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ULTRASTRUCTURE OF SENSILLA OF THE FEMALE MOUNTAIN PINE BEETLE, *DENDROCTONUS PONDEROSAE* HOPKINS (COLEOPTERA : SCOLYTIDAE)

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Abstract—The objective of this study is to provide a morphological foundation for electrophysiological studies on the sensilla of *D. ponderosae*. The sensilla on the antennae, labial and maxillary palps, galeae and fore-tarsi are described. The antennal club has several types of sensilla: (1) multiporous non-socketed pegs of varying lengths innervated by 2 neurons, (2) uniporous socketed pegs innervated by 5 neurons, (3) pegs innervated by only 1 neuron at the base, (4) tapered uniporous cones innervated by 4 neurons, and (5) fluted multiporous, non-socketed cones innervated by 4 neurons. All hairs on the fore-tarsi are innervated by 1 neuron at the base. The labial and maxillary palp-tips have: (1) digitiform organs, (2) campaniform organs, (3) uniporous, socketed pegs innervated by 5 neurons, and (4) non-porpus pegs innervated by 3 neurons. Two small, uniporous, socketed pegs innervated by 4 neurons, are set into the maxillary palp-tip sidewall, and a single, sharp-tipped peg, innervated by 1 neuron, is found on the tip. These 2 types are not seen on the labial palps. The ultrastructure of each type of sensillum found on both the maxillary and labial palps is similar; however, the number of uniporous and non-porous pegs on the labial palps is about half those of the maxilla. The maxillary galeae each have 3 types of sensilla: (1) numerous pegs of various sizes innervated by 1 neuron, (2) a single, possibly uniporous socketed peg innervated by 5 neurons, and (3) another single non-porous non-socketed peg innervated by 2 neurons.

Index descriptors (in addition to those in the title: Contact chemosensilla, mechanosensilla, olfactory chemosensilla, digitiform organs, campaniform organs, bark beetle, forest insects.

INTRODUCTION

THE MOUNTAIN pine beetle (*Dendroctonus ponderosae*) H. is an important pest of lodgepole pine forests in the western United States and Canada. Although several papers have been published in recent years on antennal and mouthpart sensilla of bark beetles, they have mostly considered only thin-walled multiporous chemonsensilla and mechanosensilla (Borden, 1968; Moeck, 1968; Borg and Norris, 1971; Payne *et al.*, 1973; Ryan and Behan, 1973; Behan and Ryan, 1978; Dickens and Payne, 1978). No work has been done on the chemonsensilla of *D. ponderosae* with the exception of a brief scanning electron microscope description of the antennal sensilla by Payne *et al.* (1973). This study was undertaken to provide a morphological foundation for electrophysiological investigations of the chemosensilla of *D. ponderosae*.

MATERIALS AND METHODS

D. ponderosae adults were removed from their galleries in lodgepole pine billets and sexed according to the method described by Schofer and Lanier (1970). Only females were used.

Tissue for transmission electron microscopy (TEM) was processed after the method of Harbach and Larsen (1976), under partial vacuum and cold (about 4°C), and using pieces no longer than 1.5 mm. The material was dissected in 2.5% glutaraldehyde (pH 7.0), placed under vacuum for 2 – 3 hr, washed in cacodylate buffer, and

left overnight under vacuum. The material was post-fixed in 1% osmium tetroxide for 2 – 3 hr, dehydrated in ethanol, followed by propylene oxide and embedded in Luft's (hard mixture) Epon (Pease, 1964). After sectioning, the grids were stained in ethanolic uranyl acetate (1%) for 1 hr.

For scanning electron microscopy (SEM), excised mouthparts, antennae and tarsi were fixed in cold glutaraldehyde, washed, sonicated in a detergent solution for 1 min, dehydrated in graded alcohol series to acetone, and critical-point dried. The parts were mounted on SEM stubs with silver paint and sputter-coated with gold prior to viewing. The terminology used in this study is that of Zacharuk (1980).

OBSERVATIONS

Antennal sensilla

Since the size-range and location of the various chemosensilla on the antennae of *D. ponderosae* were described by Payne *et al.* (1973), only the ultrastructure is described in this study. The antennal club (Fig. 1) is studded with relatively long uniporous pegs (Table 1) that project from the antennal surface at approximately right angles. They are more numerous towards the club apex, and they are intermingled in a somewhat random fashion with other sensilla. Although no pores were seen by SEM, electrophysiological studies (Whitehead, unpublished observations) on these pegs provide indirect evidence for a pore at the tip. These pegs have 2 lumina: one containing 4 dendrites in a dendritic sheath, the other containing an electron-transparent substance of unknown composition (Fig. 3). Sections through the bases of these pegs show them to have a tubular body (Fig. 4) that is the terminus of the fifth dendrite and is probably part of the mechanism for the mechanosensitivity shown by these sensilla (Whitehead, unpublished observations).

Interspersed with the uniporous pegs are shorter multiporous pegs (Fig. 1) having a slightly narrower wall that surrounds a single lumen containing 2 dendrites (Fig. 2). The length of these pegs is quite variable (Table 1). These pegs also protrude from the antennal surface but at a more acute angle than the uniporous pegs (Fig. 1). These multiporous pegs are also more numerous towards the club apex. Serial sections of these sensilla show not only their multiporosity but that the 2 dendrites branch extensively in the distal two-thirds of the peg shaft. No tubular body is seen in the socket area.

The sensory bands (Fig. 1) of the club have 3 types of chemosensilla (Table 1): (1) multiporous non-socketed pegs (Fig. 5), (2) shorter uniporous cones with tapered tips (Fig. 5), and (3) fluted cones (Fig. 6). The tapered uniporous cones contain 4 dendrites. Their structure lacks a socket at the base, also no tubular body is present; otherwise it is similar to the long uniporous pegs on the club. The fluted cones are non-socketed and multiporous, and they are innervated by 4 neurons (Fig. 7). All of the sensilla in the sensory bands lie approximately parallel to the antennal surface (Fig. 1).

Tarsal sensilla

Only prothoracic tarsi were examined. All hairs on them have a single dendrite ending in a tubular body located at the sensillum base. No lumen is seen in the hair shafts.

Maxillary sensilla

Chemosensilla are located on the maxilla and labium (Fig. 8). The labrum, mandibles and hypopharynx were not investigated.

The maxillary palps are 3-segmented. Only sensilla located on the distal segment were examined. Figure 9 shows a large cluster of sensilla located on the palp-tip with several others scattered around the sides of the segment. A digitiform organ (Zacharuk *et al.*, 1977) occurs on the lateral surface and usually consists of 5 thick-walled pegs (2.5 μm in

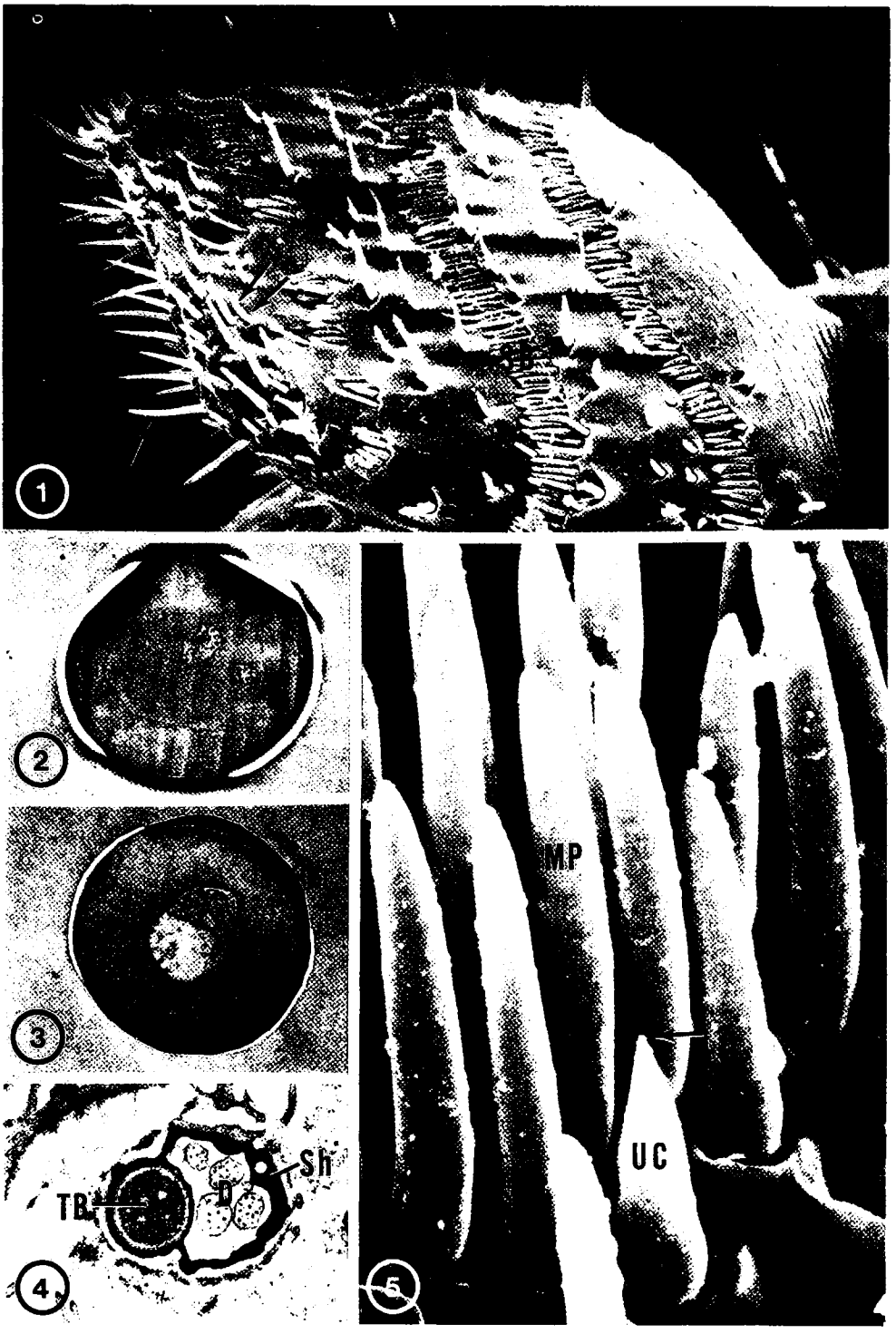
TABLE 1. LOCATION AND DESCRIPTION OF SENSILLA OF *Dendroctonus ponderosae*

Location	Type	Designation	Porosity	Length (μm)	Wall (μm)	Socket (Y/N)	Tubular body (Y/N)	Number of neurons	Number† of sensilla
Antennal									
Club	Peg	Trichoid III*	U	32 – 34	0.8	Y	Y	5 – 6	~ 30
Club	Peg	Trichoid II*	M	10 – 24	0.3 – 0.6	N	N	2	~ 180
Sensory									
Bands	Peg	Trichoid II*	M	8 – 13	0.3 – 0.6	N	N	2	~ 250
Bands	Cone	Basiconic*	U	6	0.8	N	N	4	~ 30
Bands	Cone	Basiconic*	M	4	0.5	N	N	4	~ 15
Maxillary									
Palp wall	Peg	–	U	2	–	Y	Y	4	2
Palp tip	Peg	Type I	U	3	0.4	Y	Y	5	~ 14
Palp tip	Peg	Type II	N	4.5	0.4	N	N	3	~ 6
Palp tip	Peg	Type III	N	3	–	Y	Y	1	1
Palp tip	Camp.	Camp.	–	2	–	N	N	1	2
Galea	Peg	–	U?	~ 30	~ 1·4	Y	Y	5	1
Galea	Peg	–	N	~ 30	~ 1·4	N	N	2	1
Labial									
Palp tip	Peg	Type I	U	3	0.4	Y	Y	5	~ 7
Palp tip	Peg	Type II	N	4.5	0.4	N	N	3	~ 4
Palp tip	Peg	Type III	N	3	–	Y	Y	1	1
Palp tip	Camp.	Camp.	–	2	–	N	N	1	2

U = uniporous, M = multiporous, N = non-porous.

† Number of sensilla on a single morphological unit, e.g. single antennal club, etc.

* Designation of Moeck (1968) for antennal sensilla only.



FIGS. 1 – 5. Captions on page 23.

diameter and 20-μm long) recessed into deep longitudinal grooves in the palp wall (Fig. 9). Thin sections of these sensilla reveal the presence of 1 dendrite in the peg shaft, branching considerably toward the tip. No pores were observed.

Two small uniporous socketed pegs 2-μm long and 1.25 μm in diameter (Table 1) are located on the wall of the distal segment where they occur in a depression (Fig. 10) on the posterior and mesal surfaces. They contain 4 dendrites; the fourth one terminates in a tubular body in the sensillum base (Fig. 11). No distinct pore was observed although during observation on the SEM a hint of one was seen, but I was unable to make a satisfactory micrograph of it.

There are 4 types of sensilla on the palp-tip (Table 1). Type I (Fig. 12) is a uniporous socketed peg 3-μm long and 1.25 μm in diameter. There are about 14 of these distributed around the periphery of the tip. Each contains 4 dendrites in a dendritic sheath (Fig. 13). A fifth dendrite forms a tubular body at the base. Most have a single pore at the tip (Figs. 12, 14).

Type II (Fig. 12) is a larger non-socketed peg 4.5-μm long and 2 μm in diameter. There are about 6 of these located mostly in the central area of the tip (Fig. 9). No pores were observed on them either with thin sections or the SEM. They contain 3 dendrites (Fig. 15), branching in a dendritic sheath (Fig. 16) and lacking a tubular body in the sensillum base.

Type III is a socketed peg with only 1 dendrite ending in a tubular body in the sensillum base. Only one of these is seen on the palp-tip. No lumen or dendrites are seen in its shaft. It is located distal to the digitiform organ on the tip periphery (Fig. 9).

Two campaniform organs (Fig. 12) (cupola-like sense organs of Bellamy, 1973) are on the tip. One is on the lateral side (Fig. 9), and the other is on the mesal surface of the tip periphery. They have no pores and contain only 1 neuron at their bases.

The maxillary galea (Fig. 17) has only 2 sensilla (Table 1) that contain dendrites in their shafts. They are a pair of pegs occurring apically on the adoral surface and are hidden among numerous other pegs. Although it was not possible to identify the pegs with the SEM, Fig. 18 shows 2 pegs that, from their position relative to the other pegs in the area as observed with thin sections, could be the ones. These pegs showed no pores in thin sections, are about 4 μm in diameter (their lengths are not known exactly, but they may be about 30-μm long), are thick-walled and have lumina containing dendrites (Fig. 19). One peg (similar to the lateral sensillum of Mitchell *et al.*, 1980) is socketed with a tubular body at the base and has a dendritic sheath containing an additional 4 dendrites in the peg shaft. The other sensillum (similar to the medial sensillum of Mitchell *et al.*, 1980) has no socket, lacks a dendritic sheath, has a thick wall and contains 2 dendrites in the peg. None of the other pegs on the galea have a dendritic lumen; they are socketed and have 1 dendrite ending in a tubular body in the sensillum base.

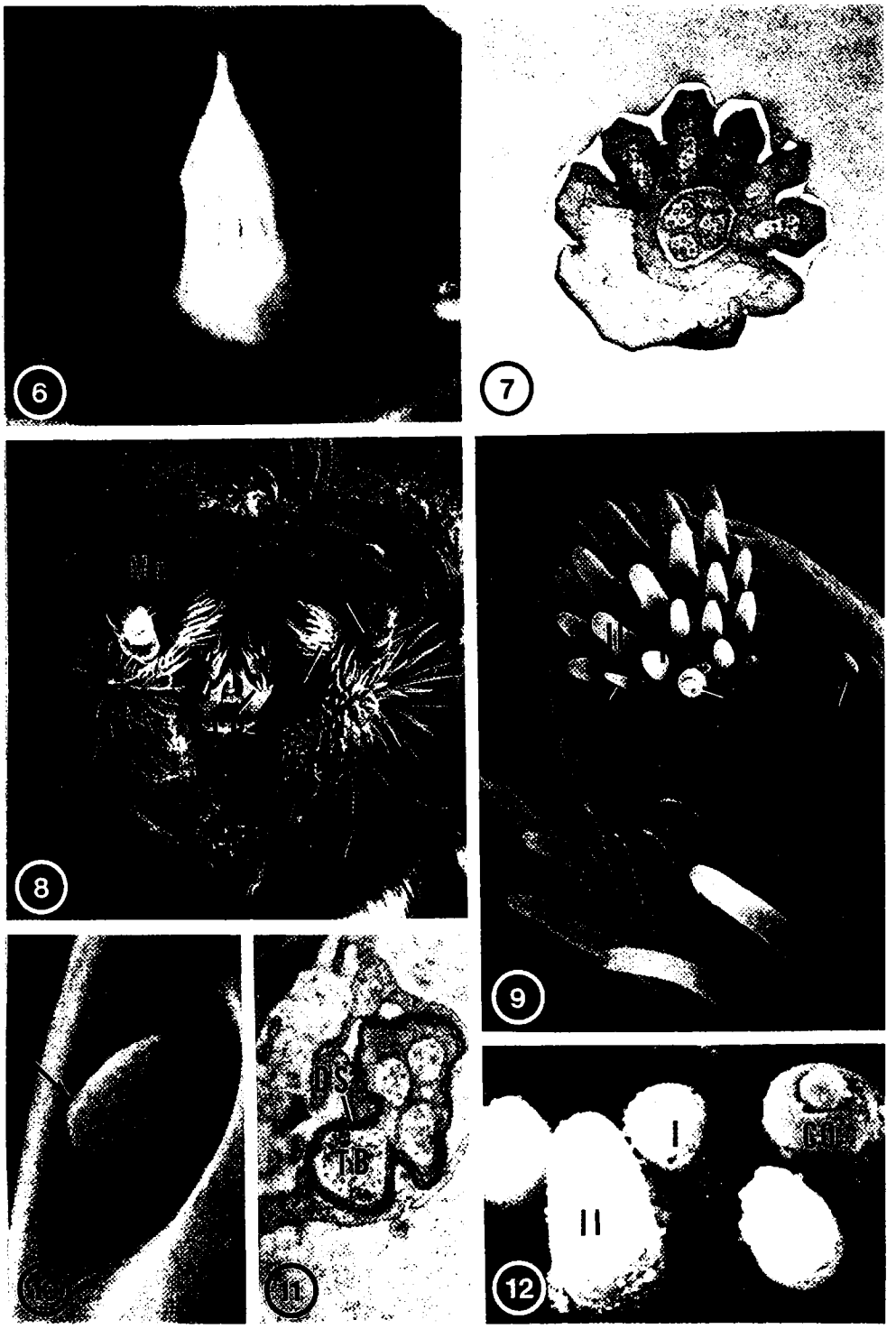
FIG. 1. Posterior aspect of right antennal club showing longer uniporous peg (arrow), shorter multiporous peg (double arrows), and sensory bands (SB). × 380.

FIG. 2. Cross-section of multiporous peg on antennal tip. Dendritic sheath is absent. × 19,800.

FIG. 3. Cross-section of uniporous peg on antennal tip showing 4 dendrites in sheath. × 13,000.

FIG. 4. Cross-section through base of uniporous peg from antennal tip showing tubular body (TB) and dendrites (D) within dendritic sheath (Sh). × 14,300.

FIG. 5. Portion of sensory band from antenna showing multiporous peg (MP) and uniporous cone (UC). A pore (arrow) was seen at tip of cone during SEM operation but is not visible in this photo. × 6900.



FIGS. 6 – 12. Captions on page 25.

Labial sensilla

The structure of the labial palps is similar to that of the maxillary palps. They are 3-segmented, bearing a cluster of sensilla at the tip (Fig. 20). Similarly, they have a digitiform organ on the distal segment located on the anterior surface. However, the number of uniporous and non-porous pegs on the tip is about half that on the maxilla. Figure 20 shows about 4 Type II, non-porous, non-socketed pegs distributed from the tip center to the periphery. Two campaniform organs are located in similar positions to those on the maxilla. About 6 Type I pegs are found on the tip periphary, but no Type III pegs are seen. Also there seem to be no short uniporous pegs on the tip side wall. The ultrastructure of these sensilla as seen in thin sections appears identical to that of their counterparts on the maxilla.

DISCUSSION

My investigation of the antennal chemosensilla of *D. ponderosae* confirms the findings of previous investigations of *Dendroctonus* sp. (Payne *et al.*, 1973; Dickens and Payne, 1978).

The antennal sensilla trichodea III of *D. frontalis* described by Dickens and Payne (1978) are singly innervated and possess a basal tubular body. This is true in *D. ponderosae,* although an occasional thick-walled, possibly uniporous, multiply-innervated sensillum similar to those described on the antennae of other beetles (Moeck, 1968; Mustaparta, 1973; Hatfield *et al.*, 1976) was encountered. These sensilla are possibly contact chemosensilla similar to those found on the antennae of other insects, e.g. the honey bee worker (Whitehead and Larsen, 1976).

The fluted cones were described by Dickens and Payne (1978) as scattered in the antennal sensory bands of *D. frontalis,* but Payne *et al.* (1973) did not mention them in the 16 species of bark beetles they surveyed. The cones may be olfactory because the side wall is porous. They have also been reported in Diptera (Bay and Pitts, 1976; Boo and McIver, 1976) and other orders (Slifer, 1970).

The digitiform organs on the maxillary and labial palps of *D. ponderosae* are very similar to those reported in other species. Zacharuk *et al.* (1977) described them on the labial palps of larvae of the elaterid, *Ctenicera destructor,* where they appear to function as vibration-sensitive sensilla. Doane and Klinger (1978) reported a single digitiform sensillum on the tips of both maxillary and labial palps of another species of elaterid larvae, *Limonius californicus.* This organ may be important in the female *D. ponderosae*

FIG. 6. Fluted cone located in antennal sensory band. × 11,400.

FIG. 7. Cross-section of fluted cone showing 4 dendrites in lumen. × 28,000.

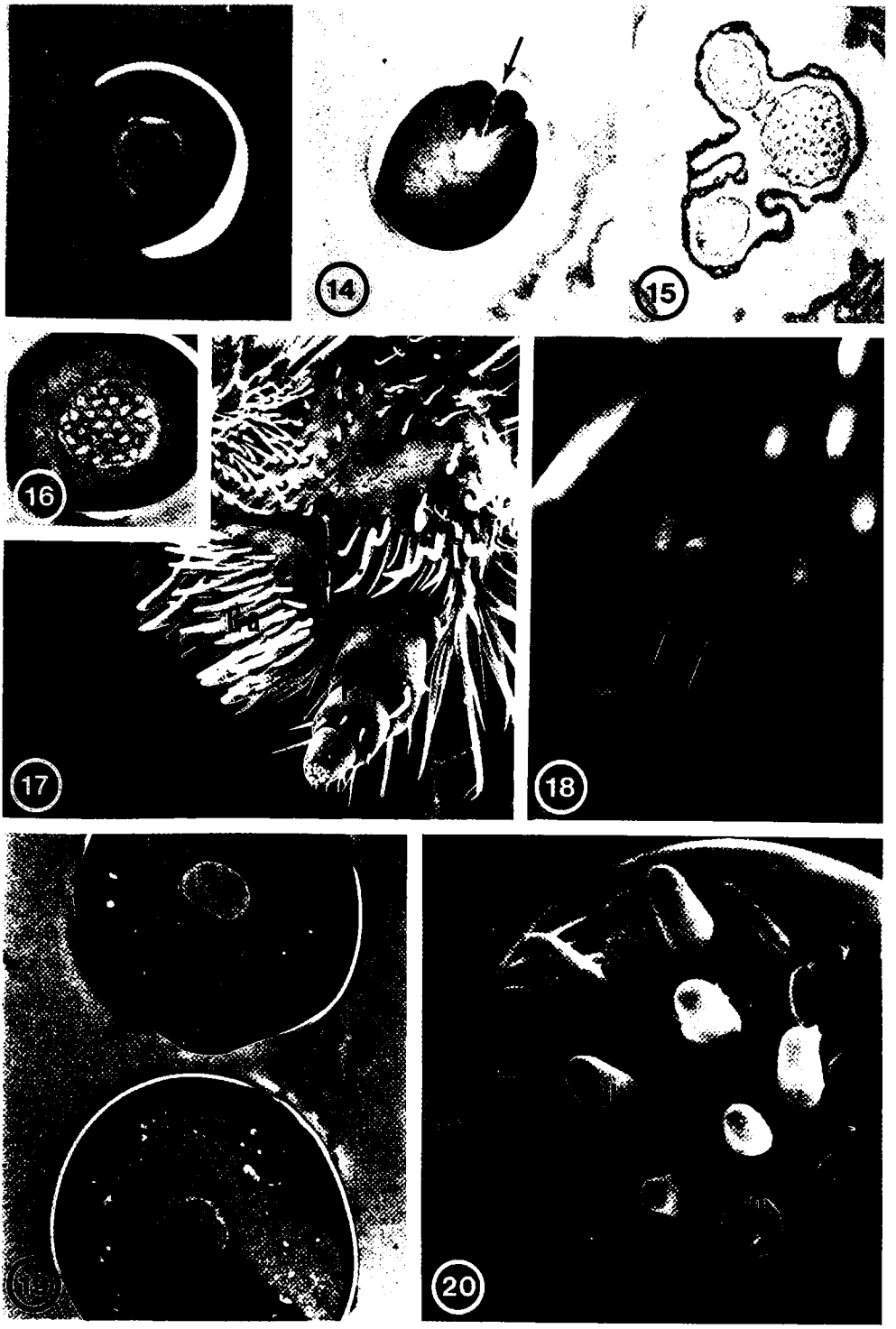
FIG. 8. Ventral aspect of mouthparts showing mandible (Mn), labial palp (LP), maxillary palp (MP), and galea (Ga). × 70.

FIG. 9. Maxillary palp-tip showing digitiform organ (DO), small uniporous peg (SUP), uniporous peg (I), non-porous, non-socketed peg (II), mechanosensitive peg (III) and campaniform organ (CO). × 2000.

FIG. 10. Small uniporous peg on distal segment of maxillary palp. A possible pore (arrow) is visible near tip. × 9000.

FIG. 11. Cross-section through base of small uniporous peg showing tubular body (TB) and 3 dendrites enclosed in dendritic sheath (DS). × 19,300.

FIG. 12. Close-up of sensilla on maxillary palp-tip showing uniporous peg (I), non-porous peg (II), and campaniform organ (CO). × 5200.



FIGS. 13 – 20. Captions on page 27.

for detecting the stridulation of the male. It is not known, however, whether the organ exists in the male.

The Type I pegs found on the tips of the maxillary and labial palps may be contact chemosensilla with a mechanosensitive neuron because their morphology also resembles those of 'classic' contact chemosensilla. Electrophysiological studies are currently being performed in my laboratory to investigate these sensilla and the effects of naturally-occurring chemicals of lodgepole pines (one of the hosts of *D. ponderosae*).

The structure of the Type II sensilla has not been described in the literature in any detail; these sensilla are referred to as "sensilla basiconica or coronal pegs" (Bellamy, 1973). Doane and Klinger (1978) mentioned their occurrence on the tips of the maxillary and labial palps of elaterid larvae, but they did not study them by the TEM. Bellamy (1973) called them thick-walled chemoreceptors but assigned them no function. There is no way of determining their function until electrophysiological studies are made. However, they may be a form of mechanosensillum, because their dendrites branch in a non-porous lumen similar to that seen in the digitiform organ sensilla.

The campaniform organ function is also not known although they are probably mechanosensitive. Bellamy (1973) described similar structures on the palp-tips of the wireworm, *Ctenicera destructor,* and Doane and Klinger (1978) reported them on 2 other species of wireworms.

The 2 sensilla from the galea have a striking similarity in cross-section to pegs found on the galea of the larval red turnip beetle, *Entomoscelis americana* Brown (Mitchell *et al.*, 1980) and on the adult (Mitchell, personal communication). However, the external morphology of these possibly homologous pegs is quite dissimilar in the 2 insects. In the red turnip beetle, Mitchell and Gregory (1979) determined that one of these pegs, the lateral sensillum, is definitely a contact chemosensillum sensitive to several sugars and amino acids; therefore, it is possible that the equivalent peg on *D. ponderosae* has this function. Mitchell and Gregory (1979) were unable to determine the function of the other peg, the medial sensillum. They suggested that it may be a mechanosensillum. Indeed, the supposedly equivalent sensillum on *D. ponderosae* and the medial sensillum of the red turnip beetle have a similar internal morphology to the Type II non-porous peg on the tips of the palps of *D. ponderosae*. Electrophysiological recordings made from the base of the sensillum could help in determining function.

FIG. 13. Cross-section of uniporous Type I peg. × 14,800.

FIG. 14. Tangential section of tip of uniporous Type I peg showing 18 nM pore (arrow) leading into dendritic lumen. × 22,200.

FIG. 15. Cross-section through base of non-porous Type II peg near distal end showing 3 dendrites within dendritic sheath. × 19,300.

FIG. 16. Cross-section through non-porous Type II peg near distal end showing numerous dendritic branches. × 15,000.

FIG. 17. Posterior aspect of left maxilla showing palp (Plp) and galea (Ga.) × 190.

FIG. 18. Mesal aspect of distal portion of galea showing 2 pegs (arrows) which might be chemosensilla. Other pegs are probably mechanosensilla. × 970.

FIG. 19. Cross-section of 2 possibly chemosensitive pegs on maxillary galea. × 10,600.

FIG. 20. Tip of labial palp showing uniporous peg (I), non-porous peg (II), and campaniform organ (CO). × 4500.

The smaller number and similar structure of the sensilla on the labial palp-tip compared with those on the maxillary palp seen in *D. ponderosae* have been reported by Doane and Klinger (1978) for the larval wireworm, *Limonius californicus*. However, they reported even more sensilla on the maxillary palp than on the labial palp compared with *D. ponderosae*. The significance of these observations is unknown.

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REFERENCES

BAY, D. E. and C. W. PITTS. 1976. Antennal olfactory sensilla of the face fly *Musca autumnalis* De Geer. *Int. J. Insect Morphol. Embryol.* **5**: 1 – 16.

BEHAN, M. and M. F. RYAN. 1978. Ultrastructure of antennal sensory receptors of *Tribolium* larvae (Coleoptera : Tenebrionidae). *Int. J. Insect Morphol. Embryol.* **7**: 221 – 36.

BELLAMY, F. W. 1973. Ultrastructure of the labial palp and its associated sensilla of the prairie grain wireworm *Ctenicera destructor* (Brown). Ph.D. Thesis, University of Saskatchewan, Regina, Saskatchewan.

BOO, K. S. and S. B. MCIVER. 1976. Fine structure of surface and sunken grooved pegs on the antennae of female *Anopheles stephensi* (Diptera : Culicidae). *Can. J. Zool.* **54**: 235 – 44.

BORDEN, J. H. 1968. Antennal morphology of *Ips confusus* (Coleoptera : Scolytidae). *Ann. Entomol. Soc. Amer.* **61**: 10 – 13.

BORG, T. K. and D. M. NORRIS. 1971. Ultrastructure of sensory receptors on the antennae of *Scolytus multistriatus* (Marsh). *Z. Zellforsch. Mikrosk. Anat.* **113**: 13 – 28.

DICKENS, J. C. and T. L. PAYNE. 1978. Structure and function of the sensilla on the antennal club of the southern pine beetle, *Dendroctonus frontalis* (Zimmerman) (Coleoptera : Scolytidae). *Int. J. Insect Morphol. Embryol.* **7**: 251 – 65.

DOANE, J. F. and J. KLINGER. 1978. Location of CO_2-receptive sensilla on larvae of the wireworms *Agriotes lineaus-obscurus* and *Limonius californicus*. *Ann. Entomol. Soc. Amer.* **71**: 357 – 63.

HARBACH, R. E. and J. R. LARSEN. 1976. Ultrastructure of sensilla on the distal segment of adult *Oncopeltus fasciatus* (Dallas) (Hemiptera : Lygaeidae). *Int. J. Insect Morphol. Embryol.* **5**: 23 – 33.

HATFIELD, L. D., J. L. FRAZIER and L. B. COONS. 1976. Antennal sensilla of the pecan weevil. *Curculio caryae* (Horn) (Coleoptera : Curculionidae). *Int. J. Insect Morphol. Embryol.* **5**: 279 – 87.

MITCHELL, B. K. and P. GREGORY. 1979. Physiology of the maxillary sugar-sensitive cell in the red turnip beetle, *Entomoscelis americana*. *J. Comp. Physiol.* **132**: 167 – 78.

MITCHELL, B. K., A. T. WHITEHEAD and E. BACHUS. 1980. Ultrastructure of the lateral and medial galeal sensilla of the larva of the red turnip beetle, *Entomoscelis americana* Brown (Coleoptera: Chrysomelidae). *Int. J. Insect Morphol. Embryol.* **8**: 289 – 95.

MOECK, H. A. 1968. Electron microscopic studies of antennal sensilla in the ambrosia beetle, *Trypodendron lineatum* Olivier (Scolytidae). *Can. J. Zool.* **46**: 521 – 56.

MUSTAPARTA, H. 1973. Olfactory sensilla on the antennae of the pine weevil, *Hylobius abietis*. *Z. Zellforsch. Mikrosk. Anat.* **144**: 559 – 71.

PAYNE, T. L., H. A. MOECK, C. D. WILSON, R. N. COULSON and W. J. HUMPHREYS. 1973. Bark beetle olfaction—II. Antennal morphology of sixteen species of Scolytidae (Coleoptera). *Int. J. Insect Morphol. Embryol.* **2**: 177 – 92.

PEASE, D. C. 1964. *Histological techniques for electron microscopy*. Academic Press, New York.

RYAN, M. F. and M. BEHAN. 1973. The sensory receptors of *Tribolium* larvae. *Physiol. Zool.* **46**: 238 – 44.

SCHOFER, G. A. and G. N. LANIER. 1970. A sexual character in pupae of *Dendroctonus* (Coleoptera: Scolytidae). *Can. Entomol.* **102**: 1487 – 88.

SLIFER, E. H. 1970. The structure of arthropod chemoreceptors. *Annu. Rev. Entomol.* **15**: 121 – 42.

WHITEHEAD, A. T. and J. R. LARSEN. 1976. Ultrastructure of the contact chemoreceptors of *Apis mellifera* L. (Hymenoptera : Apidae). *Int. J. Insect Morphol. Embryol.* **5**: 301 – 15.

ZACHARUK, R. Y. 1980. Ultrastructure and function of insect chemosensilla. *Annu. Rev. Entomol.* **25**: 27 – 47.

ZACHARUK, R. Y., P. J. ALBERT and F. W. BELLAMY. 1977. Ultrastructure and function of digitiform sensilla on the labial palp of a larval elaterid (Coleoptera). *Can. J. Zool.* **55**: 569 – 78.