THE LEAFHOPPERS AND PLANTHOPPERS

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Anatomical and Sensory Mechanisms of Leafhopper and Planthopper Feeding Behavior

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7.1 INTRODUCTION

The success of leafhoppers and planthoppers as worldwide agricultural pests is dependent on their method of feeding. Like other homopterans, they pierce plant parts to suck fluid, and in so doing can extract vital nutrients, inject toxic saliva, and/or transmit plant pathogens. Host diversity is another trait which makes these insects serious pests. Some species are monophagous; others are polyphagous, feeding on a very broad range of plants. Because of this diversity, nearly every crop in the world can serve as a host for auchenorrhynchan species.

The objectives of this chapter are to discuss (a) the structure of auchenorrhynchan mouth parts, (b) the chemistry of salivary secretions (briefly), and (c) the mechanisms of feeding behavior. Emphasis will be placed on previously unreviewed aspects of host acceptance and probing, especially recent work on the sensory apparatus and mechanisms mediating those behaviors. Whenever possible, planthoppers will be compared with leafhoppers, pointing out differences as well as similarities between them. Such comparisons may aid future study of the evolution of these insects.

For future reference, several recent reviews are recommended. Basic behavioral mechanisms are discussed by Alcock (1) and Gould (33). The physiological mechanisms of behavior are covered by Camhi (12) and Kandel (41).

Dethier (20, 21) provides excellent general references for insect feeding behavior and physiology. For general homopteran feeding, see Pollard (64); for planthoppers, see Sogawa (82); for aphids, see Pollard (66). Insect sensory systems have also been recently reviewed. Chemosensilla are discussed by Zacharuk (95); mechanosensilla by McIver (47).

7.2 STRUCTURE OF MOUTHPARTS

Leafhoppers and planthoppers have highly modified mouthparts suitable for piercing and sucking sap from their host plants. The mouthparts in these two groups of insects are very similar, and consist of the labrum, labium, and stylets. Labial and maxillary palpi are absent. The anterior regions of the alimentary canal (the precibarium and cibarium), although not strictly mouth parts, function in close concert with the mouthparts.

Most detailed, morphological studies of homopteran mouthparts have described aphids (Homoptera: Sternorrhyncha: Aphididae), rather than leafhoppers and planthoppers (27, 67). References to heteropteran mouthparts may be found in Cobben (13).

7.2.1 Labrum, Labium, and Stylets

The labrum is a narrow, triangular appendage atop the labium, with its basal portion attached to the clypellus (or anteclypeus; 77) (Fig. 7.1). The inner surface of the labrum is indented, forming part of the stylet groove, which positions the stylets where they exit the head.

The modified labium comprises most of the visible proboscis [rostrum or "beak" (77)]. This tubular, segmented appendage has a deep groove on its anterior surface, which houses the stylets. In both planthoppers and leafhoppers, the labium bears many long setae, as well as other hairs and pegs of a presumed sensory function (see section on *Labial sensilla*).

The mouthparts that actually penetrate the plant are the four stylets. Each pair is derived from highly modified mandibles and maxillae. The maxillary stylets lie in the center of the bundle and are held tightly together by interlocking ridges and grooves (Fig. 7.1). When apposed this way, the maxillary stylets form the dorsal food canal, and the much smaller, ventral, salivary canal. At the tip of the maxillary stylets, these canals join to form a single canal, where their contents mix. The mandibular stylets lie outside the maxillary stylets, partly surrounding and enveloping them. The outer surface of each mandibular stylet has concentric ridges at the tip, forming distinct barbs. All four stylets are sharply pointed and, if each were removed from the bundle and stood alone, would naturally in-curve (especially the maxillary stylets) (64).

All auchenorrhynchan species examined thus far have dendritic canals within both pairs of stylets (Figs. 7.1, 7.7a, and 7.7c). Within these canals lie

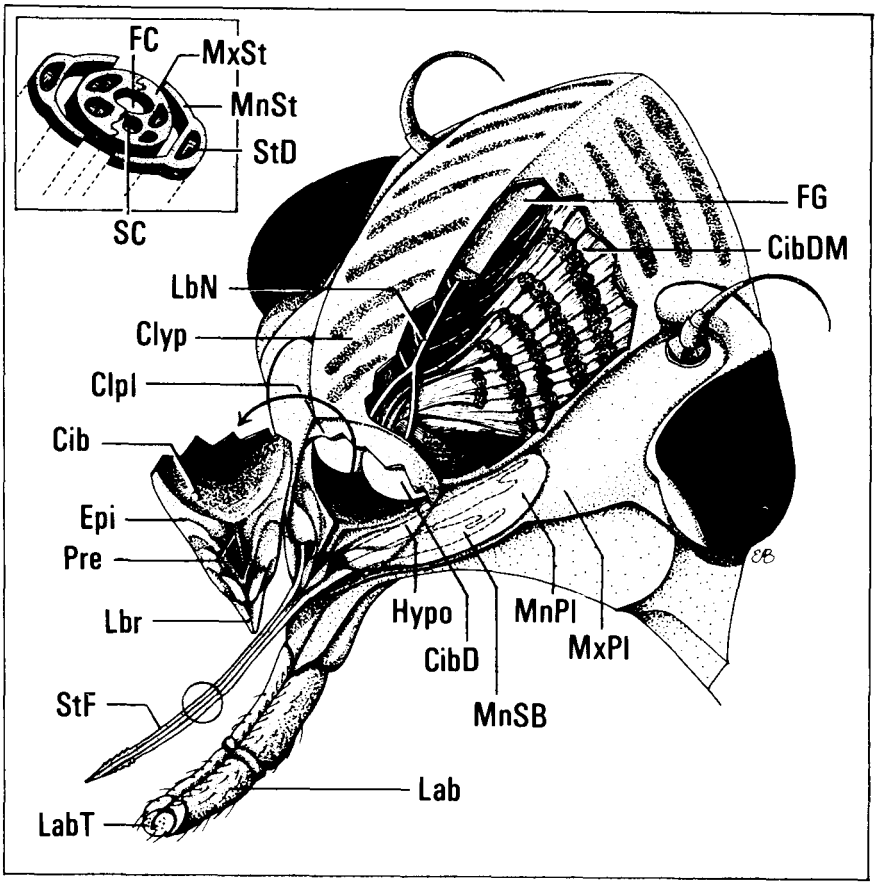

Fig. 7.1 Ventral view of the head of a leafhopper, showing an exploded view of the mouthparts and anatomy of the distal alimentary canal. Cib, cibarium; CibD, cibarial diaphragm; CibDM, cibarial dilator muscle; Clpl, clypellus; Clyp, clypeus; Epi, epipharynx; FC, food canal; FG, frontal ganglion; Hypo, hypopharynx; Lab, labium; LabT, labial tip; LbN, labral nerve; Lbr, labrum; MnPl, mandibular plate; MnSB, mandibular stylet base; MnSt, mandibular stylet; MxPl, maxillary plate; MxSt, maxillary stylet; Pre, precibarium; SC, salivary canal; StD, stylet dendrite; StF, stylet fascicle.

interspecifically varying numbers of sensory dendrites (see section on *Stylet sensilla*).

The major difference in stylet structure between leafhoppers and planthoppers is in the relative length of stylet pairs. In leafhoppers, the mandibles are significantly shorter than the maxillae, only 74–79% as long. Planthopper mandibles, in contrast, are 93–99% the length of the maxillae (79). Slight differences exist between the two insect types in the thickness and position of the mandibular stylets as they envelope the maxillae (Figs. 7.7a and 7.7c).

The stylets arise in the head, where their enlarged bases lie beneath the hypopharynx and maxillary plate (Fig. 7.1). Powerful retractor and protractor muscles insert on the enlarged bases and, in combination with the natural curvature of the stylets, facilitate precise directional control during probing (64).

7.2.2 Precibarium and Cibarium

Within the head, the maxillary stylets diverge from one another shortly before widening to form the stylet bases. Fluid flowing upward through the stylets passes this point and enters a narrow chamber, whence it is conveyed to the cibarium (food or sucking pump) (Figs. 7.1 and 7.2). Because of nomenclature uncertainty, Backus and McLean (3) have renamed this chamber the *precibarium* to indicate its functional and anatomical relationship to the cibarium. (For a detailed explanation of previous nomenclatures, see the footnote in 3.)

The precibarium has a complex structure that appears to have multiple functions in the feeding process. In all nine leafhopper species examined (3, 4) the precibarium houses a small valve (Figs. 7.1 and 7.8b). While the precibarial valve has not been looked for or detected in planthoppers, its presence is likely. It has been observed in aphids (49, 67) cicadas *(Magicicada sp.)*, cercopids *(Philaenus spumarious)* (L.), fulgorids (unknown sp.), and mirids (Heteroptera: Geocorizae: *Lygus hesperus* Knight) (Backus, unpublished). It now appears probable that the precibarial valve is a critical and widespread feature of the hemipteran (homopteran and heteropteran) feeding mechanism (Backus, unpublished).

No direct evidence regarding the function of the precibarial valve in homopteran feeding is yet available. However, it appears to act as both a precisely controlled regulator of fluid flow into the cibarium and as a pressure-sensitive check valve preventing backflow into the stylets. These inferences are based on the position of the valve, as well as its innervated extensor musculature (separate from the nearby dilator muscles of the cibarium). Innervation of the valve muscle indicates voluntary control over its contraction, and therefore closure of the valve. This closure probably acts to regulate flow of high-pressure fluids from such sources as phloem tissues. A possible third function of the valve relates to other structures in the precibarium: the precibarial chemosensilla (see section on *Precibarial sensilla*). In all species examined thus far, the valve separates two morphologically dissimilar groups of sensilla, and hence may function in separate monitoring of chemostimuli. (For more detail on inferred valve functions, see 3.)

Fluid taken up by the insect flows from the precibarium to the cibarium (Figs. 7.1 and 7.2). In cases of zero or negative hydrostatic pressure flow, the cibarium allows for suction by the insect. Contraction of powerful dilator muscles attached to the cibarial diaphragm (Fig. 7.1) causes a rapid, piston-like pumping that draws fluid from the precibarium and pumps it into the esophagus. Xylem-feeding leafhoppers (Cicadellinae) typically have enlarged

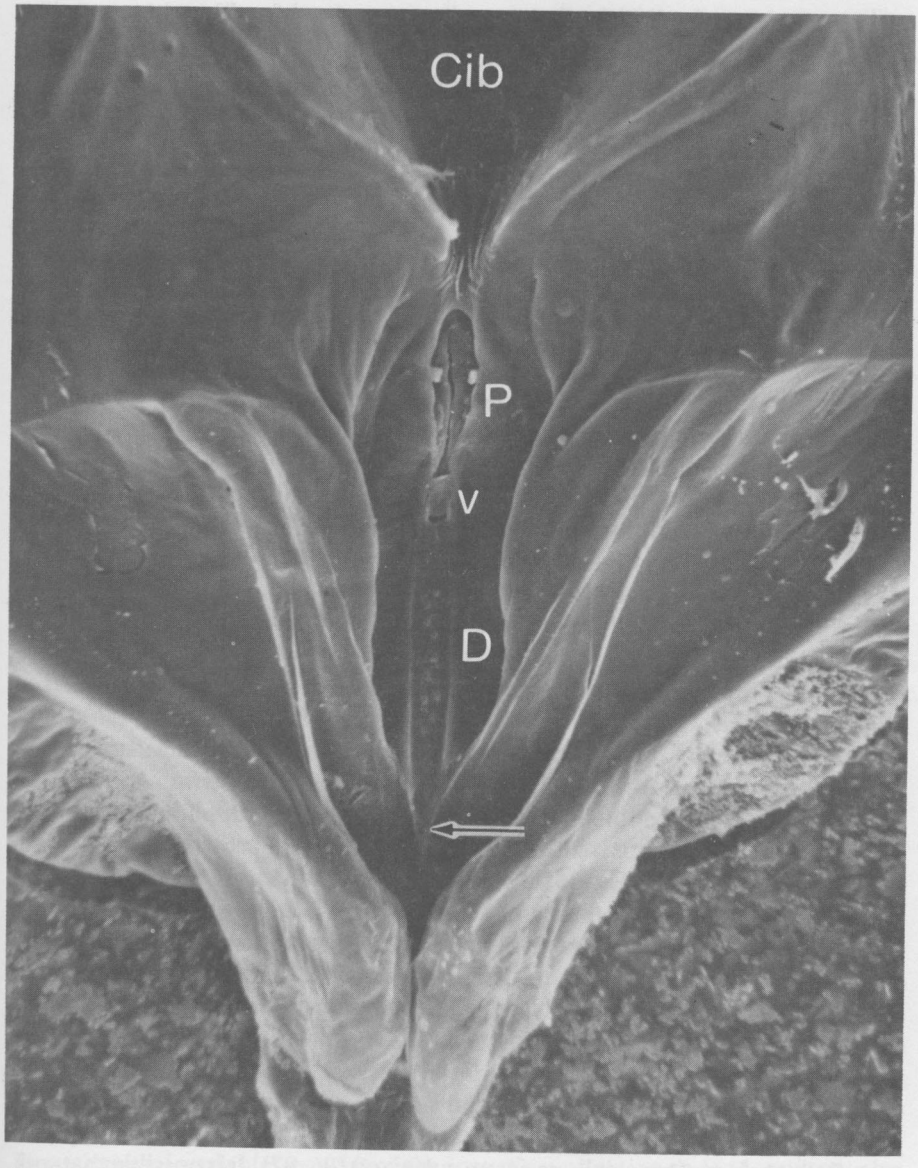

Fig. 7.2 The epipharynx of *Macrosteles fascifrons*. Arrow denotes point at which the stylets (removed) diverge to empty their contents into the precibarium. Cib, cibarium; D, D sensilla; P, P sensilla; v, precibarial valve. (1300X) [From Backus and McLean (3).]

dilator muscles, which can pull against the xylem's negative pressure. Also, their precibaria are very broad and heavily sclerotized. The breadth presumably provides less resistance to fluid flow, while the heavy sclerotization braces the structure against the tremendous force exhibited by the cibarial dilators. In

contrast, phloem-feeding leafhoppers (in several subfamilies) have smaller cibarial dilators and probably rely as much or more on the precibarial valve to regulate amounts of high-pressure fluids being forced through the stylets. The precibaria of these insects are very narrow and less-sclerotized. The narrowness may provide greater resistance to incoming fluids. (For more detail, see 4.) For comparison, pertinent discussion of cibarial function in aphids has been published (6,17, 27, 57).

7.3 SALIVARY SECRETIONS

It is not within the scope of this chapter to thoroughly review homopteran salivary secretion. For greater depth, see Miles (54). However, brief mention of the chemistry of saliva will be made here, and the use of saliva in feeding will be discussed in subsequent sections.

The salivary glands of homopterans (see Ammar, Chapter 6) produce two different types of secretions known to be important for feeding: sheath saliva and watery saliva. Sheath saliva solidifies immediately on contact with air or fluid and completely covers the stylets during probing (see Section 7.4.2). It is primarily protein, though it also contains some phospholipid and conjugated carbohydrate (54). Hardening may occur through a process similar to sclerotization (52, 78). Sogawa (82) notes the presence of salivary phenolase in *Nilaparvata lugens* (Stål), the brown planthopper. However, Miles (54) states that the sheath can form in the absence of such oxidizing enzymes. Instead, he believes that diffusion of amino acids away from the sheath, combined with the presence of free oxygen, lead to formation of hydrogen bonds and disulphide bonds, respectively. Thus, oxidizing enzymes probably participate in the solidification process, but may not be essential.

Watery saliva is secreted as a medium for digestive enzymes that aid in the feeding process (54) by liquifying plant cellular contents and walls. Several enzymes have been found in leafhoppers, among them amylase, oligosaccharases and proteinases (8). Among planthoppers, *N. lugens* secretes several carbohydrases, including α- and β-glucosidase (78). Pectinase activity has been found in a wide variety of hemipterans (46). Recently, aphids have been found to possess hemicellulase, cellulase, and several other polysaccharases, whose presence and activity seems to be correlated with adaptations of biotypes to specific host plants (especially resistant cultivars) (96, 97). It is possible that such correlations could be found with auchenorrhynchan salivary enzymes also.

7.4 HOST SELECTION AND FEEDING BEHAVIOR

Like all other complex insect behaviors, host selection and feeding by leafhoppers and planthoppers can be studied by analogy to an input–output relationship. Input in such a system is a stimulus; output is the insect's response. The connection between the two is the insect nervous system. The peripheral sensory system is the means of initially perceiving a stimulus. Without it, even a huge surfeit of stimuli would be meaningless to the insect. Behavior encompasses the acts of perceiving stimuli and all responses to them. The central nervous system (CNS) integrates sensory input with other information, then triggers the proper effector organs (glands and muscles) to move the insect through the behavior.

To understand a particular behavioral response such as selection of a proper food (or rejection of an improper food), we must dissect it by studying the stimuli (input) and neural mechanisms that elicit it. Knowledge of neural mechanisms of behavior has increased dramatically in the last 30 years. Based on the pioneering work done with feeding in flies (20, 21) and in invertebrate neurophysiology (41), feeding mechanisms of agricultural pest species can now begin to be understood.

Auchenorrhynchan feeding commences with the arrival of the insect on a potential host plant. Once on a plant, the insect rapidly proceeds through a sequence of brief, stereotypical behaviors (Fig. 7.3). Assuming that all key stimuli were adequate, a typical sequence would consist of (a) plant surface exploration, (b) stylet probing, (c) plant fluid ingestion, and (d) probe termination (63, 82).

It is likely that parts of each behavioral step in this sequence are composed of *fixed action patterns* (FAPs). In ethological terminology, a FAP is a behavioral response triggered by very specific sensory stimuli. But once triggered, it can proceed to completion without sensory feedback (1). Complex behaviors, such as feeding, are often composed of many overlapping FAPs, hierarchically arranged in sequences that are linked and modulated by sensory feedback (20). A simplified version of such a hierarchical array is diagrammed in Fig. 7.3. Each FAP is probably the output of one or more *central pattern generators:* interneurons in the CNS whose circuit controls a given set of muscles. As an example, the rhythmic pumping of the cibarium during ingestion is probably a FAP that is controlled by a pattern generator in the CNS. Sensory inputs modulate the rhythmic pulsing of the pump, but do not generate its rhythm (see discussion of fly feeding in 20, pp. 102–104). While such responses can be thought of as "innate," it is now known that they can also be modified by such variables as the insect's recent experience and internal physiological state. These internal variables consist of the insect's *motivation* to feed, and are also integrated by the CNS.

The rest of this chapter will discuss the peripheral sensory mechanisms of host selection and feeding behaviors in auchenorrhynchans, as well as clues about how information is integrated by the CNS to elicit behavior. A step-by-step description of feeding behavior will be given, drawing on our knowledge of mouthpart morphology. Then the sensory mechanisms underlying feedback in this system will be discussed.

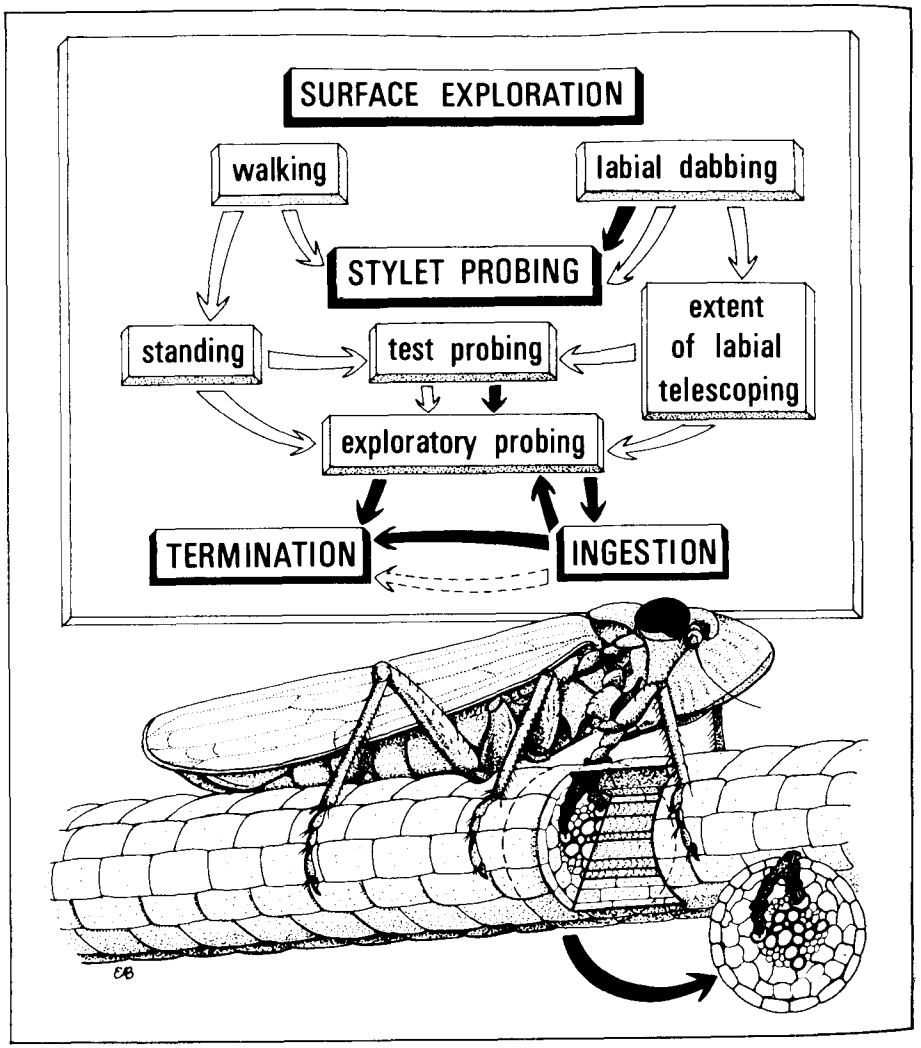

Fig. 7.3 Flowchart showing the sequence of behaviors involved in auchenorrhynchan feeding. Dark-edged boxes indicate major categories of the behavior, which consist of the behavioral steps named in light-edged boxes below them. Light arrows indicate mechanical cues; dark arrows indicate chemical cues; broken line arrow indicates postulated mechanical cues used during ingestion. The leafhopper pictured has probed a plant stem. If the stem is cross-sectioned (cutaway) the salivary sheath and stylets, terminating in a xylem vessel element, are revealed.

7.4.1 Plant Surface Exploration

After the arrival of the insect on the plant, surface exploration begins. During this time, the insect walks about on the surface of the plant (either leaf or stem) for a short time. Often, the insect will quickly move about the plant, searching

for, orienting to, and selecting a particular position and location on the plant. During this "exploring phase," or afterward while standing in one place, the insect will exhibit "labial dabbing." In this behavior, the tip of the labium is repeatedly touched to the plant surface (66, 82). It is usually accompanied by secretion of a drop of sheath saliva at the tip of the stylets (54). Bits of saliva are often left behind on the plant where the labium has touched. Also, some saliva is drawn back up the stylets at times [Backus, unpublished; this phenomenon has also been observed in heteropterans (59)]. It is not known whether such saliva is drawn up the food or salivary canals, though some believe that it interacts with the precibarial chemosensilla (54, 59). This testing of the plant surface has been observed in all examined leafhoppers (86) and planthoppers (81).

7.4.2 Stylet Probing

After repeatedly dabbing in one area for a few seconds, the insect will firmly appress its labium to the surface and insert its stylets into the plant. While the stylets penetrate downward, the labium telescopes upward as its tip is pushed against the plant cuticle (63). The stylets are thrust through a drop of sheath saliva, which adheres to the plant surface and forms the salivary flange. The insect continues to salivate while penetrating tissues, and the saliva, which solidifies around the stylets, forms a salivary (or stylet) sheath that is continuous with the salivary flange (54).

Construction of the salivary sheath is an intricate and important process for feeding. A drop of saliva forms at the tip of the maxillary stylets, and quickly begins to solidify. As it does, the insect will push the stylets through this drop, until the tips emerge through the other side. At this time, brief uptake of plant fluid can occur. The insect will then repeat the process. This step-by-step progression is reflected in the beaded appearance of most unconfined salivary sheaths. When formed in this manner, the sheath serves to hold the stylet bundle together during the probe, seal it into place, lubricate it, and aid in directional control and withdrawal (66).

Generally, leafhoppers and planthoppers will insert their mandibular stylets only a short distance into the leaf (63, 64, 68). They will then brace them there, using the barbs on their outer surface, embedded within the salivary sheath. The maxillary stylets will simultaneously push through and beyond the mandibular stylets, while continuing to secrete the sheath. In their progress, the maxillary stylets will sometimes be retracted a short distance, then redirected to form another branch of the sheath. This probing behavior is very different from that exhibited by aphids, which insert both pairs of stylets the full distance to the feeding tissue (64). In this case, the mandibular stylets are pushed ahead, with the maxillary stylets slightly retracted and passively following behind. Although these movements are fairly stereotypical in homopterans, they can vary with the viscosity of the probing medium (65).

Auchenorrhynchans also differ from aphids in that they usually probe tis-

sues intracellularly, rather than intercellularly (63). Like aphids, they may begin a probe by inserting the stylets into the interclinal junction between epidermal cells, but later their maxillary stylets usually penetrate in a straight line through cells in their path, rather than continuing to follow cell walls, as aphids do. Initially a probe is made perpendicular to the plant epidermis. However, subsequently, their tracks usually curve right or left. By rotating their stylets during penetration, most homopterans can later bend the stylets in more than one plane (64).

Probing can be divided into two stages: test probing and exploratory probing (82) (Fig. 7.3). Test probing is the earliest stage of stylet probing, and involves shallow penetration into or just past the epidermis. Exploratory probing is a continuation of test probing, during which the stylets penetrate more deeply into the plant, search for, and locate a preferred feeding tissue.

Homopterans add a level of complexity to most herbivore studies, since most not only specialize on a certain range of host plants but also on certain tissues within a host. For example, leafhoppers and planthoppers exploit phloem, xylem, mesophyll, or all three tissues (depending on the species), whereas most aphids are phloem feeders. Such tissue specialization implies that some chemical stimuli present in a plant may not actually be sensed by a probing insect. Limited ingestion (and therefore, chemical sampling) can occur from any tissues the insect's stylets pass through. However, the wholesale mastication and mixing of plant tissues which is common in mandibulate feeding does not occur.

7.4.3 Plant Fluid Ingestion

Once a suitable tissue has been located, the insect will begin ingesting plant fluid. The amount of ingestion time is variable, both on a species and an individual level. Therefore, the amount of fluid taken up can vary depending on time spent ingesting, stimuli from the type of tissue probed, and size of the insect. For example, some small mesophyll-feeding leafhoppers, such as *Empoasca abrupta* (DeLong), ingest very tiny quantities of fluid (Backus, unpublished) while other, xylem-feeding leafhoppers ingest and then excrete large amounts. A single *Graphocephala atropunctata* (Signoret) has been recorded to produce as much as 2.5 ml of excreta in a 24-hr period (39). Possible reasons for such variation are motivational and physiological; they may involve nutrition, or sensory stimuli (see Section 7.5).

During ingestion, auchenorrhynchans secrete watery saliva to aid in digestion of sap (see Section 7.3). Also, should the stylet opening become clogged by callose formation, a brief spurt of watery saliva serves to unblock it (54). If this is not successful, the insect can produce a new branch of the salivary sheath.

7.4.4 Probe Termination

The insect will eventually terminate its probe by retracting its stylets from the plant while simultaneously salivating. This action fills the lumen of the sheath

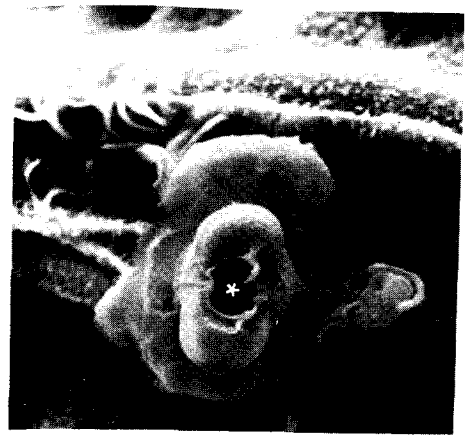

Fig. 7.4 Salivary flange produced by *Peregrinus maidis*. Note the perfect imprint of the labial tip, including dents made by sensory pegs, and the hole left by the stylets (asterisk). (2000X) (Courtesy of E. A. Bernays.)

with saliva, forming a compact, branching structure that is left behind in the plant (54). Retraction and salivation can occur very rapidly (in less than a second; Backus, unpublished). This final salivary secretion, combined with the original salivary flange, forms a "feeding mark" on the surface of the leaf (34) (also called a salivary flange in some literature, as in 58). This mark is often distinctively shaped, forming a mold of the labial tip (54) (Fig. 7.4).

7.5 SENSORY MECHANISMS OF FEEDING

The behaviors described above have been observed and documented for many years. Past research has emphasized any aspect of homopteran biology that could conceivably be involved in transmission of plant pathogens. Feeding was, and is, a favorite subject. Yet, most basic questions surrounding the *sensory* mediation of such behaviors have remained unanswered and controversial. As an example, the means by which the insect guides its stylets through the plant has long been debated in the literature (19, 23, 35, 64). Only recently have we begun to understand the sensory mechanisms used to locate a preferred feeding tissue (3, 4).

In comparison to other insects (especially lepidopterans and dipterans) very little is known about sensory organs in homopterans, and that which is known comes mostly from aphids. Most aphid sensory organs used in host selection and feeding have been anatomically characterized in at least one species. These include antennal sensilla (10, 22, 76), labial sensilla (85, 90), internal, stylet sensilla (25, 88), and internal, precibarial sensilla (90). Many hypotheses, both accurate and inaccurate, regarding the functions of these sensilla abound in aphid-vector literature. However, very few experimental tests of these theories have been carried out. Notable exceptions include two electrophysiological studies of olfaction by antennal sensilla in three aphid species (11, 91).

When we consider homopterans other than aphids, the sensory literature becomes very sparse. However, the few studies performed to date are a good

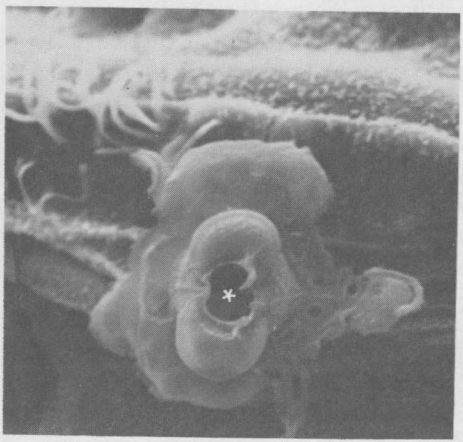

Fig. 7.4 Salivary flange produced by *Peregrinus maidis*. Note the perfect imprint of the labial tip, including dents made by sensory pegs, and the hole left by the stylets (asterisk). (2000X) (Courtesy of E. A. Bernays.)

start. The following discussion will emphasize leafhoppers and planthoppers, though some landmark studies with aphids and heteropterans will also be mentioned. In addition, since it now seems that homopterans have separate sensory systems that mediate perception of different feeding cues, each system will be examined individually. It should be kept in mind, however, that these systems function in concert, virtually simultaneously during rapid feeding probes. First, those sensory organs used to detect external plant cues during leaf surface exploration will be discussed. Then, other sets of sensilla that sense internal plant cues during stylet probing and plant fluid ingestion will be described.

7.5.1 Plant Surface Exploration

Tarsal Sensilla. Some insects (e.g., the blowfly, *Phormia regina* Meigen) have chemosensory organs on their tarsi that can taste substances on which the insect walks (20). No morphological studies of leafhopper or planthopper tarsi have been published, however, some evidence exists indicating the absence of tarsal sensory ability. Cursory examination of *Dalbulus maidis* (DeLong and Wolcott) tarsi using scanning electron microscopy indicates absence of sensilla (Backus, unpublished). Also, K. F. Harris (personal communication) has observed no overt behavioral evidence of tarsal chemosensing by *Graminella nigrifrons* (Forbes). In these studies, sucrose-coated Parafilm membranes were being used to test the effect of external, contact chemostimuli on leafhopper feeding. Harris and his colleagues found that when tarsi were coated with oil or "wax boots," there was no inhibition of the positive feeding response usually elicited by such membranes (38). Taken together, these circumstantial evidences seem to indicate a lack of tarsal chemosensory abilities. Thus, walking over the surface of the leaf probably helps the insect to distinguish gross mechanical features, such as large veins and hairs, but does not appear to provide information about the chemical nature of the surface.

Labial Sensilla. Tasting the surface chemical constituents of a plant seems to be important for optimal host selection in auchenorrhynchans, even though such stimuli are not sensed by tarsal organs. Instead, labial dabbing probably performs this function. Evidence for this again comes from observation of *G. nigrifrons* leafhoppers feeding on sucrose-coated membranes (K. F. Harris, personal communication). Insects that fed preferentially on such membranes were inhibited in this response when their labia were coated with oil (38).

Relatively few morphological studies have been performed on auchenorrhychan labial sensilla. However, recent work by Foster and his colleagues (29) has elucidated the structures of mechano- and chemosensory organs on the labium of *N. lugens*, the brown planthopper (Figs. 7.5a and c). Previously unpublished views of the labium of *Peregrinus maidis* (Ashmead) (Fig. 7.6) show it to be similar (E. A. Bernays, personal communication).

The labium of *N. lugens* is composed of two segments. The distal, smaller

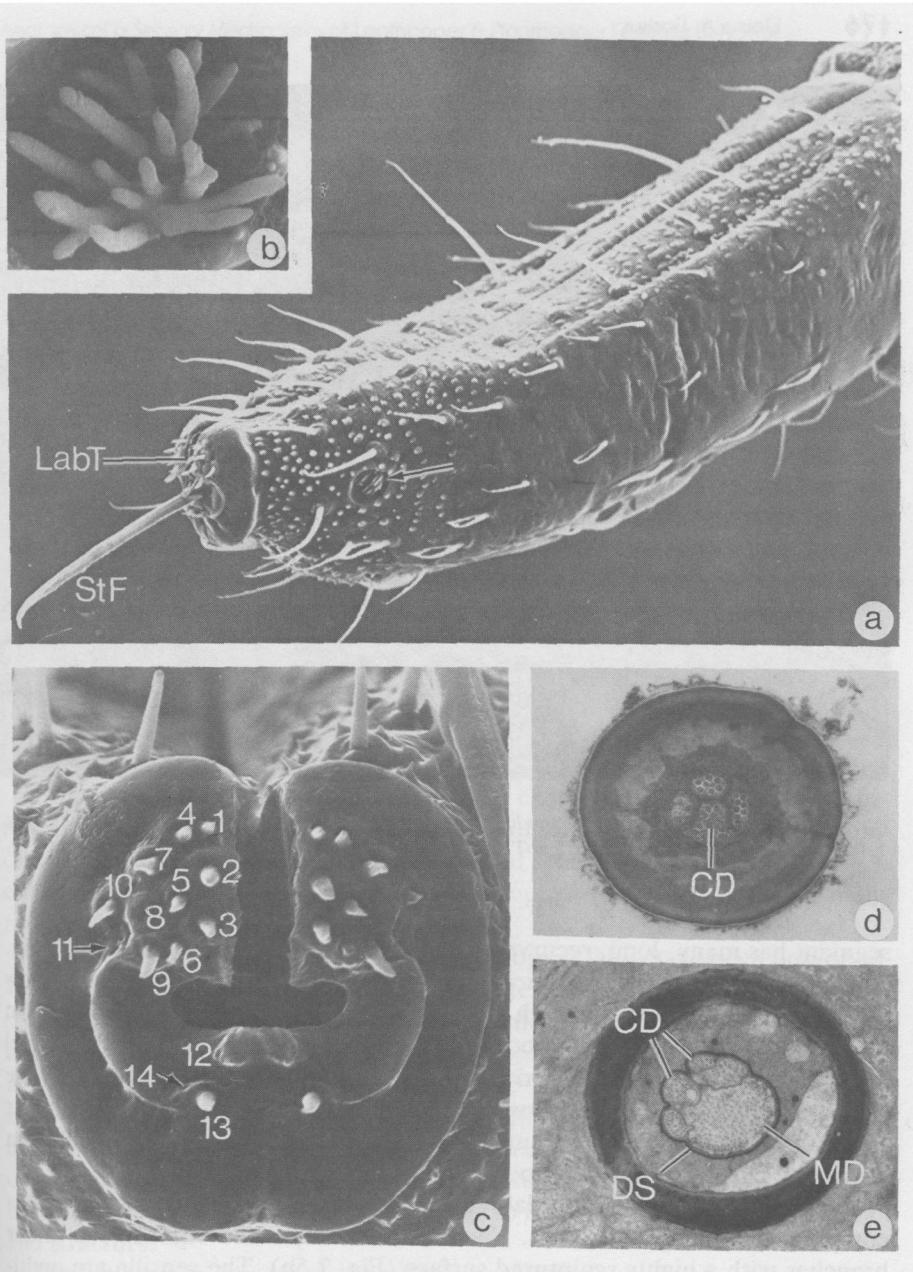

Fig. 7.5 (a) The labium of *Nilaparvata lugens*, showing large setae, the multilobed sensillum in its cavity (arrow), and the labial tip (LabT). StF, stylet fascicle (mostly maxillary stylets visible). (1000X) (b) Close-up of the multilobed sensillum. (3000X) (c) Close-up of the labial tip showing the symmetrical sensory fields on either side of the stylet groove. Each pair of sensilla is numbered. (3200X) (d) and (e) Transverse sections taken at two levels through peg no. 9. (d) Close to tip of the peg showing four chemosensory dendrites (CD). (70,000X) (e) At the base of the peg showing the four chemosensory dendrites (CD) and one mechanosensory dendrite (MD). DS, dendrite sheath. (14,000X) [From Foster and co-workers (29).]

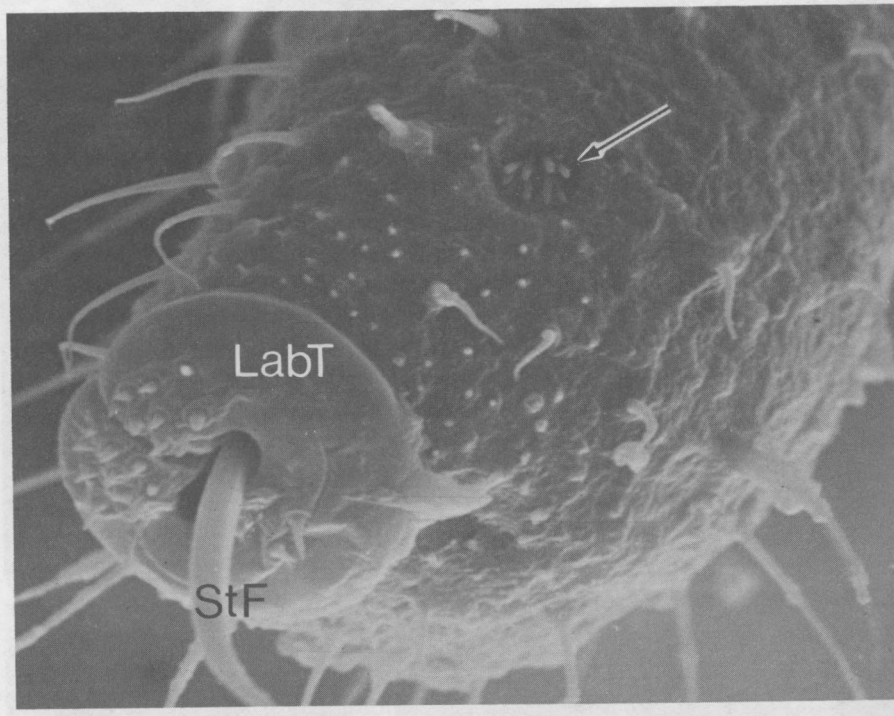

Fig. 7.6 The labium of *Peregrinus maidis*, showing its similarity to that of *Nilaparvata lugens* (Fig. 7.4). Arrow, multilobed sensillum; LabT, labial tip; StF, stylet fascile. (5000X) (Courtesy of E. A. Bernays.)

segment has many, long, recurved setae, which all point toward the tip (Fig. 7.5a). Transmission electron micrographs of sections through these hairs show that they are all innervated with a single bipolar neuron, which terminates at the base of the hair in a tubular body (29). A tubular body is a compact, parallel array of microtubules embedded within an electron-dense material (84). These bodies are a typical feature of insect cuticular mechanosensilla (47). Each hair is housed in a socket whose cuticle can articulate. Thus, these sensilla can clearly be classed as typical type I (cuticular) mechnosensilla (47).

On each side of the distal labial segment there is a cavity that houses a complex, multilobed sensillum. Each has two major and eight to ten minor branches with a highly sculptured surface (Fig. 7.5b). The sensilla are multiporous, and innervated by three repeatedly branching dendrites. Foster and his colleagues (29) are unsure of the function of these sensilla, although they resemble humidity receptors found on some coleopteran antennae (69). Alternatively, they also resemble presumed olfactory sensilla on the antennae of a lamelicornian beetle (51). These sensilla seem to be widespread in delphacids, having also been observed in other species (S. Foster, personal communication; E. A. Bernays, personal communication; Fig. 7.6). However, they have not been seen in leafhoppers (Backus, unpublished).

At the tip of the labium of *N. lugens* is a bilobed, circular field of sensory organs. There are 14 pairs of sensilla on this field, symmetrically arranged around the groove from which the stylets exit. Each pair of tip sensilla has been numbered for identification (Fig. 7.5c). While no morphological trait can be considered a sure indication of physiological function, sensory morphology is well-known and seems to be highly correlated with function (47, 95). Thus, well-based guesses on functions of labial sensilla can be made.

In the uniporous peg sensilla (numbers 4, 7, and 9), one neuron is always larger than the others and terminates at the base of the peg (compare Figs. 7.5d and e) in a tubular body, like that of a mechanosensillum. The other dendrites enter the hollow peg and terminate at the pore in a manner typical of a uniporous chemosensillum (95). These pegs seem to function both as type I mechanosensilla and chemosensilla. Some pegs (numbers 1, 6, 10, 12, and 13) lack a pore, and have a single dendrite that terminates at the base of the peg; again, they are type I mechanosensilla. Pair number 8 are multiporous dome-sensilla, which are each innervated by two, highly branching neurons. No tubular body is present, and these sensilla appear to be strictly chemosensory. The pit sensilla (numbers 11 and 14) are innervated by a single unbranching neuron and are probably also strictly chemosensory. In addition to these paired sensilla on the labial tip, there is also a single peg (number 15) inside the stylet groove, which is not visible from the outside. It is also innervated by a single neuron, and is chemosensory.

Thus, based on diagnostic morphological characteristics, we can hypothesize that the labial tip houses organs capable of sensing mechanical and chemical cues. Above the tip, there is also a pair of sensilla, which may function as either hygroreceptors or olfactory chemoreceptors (or both), as well as many mechanosensitive hairs (29).

To date, no morphological studies of leafhopper labia have been published. However, some recent observations indicate variation in leafhopper labial sensilla among the few species observed, and differences compared to the labium of *N. lugens*. While the labium of *D. maidis* resembles that of *N. lugens* in the presence of both pegs and pits on the labial tip, it differs in having a smaller number of organs and in lacking multilobed sensilla (Backus, unpublished). In contrast, the labium of *G. nigrifrons* is relatively depauperate, with only two small pit organs (K. F. Harris, personal communication). It will be interesting to see if future studies continue to find diversity in sensilla number and structure.

The labial tip is, of course, the surface that is appressed to the plant surface during dabbing. With its array of sensilla, it is probably responsive to both leaf microtopography and chemical constituents (29). It seems likely that chemicals within the plant's waxy cuticle solubilize on contact with the insect's saliva, and it is this saliva–plant chemical mixture that is sensed by the chemosensilla. Through capillarity, small quantities of such fluid may flow up the stylet groove (outside the stylets), where they would be detected by peg number 15.

The mechanosensilla on the tip probably detect the texture of the surface, presence of anticlinal grooves, and vein contours. Peg number 12 and its

companion are located very close to the point at which the stylets emerge from the labium, and probably provide information on stylet protraction. Also, mechanosensitive setae on the sides of the labium may brush the surface during dabbing, but most likely function to monitor the degree of labial telescoping during probing (29).

The possible role of the multilobed sensilla in feeding is unknown. However, given their location away from the labial tip, recessed in a cavity, it is most likely that they detect volatiles very near the plant surface. This fits their hypothesized olfactory or hygroreceptor function.

The ability of leafhoppers and planthoppers to taste external plant chemicals is interesting and unique with respect to other Homoptera, since aphids seem to lack this ability. Ultrastructural studies of the eight paired labial sensilla in the cabbage aphid, *Brevicornye brassicae* (L.), indicate that they are all probably mechanosensitive (89). This work is supported by electrophysiological evidence, which showed the sensilla's lack of response to chemicals (85). Aphids appear to use only mechanical cues, not gustatory cues, during leaf surface exploration. Also, there seems to be much less interspecific variation in sensillar number among aphids. When Harris and Childress (38) examined the labia of ten different species, they found eight pairs of pegs in each case. Thus, while generally the sensory mechanisms of homopteran feeding appear to be similar, some specific aspects may vary considerably among families.

7.5.2 Stylet Probing

As it inserts its stylets into the plant, the insect again senses both chemical and mechanical cues. In this case, however, each modality is sensed by a different set of internal sensory organs. As is discussed in the next section, mechanical stimuli in the interior of the leaf are detected by the stylet sensilla.

Stylet Sensilla. The existence of these sensory organs was unknown until the advent of the electron microscope. They were first observed in the stylets of *Rhodnius prolixus* Stål (61), and later found in the green peach aphid, *Myzus persicae* (Sulzer) (25). Subsequently, stylet sensory organs have been found in all hemipterans examined. They seem to be a characteristic trait of the order and to exhibit consistently similar morphological features (see, for example, 13, 25, 26, 88). Other piercing-sucking feeders, like mosquitoes (44), do not have the same type of stylet sensilla. Therefore, these are unique sensory organs. Their function and role in feeding have been controversial topics in homopteran-vector literature (35, 36, 48) (see Section 7.6). For this reason, these sensilla will be discussed here in some detail with the hope of laying this issue to rest. Combining morphological, physiological, and behavioral evidence, as well as comparative studies between hemipteran species will allow us to conclude with little doubt that these are unique mechanosensory organs.

As mentioned earlier, all four stylets of the two leafhopper and planthopper species examined have hollow canals within them that house sensory dendrites

(Figs. 7.7a and b). Each maxillary stylet has one canal at the base that splits into two canals distally; each mandibular stylet has a single canal. Morphological studies of the aster leafhopper, *Macrosteles fascifrons* Stål (3, 28), and the brown planthopper, *N. lugens* (30), show differences in number and arrangement of mandibular stylet dendrites in each species (Table 7.1). These differences will be briefly discussed since they may be correlated with variations in feeding behavior between the two species, and because they provide evidence for the mechanosensory function of stylet sensilla.

The most unusual property of homopteran stylet sensilla is their ultrastructure. Its role in transduction of mechanical information has yet to be determined, though some hypotheses exist. The dendrites within the canals *appear* to be free-floating extensions of the neuron cell bodies located within the stylet bases (Figs. 7.7c). They are attached to the wall of the stylet canals at the base where they emerge, and at their tips (28, 30, 88). Axons from the cell bodies exit the stylet bases and form nerves that lead to the subesophageal ganglion (62).

When sectioned in the hollow stylet canal, the dendrites exhibit two types of ultrastructure (Figs. 7.7a, b, and c). Some dendrites are surrounded by five to seven, radially arrayed, protoplasmic processes (Fig. 7.7c), which are extensions of the glial, or sheath, cells that envelope the cell bodies in the base. These protoplasmic processes are attached to the thickened cuticular sheath, which surrounds each dendrite (Fig. 7.7c). The processes do not always extend the full length of the stylet, but are always present (at least) at the base. It is possible that these processes function in nutritional support of the dendrites, as do the sheath cells (95). This type of dendritic ultrastructure shall be designated as *type p*. The other dendrites are not surrounded by protoplasmic processes, and often have somewhat thinner dendritic sheaths. These dendrites shall be designated as *type n*. Type n dendrites are often, though not always, larger than type p dendrites.

M. fascifrons and *N. lugens* differ in their numbers of types n and p dendrites, as can be seen in Table 7.1. If Fig. 7.7a and b are compared with Table 7.1, it can be seen that one of the type p maxillary dendrites in *M. fascifrons* corresponds to a type n dendrite in *N. lugens*. In the mandibular stylets, all three dendrites of *M. fascifrons* are usually type p, whereas in *N. lugens* all five dendrites are usually type n.

The two species also differ in another respect: dendrite length and number per sensillum. In *M. fascifrons*, both maxillae and mandibles each have three sensilla. The maxillary sensilla each have two dendrites (for a total of six), one of which does not enter the stylet canal. Instead, it terminates at the stylet base. In contrast, each mandibular sensillum is composed of a single dendrite, and all three extend the full length of the stylet (3). *N. lugens* also has both long and short dendrites. However, in this case it is the *mandibular* dendrites whose six dendrites are paired, forming three sensilla, with one dendrite being short. All five of the *maxillary* dendrites are unpaired and extend the length of the canal. Therefore, the short dendrites are located in the maxillary stylets in the

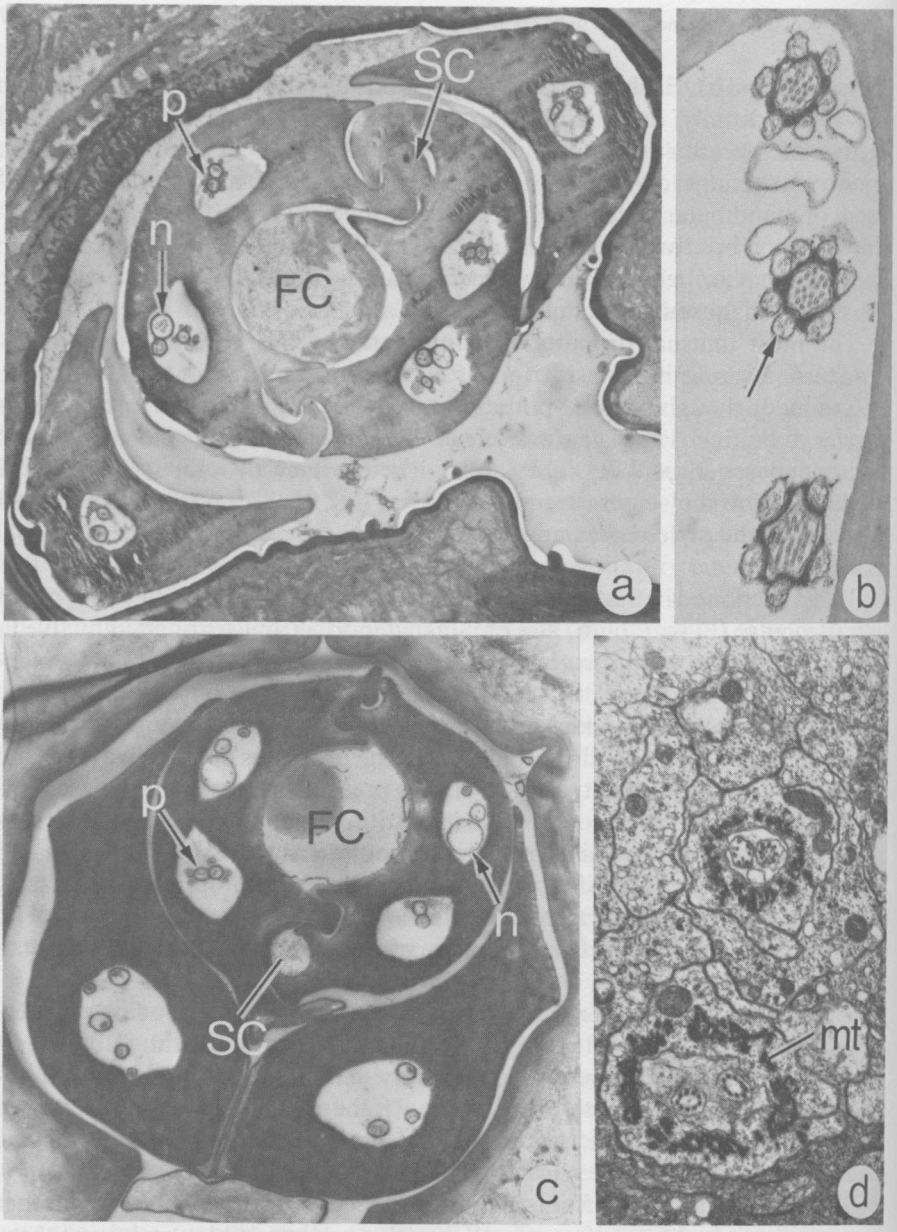

Fig. 7.7 (a) Cross section of the stylet bundle of *Macrosteles ascifrons*, in the distal half of the shafts. Note the two maxillary dendritic canals, containing bo ı type n dendrites (n) and type p dendrites (p). FC, food canal; SC, salivary canal. (7000X) [I om Forbes and Raine (28).] (b) Close-up cross section of three type p dendrites in a mandibuıar canal of *M. fascifrons*. Arrow indicates a protoplasmic process. (25,300X) [From Backus and McLean (3).] (c) Cross section of the stylet bundle of *Nilaparvata lugens*, near stylet tips. Note that a dendrite in the mandibular canal on the right is absent, since it has terminated above the level of the section. Three other mandibular dendrites are close to termination. (13,000X) [From Foster and co-workers (30).] (d) Cross section through the ciliary regions of two of the three maxillary stylet mechanosensilla of *M. fascifrons*. Note that each sensillum consists of two dendrites, surrounded by a glial cell that contains an array of electron-dense microtubules (mt). (11,000X)

Table 7.1 Characteristics of the Stylet Sensilla of *Macrosteles fascifrons* and *Nilaparvata lugens*[a]

Stylet	Total Number of Dendrites per Stylet	Total Number of[b] Dendrites in Canals	Number of Dendrites[b] in Canals		Total Number of Sensilla per Stylet	Number of Dendrites per Sensillum	Dendrite[c] Length
			Type p	Type n			
M. fascifrons							
maxillary	6	5 = (2 + 3)	(2 + 1)	(0 + 2)	3	2	5L,1S
mandibular	3	3	3	0	3	1	3L
N. lugens							
maxillary	5	5 = (2 + 3)	(2 + 0)	(0 + 3)	5	1	5L
mandibular	6	5	0	5	3	2	5L,1S

[a]Adapted from Backus and McLean (3), Forbes and Raine (28), and Foster and co-workers (30).
[b]Parentheses indicate number of dendrites in each maxillary canal. The left number always represents the dendritic canal nearest the salivary canal; the right number represents the one nearest the food canal.
[c]L, long (number of stylet dendrites extending to the tip, within stylet canals). S, short (number of dendrites terminating at base, not entering canal).

leafhopper, and in the mandibular stylets in the planthopper (30; S. Foster, personal communication). This is in contrast to the innervation pattern of the aphid *B. brassicae*, which has sensilla only in the mandibular stylets, wherein one dendrite is short and three are long (88).

Another, somewhat unique morphological characteristic of stylet sensilla is the presence of electron-dense microtubules or scolopale rods, which surround each sensillum in the stylet base (Fig. 7.7d). These fibers are embedded in the cytoplasm of the sheath cells that surround each sensillum, yet do not extend into the protoplasmic processes within the stylet canals (3). This type of scolopale has only been observed in leafhopper stylets (3), aphid stylets (88), and (according to 88) crustacean limb proprioceptors (55) and a chordotonal organ in the lacineae of the larval coleopteran *Speophyes lucidulus* DeLar (14). In each of these cases, the rods form a skeletal structure, which rigidly supports the dendrites proximally.

The free-floating nature of the distal dendritic shaft, the protoplasmic processes, and the anchoring scolopale rods are the most unusual properties of these organs, making them somewhat resemble chordotonal organs (40). Yet no other insect sensory organs, mechano- or chemosensory, are known to have all of these properties. The stylet sensilla certainly do not, as some have suggested, physically resemble "arthropodan chemoreceptors" (35).

Wensler (88), in her study of *B. brassicae*, was the first to propose that homopteran stylet organs were proprioceptive mechanosensilla. Her contention is now supported by the examinations of *M. fascifrons* and *N. lugens* in which the above three properties were also observed. Wensler hypothesized that the long dendrites monitor lateromedial movement of the stylet tips, and its direction of penetration. Bending the stylets mechanically distorts the unanchored, distal portion of the dendrites relative to the anchored, proximal portion within the stylet bases. At the tips of the dendrites, the sheaths are attached to the stylet wall and are asymmetrically thickened. During deflection of the stylets, the side of the sheath that is thinner would be bent more than the thick side. Such unequal mechanical strain on the dendroplasmic membrane beneath could trigger depolarization. Different directions of curvature might be indicated by depolarization of different dendrites. Whether this hypothesis is reasonable, given recent theories of mechanosensory transduction, cannot yet be stated. Tubular bodies and their viscoelastic properties are emphasized in such theories (31, 45), yet are not evident here.

Wensler (88) also hypothesized that the short dendrites monitor tension on and stretch of the stylet relative to the dendrites' attachment site. This is possible because each short dendrite is anchored only to a long dendrite, and is surrounded by extracellular fluid.

It is interesting that *B. brassicae* detects both bending and tension only in the mandibular stylets (88). *M. fascifrons* detects bending in both stylets, but tension on only the maxillary stylets (3), while *N. lugens* detects bending in both stylets, but tension on only the mandibular stylets (30).

Until now, no one has speculated on any proximate significance for this difference in innervation pattern between these several homopteran species. It can, however, be linked to behavioral evidence of the mechanosensory function of stylet sensilla by considering its correlation with insect feeding style. Recall that aphids and auchenorrhynchans probe plants differently (see Section 7.4.2). In the case of aphids, the maxillary stylets are somewhat passive followers of the mandibulars. If the stylet sensilla monitor movement, then it is economical for aphids to innervate only the mandibular stylets. In leafhoppers and planthoppers, the independent movement of both stylets necessitates innervation of both. Also, feeding patterns of auchenorrhychans may differ slightly enough to explain the maxillary versus mandibular location of tension receptors. In any case, this innervation difference cannot be explained as well if the stylet sensilla are chemosensory.

Finally, some electrophysiological work has been performed on stylet sensilla in a heteropteran. Bernard and co-workers (9) and Pinet and Bernard (62) describe the results of extracellular recordings of action potentials in the maxillary stylet nerves of *Triatoma infestans* (Klug) (Heteroptera: Reduviidae). They found that three neuronal units (P, G, and M), corresponding to the three dendrites in the maxillary canal, produce bursting spike discharges when stimulated by deformation of the stylet cuticle. For their experiments, they used dry and humid air blown on the stylets as a handy means of effecting gradual and reproducible deformations. The stylets reacted to humid air in a manner similar to a hair hygrometer; the extremely hygroscopic cuticle absorbed moisture, causing it to warp. This mechanical deformation triggered dendroplasmic depolarization. Thus, the dendrites within the stylets could act as both mechanoreceptors (detecting any physical movement causing stylet deformation) and hygroreceptors. The G and M units acted antagonistically, reacting to different modalities. Unit G fired in response to increased relative humidity and/or rising temperature. Unit M would be inhibited under those conditions and would, instead, fire in response to dry air movement and/or decreasing temperature. Conversely, unit G would be inhibited. Such (reciprocal?) antagonism between the dendrites supports Wensler's (88) hypothesis for the mechanism of transduction of mechanical information in these sensilla.

Pinet and Bernard (61) speculate that hemipteran stylet sensilla evolved as mechanosensilla and then, secondarily, adapted to the hygroreceptor function (at least in *T. infestans*). Clearly, however, their elegant and carefully quantified study leaves no doubt that stylet deformation alone stimulates these sensilla, and provides a fitting capstone for the contention that they are mechanosensory.

Precibarial Sensilla. Unlike the recent discovery of the stylet sensilla, homopteran precibarial sensilla have been known since 1914, when Davidson first saw them in the aphid, *Schizoneura lanigera* Hausmann (17). Weber (87) described and named them the *epipharngeal organ*, an unsatisfactory term frequently used since then. No ultrastructural examination, however, was made until 1969, when Wensler and Filshie (90) examined *B. brassicae* using

electron microscopy. Very few other hemipterans had been examined in any way (7, 60) until recent ultrastructural studies of several leafhopper species (3, 4) and a planthopper (30). The latter studies confirmed early speculation that these are gustatory chemosensilla, since their internal ultrastructure is very typical of such organs. Thus, these structures have been renamed the *precibarial chemosensilla* because of their location and presence on both the epi- and hypopharynges (3).

In ten leafhopper species examined, SEM reveals that twenty, small, papilla-like sensilla line the walls of the precibarium within the head (see Section 7.2.2). They are separated into two groups of ten by the precibarial valve (Fig. 7.2). Nine out of ten species examined with SEM have ten sensilla in the distal group, below the valve (Fig. 7.8a). In one case, *Oncometopia nigricans* (Walker), there are twenty distal (D-) sensilla. In all species, the proximal sensilla (above the valve) number eight on the epipharyngeal side (P-sensilla) and two on the hypopharyngeal side (H-sensilla). Those on the epipharyngeal side line the walls of a recessed, basin-like structure (Fig. 7.8b).

Generally, the external sensillar morphology of all observed leafhopper species is similar, differing only slightly in arrangement (and in one case, number) of the sensory organs, especially the D-sensilla. These variations are dependent on width and length of the precibaria, which in turn are correlated with the preferred feeding site of the species (see Section 7.2.2). For example, xylem-feeding cicadellinines have widely spaced D-sensilla grouped over their broad distal precibaria, whereas phloem-feeders have paired or single-file sensilla within very narrow precibaria (4).

Only TEM, not SEM studies, have been performed on a planthopper, *N. lugens* (30). Therefore, while internal sensillar ultrastructure is known, external morphology and arrangement remain unknown. *N. lugens* does, however, have two separate groups of epipharyngeal papillae, consisting of ten paired distal sensilla and ten paired proximal sensilla. There is also a pair of hypophyaryngeal sensilla, for a total of twenty-two sensory organs. Thus, *N. lugens* has two more precibarial papillae than most leafhoppers examined (Fig. 7.9a). It is likely that they are arranged in a manner similar to leafhoppers, given the remarkable similarity in sensilla among homopterans observed: cercopids, fulgorids, cicadas, and leafhoppers (Backus, unpublished).

TEM sections through the precibarial papillae of both *M. fascifrons* (3) and *N. lugens* (30) reveal features typical of gustatory chemosensilla. Each papilla has a deep, longitudinal slit that allows fluid to impinge on the dendritic bundles beneath. An electron-dense sensillum liquor is commonly observed in the distal 5 m of the dendritic bundle, and can be seen exuding through the papilla's slit (Fig. 7.8c). Sensillum liquor is thought to aid absorption of chemical stimuli and diffusion to the dendrite's membrane receptors (2, 83). Two to five unbranching dendrites from bipolar neurons innervate each papilla. Surrounding each dendritic bundle are several, highly interdigitating sheath cells, whose cell membranes form nest-like arrays (Fig. 7.8d).

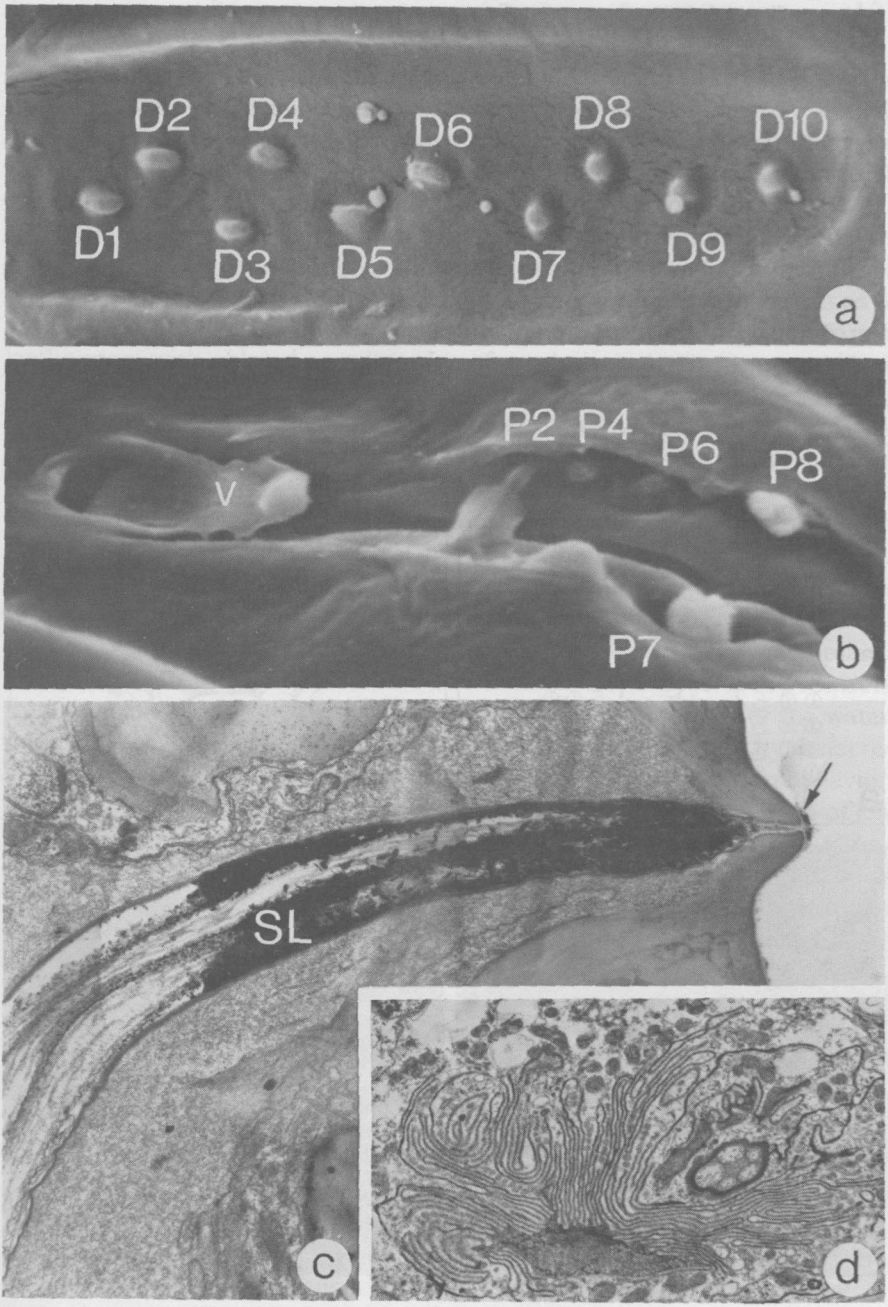

Fig. 7.8 Precibarial sensilla of *Macrosteles fascifrons*. (a) Distal portion of the epipharynx showing the D sensilla, numbered. The cibarium is to the right. (6000X) (b) Proximal portion of the epipharynx showing the precibarial valve (v) and four of the six P sensilla (numbered). The cibarium is to the right. (5200X) (c) Longitudinal section of one H sensillum. Note the electron-dense sensillum liquor (*SL*) and evidence that it has flowed out the pore (arrow). (18,000X) [(a), (b), and (c) from Backus and McLean (3).] (d) Cross section of a sensillum, showing the nest-like interdigitation of the sheath cell membranes. (11,000X)

The numbers of unbranching neurons within each sensillum vary between the two species, as shown in Fig. 7.9a. Thus, while markedly similar, the precibarial sensory systems of leafhoppers and planthoppers do vary somewhat. See Backus and McLean (3) for a comparison of aphids and leafhoppers.

In observations of leafhoppers, it is striking that sensillum *number* does not vary between species (with the exception of *O. nigricans,* which has 30 instead of 20), but *arrangement* within sensilla groups does vary. Sensory organs seem to be aligned to utilize optimally available space. Such evolutionary conservatism of sensory number may reflect the importance of these sensilla for feeding,

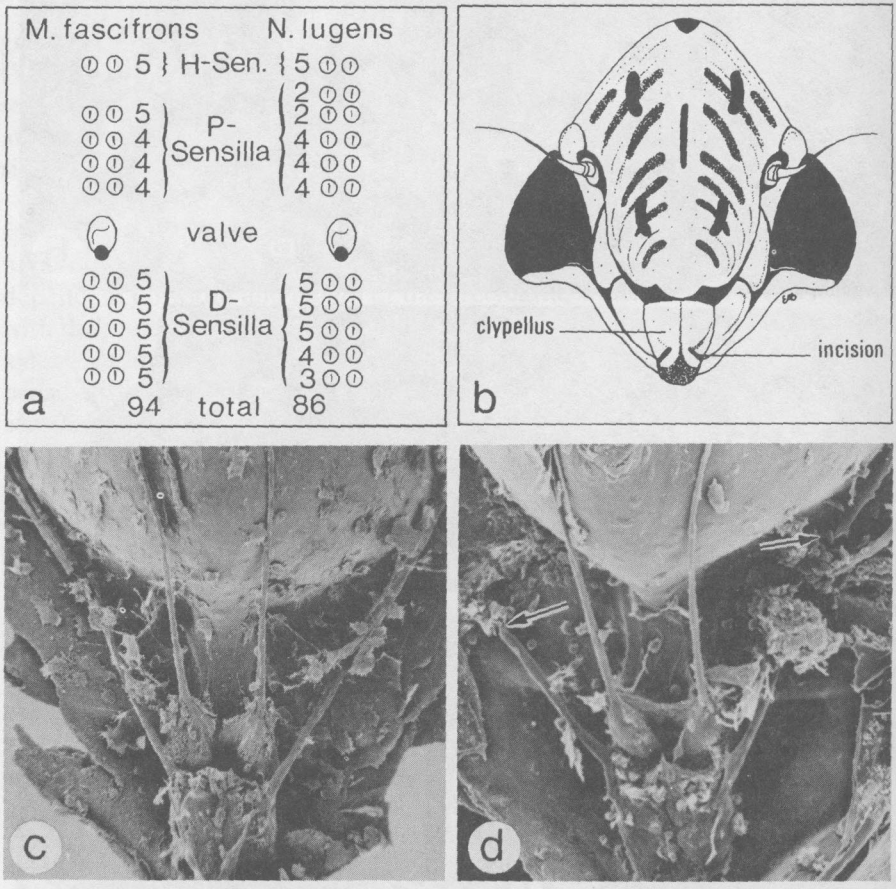

Fig. 7.9 (a) Diagrammatic representation of the precibaria of *Macrosteles fascifrons* and *Nilaparvata lugens*, for comparison. Numbers indicate how many dendrites are found in each sensillum in a pair, with totals for all precibarial sensilla at bottom. (b) Head of *Graphocephala atropunctata* showing the location of the surgical incisions used to sever epipharyngeal nerves. (c) and (d) Before-and-after views of surgery on *G. atropunctata*. Arrows denote cut lateral epipharyngeal nerves. Valve muscle and nerves are missing. (Both 190X.) [(b), (c), and (d) from Backus and McLean (5).]

and perhaps a common peripheral mechanism underlying perception of internal plant chemicals. This is in contrast to the possible variations in sensillar complement of the labium observed among different species (see section on *Labial sensilla*), which may indicate greater variability in mechanisms of sensing external plant cues.

To more directly test the importance of precibarial sensilla in leafhopper host selection and tissue-location behaviors, Backus and McLean (5) developed a technique of severing nerves that lead from half the sensory organs of *G. atropunctata* (75). Thus, it was possible to observe the feeding behaviors of leafhoppers with ablated sensilla. Use of a relatively large (8 mm), xylem-feeding leafhopper, *G. atropunctata* [vector of Pierce's disease bacterium in grapes (18)] made the surgery possible. Surgery consisted of making an incision in the cuticle of the clypellus (Fig. 7.9b) severing (Figs. 7.9c and d) the lateral nerves of the distal organs (4).

The behavioral responses of three cohorts of insects were tested by offering them a two-choice preference test between a highly preferred substrate [a mustard leaf infused with a 5% (w:w) sucrose solution] and a less-preferred substrate (a mustard leaf infused with distilled water). After tabulating the distributions of insects on or off leaves, it was clear that the host acceptance abilities of denerved insects differed substantially from those of the controls. Both controls significantly preferred the sucrose-treated leaf over the water-treated leaf, whereas there was no difference in choice of leaves by denerved insects. Also, there was a difference in the *quality* of host selection behaviors between leafhoppers. Both controls tended to undergo a short period of leaf surface exploration before commencing to probe and feed in one spot. Often, they would remain there for several observation time periods. Thus, the same insects would be counted repeatedly on the same leaf. In contrast, denerved insects rarely settled on a leaf for very long. Instead, they spent a large percentage of time off leaves (5).

Thus, depriving leafhoppers of only half of their precibarial sensilla had a profound effect on host discrimination and acceptance. This difference was not due to the trauma of the surgery, since the sham-operated controls exhibited a definite preference for the sucrose-treated leaf over water-treated leaf, though not to the same extent as normal controls. However, sham-operated controls were capable of making the distinction between leaves, while denerved insects could not. The only detectable difference between test leaves was in their internal chemistry. Since denerved insects could not perceive that difference, the precibarial chemosensilla likely were the major means of sensing those chemicals. For further discussion, see Backus and McLean (5).

Further quantification of the mediation of feeding by the precibarial chemosensilla, especially as related to the location of preferred feeding tissues, is currently being undertaken. For this second test, an electronic measurement system to record feeding behavior (42, 43, 48, 50) is being used. In these studies, the same three cohorts of insects are being examined, and each subject is given two hr of access time to a 5% sucrose-infused mustard leaf.

Results of the second study have not yet been analyzed. However, preliminary observations indicate that, once again, there seems to be a dramatic behavioral difference between controls and denerved insects. It seems likely that significant differences will be seen in probing frequencies and durations, salivation and ingestion times, and tissues from which ingestion occurs, and that these will be related to mechanisms underlying test and exploratory probing (Backus and McLean, unpublished).

Thus, current evidence indicates that the precibarial chemosensilla are vital for mediation of host selection and feeding. They are the major means by which leafhoppers, planthoppers, and probably all homopterans taste internal plant chemicals. Therefore, they are an important key to our understanding of behavioral mechanisms of feeding in these insects.

7.6 CONCLUDING REMARKS

The complex interactions that occur between a homopeteran and its host plant during feeding have been studied by many researchers for a number of years. The depth of this work is demonstrated by the detail to which some morphological and physiological factors are known (e.g., see 54, 64). Because of this knowledge, and the general similarity in feeding among homopterans, it is now possible to analyze the underlying mechanism of feeding in a stepwise fashion. In the case of auchenorrhynchans, the flowchart in Fig. 7.3 summarizes this sequence. Such a mechanistic view of feeding will allow researchers to apply basic principles of behavioral theory to this system. The simplicity of homopteran sensory systems (compared to such insects as beetles and flies) augurs well for their future use as a basic model system for behavior.

One outcome of the search for sensory mechanisms of feeding is an answer to the question, How do homopterans locate a specific feeding tissue? In the case of leafhoppers and planthoppers, *one* answer is as follows. They sense internal mechanical cues of the plant by detecting the precise movements of their stylets as they probe through tissues. They detect chemical cues by pulling fluids (probably a mixture of plant and salivary juices) up their stylets to the precibarium, where chemosensilla monitor chemical constituents. These two sensory events probably occur simultaneously during stylet probing. While the chemical stimuli involved are hardly understood, at least now the organs that sense them are known.

Knowledge of homopteran sensory mechanisms promises to have a profound effect on studies of plant pathogen–vector relationships, as well as development of host plant resistance in crop cultivars. For example, knowing that plant fluid must be drawn up the stylets to the precibarium before it can be tasted by homopterans has implications for acquisition and transmission of non-persistent viruses by aphids and semipersistent viruses by aphids and leafhoppers [these were the crux of the controversy surrounding function of the stylet sensilla (35)]. We now suspect that even the shallowest probes involve uptake of tiny quantities of fluid, which may contain virus particles that render

a vector viruliferous (49). Also, advanced knowledge of sensory perception, and the specific chemical stimuli that mediate feeding, may aid plant geneticists in designing future cultivars resistant to leafhopper or planthopper feeding. With more rapid, recombinant DNA and tissue culture technologies now becoming available, resistance factors based on an insect's behavioral avoidance of feeding could potentially be incorporated into crop genomes. This may facilitate development of vertical host plant resistance, which would be less easily overcome by pest populations.

While the considerable literature may indicate how much is known about homopteran feeding, there still remain many unanswered questions. Knowledge of specific chemical deterrents, antifeedants, and/or other stimuli was not discussed in detail here. Chemical cues for some species are known, for example, *N. lugens* and deltocephaline leafhoppers (70, 74, 80–82, 93, 94), *Empoasca fabae* (Harris) (15, 16), *P. maidis* (24), and aphids (92). Much of this knowledge stems from the development of artificial diets for rearing homopeterans (56) (see also Brooks, Chapter 8). For the majority of auchenorrhynchans, however, feeding stimuli remain unknown.

Many questions still remain about auchenorrhynchan sensory systems. Possible sensilla on the antennae may play a role during host acceptance and feeding by detecting volatiles emanating from the plant surface. Since so little is known about antennal sensilla, these were neither included in Fig. 7.3 nor discussed in the text. Electrophysiological studies of auchenorrhynchan sensilla have yet to be performed, and only they can provide some answers. For example, the true function of the multilobed sensillum on the labium of *N. lugens* will only be learned using electrophysiology. Also, attraction to and orientation toward the host plant has scarcely been studied, though often observed anecdotally. Actual sensory systems mediating orientation behavior have been little researched (71–73) and, thus, have not been discussed here.

An understanding of auchenorrhynchan sensory mechanisms from an evolutionary standpoint remains unknown. The amount of variation in sensory organs among species is barely appreciated, although the wide divergence in feeding behaviors and host specificities (see Section 7.1) is realized. To what extent such behavioral diversity is correlated with the evolution of sensory mechanisms is unknown. However, current theories on the evolution of insect herbivory emphasize changes in sensory perception of plant cues as a first step in adaptation to a new host plant (32). Such subtle changes can be rapidly followed by shifts in feeding behavior. Thus, comparative studies of sensory mechanisms in leafhoppers and planthoppers will aid in an understanding of the evolution of potential agricultural pests (see Nault, Chapter 13).

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