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Sensory receptors associated with the stylets and cibarium of the rice brown planthopper, *Nilapavarta lugens*

S. Foster, L.J. Goodman, and J.G. Duckett
School of Biological Sciences, Queen Mary College, London, England

Summary. The stylets of *Nilapavarta lugens* consist of two maxillae that interlock to form separate food and salivary ducts partially surrounded by two mandibles. The ultrastructure of the sensory innervation of the stylets is described. Each maxilla possesses five neurones which extend to the tip of the stylet. The mandibles also contain five neurones, four of which are paired. The paired neurones comprise a shorter dendrite extending part of the way along the stylet and a longer one extending to the tip. The possible functions of these neurones are discussed.

Gustatory receptors are located in the small passageway leading from the food duct to the cibarium. The receptors are in two distinct groups on the epipharyngeal side and one group on the hypopharyngeal side of the food canal. Two to five neurones innervate each receptor which connects to the food canal via a small pore.

Key words: Homoptera – Stylets – Cibarium – Sensilla – Ultrastructure

N. lugens, the rice brown planthopper, feeds by sucking sap from the phloem of the host plant. It can discriminate between host and non-host plants (Sogawa 1977) and work on other sap suckers suggests that chemical stimuli encountered below the leaf surface play a part in host plant selection. Wensler and Filshie (1969) have shown that aphids can distinguish between test plants ensheathed in a thin celloidin layer. *N. lugens* (Sogawa 1977) and *Myzus persicae* Sulzer (Mittler and Dadd 1965) can distinguish between test solutions under a 'parafilm' membrane after surface penetration by the stylets. The sensory receptors, which might assist *N. lugens* in guiding the stylets to the phloem and in discriminating between host and non-host tissues, are unknown but receptors which may perform these functions have been described in several homopterans. The stylets have been found to

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Send offprint requests to: Dr. Stephen Foster, School of Biological Sciences, Queen Mary College, Mile End Road, London E1 4NS, England

be innervated in several species of aphids (Forbes 1966; Forbes and Mullick 1970; Parrish 1967) in *Oncopeltus fasciatus* Dallas (Forbes 1976) and in the blood sucking heteropteran *Rhodnius prolixus* (Pinet 1970), but there is some debate about the nature of the receptors present in the stylets. Forbes and Raine (1973) suggest that the receptors present in the stylets of *Macrosteles fascifrons* Stål. are contact chemoreceptors whilst Wensler (1974) postulates a mechanoreceptive role for the sensory dendrites found in the mandibular stylets of *Brevicoryne brassicae*. Pinet's (1970) study of the receptors of the mandibular and maxillary stylets of *R. prolixus* support Wensler's observations.

The food canal in the Hemiptera leads off from the stylets through a narrow passageway into the cibarium. The presence in this passageway of an epipharyngeal organ containing gustatory receptors for sampling ingested sap was initially suggested by Davidson in 1914, and more recently by de Carlo (1970), Khan (1972), Forbes (1977) and Sogawa (1977). Wensler and Filshie's (1969) examination of the ultrastructure of the epipharyngeal organ of *B. brassicae,* and Backus and McLean's (1982) study of the same organ in *M. fascifrons* have demonstrated that it contains a number of chemoreceptors so situated that their dendrites will make contact with the ingested foods passing through the food canal.

This paper describes the structure and disposition of the sensory receptors of the mandibular and maxillary stylets and of the cibarial receptors of the rice brown planthopper.

Materials and methods

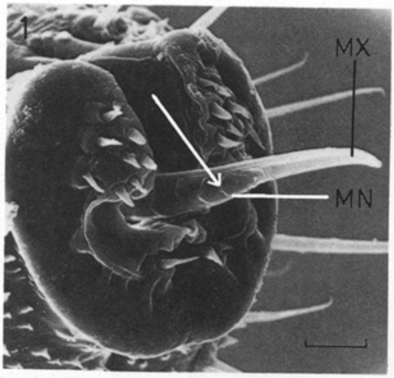
Nilapavarta lugens Stål. were reared as described previously (Foster et al. 1983). Full details of specimen preparation are cited in that publication. Problems encountered in trying to get fixative to flow into the very narrow neural cavities of the stylet bundle were reduced by gently pulling the stylets out of the stylet groove of the labium.

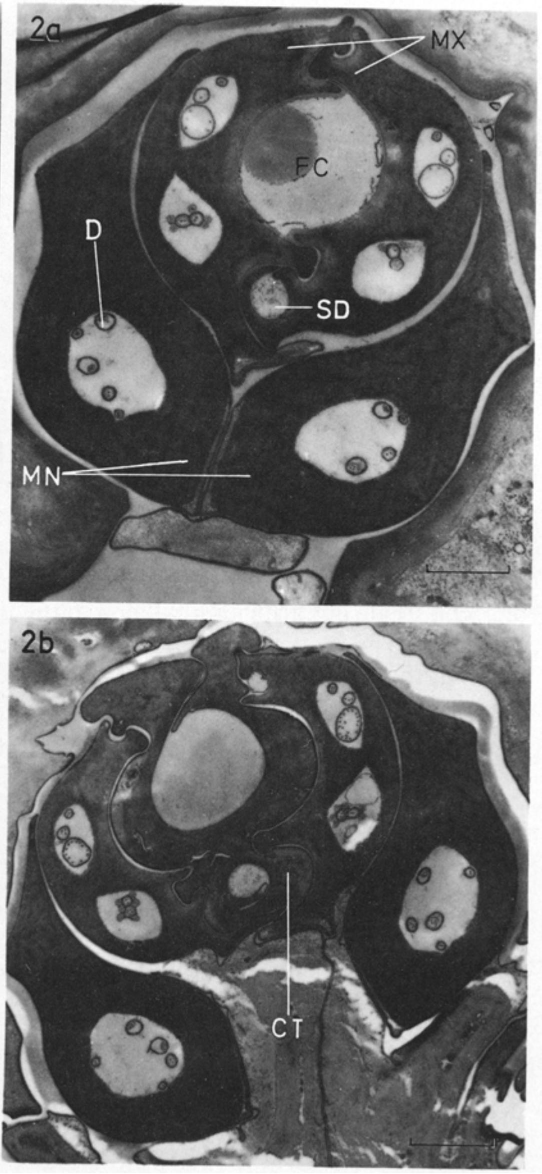
Results

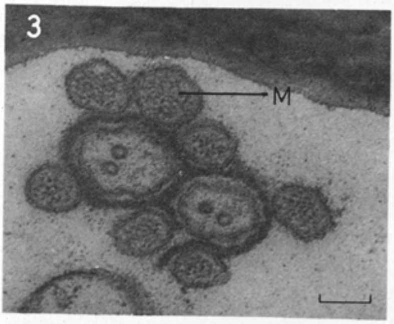
The mandibular and maxillary stylet receptors

The stylet bundle of the rice brown planthopper consists of a pair of maxillary stylets partially surrounded by a pair of mandibular stylets. The average length of the stylets is about 650 μm and 700 μm for the mandibular and maxillary stylets respectively. They originate in the head capsule lateral and ventral to the cibarium. They interlock with each other beneath the labrum and then run in the stylet groove of the labium protruding from the flattened labial tip (Fig. 1). The labium braces the stylets during penetration of plant tissues.

The maxillae curve slightly at their tips, coming to a fine point (Fig. 1). It is this part of the stylets which penetrates the phloem cells. The somewhat shorter mandibles are serrated on their external convex edges and are involved in cutting through the plant towards the phloem. The mandibular stylets which move alternately during plant penetration are prevented from







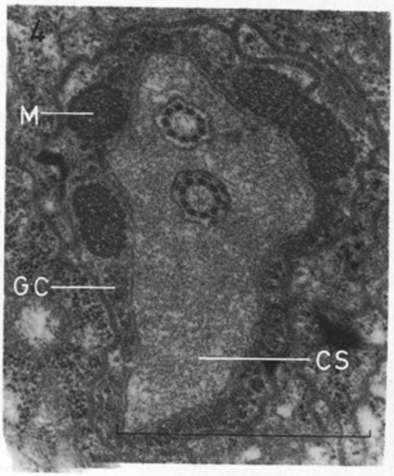


Fig. 1. A scanning electron micrograph of the labial tip showing the stylet bundle protruding from the labial groove. The stylets consist of the longer maxillae (*MX*), which curve to a fine point, and the mandibles (*MN*) with serrated edges (*arrow*). Bar = 10 μm

Fig. 2. Transverse sections through the stylet bundle. (**a**) The two interlocking maxillae (*MX*) form the salivary duct (*SD*) and the food canal (*FC*). The maxillae have two neural cavities, one containing two dendrites (*D*), the other three dendrites. The outer mandibles (*MN*) have one cavity which contains five dendrites. In the mandible on the right one of the dendrites has terminated below the level of the section. Bar = 1 μm. **b** A transverse section through the stylets proximal to the point of their separation showing the cuticular template (*CT*) which maintains the integrity of the food and salivary ducts. Bar = 1 μm

Fig. 3. Transverse section through a neural cavity of a maxilla showing two dendrites surrounded by glial cell extensions containing microfilaments (*M*). Bar = 0.1 μm

Fig. 4. Transverse section through the ciliary region of a pair of dendrites innervating a mandible showing the 9 + 2 + 0 arrangement of the microtubules. *CS* ciliary sinus. *GC* glial cells. *M* microfilaments. Bar = 1 μm

slipping back by a series of grooves and ridges on their internal concave surfaces.

Transverse sections along the length of the stylet bundle show that the two maxillae interlock by a system of ridges and grooves forming a larger food duct and a smaller salivary duct (Fig. 2a). As the stylets converge within the head, the maxillae are guided into position by a cuticular template (Fig. 2b). This structure allows the grooves and ridges of the two maxillae to interlock as they come together and also maintains the integrity of the food and salivary ducts.

Within the wall of each maxillary stylet are two cavities containing the dendrites of bipolar neurones (Fig. 2). Serial sections show that the maxillae contain three dendrites in one cavity and two in the other. It is the distal part of the dendrites that extends along the whole length of the maxilla. Sections through the mandibles show two groups of two dendrites plus another single dendrite all within one cavity (Fig. 2). Of the dendrites within the two groups, one is short, terminating at the level where the stylets enter the labial groove; the other is long, extending to the tip of the mandible. The single dendrite also extends to the tip of the mandible. The dendrites are encased in a narrow glial cell that contains bundles of microfilaments (Fig.4). In some cases fingerlike processes of glial cytoplasm containing microfilaments extend along the length of the stylets (Fig. 3). Careful examination of serial sections revealed no means of contact between the dendrites of either the mandibles or the maxillae and the exterior.

The cibarial receptors

The food canal bends dorsally and to the posterior after it has separated from the stylets (Fig. 5). For the first 40 μm the canal maintains its narrow lumen before widening into the cibarium. It is along this narrow part of the gut that three groups of receptors (commonly called the epipharyngeal

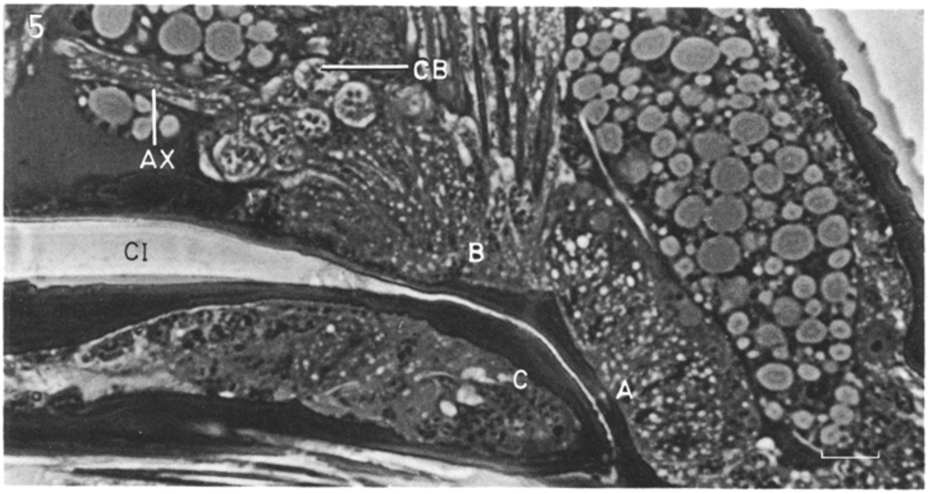
Fig. 5. A light microscope longitudinal section through the head showing the narrow food canal along which the receptors are located in areas *A*, *B*, and *C*, opening into the cibarium (*CI*). The axons (*AX*) and cell bodies (*CB*) of receptors from area *B* are indicated. Bar = 10 μm

Fig. 6. A transverse section through a receptor from area A showing the dendrites (*D*), surrounded by a densely staining lymph sinus (*LS*) and connected by a small pore (*P*) in the cuticle (*C*) to the foregut (*F*). Bar = 1 μm

Fig. 7. An oblique longitudinal section across three cibarial receptors from area *B*. The dendrites are surrounded by dendritic sheath (*DS*) and a densely stained extracellular lymph sinus (*LS*). *C* cuticle. Bar = 1 μm

Fig. 8. A transverse section through the dendrites (*D*) of a receptor showing them passing through the gut cuticle (*C*). Bar = 1 μm

Fig. 9. A transverse section through the dendrites distal to the ciliary region, showing five dendrites (*D*) tightly packed within a dendritic sheath (*DS*). Two sheath cells (*SC1*, *SC2*) are visible. Bar = 1 μm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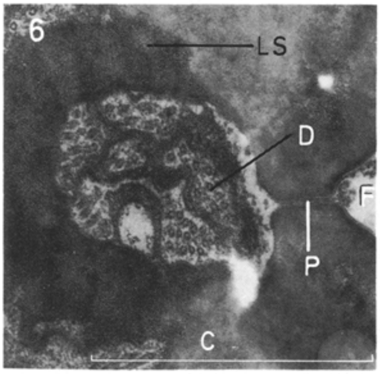
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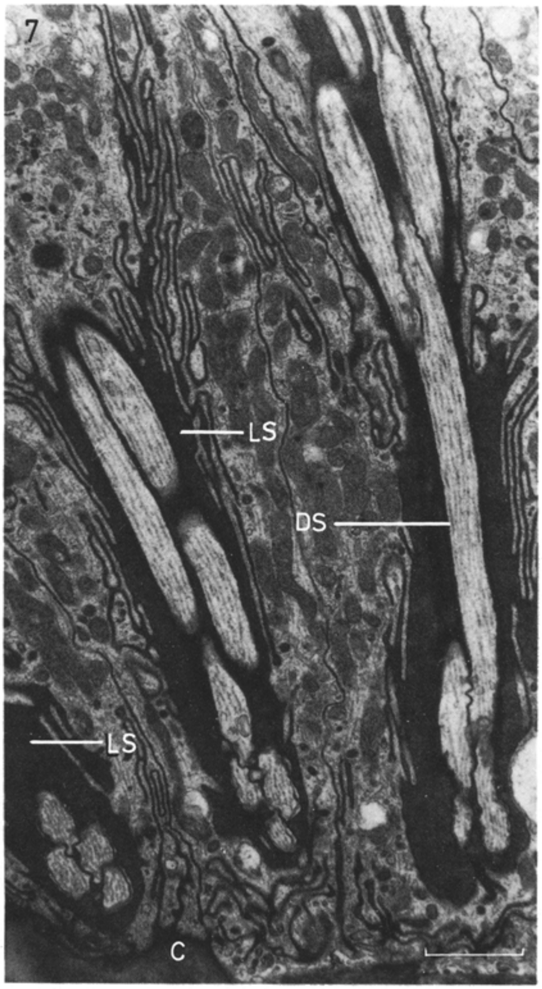
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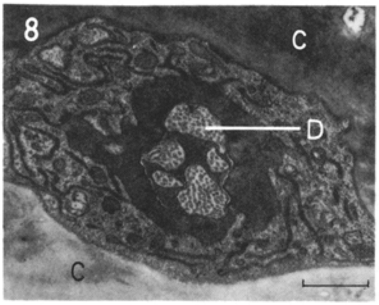
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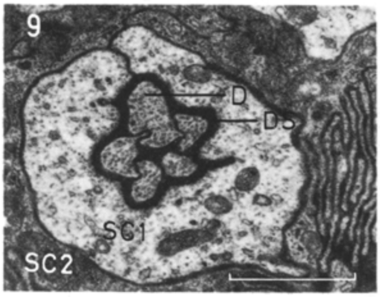
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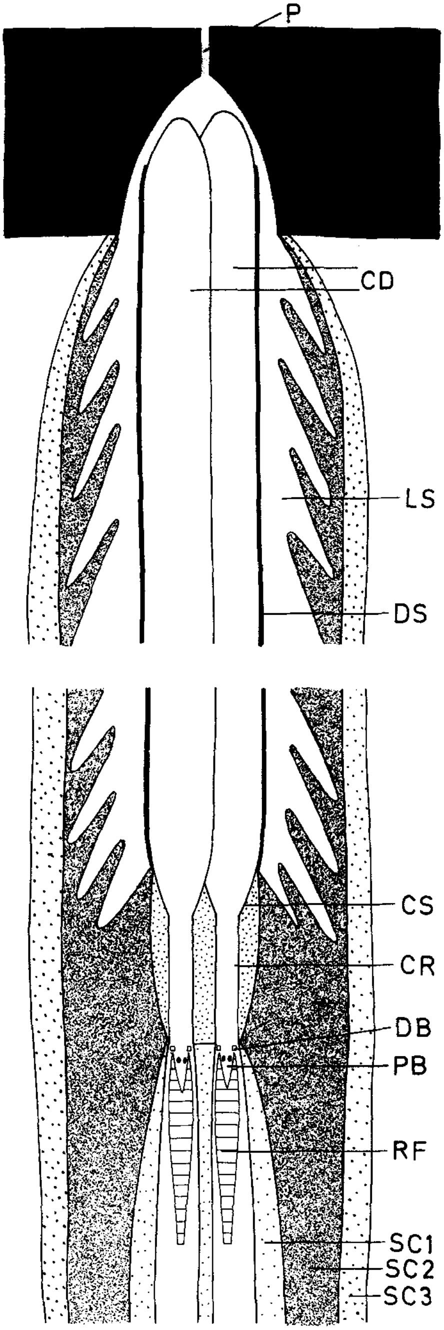

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Fig. 10. Diagrammatic representation of a cibarial receptor. *CD* Chemoreceptive dendrite. *CR* Ciliary region. *CS* Ciliary sinus. *DB* Distal basal body. *DS* Dendritic sheath. *LS* Lymph sinus. *P* Pore through cuticle. *PB* Proximal basal body. *RF* Root fibril. *SC1, SC2, SC3* Sheath cells

organ after Davidson (1914)) are located. There are two distinct groups of five paired receptors (labelled A and B) on the dorsal (epipharyngeal) side of the canal and one pair on the ventral (or hypopharyngeal) side of the canal (labelled C).

Examination of the ciliary regions of the neurones innervating these receptors shows that the receptors contain two to five unbranched dendrites (Figs. 6–9). Progressing along the food canal from the anterior to posterior, the first receptor in Group A has three neurones, the second, four neurones, and the remaining two have five neurones each. Similarly, the first three receptors in Group B each contain four neurones and the last two possess two neurones each. There are five neurones present in the receptors of Group C (Fig. 9).

The distal section of the receptor neurones extends from the ciliary region to the food canal for a distance of about 12 μm (Fig. 7). The dendrites pass through a cavity in the cuticle lining the alimentary canal (Fig. 8), terminating in a pore kettle within the cuticle (Fig. 6). A single pore about 30 nm in diameter opens into the lumen of the gut. The dendrites are enclosed within a dendritic sheath (Figs. 7, 9) which extends from the ciliary region to the pore kettle. The receptor lymph is extremely dense in these sensilla (Figs. 6, 7). Fig. 10 is a diagrammatic representation of the distal section of one of these receptors.

Discussion

Studies on the stylets of other Homoptera (Pinet 1970; Forbes and Mullick 1970; Wensler 1974) have shown that the maxillae interlock to form the food and salivary ducts and are surrounded by the mandibles. The difference between the species described lies in the innervation of the stylets. In *Adelges picae* (Forbes and Mullick 1970), *Oncopeltus fasciatus* (Forbes 1967) and *Brevicoryrne brassicae* (Wensler 1974) only the mandibles are innervated. Both the mandibles and the maxillae of *Rhodnius prolixus* (Pinet 1970), *Macrosteles fascifrons* (Forbes and Raine 1973; Backus and McLean 1982), and *Triatoma infestans* (Bernard 1974) are innervated and this is the case in *N. lugens.*

Observations reported here have indicated that the dendrites within the stylets do not make contact with the exterior and it is unlikely that they function as contact chemoreceptors when the stylets are within the plant tissues. The mode of termination of the dendrites within the stylet cuticle closely resembles that of the stylet receptors of *B. brassicae* described by Wensler (1974) to which she ascribed a mechanosensory function. Sogawa (1977) has shown that, during exploratory probing, the stylets of *N. lugens* terminate most frequently in the phloem cells of the vascular bundle. Mechanoreceptors within the stylet would allow the insect to discriminate between tissues of varying rigidity encountered during probing which might aid in the location of the phloem.

Gustatory responses may be involved in the initial stages of probing and in the maintenance of sap ingestion. de Carlo (1970) suggests a chemosensory function for 20 receptors identified by light microscopy in the pharyngeal region of *Lethocerus mazzai* and Khan (1972) showed that there were six sensilla in the same region of *Dysdercus fasciatus* Sign. Wensler and Filshie (1969) using electron microscopy demonstrated that 60 neurones terminated in groups at 14 porous papillae on the dorsal wall of the cibarium, and suggested that there were paired papillae on the ventral wall. Likewise, Backus and McLean (1982) have presented an ultrastructural study on ten paired sensilla located in the pre-cibarium of *M. fascifrons*. The morphology of these receptors suggests that they have a chemosensory function.

This investigation has shown the presence of ten paired sensilla in the cibarium. They have been called 'gustatory receptors' rather than using the term epipharyngeal organ as suggested by Davidson (1914), since they are located on both the hypopharyngeal and epipharyngeal sides of the alimentary canal. The receptor neurones terminate in a small cavity which is connected to the food canal via a small and very narrow pore, thus allowing direct contact with fluids passing along the canal. Contraction of the dilator muscles of the cibarium will draw plant sap past these receptors into the cibarium. Relaxing the dilators will expel the fluid towards the foregut. In this manner the insect can sample the plant sap.

N. lugens, once it has alighted on a plant, may perform a sequence of behavioural acts starting with extension of the labium, followed by dabbing the substrate surface, insertion of the stylets and then ingestion of food. Analysis of the ultrastructure of the external sensory receptors on the labium has indicated their possible role in the behaviour involved in the initial preprobing and penetration of the plant surface (Foster et al. 1983). This investigation shows the presence of receptors within the stylets and cibarium which may provide the sensory control of stylet movements within the plant tissues and the ingestion of sap.

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