

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 denervated 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 homopteran 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 homopterans (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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