting case of the absence of a mycetome from the eggs of the fulgoroid *Scolypopa australis* (Walker) (Ricaniidae) has been reported (25). More details on symbiotes and symbiosis are found in Chapter 8.

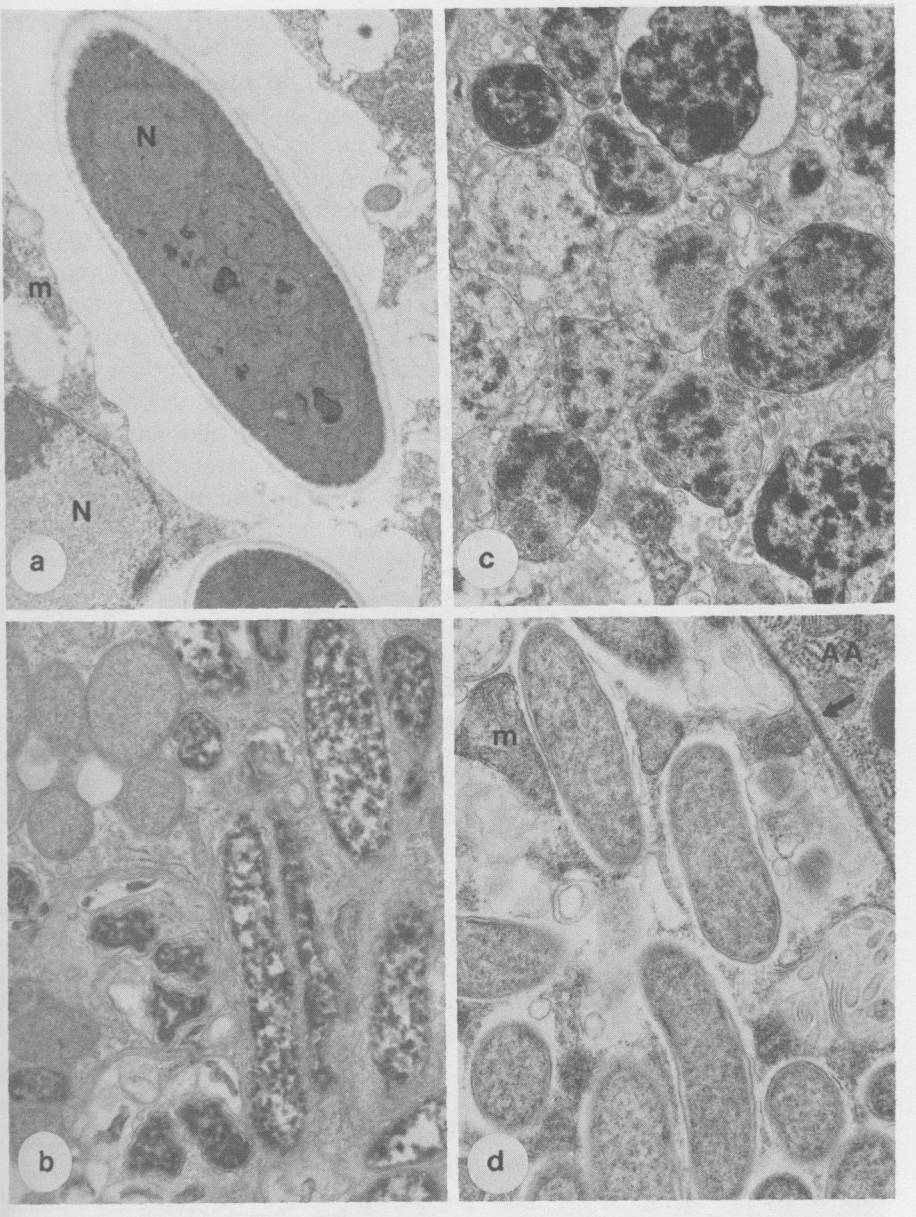

Fig. 6.9 Structures resembling microorganisms in various tissues of *Peregrinus maidis*. **(a)** Yeast-like and **(b)** other structures found in fat tissue of the head. (a, 9000x; b, 13,500x.) **(c)** Unidentified bodies in the muscle connective tissue surrounding the midgut. 21,000x. **(d)** Rickettsia-like structures in a membrane-bound pocket (arrow) in acinus A (AA) of the salivary gland 21,000x. m, mitochondrion; N, nucleus.

6.6 CIRCULATORY SYSTEM

The circulatory system in Auchenorrhyncha has been investigated in very few species. In the fulgorid *P. candelaria*, the heart and dorsal vessel were described as a long simple tube, slightly swollen at each segment of the abdomen, whereas in the thorax and head it narrows to a very slender tube, which passes medially over the anterior diverticulum (40). In the cicadellid *A. constricta*, the heart, situated dorsally (mostly in the abdomen) is divided by constrictions into seven chambers, with ostioles at the constrictions. The aorta extends from the heart through the thorax into the head, passing above the salivary glands. The heart is composed of one layer of cells, with elongated nuclei, surrounded by muscle fibers. The alary muscles and connective tissue stretch from the heart, on both sides to the integument forming a dorsal diaphragm. Blood cells, seen in the heart lumen,were elongated with oval nuclei. The abdominal pulsatory organ consists of sac-like structures, situated on both sides of the heart in the second through fourth abdominal segments,just underneath the integument. These structures exhibit a rapid strong pulsation, moving the blood to and from the insect legs (28). In Peloridiidae (Coleorrhyncha), the heart occupies six abdominal segments with six sets of alary muscles (69).

Circulative viruses are assumed to be carried with their vector's blood, from their point of entry into the hemocoel from the gut, to various organs including the salivary glands (33). However, little is known about Homopteran blood. In the aphid *M. persicae*, the hemolymph is characterized by the absence of circulatory hemocytes (72).

6.7 NERVOUS AND NEUROENDOCRINE SYSTEMS

The central nervous system in Auchenorrhyncha is formed by the fusion of the abdominal and thoracic ganglia and is concentrated in the head and thorax. In the cicadellid *A. constricta*, the brain, or supraesophageal ganglion, situated dorsally in the head, consists of three pairs of ganglia forming the proto-, deuto-, and tritocerebrum. Around the pharynx, circumesophageal connectives connect the posterior part of the tritocerebrum to the paired subesophageal ganglia, which form the first of three ventral ganglionic masses. The subesophageal ganglia, situated in the head, are joined by two connectives to the prothoracic ganglion found in the thorax. The third ganglionic mass is formed by the fusion of the mesothoracic, metathoracic, and all abdominal ganglia (28). In the fulgorid *P. candelaria*, the central nervous system, is basically similar to that described above for Cicadellidae (40).

Histological and ultrastructural studies of the nervous system in *A. constricta* (36) indicated that the entire system is enclosed in the perilemma which is formed by an outer noncellular layer (neural lamella or basement membrane) and an inner cellular layer (the perineurium). In the ganglia, most of the ganglion cell bodies are situated in the periphery. The central core of the

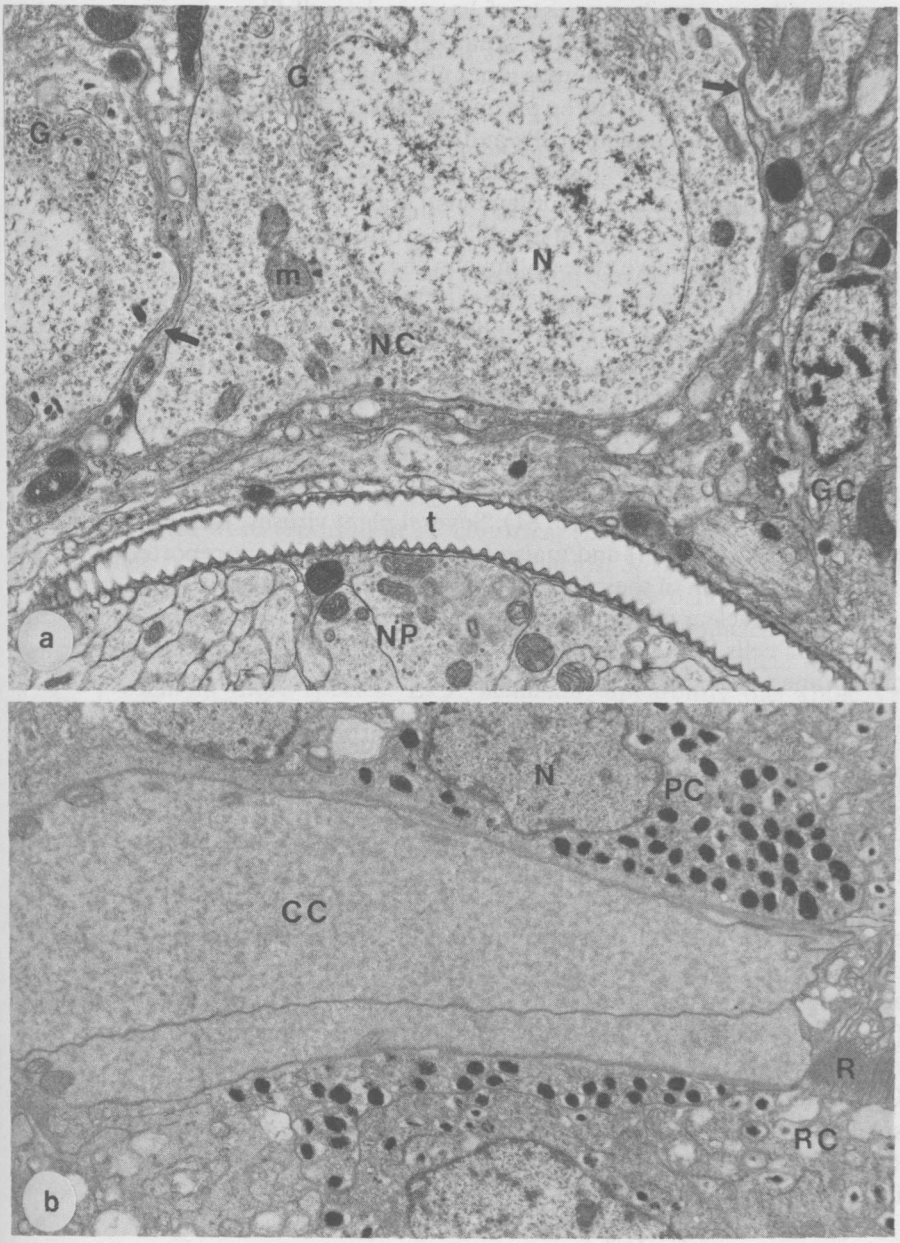

Fig. 6.10 **(a)** Neuron cell bodies (NC) around the neuropile (NP) in a nerve ganglion of *Peregrinus maidis*. Note glial cell (GC) and tracheole (t) at the periphery of neuropile, and glial processes (arrows) ensheathing neuron cell bodies. 9000x. **(b)** Part of a longitudinal section through an ommatidium in the compound eye of *P. maidis*. 6000x. CC, crystalline cone; G, Golgi body; m, mitochondrion; N, nucleus; PC, pigment cell; R, rhabdom; RC, retinula cell.

ganglion, the neuropile, consists of large and small fibers forming complex fiber networks. Outer glial cells, situated beneath the perineurium, surround the ganglion cell bodies, whereas inner glial cells are present in the neuropile. Synapses are observed between plasma membranes of the fibers and inner glial cells, and between ganglion cells and outer glial cells. Synaptic vesicles are found in the synaptic region of the axoplasm, which contains a few mitochondria and numerous neurofilaments. The cytoplasm of the glial cells is composed of loosely scattered cytoplasmic organelles. Some nerve axons are invested with a primitive type of "myelin sheath" in a spiral course formed by the glial cells. The tracheae penetrate into the perineurium of the ganglia and lateral nerves as well as to the periphery of the neuropile. The latter observation is true also in the nerve ganglia of *P. maidis* (Fig. 6.10a). In this delphacid, the cytoplasm of the glial cells is more electron dense than that of nerve cells. Electron-dense, probably neurosecretory vesicles were found in some nerve cells and axons of the neuropile. The ultrastructure of an ommatidium from the compound eye of *P. maidis* (Fig. 6.10b) is generally consistent with that described for other insects (16, 81). Several plant viruses, for example, clover wound tumor virus (36) and maize mosaic virus (5), were reported to invade the nervous system of their leafhopper or planthopper vectors. The latter virus buds on the nuclear membrane of nerve cells in the brain and other ganglia and of retinula cells in the compound eye, in addition to the axolemma and other membranes of nerve axons in its vector, *P. maidis* (5).

Little work has been reported on the neuroendocrine system in Auchenorrhyncha. Cazal (15) distinguished five anatomical variations of this system in five species belonging to Cicadidae, Aphididae, and Coccidae. Dogra and Srivastava (24) studied the neuroendocrine system in the fulgorid, *P. perpusilla*. They reported neurosecretory cells in the brain, ventral ganglia, and the postcerebral endocrine glands, the corpora cardiaca (CC), and the corpus allatum (CA). CC are paired, oblong glands situated between the aorta and the esophagus, posterior to the brain, and are connected posteriorly through commissures. Each of two nerves enters the CC lateromedially. A single CA is attached to the posterior of CC by a short nerve. Four groups of neurosecretory (NS) cells, designated A_1, A_2, A_3, and B, were detected in the brain. Subesophageal and thoracic ganglia possess two cell groups, each of A and B types. CC contain two cell types, A_1 and an unclassified type. CA is considerably smaller in size and has a few NS cells of a single type enveloped by a layer of small flattened cells. More studies on the NS system in Homoptera have been reported with aphids (38, 72).

6.8 MALE REPRODUCTIVE SYSTEM

In Cicadoidea, the male reproductive system has been studied in *A. constricta* (28), *Macrosteles sexnotatus* (Fall.) (10), *Cicadella spectra* Dist., *Kolla unimaculata* Sign., *Amritodus atkinsoni* Leth. (all Cicadellidae), *Atinotus elongatus* Dist. (Membracidae), and *Clovia puncta* Walk. (Cercopidae) (57). These species have two lateral testes situated at the anterior part of the abdomen. Each testis consists of oval testicular follicles numbering three to six in Cicadellidae, four in the membracid, and 17 in the cercopid. The follicles of each testis open collectively into a slender tubular vas deferens of a uniform length throughout, except for a much wider part that forms the seminal vesicle. The two seminal vesicles are usually separated from one another, but in *C. spectra* and *K. unimaculata* they are enclosed together in a common sheath. The seminal vesicles open into two narrow lateral ejaculatory ducts that merge into a pear-shaped median, or common, ejaculatory duct. This ends posteriorly with a narrow part continuing into the endophallus of the aedeagus. Two long accessory glands open in the lateral ejaculatory ducts adjacent to their junction with the seminal vesicles. These glands are usually tubular with a somewhat constant diameter throughout, but in *A. atkinsoni* and *C. puncta*, their anterior parts are much narrower, forming long coiled distal tubes. Strong peristaltic movements in the bases of the accessory glands and the seminal vesicles were reported in *A. constricta* (28).

The male reproductive system of the delphacids, *Sogatodes (Sogata) orizicola* Muir (54), *J. pellucida* (60), and *P. maidis* (Fig. 6.11a), is essentially similar to that described above for Cicadoidea, with three follicles per testis in the delphacids mentioned. However, no lateral ejaculatory ducts were evidently present in these species. In *J. pellucida*, apparently the whole vas deferens was enlarged in mature males for the storage of sperm. This was also reported in another delphacid, *N. lugens* (59). The accessory glands in both *J. pellucida* and *P. maidis* are trilobed, but in the former species they are more compact and broad-bean shaped, whereas in the latter they are enlarged and nearly tubular. In *S. orizicola*, the peanut-shaped accessory glands are divided

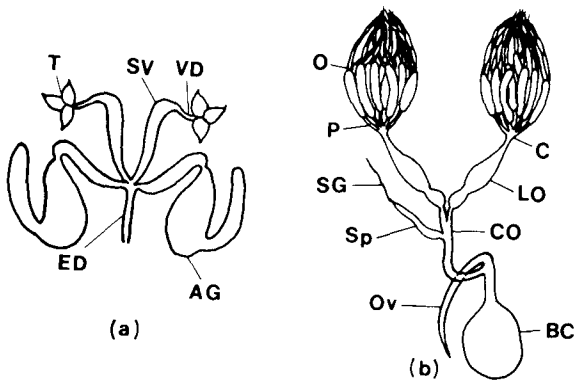

Fig. 6.11 Reproductive system in *Peregrinus maidis*. **(a)** Male: AG, accessory gland; ED, ejaculatory duct; SV, seminal vesicle; T, testis; VD, vas deferens. **(b)** Female: BC, bursa copulatrix; C, calyx; CO, common oviduct; LO, lateral oviduct; O, ovariole; Ov, ovipositor; P, pedicel; Sp, spermatheca; SG, spermathecal gland. (Courtesy of W. E. Styer.)

into four chambers that are separated from each other by a constricting valve-like muscle. Sperm was found only in the two chambers nearest the ejaculatory duct, but the other two chambers contained only granular material of unknown nature (54). In *P. candelaria*, six follicles per testis were reported; the tubular vasa deferantia and accessory glands were eight and 16 times the length of the abdomen, respectively (40).

Ultrastrucutral studies on the cicadellid *Dalbulus maidis* (Delong and Wolcott) (43), indicated that spermiogenesis was essentially similar to that reported for other insects. But homopteran spermatozoa have some interesting ultrastructural features (6). In most of the Auchenorrhynchan species studied, the head or acrosome region is not at the very tip of the spermatozoan, for there is an anteacrosomal cytoplasmic bleb as long as the acrosome (26). Also, in addition to the usual axial flagellar filament or axoneme, with its set of 9 + 9 + 2 microtubular elements, and the mitochondrial derivatives found in other insects, the sperm tails in Homoptera possess two accessory structures or bodies symmetrically positioned on either side of the axoneme (Fig. 6.12a–c). Only in aphids has the origin of these structures from Golgi-derived cisternae been ascertained (6). The shape of the mitochondrial derivatives are reported to be species-specific (70). Some authors have suggested the use of sperm-tail structures in taxonomy (43). However, very little difference was found in the ultrastructure of sperm tails of six cicadellid species: *D. maidis* (43), *G. nigrifrons* (Fig. 6.12a), *M. fascifrons*, *Dalbulus elimatus* (Ball), *D. gelbus* DeLong, and *Baldulus tripsaci* Kramer and Whitcomb (Ammar and Styer, unpublished). Nevertheless, significant differences were found in the ultrastructure of sperm tails between the above cicadellids and two delphacids: *J. pellucida* (Fig. 6.12b) and *P. maidis* (Fig. 6.12c). In cross sections of cicadellid sperm tails, the mitochondrial derivates are pear- or mango-shaped, and the accessory bodies, or deltoid structures (43), are almost curved triangles. The size of each is smaller than the axoneme. In cross sections of sperm tails in the above delphacids, the mitochondrial derivatives are either rounded triangles (in *P. maidis*) or hemispherical (in *J. pellucida*). Each of the accessory bodies, or wing-shaped structures (35), is nearly S-shaped and is larger than the axoneme. Spermiogenesis and spermatozoa of several Auchenorrhynchans have been studied by Folliot and Maillet (26) who demonstrated that accessory structures in *Cixius nervosus* L. (Cixiidae) are similar to, but distinguishable from, those described above for the Delphacidae. These authors also reported that in Cicadidae and Typhlocybinae (Cicadellidae), rickettsia-like organisms are often present in the spermatozoan nucleus and in this way can be transported into the female genital duct.

The ultrastructure of the male accessory gland in *P. maidis* revealed an epithelial layer rich in cisternae of the rough endoplasmic reticulum, electron-dense bodies, and semiopaque globular secretory vesicles with similar ones being released into the lumen (Fig. 6.12d). Such cells are clearly equipped for protein synthesis and secretion (81). Although their function in Auchenorrhyncha is yet unknown, secretions of the male accessory glands in other

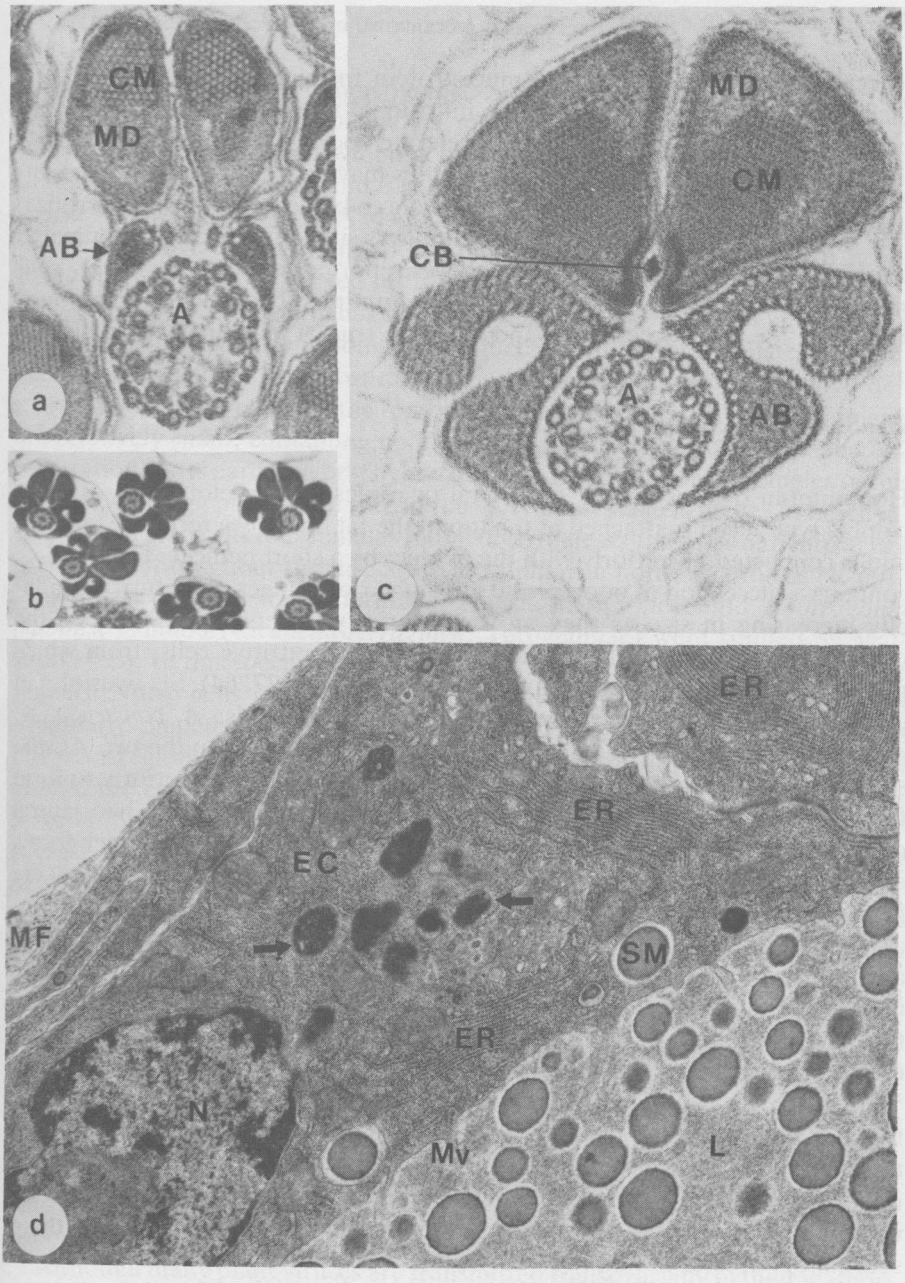

Fig. 6.12 **(a-c)** Cross sections in sperm tails of **(a)***Graminella nigrifrons*, **(b)** *Javesella pellucida*, and **(c)** *Peregrinus maidis*. A, axoneme; AB, accessory body; CB, central body; CM, crystalline part of mitochondrial derivative (MD). (a, 90,000x; b, 15,000x; c, 94,500x). **(d)** Male accessory gland in *P. maidis*. Epithelial cells (EC) with extensive rough endoplasmic reticulum (ER), dense vesicles (arrows), and semiopaque secretory material (SM) found also in the lumen (L). MF, muscle fibers; Mv, microvilli; N, nucleus. 13,500x.

insects are known to constitute mucoprotein forming the spermatophores, facilitate sperm transfer, have some nutritional value for the female, act as barriers to further insemination, or accelerate oocyte formation (16). At least in the Delphacidae, the last two possibilities may be excluded. Multiple matings of females have been reported and seem to be necessary for full fertilization of eggs, although total egg production was similar in mated and unmated females (2, 54, 60). If the spermatophores reported in the cicadellid *A. constricta* (28) are found in other species, the first possible function mentioned above for the male accessory gland could be true at least in such species.

6.9 FEMALE REPRODUCTIVE SYSTEM

Homopteran ovaries consist of several ovarioles of the telotrophic or acrotrophic type; each is attached at the top to the fat body by a terminal filament and is connected posteriorly with the oviduct by a short pedicel. The ovariole contains a succession of oocytes and eggs in various stages of maturity, gradually increasing in size as they move posteriorly. Interspersed between the oocytes and clustered near the apex are nurse or nutritive cells, from which nurse or nutritive cords lead into developing oocytes (27, 64). Six ovarioles in each of the two ovaries were reported in three cicadellids: *A. constricta*, *A. quadripunctata* (Provancher) (28), and *M. sexnotatus* (10). In the two *Agallia* species mentioned, the ovarioles of each ovary are joined posteriorly to form the calyx, which connects them to a short lateral oviduct. The two lateral oviducts merge to form a thick, tubular main or common oviduct, which forms an elbow-like bend coated with circular muscles before opening at the wide genital chamber or vagina. Also connected to this chamber is the spermatheca, a sac-like structure for storing sperm, two slender tubular accessory glands, and a thicker tubular collateral gland (28). In *M. sexnotatus* (10), only a single, accessory gland has been reported, but this is apparently more comparable to the collateral gland in *Agallia*. It is noteworthy that Gil-Fernandez and Black (28) indicated that the two accessory glands in *Agallia* are very slender and "difficult to see." In *M. sexnotatus*, one fully mature, chorionated egg is usually found in the ovariole at any time. In unmated females, the transparent walls of the spermatheca are close together, but mated females have a distended and milky spermatheca (10). In smears of different spermathecae from adult females of *A. constricta*, spermatozoa were either confined to two to three spermatophores or swimming freely (28).

In Delphacidae (Fulgoroidea) the number of ovarioles reported per ovary was usually much greater than that reported above for Cicadellidae, for example, 14 ovarioles in *S. orizicola* (54), 17–18 ovarioles in *J. pellucida* (60), and about 21–27 ovarioles in *N. lugens* (18, 42). The female reproductive system in these species, and in another delphacid, *P. maidis* (Fig. 6.11b), share the following characteristics. At the posterior end of each ovary, the calyx is connected to a long, usually constricted, lateral oviduct. The two lateral

oviducts join to form a common oviduct. A tubular spermatheca opens into the common oviduct slightly below its juncture with the lateral oviducts. A spermathecal gland, usually globular or pyriform, is connected to the distal end of the spermatheca. This gland is generally thought to secrete nutrients for the sperm in other insects (16). A bladder-shaped bursa copulatrix also opens into the common oviduct below the spermatheca. Pulsating movements with movement of sperm were observed in the spermatheca and bursa copulatrix of *S. orizicola* (54). *P. candelaria* has 10 ovarioles per ovary, two globular accessory glands, a complicated and long spermathecal gland, and a collateral gland, comparable in shape and position to the bursa copulatrix of the above delphacids (40). In *J. pellucida*, the reproductive organs of newly emerged females are relatively small, containing no mature eggs. Both yolk formation and egg maturation starts earlier in brachypterous than in macropterous females of this species. Also egg production rate in the early adult stage is higher in brachypterous than macropterous females (60). Nevertheless, longevity and rate of egg production throughout the insect life are similar in both wing forms (1, 60).

Ultrastrucutral changes during oogenesis in the cicadellid *Bothrogonia japonica* Ishihara (*Cicadella ferruginea*, Tettigellinae) were studied by Matsuzaki (52). In this species, nutritive tissue in the germarium consists of three regions. Nurse cells in the anterior region are uninucleate, small, and with irregularly shaped nuclei. Those in the middle region are binucleate. In the posterior region, cells and their nuclei become greatly enlarged and arranged around the central core; successive degenerating changes in nurse cells take place in this region. The cytoplasm of the nutritive core and cord are densely packed with ribosomes and microtubles. Oogenesis was divided into five developmental stages, two of which are vitellogenic. The lipid and proteid yolk seem to be formed by a similar method to that reported in other insects. The vitelline membrane and chorion are apparently depositied by the follicular cells after yolk formation. Extensive microvilli are found at the interface between the follicular epithelium and the oocyte with the micropinocytosis starting actively. At the final stage of vitellogenesis, the pinocytotic activity in the oocyte surface is remarkably reduced, and large lipid droplets and proteid yolk spheres are found throughout the oocyte cytoplasm. The anterior part of the germarium and the vitellarium in ovarioles of *P. maidis* are shown in Figs. 6.13a and b, respectively. Bacteroids similar to those found in the cytoplasm of nurse and follicular cells in this insect have been reported and considered as symbionts in similar cells of *N. cincticeps* (64).

Although many plant viruses are transmitted transovarially in their leafhopper or planthopper vectors (33), the mechanism involved in transovarial transmission has been studied only with rice dwarf virus (RDV) in *N. cincticeps* (64). In each ovariole of the latter species, a mycetocyte is found at the place where the follicular layer comes into contact with the pedicel. This mycetocyte contains L and H symbiotes and smaller bacteroids. RDV particles were reported to attach selectively to the surface of the L symbiotes, and thus are apparently carried with them when part of the ovariole mycetocyte enters into

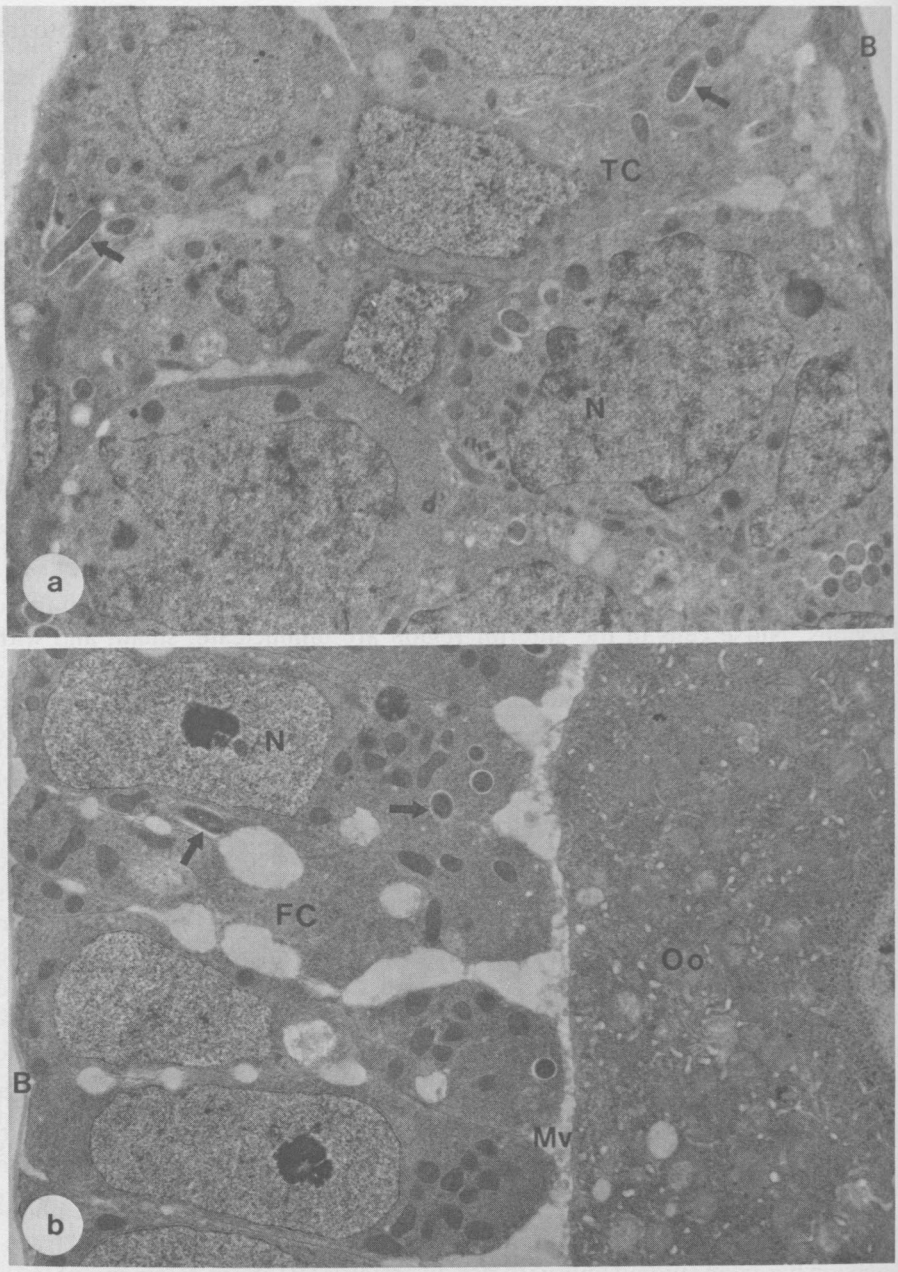

Fig. 6.13 **(a)** Anterior part of the germarium in an ovariole of *Peregrinus maidis*. Note irregular-shaped nuclei (N) of trophic cells (TC), and bacteroid microorganisms in the cytoplasm (arrows). 6000x. **(b)** Part of the vitellarium in an ovariole of *P. maidis*. Follicular cells (FC) surrounding a developing oocyte (Oo), with microvilli (Mv) at the interface between them; arrows indicate bacteroids. 6000x. B, basal lamina; N, nucleus.

the neighboring oocyte to form the egg mycetome. However, Nasu (64) indicated two other possible mechanisms for transovarial transmission, neither of which have been investigated so far. More work is clearly needed in this area on other viruses and vectors. Some plant viruses, apparently not transmitted transovarially, have been reported in follicular or other somatic cells in the ovaries of their vectors (5). Although it is possible that these viruses may be truly restricted to somatic tissues without moving into the eggs, a very low rate of transovarial transmission is difficult to prove, and such a possibility cannot be excluded without extensive trials in each case.

6.10 CONCLUSIONS

In this chapter, the morphology, histology, and ultrastructure of the internal organs of the Auchenorrhyncha have been reviewed. Essential differences are found in several structures, notably the alimentary canal, salivary glands, mycetome, and the reproductive system between the two superfamilies Cicadoidea and Fulgoroidea, and sometimes between families, subfamilies, or tribes within each. Miles (55) used characteristics of the salivary glands in the Hemiptera to discuss the evolution of this order from other insects, and Goodchild (30) used characteristics of the alimentary canal to suggest the evolutionary interrelationships of various divisions within the Hemiptera. Harris (33) and Nielson (66) indicated that most of the Auchenorrhyncha-borne plant disease agents are transmitted within limited taxonomic groups, a concept consistent with group specificity. Furthermore, Nielson (66) noted interesting differences in the frequency of vector genera and species between various taxonomic groups of leafhoppers. For example, the Deltocephalinae, which include about 60% of the vector genera and 59% of the vector species, transmit 70% of the known phytopathogenic agents. The Agallinae include the highest percentage of vector species (4.3%). It is possible that some anatomical or ultrastructural differences among these groups, in addition to other differences in feeding behavior and physiology, may account for their varied efficiency as vectors of disease agents. The classical example of puncturing the gut wall of *Cicadulina* and rendering inactive "races" to active ones in transmitting maize streak virus (85), illustrates that anatomical differences may be important. However, permeability of the gut wall is probably but one of many anatomical, physiological, and behavioral factors that collectively determine whether a group, species, or race will transmit a certain plant pathogen. Since we seem to be far from an understanding of most of these factors, some basic knowledge on the anatomy and physiology of vector species or groups may pave the way to that end. At present, ultrastructural and cytochemical studies on many important structures, for example, salivary glands, alimentary canal, and mycetomes of several vector groups, are still scanty. Such studies are important not only for understanding various aspects of pathogen–vector relationships, but also for better identification of disease agents *in situ* in the vector, or their effects on its cells and tissues.

Finally, some problems that need special attention from researchers are (a) the problem of osmoregulation in the Fulgoroidea lacking a filter chamber, particularly Delphacidae, (b) the mechanism(s) for transovarial transmission of disease agents, (c) salivary secretions, their sources in the salivary glands and their effects on disease agents and, (d) characteristics of the hemolymph and its effect on disease agents in the hemocoel.

ACKNOWLEDGMENTS

Most of the electron micrographs included here, and the literature search, were undertaken at the Ohio State University, Ohio Agricultural Research and Development Center (OARDC), Wooster, Ohio, where the author was on leave from Cairo University as a visiting professor on a Fulbright Scholarship. From the OARDC, I thank Dr. L. R. Nault for stimulating discussions and for reading the manuscript, W. E. Styer for his help in many ways and for Fig. 6.11, personnel of the library, Electron Microscopy Laboratory and Photography Laboratory for their valuable assistance. From Cairo University, I thank Dr. M. M. Megahed for constant encouragement, Dr. S. H. Fouad for reading the manuscript, and G. H. Sewaify for redrawing some of the figures.

LITERATURE CITED

1. E. D. Ammar, Factors related to the two wing forms in *Javesella pellucida* (Fab.) (Homoptera: Delphacidae). *Z. Angew, Entomol.* **74**, 211–216 (1973).
2. E. D. Ammar, Biology of the nymphal and adult stages of *Javesella pellucida*, vector of European wheat striate mosaic virus (Homoptera, Delphacidae). *Dtsch. Entomol. Z.* **22**, 67–77 (1975).
3. E. D. Ammar, Muscle cells in the salivary glands of a planthopper *Peregrinus maidis* (Ashmead) and a leafhopper *Macrosteles fascifrons* (Stål) (Homoptera, Auchenorrhyncha). *Int. J. Insect Morphol. Embryol.* **13**, 425–428 (1984).
4. E. D. Ammar, R. G. Milne, and M. A. Watson, Virus-like particles in the planthopper *Javesella pellucida*. Fab. *J. Gen. Virol.* **6**, 315–318 (1970).
5. E. D. Ammar and L. R. Nault, Assembly and accumulation sites of maize mosaic virus in its planthopper vector. *Intervirology* (in press).
6. B. Baccetti, Insect sperm cells. *Adv. Insect Physiol.* **9**, 315–397 (1972).
7. A. Balasubramanian, Morphology and histology of salivary glands of *Idiocerus atkinsoni* L. and *I. clypealis* L. (Homoptera, Jassidae). *Indian Cong. Assoc. Proc.* **59**, 443–444 (Abstr.) (1972).
8. A. Balasubramanian, Morphology and histology of the salivary glands of the shoot bug, *Peregrinus maidis* Ashmead (Homoptera: Fulgoroidea). *Indian Sci. Cong. Assoc. Proc.* **60**, 436 (Abstr.) (1973).
9. A. Balasubramanian and R. G. Davies, The histology of the labial glands of some Delphacidae (Hemiptera: Homoptera). *Trans. R. Entomol. Soc. London* **120**, 239–251 (1968).
10. M. Becker, The nymphal stages and internal reproductive organs of *Macrosteles sexnotatus* (Fall.) (Hem., Cicadellidae). *Entomol. Mon. Mag.* **115**, 11–16 (1979).

11. L. C. Berlin and E. J. Hibbs, Digestive system morphology and salivary enzymes of the potato leafhopper, *Empoasca fabae* (Harris). *Iowa Acad. Sci.* **70**, 527–540 (1963).
12. R. K. Bharadwaj, D. V. R. Reddy, and R. C. Sinha, A reinvestigation of the alimentary canal in the leafhopper *Agallia constricta* (Homoptera: Cicadellidae). *Ann. Entomol. Soc. Am.* **59**, 616–617 (1966).
13. J. Brcak, and O. Kralik, Electron microscopy of the striated border of the midgut cells of *Javesella pellucida* (F.) (Homoptera, Delphacidae). *Acta Entomol. Bohemoslov.* **64**, 173–178 (1967).
14. P. Buchner, *Endosymbiosis of Animals with Plant Microorganisms*. Wiley-Interscience, New York, 1965.
15. P. Cazal, Les glandes endocrines rétrocérébrales des insectes (étude morphologique). *Bull. Biol. Fr. Belgique* **32**, 1–228 (1948); through Dogra and Srivastava (24).
16. R. F. Chapman, *The Insects Structure and Function*, 3rd ed., Harvard University, Cambridge, Massachusetts, 1982.
17. C. C. Chen, L. L. Cheng, C. C. Kuan and R. F. Hou, Studies on the intracellular yeast-like symbiote in the brown planthopper. *Nilaparvata lugens* Stål. 1. Histological observations and population changes of the symbiote. *Z. Angew. Entomol.* **91**, 321–327 (1981).
18. J. C. Chen, S. N. Cheng, L. M. Yan, and H. T. Yin, The ovarial development of the brown planthopper (*Nilaparvata lugens* Stål) and its relations to migration. *Acta Entomol. Sinica.* **22**, 280–288 (1979) (Chinese, English summary).
19. W. W. K. Cheung, An electron microscopic observation of the rectum of the lantern bug, *Pyrops candelaria* Linn. (Homoptera: Fulgoridae). *J. Chinese Univ. Hong Kong* **5**, 521–533 (1979).
20. W. W. K. Cheung, Ultrastructural and functional differentiation of the Malpighian tubules of the lantern bug, *Pyrops candelaria* Linn. (Homoptera: Fulgoridae). *Cytologia* **46**, 241–254 (1981).
21. W. W. K. Cheung, and A. T. Marshall, Studies on water and ion transport in homopteran insects: Ultrastructure and cytochemistry of the cicadoid and cercopoid midgut. *Tiss. Cell* **5**, 651–669 (1973).
22. W. W. K. Cheung, and A. T. Marshall, Ultrastructural and functional differentiation of the midgut of the lantern bug, *Pyrops candelaria* Linn. (Homoptera: Fulgoridae). *Cytologia* **47**, 325–339 (1982).
23. I. D. Dobroscky, Morphological and cytological studies on the salivary glands and alimentary tract of *Cicadula sexnotata* (Fallen), the carrier of aster yellows virus. *Contrib. Boyce Thompson Inst.* **3**, 39–58 (1931).
24. G. S. Dogra, and R. C. Srivastava, Morphological and histological studies on the neuroendocrine system of the sugarcane leafhopper, *Pyrilla perpusilla* Wlk. (Fulgoridae: Homoptera). *Z. Mikrosk. Anat. Forsch. Leipz.* **91**, 41–51 (1977).
25. M. J. Fletcher and D. T. Anderson, Unusual features in the embryonic development of *Scolypopa australis* (Walker) (Homoptera: Fulgoroidea: Ricaniidae). *Int. J. Insect Morphol. Embryol.* **9**, 129–134 (1980).
26. R. Folliot and P. L. Maillet, Ultrastructure de la spermiogenése et du spermatozoide de divers insectes Homoptéres. In, *Comparative Spermatology*, B. Baccetti (ed.), Academic, New York, 1970, pp. 289–300.
27. A. R. Forbes and H. R. MacCarthy, Morphology of the Homoptera, with emphasis on virus vectors. In, *Viruses, Vectors, and Vegetation*, K. Maramorosch (ed.) Wiley-Interscience, New York, 1969, pp 211–234.
28. C. Gil-Fernandez and L. M. Black, Some aspects of the internal anatomy of the leafhopper *Agallia constricta* (Homoptera: Cicadellidae). *Ann. Entomol. Soc. Am.* **58**, 275–284 (1965).
29. A. J. P. Goodchild, Some new observations on the intestinal structures concerned with water disposal in sap-sucking Hemiptera. *Trans. R. Entomol. Soc. London* **115**, 217–237 (1963).

72. M. B. Ponsen, Anatomy of an aphid vector: *Myzus persicae*. In, *Aphids as Virus Vectors*, K. F. Harris and K. Maramorosch (eds.), Academic, New York, 1977, pp. 63–82.

73. J. Raine, and A. R. Forbes, The salivary syringe of the leafhopper *Macrosteles fascifrons* (Homoptera: Cicadellidae) and the occurrence of Mycoplasma-like organisms in its ducts. *Can. Entomol.* **103**, 110–116 (1971).

74. J. Raine, A. R. Forbes, and F. E. Skelton, Mycoplasma-like bodies, rickettsia-like bodies, and salivary bodies in the salivary glands and saliva of the leafhopper *Macrosteles fascifrons* (Homoptera: Cicadellidae). *Can. Entomol.* **108**, 1009–1019 (1976).

75. K. N. Saxena, The anatomy and histology of the digestive organs and Malpighian tubes of the Jassidae (Homoptera). *J. Zool. Soc. India* **7**, 41–52 (1955).

76. E. Shikata, Cytopathological changes in leafhopper vectors of plant viruses. In, *Leafhopper Vectors and Plant Disease Agents*, K. Maramorosch and K. F. Harris (eds.), Academic, New York, 1979, pp. 309–325.

77. E. Shikata and K. Maramorosch, Electron microscopy of wound tumor virus assembly sites in insect vectors and plants. *Virology* **32**, 363–377 (1967).

78. E. Shikata and K. Maramorosch, Electron microscopy of insect-borne viruses *in situ*. In, *Viruses, Vectors, and Vegetation*, K. Maramorosch (ed.), Wiley-Interscience, New York, 1969, pp. 393–415.

79. R. C. Sinha, Virus-like particles in salivary glands of leafhoppers *Endria inimica*. *Virology* **51**, 244–246 (1973).

80. R. C. Sinha, and L. M. Black, Wound-tumor virus antigens in the internal organs of an insect vector. *Virology* **21**, 183–187 (1963).

81. D. S. Smith, *Insect Cells: Their Structure and Function*, Oliver and Boyd, Edinburgh, 1968.

82. D. S. Smith and V. C. Littau, Cellular specialization in the excretory epithelia of an insect, *Macrosteles fascifrons* Stål (Homoptera). *J. Biophys. Biochem. Cytol.* **8**, 103–133 (1960); through Smith (81).

83. K. Sogawa, Studies on the salivary glands of rice plant leafhoppers. I. Morphology and histology. *Jpn. J. Appl. Entomol. Zool.* **9**, 275–290 (1965).

84. K. Sogawa, The rice brown planthopper: Feeding physiology and host plant interactions. *Annu. Rev. Entomol.* **27**, 49–73 (1982).

85. H. H. Storey, Investigation of the mechanism of the transmission of plant viruses by insect vectors. I. *Proc. R. Soc. London B* **113**, 463–485 (1933).

86. J. H. Tsai, Vector transmission of Mycoplasmal agents of plant diseases. In, *The Mycoplasmas. Vol. 3. Plant and Insect Mycoplasmas*, R. F. Whitcomb and J. G. Tully (eds.), Academic, New York, 1979, pp. 265–307.

87. N. Waloff, Studies on grassland leafhoppers (Auchenorrhyncha, Homoptera) and their natural enemies. *Ann. Ecol. Res.* **2**, 81–215 (1980).

88. R. F. Whitcomb, D. D. Jensen, and J. Richardson, The infection of leafhoppers by Western X-disease virus VI. Cytopathological interrelationships. *J. Invert. Pathol.* **12**, 202–221 (1968).

89. D. M. Willis, The anatomy and histology of the head, gut, and associated structures of *Typhlocyba ulmi*.*Proc. Zool. Soc. London* **118**, 984–1001 (1949).