

Chemoreceptors of adult Mexican bean beetles: External morphology and role in food preference

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Keywords: Mexican bean beetle, *Epilachna varivestis*, host selection, food preference, chemoreceptors, SEM, host plant resistance, ablation, olfaction, taste

Abstract

The Mexican bean beetle, *Epilachna varivestis* Mulsant (Coleoptera; Coccinellidae), is an oligophagous insect that accepts leaves of soybean, *Glycine max* (L.) Merrill, as food but exhibits distinct preferences among varieties. It is believed that the basis for discrimination between the resistant PI 229358 and the susceptible cv. 'Williams' is chemical. By the ablation of chemosensilla on antennae, maxillary palpi, labial palpi, and foretarsi, followed with leaf disc preference tests, we found antennal and maxillary palp chemosensilla to be almost entirely responsible for Mexican bean beetles' discrimination between foliage of the resistant and susceptible genotypes. All appendages, and the epipharynx, were observed by scanning electron microscopy and, except for foretarsi, were found to bear several types of presumably olfactory and gustatory sensilla, which are figured and described. Since behavioral observations show that olfaction is usually sufficient to cause rejection of PI 229358, we conclude that olfactory sensilla mainly on antennae and maxillary palpi are critical in food discrimination in this system.

Introduction

The Mexican bean beetle (MBB), *Epilachna varivestis* Mulsant, is one of the few truly oligophagous Nearctic herbivores adapted to soybean, *Glycine max* (L.) Merrill, an introduced plant in the United States. The spatial patterns of soybean and the MBB in the United States are perfectly coincidental in the east but, the pattern of soybean exploitation by the MBB is disjunct (Kogan, 1980). Although capable of exploiting soybean resources in some areas, the MBB still prefers feeding on its native hosts, *Phaseolus* spp.

The MBB displays a remarkable ability to discriminate among its potential leguminous hosts. It was used to screen, from among hundreds of genotypes of soybean, a few with high levels of resistance to foliage-feeding arthropods (Van Duyn *et al.*, 1971). These lines – plant introductions (PI's) 171451, 227687 and 229358, have been investigated

with regard to possible physiological processes associated with resistance (Van Duyn *et al.*, 1972; Kogan, 1972; Tester, 1977; Dreyer *et al.*, 1979; Smith & Brim, 1979; Grunwald & Kogan, 1981; Hart *et al.*, 1983; Binder & Waiss, 1984). Despite these researchers' efforts to elucidate mechanisms of soybean resistance to insects, the question is still unresolved. We believe that the answer lies in a better understanding of the fundamental host-selection mechanisms in the MBB. Therefore, we redirected our research to improve our understanding of those mechanisms at the sensory, behavioral, physiological, and broad ecological levels.

By gross examination of antennae, maxillary and labial palps, epipharynx, and tarsi we located sensory areas likely to be involved in host-selection processes. We employed scanning electron microscopy (SEM) of those sensory areas. In a preliminary attempt to connect structure and function, we systematically amputated adult beetle ap-

pendages and tested the loss of discrimination of amputated beetles by dual-choice preference tests. We describe sensory areas, as revealed by SEM, and report and discuss results of dual-choice tests with amputated adults.

Materials and methods

Insects

We used 12th and 13th generation MBB's from a laboratory culture started with specimens collected on soybean in Park County, Indiana, USA. Larvae and adults were maintained on leaves of seedling common bean, *Phaseolus vulgaris* (L.), under a 16L:8D photoperiod in a greenhouse.

Scanning electron microscopy

Heads of newly emerged adults were fixed in 2.0% glutaraldehyde and 0.1 M phosphate buffer for 24 h. Fixing was followed by dehydration in an ethanol/water series, ascending from 10 to 100% ethanol (ETOH) in 1.5 h, with a final triple rinse in 100% ETOH. The various appendages were dissected under ETOH, dried from CO₂ in a critical point drier, sputter coated with platinum and iridium at 30 ma for 40 s, and examined with a dual-stage scanning electron microscope (ISI-DS130) at accelerating voltage 7.0 Kv.

Ablation

Pairs of antennae, maxillary palps, or foretarsi were excised with iridectomy scissors. Each beetle was anesthetized under a stream of CO₂ for approximately 1 min and held ventral side up under a dissection microscope by a vacuum tweezer applied against the elytra. Excision of sensory appendages was completed in less than 1 min, and insects were immediately placed on preference tests. They recovered from anesthesia and were upright in ca. 5 min. Antennae were excised by cutting through the scape adjacent to the head. Labial palps were cut close to the labium through the basal section. The entire maxillary palp was severed. Six ablation treatments were tested: (1) antennae, (2) maxillary palps, (3) labial palps, (4) foretarsi, (5) antennae plus maxillary palps, or (6) all 4 pairs of append-

ages. Two controls were (1) CO₂ anesthetized unablated beetles and (2) beetles with only one of the pair of each of the four types of appendages excised.

Preference tests

Preference tests were conducted in a 15-cm-diam. petri dish arena. The bottom of the dish was lined with an 8-mm-thick layer of hardened plaster of Paris and covered with a filter paper disc. The plaster of Paris-filter paper linings were saturated with distilled water prior to each test. Leaf discs, each 2.5 cm in diameter, were cut with a cork borer from freshly collected leaves of the test plants. Three discs each of two varieties were skewered with map tacks in an alternating pattern along a circle ca. 1 cm away from the perimeter of the dish. Test plants were hydroponically grown 'Williams', a 'susceptible' variety, and PI 229358, a line highly resistant to the MBB. Four ♀ MBB's, 3–7 days old, were placed in each arena after 6–8 h of starvation and the ablation of selected sensory appendages. Test arenas were held in the dark 25±2 °C and 60% R.H. After either 24 or 48 h, the leaf area remaining for each disc was measured by using a leaf-area meter.

Results and discussion

Sensory structures

Antenna (Figs. 1–11)

The MBB antenna consists of 12 segments, including scape and pedicel, and is very small (ca. 2 mm long) relative to the size of the beetle (Fig. 1). Antennae might be expected to be densely covered with sensilla, since surface area is small. However, sensory hairs are rather widely spaced, and only the three terminal segments bear chemosensilla (Fig. 2). These types of sensilla were identified.

Sensilla trichodea Types I & II (Figs. 1–2). Pedicel has a cluster of 40–100 μ trichoid hairs (Type I) with straight or strongly curved, finely striated shaft, without openings or pores, and with blunt tips (Fig. 1). Remaining segments are sparsely covered with sensilla trichodea closely appressed to the integument of the antenna (Type II) (Fig. 2).

These hairs do not show openings or pits, the tip is blunt, and the shaft is also finely striated. Both types appear to be mechanoreceptors (Slifer, 1970; Zacharuk, 1980).

There appear to be five types of sensilla on the three terminal segments. They can be distinguished as:

Sensilla trichodea Type III (Figs. 2–4). A third type of trichoid sensillum extends outward, at approximately 45° from the three apical segments (Figs. 2, 4). These are $50\text{--}80\ \mu$ long and $3\ \mu$ in diameter. Strong grooves begin at the base and spiral toward the tip, where there is an opening about $0.2\ \mu$ wide (Fig. 3). There is no evidence of pores on the side-walls of these hairs, and they are probably gustatory. Similar trichoid sensilla were observed on the antennae of *Dendroctonus ponderosae* Hopkins and *Apis mellifera* L. and were considered gustatory (Whitehead & Larsen, 1976; Whitehead, 1981).

Sensilla chaetica Types I & II (Figs. 4–7). Each of the three terminal segments also bears a small field of sensilla chaetica (Fig. 2). Type I is $10\text{--}15\ \mu$ long, slightly tapered distad, $2\ \mu$ at tip and produced from a bulbous base. The tip is blunt, and the shaft is apparently multiporous (Fig. 6). Type II is identical to Type I but ranges from $22\text{--}28\ \mu$ in length and appears only on the terminal segment (Fig. 7). Examination of the interior of broken s. chaetica reveals very thin walls. A similar s. chaeticum on the antenna of *D. ponderosae* is multiporous and filled with profusely branched dendrites, indicating an olfactory function (Whitehead, 1981). Multiporous external surfaces and highly branched dendrites seem to typify olfactory sensilla in antennae of insects (Slifer, 1970; Mustaparta, 1973; Hatfield *et al.*, 1976; Dickens, 1979; Zacharuk, 1980; Bland, 1981; Rojas-Rousse & Palevody, 1983). In the MBB the size of these fields increases toward the antennal tip, with the antepenultimate segment bearing approximately 30 s. chaetica and five s. trichodea (Type III), the penultimate bearing $50\text{--}55$ s. chaetica and $8\text{--}10$ s. trichodea, and the ultimate segment bearing approximately 100 s. chaetica and $8\text{--}10$ s. trichodea.

Sensilla chaetica Type III (Figs. 8–9). This type is about the same length as s. chaetica Type I ($10\text{--}15\ \mu$) and also arises from a bulbous base, but

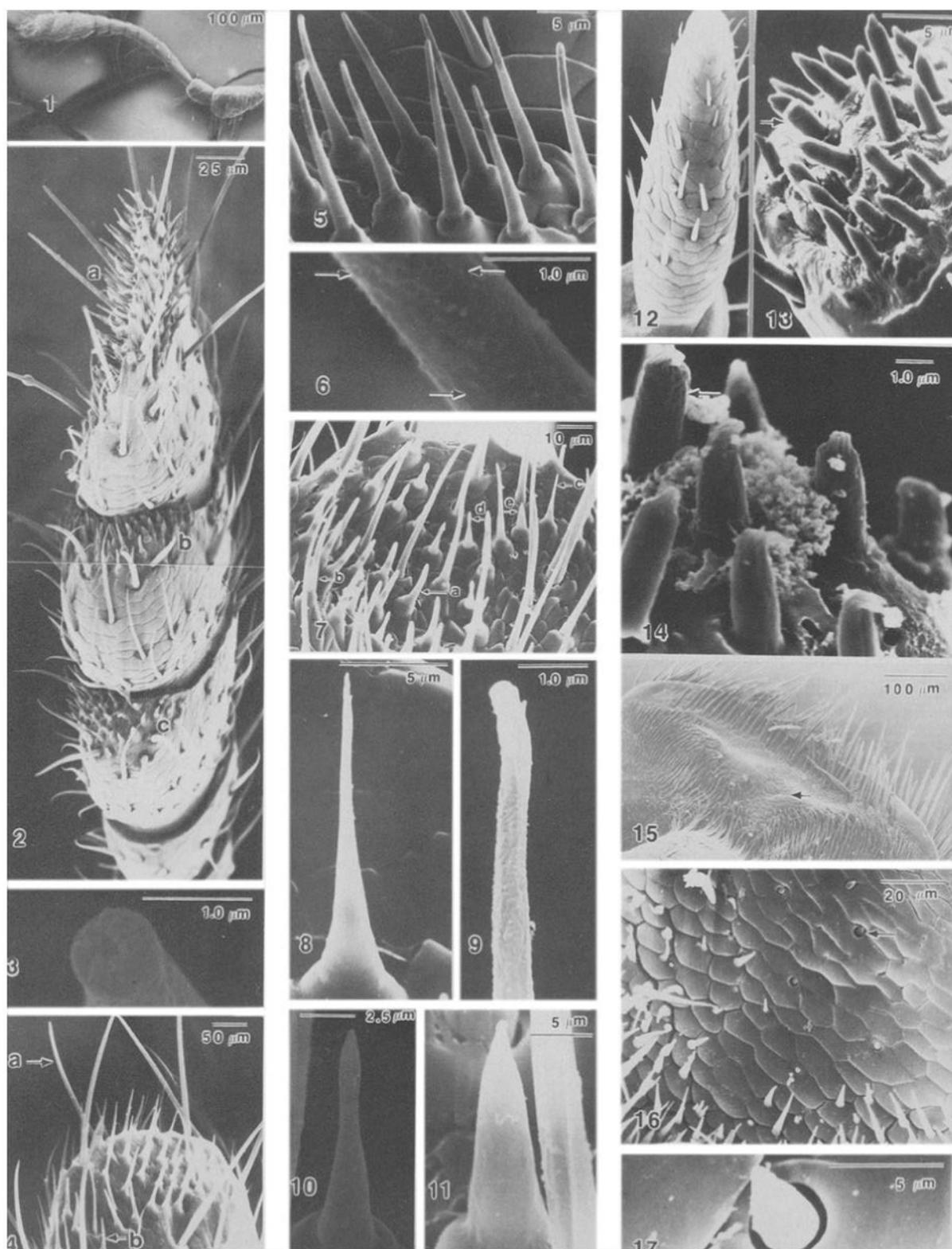
Type III is needlelike, tapering sharply from $3\ \mu$ diam to $0.5\ \mu$ through half its length and remaining at $0.5\ \mu$ diam through the tip (Fig. 8). Its surface is deeply and irregularly corrugated, and no apical pore is evident (Fig. 9). Type III sensilla are present only on the dorsal side of the terminal segment; only five were detected (Fig. 7). Honda *et al.* (1984) reported a very similar needlelike sensillum on the antenna of *Delia antiqua* (Meigen), the onion maggot, and showed by TEM examination of cross sections that it has a multiporous olfactory structure.

Sensilla basiconica Type I (Fig. 10). This peglike sensillum is $8\ \mu$ long on a bulbous base, $2.5\ \mu$ in diam at base, with tip grooved, clavate, and $1.0\ \mu$ in diam (Fig. 10). Eleven such sensilla are found on the dorsal surface of the terminal antennal segment and three on the penultimate segment just below the base of the terminal segment. This type of sensillum has been found on antennae of several insect species, usually as shorter pegs (Harbach & Larsen, 1977b; Hatfield *et al.*, 1976; Honda *et al.*, 1984). In cross section, multiple pores are found in the base of the longitudinal grooves. Harbach & Larsen (1977b) calculated the presence of approximately 214 pores in each groove of such sensilla on the antenna of *Tenebrio molitor* L. *S. basiconicum* Type I is very similar to the s. styloconicum of unknown function reported by Hatfield *et al.* (1976) on the antenna of *Hypera meles* (F.), the clover head weevil.

Sensilla basiconica Type II (Fig. 11). This stout, smooth-walled peg is $8\text{--}10\ \mu$ long, and $5\ \mu$ in diam at base, pointed at tip, and with no visible apical pore. Four s. basiconica Type II are seen on the dorsal surface of the terminal segment (Fig. 7). Smooth-walled pegs of this type are often thermoreceptors or hygroreceptors (Harbach & Larsen, 1977a; Altner & Prillinger, 1980).

Labial Palp (Figs. 12–14)

The three-segmented labial palp bears s. trichodea similar to those found along the shaft of the antenna (Type II). However the distal tip of the terminal segment bears a field of s. basiconica, the number varies from specimen to specimen but is about 20. All but one have a single terminal pore surrounded by several tubercles and a sidewall that appears to be multiporous (Fig. 14). The single ex-



ception is a central blunt sensillum also with pitted walls but no terminal pore (Fig. 13 arrow). The same arrangement was described by Mitchell & Schoonhoven (1974) for larvae of *Leptinotarsa decemlineata* (Say), the Colorado potato beetle, except that the sides of the pegs bearing an apical pore did not appear multiporous. In the Colorado potato beetle these sensilla are sensitive to salt, sucrose, chlorogenic acid, and some amino acids.

Maxillary palp (Figs. 18–23)

The three-segmented maxillary palps are also sparsely covered with s. trichodea that are presumed to be mechanoreceptive (Type II) (Fig. 18), but the subtriangular distal segment bears on its mesal face an oblong field with about 420 s. basiconica of two distinct types surrounded by ranks of appressed setae (Figs. 18–19). A similar morphology is found on the maxillary palpi of several other species of Coleoptera (Honomichl, 1980; Honomichl & Guse, 1981). Altner (1975) described a very similar field of chemosensilla on the maxillary palp of *Periplaneta americana* L. In *P. americana*, as in the MBB, the floor of this field is pliable and assumes a convex shape by hemostatic pressure. This anatomical structure allows the sensilla to maintain close contact with surfaces while protecting the sensilla from injury.

Sensilla basiconica Type I (Figs. 20–21). This sensillum is a grooved peg, 4–6 μ long, 2 μ in diam at base, and with a single terminal pore surrounded by several tubercles (Fig. 21). Some pegs are extended and appear to have no distinct base; others appear slightly withdrawn and are surrounded by a low rimmed base. This basiconic peg is a typical gustatory sensillum (Zacharuk, 1980).

Sensilla basiconica Type II (Figs. 22–23). This type is blunt, with pitted sidewalls and a tip composed

of approximately 75 tightly packed tubercles (Fig. 23). It is 4–6 μ long and 2 μ in diam. No apical pores are evident, but the sidewall is highly pitted and apparently multiporous (Fig. 22). Each Type II peg is produced from a cylindrical base with a strongly crenulated rim. The function of these sensilla is difficult to assess. The clearly pitted sidewalls suggest the likelihood of a porous wall, but the morphology of the tip seems to be unique. Histological and physiological investigations will be required to determine its function. A third type of basiconic peg may be present. One area in the proximal third of the sensory field is composed of only one type of pegs (Fig. 16b). These are very similar to Type I but have more longitudinal grooves, with terminal tubercles arising from the areas between grooves. These pegs have many more protuberances and these appear longer and not as tightly grouped as in Type I pegs. The tubercles surround an apical pore.

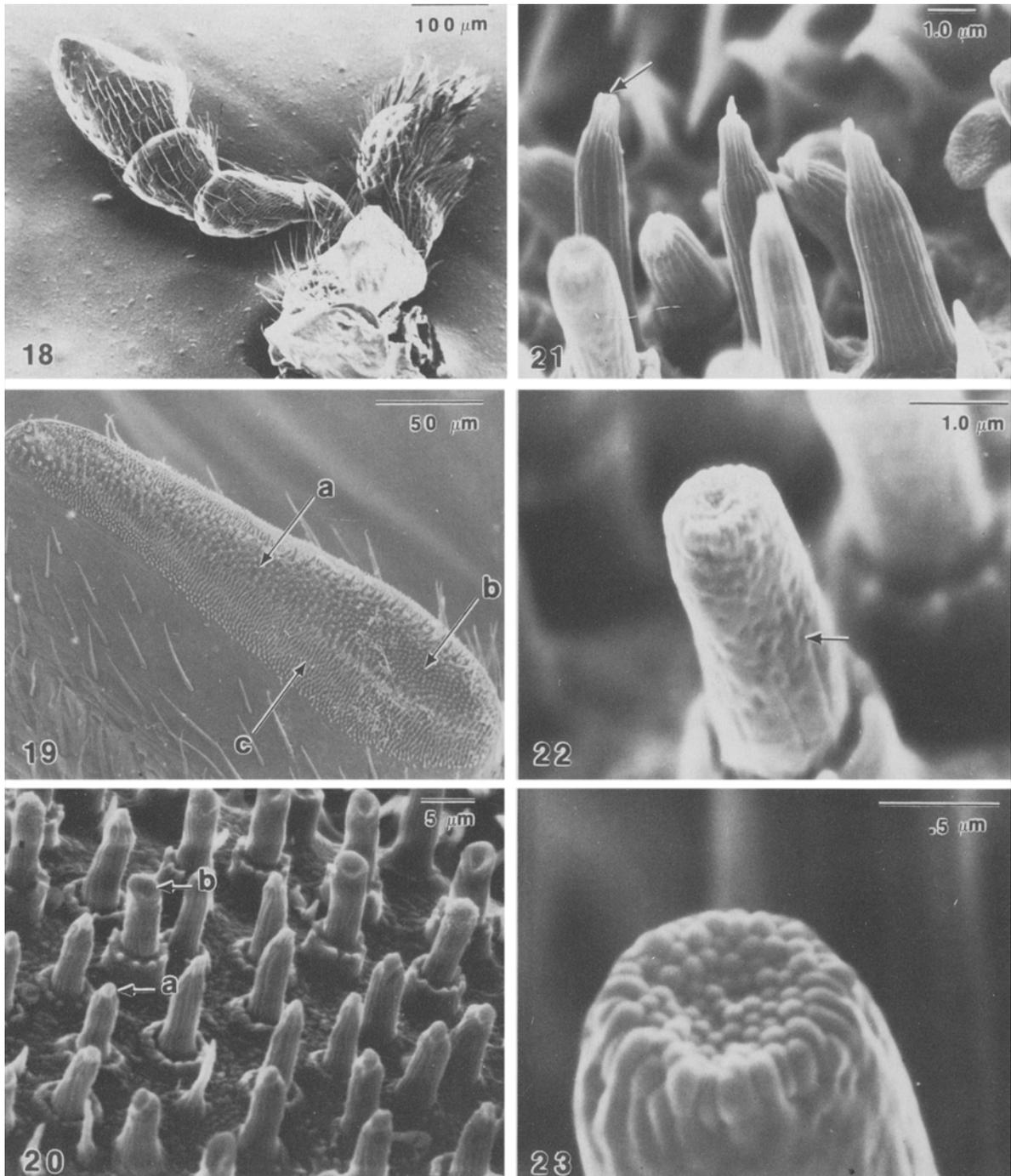
Epipharynx (Figs. 15–17)

The epipharynx is densely covered with setae except for a small bare triangular area in its center (Fig. 15 arrow). In this area are found a variable number (6–8 in our sample) of sensilla basiconica projecting from circular pits. Each is 1 μ in diam and 2 μ high and appears smooth walled and without an apical pore. Some of these pegs are also found among the dense setae toward the posterior of the epipharynx. The number of these has not been accurately determined, but it is about five to ten.

Foretarsus

Examination of the foretarsus showed a very dense covering of s. trichodea, apparently mechanoreceptive. No chemosensilla were discovered, though examination by transmission electron microscopy for nerve fibers will be necessary for a

Figs. 1–17. *MBB antennal chemosensilla*: 1) Right antenna dorsal view; 2) Distal 5 segments proximal lateral surface of left antenna (a, b, c, = sensory fields of *S. chaetica* type I and II); 3) terminal pore of *S. trichodea* type III; 4) Ventral surface of distal antennal segment (a=s.t. type III, b=s.t. type I); 5) s.t. type I on penultimate antennal segment (same as 2-b); 6) surface of s.c. type I (arrows=probable pores in sidewall); 7) Dorsal view of terminal antennal segment (a=s.c. type I; b=s.c. type II; c=s.c. type III; d=sensillum basiconicum (s.b.) type I; e=s.b. type II); 8) s.c. type III; 9) tip and corrugated sidewall of s.c. type III; 10) s.b. type I; 11) s.b. type II. *Labial palp chemosensilla*: 12) Terminal segment of labial palp; 13) Sensory field of 21 s. basiconica (arrow = single blunt tipped type similar to maxillary palp form); 14) enlarged view of s. basiconica; note probable multiporous walls and papillae surrounding apical pore (arrow designates pore). *Epipharynx chemosensilla*: 15) Inner surface of labrum (arrow=location of sensory pegs in bare triangular area); 16) Enlargement of bare triangular area from Figure 15 (arrow=single *S. basiconicum*); 17) *S. basiconicum* in pit.



Figs. 18-23. Maxillary palp sensilla. 18) Entire maxillary palp; 19) Sensory field on terminal segment (a=chemosensilla mixed type I and II; b=circular area of only type I; c=rows of setae surrounding chemosensilla; 20) Both types of max. palp s. basiconicum (a=type I; b=type II); 21) S.b. type I (arrow=apical pore); 22) S.b. type II (arrow=apparent sidewall pores); 23) Apex of s.b. type II.

conclusive statement. However, preference test results indicate that tarsi apparently are not used in discriminating among soybean varieties.

Preference tests with MBB

A preference index (C) was computed as:

$$\hat{C} = 2A / (M + A)$$

where A = leaf area eaten of the normally not preferred PI 229358 and M = leaf area eaten of cv. Williams, a susceptible type. C values fall between 0 and 2.0, and a value of 1.0 indicates no preference for either test plant (Kogan, 1972). Figure 24 dia-

grams treatments applied and average C values resulting from each. Normal MBB show a strong preference for Williams leaf discs ($C = 0.35 \pm S.D. 0.22$). Treatment wherein one antenna, one maxillary palp, one labial palp, and one foretarsus were removed slightly reduced discrimination, but differences from unablated controls are not significant. Loss of chemoreceptors on antennae and maxillary palps had the most marked effect on food choice. Ablation of maxillary palps (MP) produced the greatest single effect ($C = 0.85 \pm 0.27$), with ablation of antennae (ANT) alone somewhat less effective ($C = 0.75 \pm 0.28$). When both antennae and maxillary palpi (ANT+MP) were excised, there was complete loss of discrimination between the

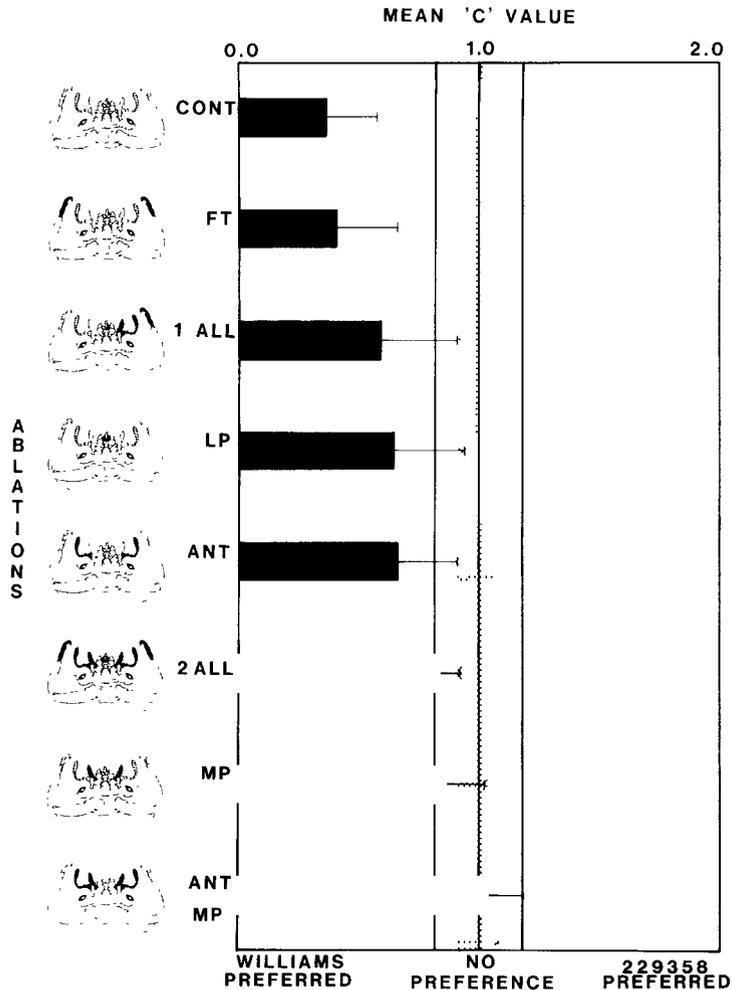


Fig. 24. Results of preference tests following ablation treatments. The shaded area represents a no preference zone bounded by the mean C values when all discs in the preference test are Williams. Vertical lines: + and - one s.d.

two soybean types ($C=1.01\pm 0.17$). When maxillary palpi alone were excised, no feeding occurred for approximately 24 h, and results were taken after 48 h. Ablation of labial palps (LP) produced a partial loss of discrimination ($C=0.65\pm 0.41$) but only slightly less than in controls in which only one of each pair of appendages tested was excised ($C=0.52\pm 0.38$). Removal of foretarsi (FT) had almost no effect on food choice ($C=0.38\pm 0.28$). In tests where all appendages were ablated (antennae, maxillary palpi, labial palpi, and foretarsi), results were erratic, in some cases indicating strong preference and in other cases indicating no preference. This result was due to the almost complete and permanent cessation of feeding, with occasional very slight random feeding by one beetle on one disc. In total ablation, no feeding was ever observed in the first 24 h after treatment, and most beetles never resumed normal feeding.

Figure 24 illustrates the intensity of ablation effects for each treatment as measured by the degree of lost discrimination between 'susceptible' and 'resistant' plants: $2ANT+MP > 2MP > 2ANT+2MP+2LP+2FT > 2ANT > 2LP > 1ANT+1MP+1LP+1FT > 2FT > CONTROL$. These results suggest that the sensilla involved in discrimination between these soybean types reside primarily on the antennae and maxillary palps.

Visual observation of MBB food selection suggests that olfaction at close range may produce the stimulus that results in the rejection of 229358 in favor of Williams. When unablated beetles are placed in a preference arena and provided with both types of leaves, they consistently wander over the discs and filter paper without feeding for several minutes, antennae and maxillary palps waving in the air. Some MMBs palpate discs with maxillary palps and eat 'preferred' discs without ever biting the 'nonpreferred' discs. On other occasions they do not seem to make physical contact with the leaf surface except with the tarsi. However, no obvious chemosensilla were observed on the tarsi. Since there are no apparent physical differences in the leaf surfaces of the soybean types, it is difficult to assume a physical basis for discrimination. Indications are that the discriminatory stimulus for initiation of feeding is primarily olfactory.

Our observations indicate that there is an olfactory signal that triggers a rejection or an acceptance response. In the former case the presence of

volatile allomones in 229358 would account for the resistance; in the latter, the absence of a required kairomone would be the main resistance factor. Experiments with very low molecular weight volatiles emitted by Williams, 229358, and common beans, suggest that volatile allelochemicals may be involved in the rejection process (Wei, Fischer, & Kogan unpublished results).

The apparent olfactory capabilities of the labial palps and maxillary palps also support the assumption of a chemosensory basis for discrimination. Sometimes, before rejection, biting and slight feeding occurs on 229358 leaf, indicating a secondary gustatory component in the discrimination process.

Ablation results clearly demonstrate the importance of the maxillary palps and the antennae in food choice among soybean genotypes. Amputation of the maxillary palps alone is nearly enough to destroy the ability to distinguish between Williams and 229358. In combination with antennal amputation, discrimination is virtually lost. The large number of sensilla on the maxillary palps (>840) and the high concentration and anatomical location of the sensory field (Figs. 15 and 16) are other signs of their importance in food selection.

We are in the process of investigating the internal structure of sensilla on antenna, maxillary palp, and labial palp to confirm function. However, external structures have been shown to correlate well with function. *S. basiconica* Type I on the maxillary palp are typical of many insect gustatory organs. Their smooth, grooved walls and apical pore strongly suggest a gustatory function. The pitted nature of the wall and lack of an apical pore indicate an olfactory function for Type II *s. basiconica*. The tight group of tubercles at its tip is not similar to any structure previously described. Thus, on the maxillary palp, *s. basiconicum* Type I is the likely olfactory structure with food selection function.

The MBB antenna is quite small by comparison with the antennae of other phytophagous Coleoptera of similar size (e.g., *Diabrotica* spp.), and it is often positioned near the mouthparts rather than extended forward. Since each bears about 30 gustatory and about 150 olfactory hairs, it appears that a significant part of the antennal function is close-range chemoreception. We are confident that the maxillary palps and antennae contain the main chemoreceptors involved in the detection of the plant stimuli that permit the MBB to discriminate

between the two genotypes. Those plant stimuli are not currently known, but they could be (a) secondary metabolites peculiar to each genotype or (b) low molecular weight plant volatiles, in unique combinations and concentrations, that provide a 'fingerprint' pattern, as proposed by Visser (1983) for plants eaten by the Colorado potato beetle.

Analysis of soybean leaf volatiles for differences among acceptable and nonacceptable leaf types is being performed in our laboratory. The activity of these compounds is being measured with standard behavioral bioassays (preference tests, olfactometry) as well as with electrophysiological techniques applied to antennal and maxillary palp chemoreceptors.

Acknowledgements

We thank Tzu-Suan Chu for providing Mexican bean beetles and technical assistance, Nancy Wiseman for technical assistance, Drs. M. R. Berenbaum and J. B. Larsen, Department of Entomology, University of Illinois, Urbana, Illinois for criticism. We acknowledge the use of facilities and assistance of the staff of the Center for Electron Microscopy, University of Illinois at Urbana. Supported in part by Hatch project ILLU-12-0324 'Insect/plant interactions: Phytophagous insects and plant defense strategies', by Regional project S-157 'Tactics for management of soybean pest complexes, and by a USDA grant, CR 806277-03, through the Consortium for Integrated Pest Management and Texas A & M University. The opinions expressed herein are those of the authors and not necessarily those of the supporting institutions or agencies.

Résumé

Chimiorécepteurs d' Epilachna varivestis adultes: Structures et importance dans la sélection des aliments

E. varivestis Mulsant, insecte oligophage, accepte les feuilles de *Glycine max* (L.) Merrill (soja) comme aliment, mais présente des préférences marquées parmi les variétés. On considère que l'origine de la discrimination entre le cultivar sensible 'Williams' et PI 229358 résistant, est chimique. Des ex-

périences de choix avec des rondelles de feuilles, après ablation des sensilles chimiques des antennes et des palpes maxillaires et labiaux, et des tarsi antérieurs, ont montré que les sensilles chimiques étaient presque entièrement responsables de la discrimination entre les feuillages de génotypes résistant et sensible. Tous les appendices ont été observés au microscope à balayage, et, à l'exception des tarsi antérieurs, ils portaient plusieurs types de sensilles gustatives et olfactives, qui ont été représentées et décrites. Puisque les observations comportementales montrent que l'olfaction est normalement suffisante pour provoquer le rejet de PI 229358, nous concluons que les sensilles olfactives des antennes et des palpes maxillaires jouent un rôle crucial dans le choix de l'aliment.

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Accepted: April 17, 1985.