SENSORY BASES OF ATTRACTANCY: MORPHOLOGY OF MOSQUITO OLFACTORY SENSILLA—A REVIEW

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ABSTRACT. The internal and external ultrastructure of virtually all of the olfactory sensilla of the mosquitoes *Aedes aegypti* and *Anopheles stephensi* have been described. Many other mosquitoes have had their olfactory complements partially described. This review summarizes ultrastructural features and suspected biological roles of the small sensilla coeloconica, large sensilla coeloconica, sensilla ampullaceae, grooved pegs and sensilla trichodea of mosquito antennae, and the capitate pegs of mosquito palps. In addition to a general review of the topic, several new points are raised: 1) the lamellate dendrite is the CO_2-sensitive element in the capitate pegs of mosquitoes and in equivalent pegs of certain other insects; 2) the presence of the purported CO_2-sensitive lamellate dendrite in many male mosquitoes and other biting flies argues for more widespread occurrence of males seeking out hosts for mating purposes; 3) the grooved pegs, considered to have a single apical pore are olfactory sensilla of the multiporous grooved type bearing many pores along their side grooves; and 4) the large sensilla coeloconica are multiporous grooved sensilla and may have structural and functional equivalences with grooved peg sensilla.

INTRODUCTION

The life of the female mosquito is governed, in large part, by its orientation responses to stimuli from important resources such as resting sites, oviposition sites, nectar sources, mates, and blood hosts. Odors emanating from these (with the probable exception of a mate) are known to be important orienting stimuli for the female mosquito. The purpose of this contribution is to briefly review our current knowledge of the morphology of the cuticular sensory receptors used by mosquitoes to detect and orient to odor-type stimuli (including heat and humidity). Orientation to these resources also involves visual and, in the case of mate-finding by the male mosquito, auditory stimuli. The morphological bases for these senses in mosquitoes are summarized by McIver (1982); Allen et al. (1987) reviewed the role of vision in biting fly (including mosquito) ecology.

NATURE OF INSECT CUTICULAR SENSORY RECEPTORS

Mosquito cuticular sensory receptors (= sensilla) are typical of those of insects in general. They consist of an external cuticular process in the form of a seta or modified seta (depending on specific function). The seta is underlain by a small group of modified epithelial cells including a bipolar sensory cell(s) and various sheath cells. Each sensory cell(s) extends a dendrite that associates with the seta in a sensory modality-specific manner. Each sensory cell also sends an axon to the central nervous system. The axon goes to the central nervous system without synapsing or fusing with others.

Insect odor-sensitive sensilla may have from one (Schmidt and Gnatzy 1972) to more than 50 (Barlin and Vinson 1981) sensory cells although 2–6 is more common (Zacharuk 1985). Dendrites from sensory cells usually extend, either branched or unbranched, into the hollow seta process where they come into contact or close proximity with pores or pore-tubules extending from the pores. Odorant molecules apparently diffuse into the pores eventually coming into contact with, or affecting in some indirect manner, the dendrites. Zacharuk (1985) reviewed insect sensillar structure and classified olfactory sensilla on the basis of pore distribution and wall thickness. He distinguished between smooth-sided "multiporous pitted" or "MPP" sensilla, which may be "thin-walled" or "thick-walled", and sculpted "multiporous grooved" or "MPG" sensilla.

Zacharuk (1985) also included an "aporous" category into which fall sensilla generally considered to be hygro-/thermoreceptive. In such sensilla, convection or conduction heat and water vapor affect the dendrites either by passing through the overlying cuticle or by altering the microconformation of the cuticle thus affecting the dendrites indirectly. Insect hygro-/thermosensilla are reviewed by Altner and Loftus (1985).

MOSQUITO OLFACTORY SENSILLA

Since McIver's major review in 1982, no new information has been published on the morphology of mosquito olfactory sensilla. The exception to this is a study of palpal pegs of the non-host-seeking mosquito, *Toxorhynchites brevipalpis* Theobald by McIver and Siemicki (1984). McIver (1982) reviewed literature dating

from the early 1950s and provided detailed summaries of sensillar distribution, numbers on different species and each sex, and of the ultrastructure of all the sensillar types discussed herein. In all, McIver's review provides information on aspects of the sensillar complement of mosquitoes from 11 genera. The most thoroughly known species are *Anopheles stephensi* Liston, *Culex pipiens* Linn., and *Aedes aegypti* (Linn.). Indeed, the claim is justifiably made that virtually all of the sensilla of *Ae. aegypti* have been mapped, counted, and described ultrastructurally (McIver 1982).

Based on a combination of detailed ultrastructural information and careful counts of sensillar types on the antennae of *Ae. aegypti* and *An. stephensi*, McIver (1982) calculated that 93% and 85%, respectively, of the neurons in the flagellar nerves of these species carry information on odors. This speaks to the importance of odor information to the mosquito and its speaks to the great variety of odor information available in the mosquito's environment.

According to McIver (1982), in *Ae. aegypti*, 5 types of olfactory sensilla occur on the antennae (large and small sensilla coeloconica, sensilla ampullaceae, grooved pegs, sensilla trichodea) and one occurs on the palps (capitate pegs). The same sensillar types appear to occur (with some variations—see below) on *An. stephensi* and other species. In addition, large sensilla coelconica occur only on anopheline mosquitoes. The morphology of these sensillar types is summarized in the following sections. In addition, the possible sensitivities and biological roles of these sensilla in mosquitoes, and in other insects where equivalent types occur, is discussed.

Capitate pegs: These sensilla occur on palpal segments 2–4 in female anophelines, on palpal segment 4 in male anophelines (McIver and Siemicki 1975), and on segment 4 only in male and female culicines studied (McIver and Charlton 1970, McIver 1971). Numbers present range from less than 20 per palp in female *Uranotaenia* sp. (Omer and Gillies 1971) to more than 200 in various *Culex* species (see for example McIver 1970). Males generally have fewer than females. Capitate pegs have been studied ultrastructurally in a number of mosquitoes including *Ae. aegypti* (McIver 1972) and *An. stephensi* (McIver and Siemicki 1975). They are thin-walled MPP sensilla possessing, in these species, 3 neurons; 2 of these produce a branching, digitiform dendrite each; the 3rd produces a highly lamellate dendrite.

Palpal ablation studies (Bassler 1958, Omer and Gillies 1971) suggest a CO_2-detection role for these sensilla in *Ae. aegypti* and *Culex quinquefasciatus* Say. Carbon dioxide responsiveness within a behaviorally significant range (additions of 0.01% to ambient CO_2 concentration) for capitate pegs of *Ae. aegypti* was confirmed electrophysiologically by Kellogg (1970). He also found that capitate pegs in this species respond to odors of n-heptane, acetone, and amyl acetate (the latter induces inhibition).

It is not possible with this information alone to determine which dendrites in the capitate pegs respond to specific stimuli. However, morphological evidence can be used to build a strong circumstantial case for which dendrite is the probable CO_2 detector. Capitate peg equivalents occur on other nematoceran biting flies such as simuliids (Mercer and McIver 1973) and ceratopogonids (Rowley and Cornford 1972) where they are found in a deep pit on the 3rd segment of the maxillary palp. In the black fly, *Simulium arcticum* Malloch, these pegs are innervated by a single neuron producing a lamellar dendrite (Sutcliffe et al. 1987), whereas in the ceratopogonid *Culicoides furens* (Poey), they are innervated by 2 neurons, one producing a digitiform dendrite, the other a lamellate dendrite (Chu-Wang et al. 1975).

Sutcliffe et al. (1987) argued that, because all 3 biting groups (Simuliidae, Ceratopogonidae, and Culicidae) respond to CO_2 and because the lamellate dendrite is the only dendrite common to the capitate pegs of all 3 groups, the lamellate dendrite is the probable CO_2 detector.

In fact, many insects, not just bloodfeeders, are known to respond to CO_2. For instance, Bogner et al. (1986) and Lee et al. (1985) described palpal sensilla possessing a lamellate dendrite (only) in the moth *Rhodogastria* sp. (Arctiidae) and in the butterfly *Pieris rapae* (Pieridae), respectively. Furthermore, Bogner et al. (1986) demonstrated electrophysiologically that these palpal sensilla (and therefore the lamellate dendrite within) are CO_2 sensitive. This provides further circumstantial support for the lamellate dendrite of mosquitoes and other biting flies being the CO_2-sensitive unit. It would be very interesting to know what it is about CO_2 detection that necessitates such an elaborate dendritic structure.

Morphological evidence also points out a seeming incongruity with respect to the sex-specific occurrence of the capitate pegs; that is, although females always have more such pegs, nematoceran males, which have no apparent need to locate the host, generally have some. What use could males make of this information? Sutcliffe et al. (1987) pointed out that some male black flies (*Simulium arcticum*, *Boophthora erythrocephala* De Geer, *Odagmia ornata* (Meigen)) intercept females at or near the host and may, therefore, orient to host odors including CO_2.

Although males of a few mosquito species (e.g., *Ae. aegypti*) are also known to seek mates at or near hosts, this is not thought to occur widely. In a study involving animal-baited trapping in Sweden, males of the mosquito, *Aedes diantaeus* Howard, Dyar and Knab made up more than 50% of trap catches and were apparently attracted by odors because the bait animals were hidden behind a screen (Jaenson 1985). Perhaps male mosquitoes, black flies, etc., orient to hosts to locate mates more than generally realized. Their absence from many trap collections may be due to differences in near-host response that normally keep them at a distance. Alternatively, perhaps males of some species only seek mates at hosts under certain special conditions.

Although still not definitive, further evidence in support of mate seeking as a role for CO_2-detection by male nematoceran biting flies come from the finding that male *Tx. brevipalpis* lack capitate pegs altogether. This mosquito species does not bloodfeed. If the females do not mass around hosts, perhaps there is no point in the males possessing sensory equipment to detect CO_2.

Grooved pegs: Males and females of all mosquito species examined to date possess the short, deeply grooved sensilla called A3 sensilla in *Ae. aegypti* by Steward and Atwood (1963). Grooved pegs occur on all flagellar segments in females varying from 10 per antenna in female *Uranotaenia lateralis* Ludlow to 350 per antenna in female *Culex restuans* Theobald (McIver 1970). Male *Ae. aegypti* and *An. stephensi* have fewer grooved pegs than conspecific females (36 in male *Ae. aegypti* vs. more than 100 in females) and they are restricted to antennal segments 12 and 13 (McIver 1970).

McIver (1974) described the grooved pegs in *Ae. aegypti* as thick-walled and having 3–5 (usually 3) unbranched dendrites that make contact with the outside by a single apical pore. In *An. stephensi* the grooved pegs are categorized into A1 and A2 subtypes but have the same number of dendrites and similar ultrastructure as in *Ae. aegypti* (Boo and McIver 1976, Boo 1980). Grooved peg sensilla in *Cx. pipiens* also resemble those of *Ae. aegypti* but possess only 2 dendrites (Elizarov and Chaika 1972).

Despite what appears to be a contact chemosensillar morphology (single apical pore), McIver (1974) concluded that the grooved pegs must operate as olfactory sensilla because their shortness and the fact that they are located among much longer setae would make contact with a substrate virtually impossible for them. Kellogg (1970) confirmed an olfactory function for the grooved pegs with physiological evidence that the grooved pegs of *Ae. aegypti* respond to vapors of ammonia, acetone, and water (by excitation) and of acetic acid and anisole (by inhibition). Davis and Sokolove (1976) could only partially confirm this response spectrum but were able to show that the grooved pegs of *Ae. aegypti* respond to lactic acid, a known mosquito attractant (Acree et al. 1968). The lactic acid response comes from 2 cells; one is inhibited by increasing lactic acid concentration whereas the other is excited by it. The grooved pegs of *Ae. aegypti* also respond to organic vapors including those of certain fatty acids (possibly skin associated) and essential oils (possibly flower/nectar-source associated) (Davis 1977). In addition, both lactic acid-sensitive cells in the grooved pegs of *Ae. aegypti* are deet-inhibited (Davis and Sokolove 1976).

The grooved pegs as described by McIver (1974) are very unusual as insect olfactory sensilla in that they have but a single apical pore instead of the usual (for olfactory sensilla) numerous pores in the side walls. According to Zacharuk (1985), MPG sensilla, which the grooved pegs resemble strongly, have very small pores that open in the bottoms of the grooves in the peg shaft. These connect by means of "spoke canals" to the lumen of the peg. Electron-dense material from the dendritic chamber often fills these spoke canals and flows out to coat the bottoms of the grooves. Odorant molecules are thought to dissolve in this material and eventually diffuse to pores and into the peg lumen through the canals. Although McIver (1974, Fig. 7) observed "electron-dense strands" that look like spoke canals, this possibility was rejected because so few were seen. Spoke canals are easily missed, however, because they are not numerous (as few as 200 per sensillum) and may be as small as 5 nm in diameter (Zacharuk 1985). The grooved pegs also have electron-dense material in their grooves. It is possible that the multiporous nature of these sensilla has been misinterpreted and that the single apical pore is actually a molting pore such as occurs at the tips of many sensilla (Zacharuk 1985). In my view, there is enough morphological evidence to justify leaving the possibility that the antennal grooved pegs of mosquitoes are conventional MPG sensilla open pending further examination of their ultrastructure.

Large sensilla coeloconica: Called "sunken pegs" by Boo and McIver (1976) and simply "sensilla coeloconica" by Ismail (1962), the large sensilla coeloconica occur only in anopheline mosquitoes. Female anophelines, which usually have a few such sensilla on each of the 7 basal flagellomeres, have more than conspecific males, which have between 8 and 14 mainly on the subterminal flagellomere (McIver 1982).

Large sensilla coeloconica consist of short pegs

(5 μm in length in *An. stephensi* [Boo and McIver 1976]) in the floor of a pit the sides of which close partly over the peg tip. Four or 5 neurons extend branched dendrites into the peg lumen. The dendrites appear to have contact with the exterior by means of up to 16 grooves that run from just above the peg base to just below its tip. These grooves contain electron-dense material along their bottoms that appears to come from the peg lumen. Although no spoke canals are observed in the micrographs, these sensilla fit the description of Zacharuk's (1985) MPG sensilla and, in my opinion, may have closer affiliations with the grooved pegs that I also suggest are MPG-type sensilla (see previous section).

The large sensilla coeloconica are probably olfactory in function although no electrophysiological evidence exists to support this, let alone to determine specific sensitivities. However, if the large sensilla coeloconica are another form of grooved pegs, they may also have grooved peg-type sensitivities to skin-associated volatiles, deet, and/or lactic acid.

Small sensilla coeloconica: Two or 3 so-called "small sensilla coeloconica" occur at the tip of both antennae of both sexes of all culicine, anopheline, and toxorhynchitine species that have been examined (McIver 1973, Boo and McIver 1975, McIver 1982). Each small sensillum coeloconicum consists of an aporous peg approximately 2–3 μm long set into the bottom of a shallow pit. Each peg is innervated by 2 neurons, the dendrites of which are closely "packed" into the peg lumen. The dendrite of a 3rd cell extends toward the peg base but stops well short of it and takes on a lamellate form.

These morphological features are consistent with the "no pore, inflexible socket" hygro-/thermosensilla of insects as reviewed by Altner and Loftus (1985). Such sensilla are widespread in insects (e.g., found in certain beetles [Arbogast et al. 1972, Haug 1985]; crickets [Itoh et al. 1984]; moths [Haug 1985]; and in the bloodfeeding bug, *Rhodnius prolixus* Stahl [McIver and Siemicki 1985]). Typically, these sensilla occur in very small numbers usually at the antennal tips and at the ends of the antennal segments and, typically, they are innervated by a "triad" of cells as in mosquitoes.

These sensilla have been studied physiologically in many insects (e.g., stick insects [Tichy 1987]; locusts [Ameismeier and Loftus 1988]; certain lepidopteran caterpillars [Schoonhoven 1967, Dethier and Schoonhoven 1968]). Although much variation in response has been found, such sensilla often have 2 cells that respond to changes in humidity (one cell being inhibited, the other excited by moisture increase) and a 3rd cell that responds positively to decreasing temperature (i.e., a "cold" cell). The fact that air temperature and relative humidity covary often poses problems in properly interpreting the responses of these sensilla.

Morphological evidence can suggest, but not establish definitively, which of the triad units are humidity sensitive and which is thermoreceptive. Altner and Loftus (1985) point out that the microtubule-filled dendrites of the aporous peg respond mechanically to moisture-induced distortions of the peg cuticle. Although morphologically similar to mechanosensitive tubular bodies (McIver 1975, 1985), these units may be functional moisture detectors. The lamellate dendrite may be the temperature sensor; the extent of development of the lamellae has been suggested to relate to the temperature range the dendrite is designed to operate in—the more lamellae, the lower the operating temperature range may be (Altner and Loftus 1985).

Early ablation experiments (Roth and Willis 1952) suggested that sensilla at the antennal tip of *Ae. aegypti* are thermosensitive. Davis and Sokolove (1975) made physiological recordings from the small sensilla coeloconica in the tip of the antennae of *Ae. aegypti* and showed that these sensilla possess 2 thermosensitive cells (one excited by increasing temperature, one inhibited by it). No evidence was found for the detection of water vapor, CO_2, or infrared radiation by these sensilla. Considering the extent of evidence showing such sensilla in other insects to be humidity sensitive, it may be premature, based on this one report, to dismiss the possibility of hygroreception for such sensilla in all mosquitoes.

It is tempting to ascribe a role in host-seeking behavior to the small sensilla coeloconica. Those of *Ae. aegypti* are capable of responding to the small temperature changes that might occur within a meter or so of the warm-blooded host (Davis and Sokolove 1975). A role for the lamellate dendrite in host seeking is also suggested by morphological evidence that this dendrite is much reduced in size in the antennae of the non-host seeker, *Tx. brevipalpis* (McIver and Siemicki 1978).

Among mosquitoes examined, the lamellate dendrite is most elaborate in male *Deinocerites cancer* Theobald, which spend much of their lives in dark crab holes where they attend female pupae and mate with the female adults as they emerge. McIver and Siemicki (1976) suggested that the elaborate lamellate dendrite of male *De. cancer* is an infrared radiation receptor used to identify the older (arguably warmer) female pupae. The highly developed lamellate dendrites of cave beetles, which also spend their lives in darkness, were also suggested as infrared detectors by Corbière-Tichané (1971). No subsequent sup-

port for infrared detection by these sensilla has been forthcoming. On the other hand, Altner and Loftus (1985) suggested that the more highly developed the lamellate dendrite, the more sensitive it may be to small temperature changes through conduction or convection. This may explain the elaborate lamellate dendrite in the crabhole mosquito because, if about-to-emerge pupae are warmer than younger ones, as McIver and Siemicki (1976) argued, temperature differences must be slight.

Although presumed thermo-/hygrosensilla on biting insects may be involved in host seeking or, in specialized cases, mate seeking, such sensilla occur in virtually all insects where they have been looked for. The function of these sensilla in insects, including mosquitoes, may be a general one because, as Altner and Loftus (1985: 273) wrote, "For animals as small as insects, sunlit biotopes may be quite unmanageable if not quickly lethal in the absence of instant clues about their temperature and humidity."

Sensilla ampullaceae (pegs in deep pits) also occur in small numbers along the antennae of male and female *An. stephensi* and *Ae. aegypti*. Their morphological similarity to small sensilla coeloconica suggests that the sensilla ampullaceae are "no pore, inflexible socket"-type sensilla (Boo and McIver 1975, McIver and Siemicki 1979) sensitive to thermal and moisture stimuli but no physiological investigations have been done to confirm their sensitivities.

Sensilla trichodea: These are the most numerous and varied sensilla on the mosquito antenna. Antennae of *Tx. brevipalpis* females bear more than 1,200 such sensilla (Omer and Gillies 1971), whereas those of females of smaller species bear fewer (*ca.* 650 in *Ae. aegypti* [Steward and Atwood 1963], 550 in *Anopheles* spp. [Omer and Gillies 1971]). Numbers of sensilla trichodea on males are significantly lower than on conspecific females. Sensilla trichodea occur generally distributed over the antennal segments, are much longer than the grooved pegs (though shorter than the mechanoreceptive sensilla chaetica at the bases of most antennal segments), and occur in a number of variants based on length and whether sharp or blunt at the tip (see McIver [1982] for a detailed discussion of variants). Irrespective of the variant, McIver (1982) noted that all sensilla trichodea of the mosquito antennae are innervated by 2 sensory cells and that each sensory cell produces an unbranched dendrite that extends the length of the inside of the seta. These conform to the thick-walled MPP-type of olfactory sensillum (Zacharuk 1985) that occurs widely in insects.

It is generally true that identifiable differences in morphology correspond to differences in sensory function (although it is not necessarily correct to conclude that sensilla of a given morphological type all share the same sensory function). Given their variety in mosquitoes then, it is probable that the sensilla trichodea serve many specific sensory functions. A number of physiological studies have been done on the response spectra of sensilla trichodea of *Ae. aegypti* and other mosquito species; many of these are summarized in detail by McIver (1982). Briefly, sensilla trichodea types and subtypes have been found that respond to oviposition site-related compounds (Davis 1976, Bentley et al. 1982), essential oils (often associated with nectar sources—Lacher 1967, Davis 1977), fatty acids and oils associated with skin, and to certain repellents (Lacher 1971, Davis and Rebert 1972). Interestingly, none of the sensilla trichodea have been found to be sensitive to lactic acid.

CONCLUSION

Through the application of morphological techniques, a thorough understanding of the sensillar complement (including olfactory sensilla) of 2 species of mosquitoes, *Ae. aegypti* and *An. stephensi*, is now available. Less comprehensive, but nonetheless useful, information is available on sensillar morphology for many other mosquito species. Unfortunately, very little new information on mosquito sensory morphology has been forthcoming in the last 10 years.

As the range of mosquito species of interest in the context of attractants research continues to grow, the information base on mosquito sensory complement becomes more and more inadequate. The foregoing summary shows that considerable variation in sensillar types, numbers, distribution, and ultrastructure occurs between species. Although across-the-board cataloging of the sensory complements of various mosquito species is no longer desirable, it is still important that proper morphological descriptions of specific sensillar types continue to be made to support electrophysiological and behavioral studies of attractants. For the electrophysiologist to acquire and interpret recordings from mosquito attractant receptors it is important to know things such as how many of the particular sensillar types occur on the antenna and where they are, how many neurons innervate the sensillum, whether this number varies from one sensillum to another, how the dendrites associate with the peg or seta, etc. Morphological information such as the presence (or absence) and abundance of sensillar types of known function may also correlate with behavior. For instance, nonbloodfeeding mosquito species and males often possess fewer sensilla for which functions in host attractant de-

tection are known or suspected than do females of host-seeking species.

Future morphological work on mosquito sensory structures will need to be closely linked to behavioral and physiological studies of attractants and other directing influences in the mosquito's life. This means that morphologists, physiologists, and behavioral researchers will need to work more closely than ever. Indeed, the combination of these approaches will be essential to the complete understanding of the mosquito's olfactory responses because no one approach provides all the pieces of the puzzle.

ACKNOWLEDGMENTS

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