

Sensilla of the Antennae and Maxillary Palps of *Culicoides hollensis* and *C. melleus* (Diptera: Ceratopogonidae)

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ABSTRACT The types and arrangement of the sensilla on the female antennae and maxillary palps of both sexes of 2 estuarine species of biting midges, *Culicoides hollensis* (Melander & Brues) and *C. melleus* (Coquillett), were studied by scanning electron microscopy. Five sensillum types are found on the antennae of both species. Both species have sharp-tipped sensilla trichodea and sensilla basiconica only on subsegments 9-13 and blunt-tipped sensilla trichodea on all subsegments. Sensilla coeloconica occur on subsegment 1 of both species and various other subsegments depending on the species. Sensilla chaetica are found on all subsegments of *C. melleus*, but only on subsegments 1-8 and 13 on *C. hollensis*. Both sexes of *C. hollensis* have either 1 or 2 pits on the 3rd segment of the maxillary palps, which contain 8-15 bulb-shaped sensilla in females compared with 5-6 in males. No pit is found on the maxillary palps of either sex of *C. melleus*, but rather the bulb-shaped sensilla are distributed individually on this segment, ranging from 13 to 29 on the female and 6-10 on the male palps. These data are compared with data obtained from previously published light and electron microscopical studies of biting midge sensory structures.

KEY WORDS biting midges, *Culicoides*, olfactory sensilla, morphology, estuarine, scanning electron microscopy

BITING MIDGES of the genus *Culicoides* are distributed widely throughout the world. The blood-sucking behavior of the females, in addition to being an irritation, can cause severe dermatitis and several species are vectors of pathogens (Linley et al. 1983). Except for mosquitoes, probably no other biting insect found in the coastal areas of the southeastern United States causes more human discomfort than *Culicoides*. Large populations of *C. furens* (Poey), *C. hollensis* (Melander & Brues), and *C. melleus* (Coquillett) are produced in or near saltmarshes, mangrove swamps, and intertidal sandy areas at certain times of the year (Kline and Axtell 1976, 1977; Blanton and Wirth 1979; Magnon and Hagan 1988). The presence of abundant populations of these biting midges has had a direct role in delaying the development of some coastal areas as tourist attractions, recreational areas, and residential subdivisions. Despite the importance of these biting midges as major pests, no effective control strategy has been achieved. Because they are so difficult to control by traditional chemical insecticide methods, our recent research efforts have focused on the development of control strategies that use behavior-modifying chemicals, such as olfactory cues used for host location (Kline et al. 1994). Crucial to the development of such an approach is a greater understanding of the life histories, behavior, and sensory morphology and physiology of these biting midges. To date, there have been

few detailed morphological studies of either the antennal or palpal sensilla of biting midges, or investigations into the physiological roles of the individual sensilla.

Chu-Wang et al. (1975) initiated development of a sensory morphology database for the estuarine species that occur in the southeastern United States to provide a basis for behavioral and electrophysiological studies. These authors conducted scanning (SEM) and transmission electron microscopical (TEM) studies of the arrangement and ultrastructure of the sensilla on the antennae and maxillary palps of *C. furens*. The types of sensilla found in these studies, as well as the ultrastructure of the various sensilla were verified by similar SEM and TEM studies by Blackwell et al. (1992) of the antennae of both sexes of *C. impunctatus* (Goetghebuer) and *C. nubeculosus* (Meigen), pestiferous species in Scotland. Felipe-Bauer et al. (1989) also conducted a SEM microscopy study of the antennae of female *C. paraensis* (Goeldi) in Brazil with similar results. Messaddeq et al. (1989, 1990) conducted a systematic SEM study of the sensilla on the antennae and palpi of both sexes of *C. nubeculosus*.

The objectives of the current article were to expand our sensory morphology database for estuarine species found in the southeastern United States by means of SEM studies of the antennae of the females and the maxillary palps of both sexes of *C. hollensis* and *C. melleus*, and to compare these results with previously published SEM studies of the antennae and maxillary palps of *C. furens* (Chu-Wang et al. 1975).

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Fig. 1. Scanning electron micrograph overview of the antenna ($\times 430$) of a female *C. hollensis* showing the 13 subsegmented flagellum. Note that proximal 8 flagellar subsegments are ovoid and distal 5 subsegments elongated. Insert shows higher magnification ($\times 1,136$) of last (distal) subsegment.

Materials and Methods

Adult female specimens used for SEM were collected near Morehead City, NC, by aspirator as they attempted to bite a human. Additional females and males (which are not hematophagous) were obtained by rearing larvae collected from soil in a marsh.

Culicoides of both sexes were prepared for SEM by a fixation, dehydration, and critical point drying (Nemanic 1970). Living specimens were refrigerated at 4°C for 2–5 min and transferred to individual vials containing 3% glutaraldehyde in 0.05 M sodium cacodylate buffer at pH 7.2 for 2–4 h at 4°C . The glutar-



Fig. 2. Scanning electron micrograph overview of the antenna ($\times 968$) of a female *C. melleus*. The insert shows higher magnification ($\times 2,816$) of last (distal) subsegment. Black triangle points to a sensillum basiconicum and the arrow to a sensillum chaeticum.

aldehyde solution was removed by pipette and replaced with a 3% sucrose-sodium cacodylate wash in which the specimens remained for 12–24 h. at 4°C. After dehydration in ethanol of concentrations increasing from 50 to 100%, the specimens were washed in a transition fluid, Freon 113, in serial concentrations

from 15 to 100% and were dried using Freon 13 with a Bomar 850EX critical point dryer (Bomar, Tacoma, WA). The dry specimens were mounted on stubs, coated with carbon/gold in a rotary vacuum evaporator, and examined in an ETEC Autoscan (Perkin-Elmer, Hayward, CA), operating voltages of 5–10 kV.

Table 1. Distribution and mean number (range) of various types of sensilla on the flagellar subsegments of the antennae of female *C. furens* (*f*; *n* = 10), *C. hollensis* (*h*; *n* = 25), and *C. melleus* (*m*; *n* = 30)

| Flagellar subsegment | <i>S. chaetica</i> | | | <i>S. trichodea</i> | | | | | | <i>S. basiconica</i> | | | <i>S. coelonica</i> | | |
|----------------------|--------------------|-----------------|-----------------|---------------------|-----------------|-----------------|-----------------|-------------------|------------------|----------------------|---------------|----------------|---------------------|---------------|---------------|
| | | | | Blunt-tipped | | | Sharp-tipped | | | | | | | | |
| | <i>f</i> | <i>h</i> | <i>m</i> | <i>f</i> | <i>h</i> | <i>m</i> | <i>f</i> | <i>h</i> | <i>m</i> | <i>f</i> | <i>h</i> | <i>m</i> | <i>f</i> | <i>h</i> | <i>m</i> |
| 1 | 5.0 (4-6) | 4.3 (2-6) | 4.8 (2-8) | 2.7 (2-3) | 1.8 (1-2) | 2.0 (2) | 0 | 0 | 0 | 0 | 0 | 0 | 2.0 (2) | 3.0 (3) | 2.4 (2-3) |
| 2 | 5.8 (4-6) | 2.9 (1-5) | 5.3 (2-8) | 3.5 (3-4) | 1.6 (1-3) | 2.1 (2-3) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3 | 5.8 (4-6) | 2.6 (1-4) | 4.8 (2-7) | 3.6 (2-4) | 1.8 (1-3) | 1.9 (1-2) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 4 | 5.6 (4-6) | 3.8 (3-5) | 4.5 (2-6) | 3.7 (3-4) | 2.1 (1-3) | 1.9 (1-3) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 5 | 4.7 (3-6) | 3.8 (2-6) | 4.7 (2-6) | 3.8 (3-4) | 2.0 (1-3) | 1.9 (1-2) | 0 | 0 | 0 | 0 | 0 | 0 | 1.0 (1) | 0 | 0 |
| 6 | 4.8 (3-6) | 3.2 (3-5) | 4.6 (2-6) | 3.6 (3-4) | 2.2 (1-3) | 1.9 (1-3) | 0 | 0 | 0 | 0 | 0 | 0 | 2.0 (2) | 0 | 0 |
| 7 | 4.7 (3-6) | 3.3 (2-5) | 5.2 (2-6) | 4.0 (4) | 2.2 (1-3) | 2.0 (1-3) | 0 | 0 | 0 | 0 | 0 | 0 | 2.0 (2) | 0 | <0.1 (0-1) |
| 8 | 4.6 (4-6) | 3.4 (2-6) | 5.7 (5-7) | 3.8 (2-4) | 2.0 (1-3) | 2.7 (2-3) | 0 | 0 | 0 | 0 | 0 | 0 | 3.0 (3) | 0 | 0.9 (0-1) |
| 9 | 0 | 0 | 1.8 (1-2) | 2.5 (2-3) | 2.7 (2-4) | 2.4 (1-4) | 12.9 (12-13) | 12.5 (11-14) | 16.0 (15-18) | 4.8 (4-5) | 0.1 (0-1) | 1.8 (2-3) | 0 | 0.7 (0-1) | 1.0 (1) |
| 10 | 0 | 0 | <0.1 (0-1) | 2.5 (2-3) | 5.0 (2-6) | 3.7 (2-5) | 12.5 (12-13) | 13.7 (12-16) | 15.4 (13-20) | 6.0 (6) | 0.4 (0-1) | 2.1 (1-3) | 0 | 0.4 (0-2) | 1.0 (1) |
| 11 | 0 | 0 | 1.5 (1-2) | 3.6 (3-4) | 6.0 (4-8) | 4.4 (2-9) | 14.7 (13-15) | 20.8 (17-26) | 16.6 (12-20) | 8.0 (8) | 2.0 (1-2) | 2.1 (1-4) | 0 | 0.9 (0-1) | 1.0 (1) |
| 12 | 0 | 0 | <0.1 (0-1) | 3.9 (3-4) | 6.2 (3-10) | 5.4 (2-8) | 17.4 (14-18) | 19.7 (15-25) | 21.2 (13-24) | 8.0 (8) | 1.8 (1-3) | 3.0 (2-4) | 0 | 2.3 (0-5) | 2.1 (1-3) |
| 13 | 1.0 | 3.3 (3-5) | 3.5 (2-5) | 6.9 (6-8) | 6.5 (2-15) | 3.5 (2-5) | 35.2 (34-36) | 33.6 (23-49) | 27.3 (23-33) | 15.4 (14-16) | 5.3 (3-7) | 3.6 (1-6) | 0 | 1.0 (1) | <0.1 (0-1) |
| Σ | 42.0 (30-49) | 30.6 (19-47) | 46.6 (23-65) | 48.1 (38-53) | 42.1 (21-66) | 35.8 (20-52) | 92.7 (85-95) | 100.3 (78-140) | 96.5 (76-115) | 42.2 (40-43) | 9.5 (5-14) | 12.6 (7-20) | 10.0 (10) | 8.3 (4-13) | 8.6 (6-12) |

Data from Chu-Wang et al. (1975).

Sensilla on antennal subsegments 1-13 were counted for 25-30 female specimens of each species. Palpal sensilla were examined on 2 male and 9 female *C. hollensis* and 5 male and 23 females of *C. melleus*.

Results

Antennal Sensilla. The antennae of female *C. hollensis* (Fig. 1) and *C. melleus* (Fig. 2), like all the other *Culicoides* species previously examined, consist of 3 segments: the 1st segment, attached to the head, is a small ring-shaped scape; the 2nd segment is an enlarged cup-shaped pedicel; and the 3rd segment is the elongated flagellum with 13 subsegments. The first 8 flagellar subsegments are ovoid, and the distal 5 subsegments are elongated and nearly cylindrical. The antennal flagellum contains ≈191 and 202 sensilla, respectively, for *C. hollensis* and *C. melleus* (Table 1). These sensilla are classified as sensilla chaetica, blunt- and sharp-tipped sensilla trichodea, sensilla basiconica, and sensilla coelonica (following terminology of Wirth and Navai 1978) (Fig. 3).

Sensilla Chaetica. The sensilla chaetica are long articulated setae, arising from a socket, with sharp tips and thick walls. These sensilla are most abundant on short flagellar segments (1-8), and less numerous on the longer distal segments (9-13). In *C. hollensis* they are arranged in whorls of 2-6 at the proximal ends of flagellar subsegments 1-8, absent on subsegments 9-12, and in a whorl of 3-5 on subsegment 13 (Table

1). In *C. melleus* this type of sensillum is found on all flagellar subsegments, but are most abundant on the proximal ends of subsegments 1-8, occurring as whorls of 2-8. On subsegments 9-12 they are found as a single sensillum, but there may be as many as 2 per segment; there are 2-5 on subsegment 13.

Sensilla Trichodea. There are 2 types of sensilla trichodea: blunt-tipped and sharp-tipped. The blunt-tipped trichodea are present on all the flagellar subsegments (Table 1). They are most numerous on the distal 4 subsegments. On the proximal subsegments they are arranged more or less in whorls of 1-3 for both species. On subsegments 10-13 of *C. hollensis* they usually occur in whorls of 5-6, but on some specimens there are as many as 10-15.

The sharp-tipped trichodea are situated exclusively on the distal 5 subsegments and are the most numerous sensory organs in this region (Table 1). Their shafts usually are curved at the distal ends, and on each subsegment the shafts gradually decrease in length distally. This type of sensilla trichodea gives each subsegment on which it occurs the appearance of a conical brush. The average number (≈100) of these sensilla is similar for both species.

Sensilla Basiconica. Sensilla basiconica have peg-shaped shafts and are located only on the distal 5 subsegments of the flagellum. On average they are more numerous on the antennae of *C. melleus* than *C. hollensis* (12.6 versus 9.5).

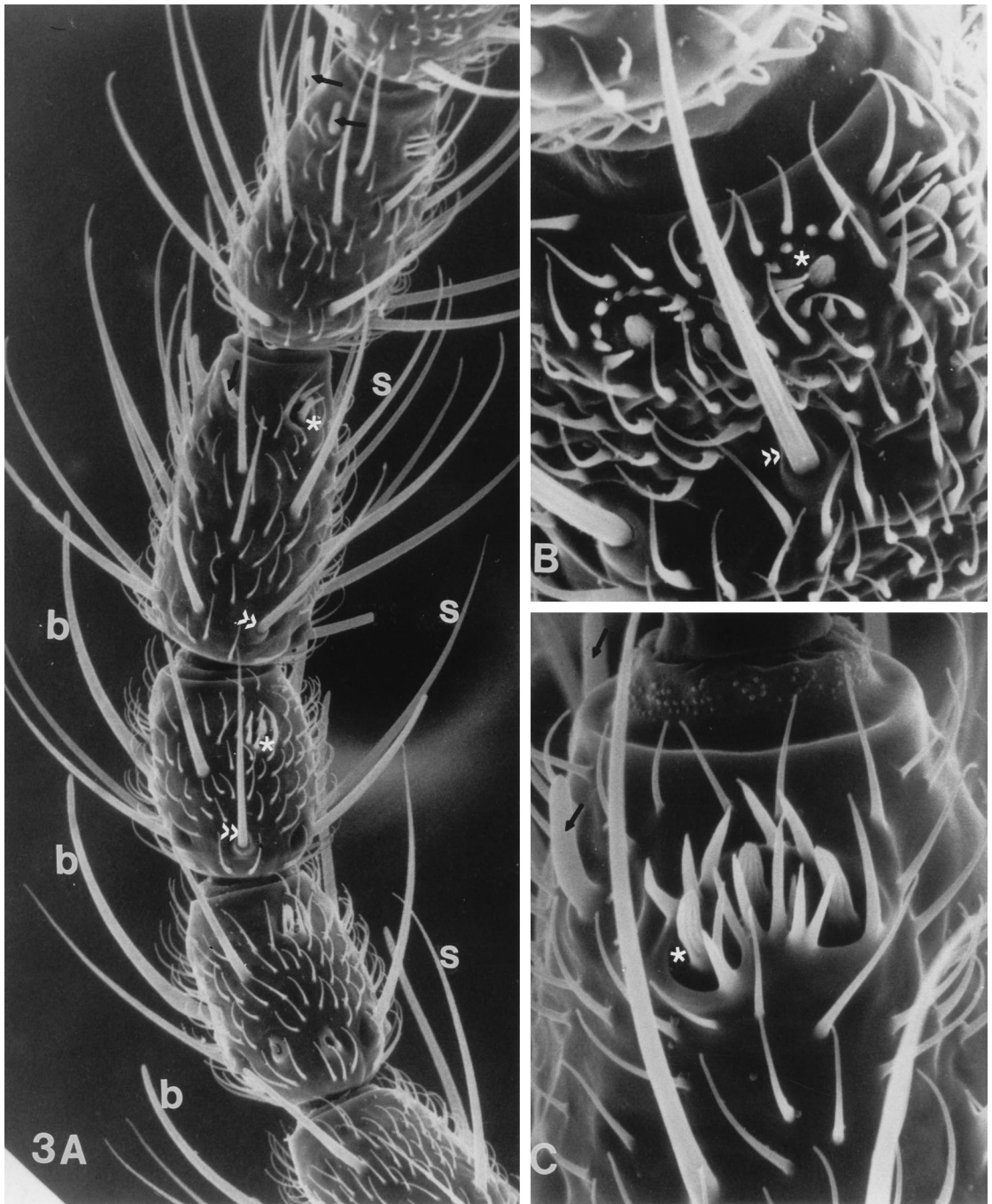


Fig. 3. (A) Scanning electron micrograph of flagellar subsegments 7-10 of *C. melleus*, each bearing a single sensory pit containing a sensillum coeloconicum (*); the other 4 types of marked sensilla are chaetica (>>), blunt-tipped (b) and sharp-tipped (s) trichodea, and basiconica (short black arrow) ($\times 2,366$). (B) The 1st flagellar subsegment of *C. hollensis* bearing 3 contiguous sensory pits containing sensilla coeloconica (*). Each pit contains 1 sensillum coeloconicum, surrounded by several microtrichia on border of pit. (C) The 12th flagellar subsegment ($\times 8,424$) of *C. melleus* bearing 3 contiguous sensory pits containing sensilla coeloconica; note the presence of sensilla basiconica marked with a solid black arrow.

Sensilla Coeloconica (Sensory Pits). Sensilla coeloconica are peg organs sunken into depressions of the body wall (Fig. 3). They appear as shallow pits

bearing a short dark hyaline peg in the middle with the margin of the pit bordered by a ring of 5-12 microtrichia. These sensilla are often referred to as

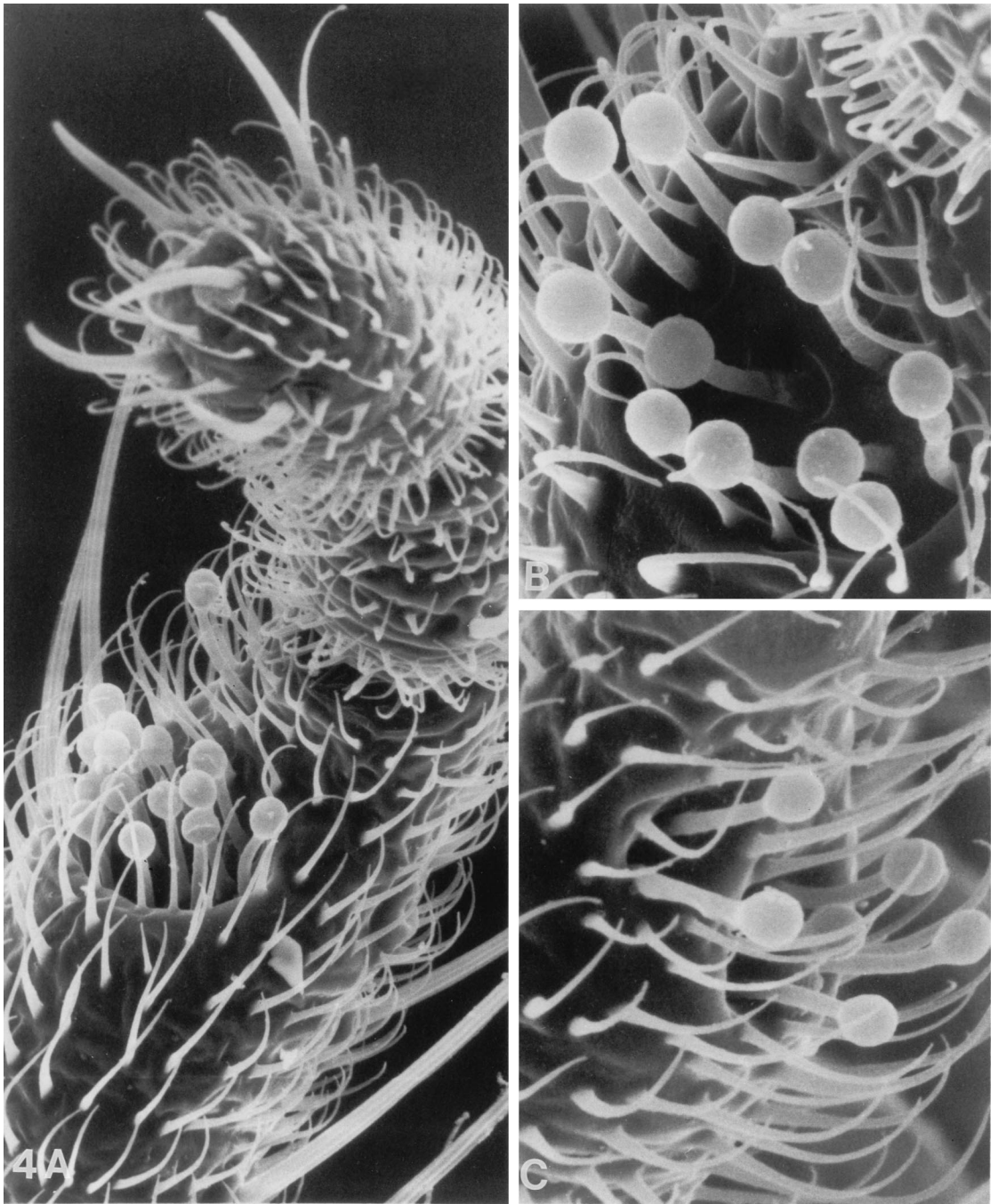


Fig. 4. Scanning electron micrographs of maxillary palps of *C. hollensis*. (A) Three distal segments of palp of female adult showing swollen 3rd segment with 1 large and 1 small palpal pit, each containing a cluster of bulb-shaped sensilla ($\times 4,509$). (B) Female palpal pit at higher magnification ($\times 7,790$) showing, shallow sunken pit with 11 bulb-shaped sensilla. (C) Portion of 3rd maxillary segment ($\times 4,140$) of a male *C. hollensis* showing 2 small pits containing 2 and 4 bulb-shaped sensilla, respectively.

olfactory pits in the biting midge literature (Jamnback 1965). The number of sensilla coeloconica varies from a single pit to 3 or 5 contiguous pits for *C. melleus* and *C. hollensis*, respectively. For *C. hollensis* these sensilla usually are found on subseg-

ments 1 and 11-13, but on some specimens they also are found on subsegments 9 or 10, or both. For *C. melleus* they are found almost always on segments 1 and 8-12; occasionally, they are found on segments 7 or 13.

Table 2. Palpal bulb-shaped sensilla arrangement and measurements (range)

| Species | ♀, ♂ (n) | Sensory pit | Mean no. | Sensilla | | |
|-------------------------------|-------------|---|----------------|--------------------|------------------|--------------------|
| | | | | Bulb | Stalk | |
| | | | | Mean diam | Mean height | Mean diam |
| <i>C. hollensis</i> | ♀ (9) | 2 separate pits or 1 single pit ≈14μ × 15μ | 10.5 (8–15) | 2.2 (2.1–2.3) | 4.2 (3.9–5.6) | 0.8 (0.75–0.81) |
| | ♂ (2) | 1 single pit~ 5μ × 7μ or 2 separate pits of unequal size, ≈10.6μ & ≈5.3μ diam | 5.5 (5–6) | 2.6 (2.1–3.1) | 4.8 (3.5–6.1) | 1.0 (0.78–1.14) |
| <i>C. melleus</i> | ♀ (23) | no single pit; sensilla arranged over entire segment in individual dual recessed sockets | 18 (13–29) | 1.5 (1.3–1.8) | 4.3 (3.5–5.0) | 0.6 (0.4–0.8) |
| | ♂ (5) | Same as ♀ | 7.8 (6–10) | 2.0 (1.99–1.97) | 5.4 (4.9–5.8) | 0.7 (0.72–0.75) |
| <i>C. furens</i> ^a | ♀ (10) | 1 single circular pit ≈ 8μ diam | (9–12) | 3.0 | 8.0 | 0.7 |
| | ♂ (10) | Same as ♀ | (4–6) | | | |
| | | | | | | |

^a Data from Chu-Wang et al. (1975).

Palpal Sensilla. The maxillary palps are 5-segmented in both sexes and species. In *C. hollensis* the 3rd segment is swollen and bears on the distal part of the medioventral surface a specialized sensory pit in which there is a scattered group of bulb-shaped sensilla (Fig. 4A). Fig. 4A and B show the arrangement and morphology of the palpal pit and individual sensilla of female *C. hollensis*. The 3rd segment has a large pit (average dimension 14 by 15 μ) with an average of 11 sensilla (range, 8–15). Fig. 4B shows a pit with 11 well-defined bulb-shaped sensilla (bulb diameter 2.2 μ, stalk height 4.2 μ) in the pit. Close examination reveals the presence of 2 smaller distinct pits within the large pit of some specimens; other specimens have only a single pit (Table 2). In both instances, the base of each sensillum is recessed in a small socket. Fig. 4C shows the 3rd palpal segment, pit and 3 bulb-shaped sensilla of male *C. hollensis*. Males have either a single pit (5 by 7 μ) or 2 separate pits of unequal size (≈10.6 μ and 5.3 μ in diameter). In both cases the mean number of bulb-shaped sensilla per maxillary palp is 5.5 (range, 5–6).

There is no pit on the 3rd segment of either sex of *C. melleus* (Fig. 5A–C) and the sensilla are arranged individually over the distal half of the segment in recessed sockets. There is a clear sexual difference in the number of sensilla located on each maxillary palp (Table 2). The female maxillary palps have 13–29 sensilla, compared with 6–10 for the males. The mean bulb diameter (1.5 versus 2.0 μ) and stalk height (4.3 versus 5.4 μ) also differ by sex (female versus male).

Discussion

This 1st detailed SEM description of the antennal and palpal sensilla of *C. melleus* and *C. hollensis* shows

that these 2 estuarine species have the same array of sense organs as *C. furens* (Chu-Wang et al. 1975). However, the number and distribution of these sensilla vary among species. On average, more sensilla chaetica (47) are found on more subsegments (1–13) of *C. melleus* than on those of *C. furens* (42; subsegments 1–8) and *C. hollensis* (31; subsegments 1–8). The distribution pattern of sensilla chaetica found on *C. furens* and *C. hollensis* is similar to that found on the antennae of female *C. paraensis* (Felippe-Bauer et al. 1989), but the pattern on female *C. melleus* is more like that on *C. impunctatus* and *C. nubeculosus* (Blackwell et al. 1992). The distribution pattern of both types of sensilla trichodea and sensilla basiconica is the same for our 3 estuarine species and *C. impunctatus* and *C. nubeculosus* (Blackwell et al. 1992). Blunt-tipped sensilla trichodea occur on all 13 subsegments. Sharp-tipped sensilla trichodea and sensilla basiconica occur on distal subsegments 9–13 only. *C. furens* has more blunt-tipped sensilla (48) than *C. hollensis* (42) or *C. melleus* (36); whereas *C. hollensis* has more sharp-tipped sensilla trichodea (100) than either *C. melleus* (97) or *C. furens* (93); *C. furens* has many more sensilla basiconica (42) than *C. melleus* (13) or *C. hollensis* (10). The subsegmental distribution of sharp-tipped sensilla trichodea and basiconica on the antennae of female *C. paraensis* is similar to these species, but Felippe-Bauer et al. (1989) found 2 types of blunt-tipped sensilla trichodea with distinct lengths, both occurring only on subsegments 1–8.

The distribution and number of sensilla coeloconica is different for all 3 estuarine species. The pattern for *C. furens* is 1, 5–8; for *C. hollensis* is most commonly, 1, 11–13, but is also found in some specimens on subsegments 9 and 10; and for *C. melleus* 1, 8–12, rarely also found on 7 or 13. Sensilla coeloconica are more

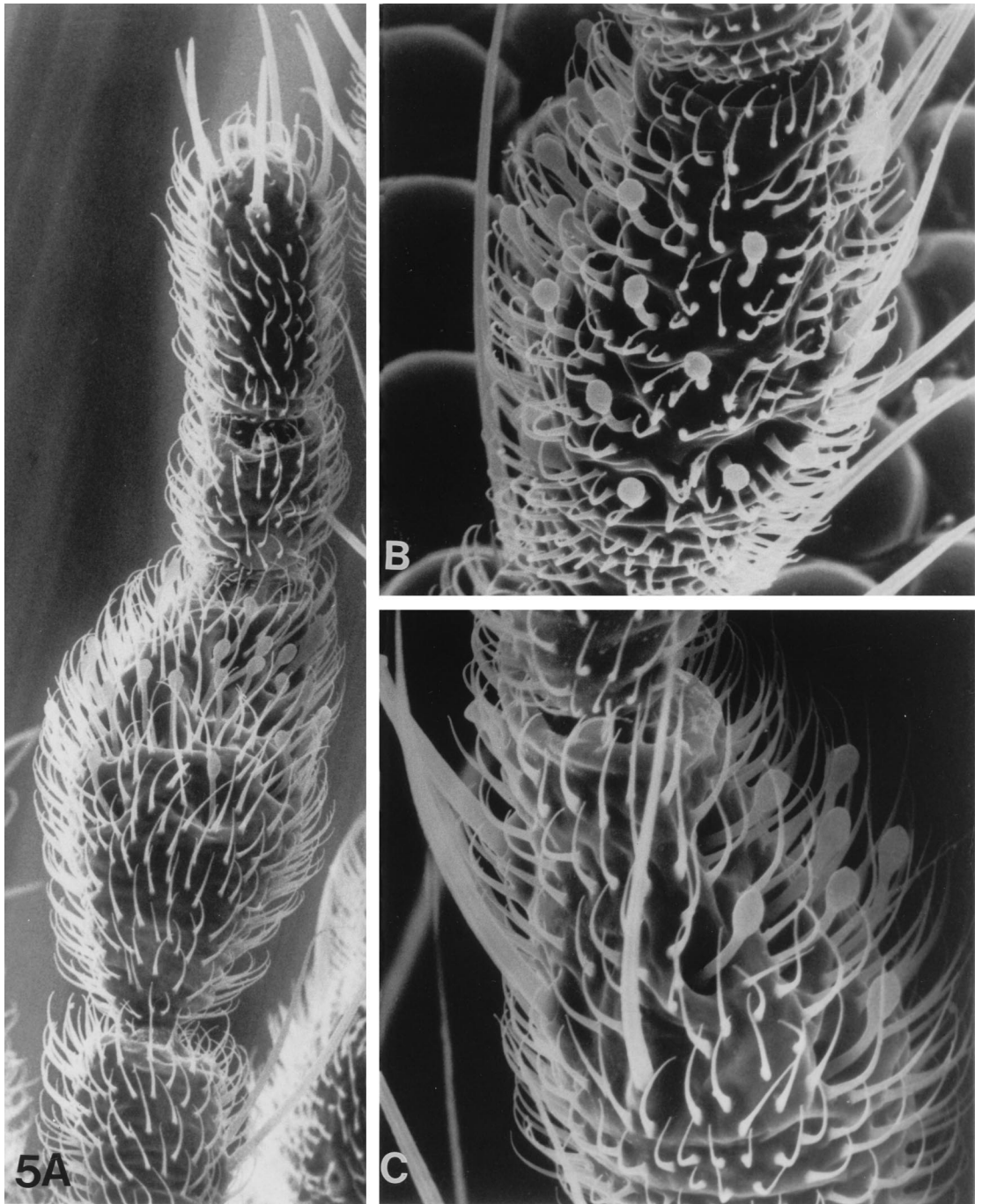


Fig. 5. Scanning electron micrographs of maxillary palp of female *C. melleus* ($\times 2,625$). (A) Three distal segments of palp of female adult showing swollen 3rd segment; 18 bulb-shaped sensilla individually distributed over distal half of 3rd segment. (B) Third segment of female at higher magnification ($\times 3,700$). (C) The 3rd segment of a male showing 7 bulb-shaped sensilla ($\times 3,998$).

abundant on *C. furens* (10); there are usually 8 on *C. hollensis* and *C. melleus*. Females of *C. paraensis* also have 8 sensilla coeloconica on subsegments 1, 6–8 (Felippe-Bauer et al. 1989). Sensilla coeloconica always occur on the distal end of subsegment 1 of both

male and female *C. impunctatus* and *C. nubeculosus* (Blackwell et al. 1992). Further coeloconic sensilla lie on subsegments 6 and 12 of female *C. impunctatus* antennae, subsegments 12 and 13 of male *C. impunctatus* antennae, subsegments 6–8 of female *C. nube-*

culosus antennae, and subsegments 7–9 of male *C. nubeculosus* antennae. In each case the number of coeloconic sensilla varies between 1 and 3 in a row.

Overall *C. furens* averaged 235 of these 5 types of sensilla per antenna per specimen, compared with 202 for *C. melleus* and 191 for *C. hollensis*. The female antennae of female *C. impunctatus* and *C. nubeculosus* have a maximum of 241 and 254, respectively, of these sensilla (Blackwell et al. 1992). The female antennal flagellum of *C. paraensis* contains ≈ 174 of these sensilla (Felippe-Bauer et al. 1989). In addition, to these 5 types of antennal sensilla, Felippe-Bauer et al. (1989) found sensilla ampullacea on subsegments 1, 2, and 13, and 4 styloconic-type sensilla on subsegment 13 of *C. paraensis*. Blackwell et al. (1992) also found sensilla ampullacea opposite sensilla coeloconica, on the distal ends of subsegments 1 and 2, but not 13, of female *C. impunctatus* and *C. nubeculosus*; these investigators did not find any styloconic-type sensilla.

The number and arrangement of bulb-shaped sensilla on the maxillary palp differs among our 3 estuarine species. In both sexes of *C. furens* there is a single circular pit (8 μ diameter) (Chu-Wang et al. 1975), compared with either 1 or 2 pits in *C. hollensis* and no pits in *C. melleus*. The size of the pit in female *C. hollensis* is almost twice the size of that in female *C. furens*. The range of bulb-shaped sensilla found on the maxillary palps of female *C. hollensis* (8–15) is similar to *C. furens* (9–12), which is less than that found on *C. melleus* (13–29). In all 3 species there is a clear sexual difference in the mean number of bulb-shaped sensilla located on each maxillary palp. Males have about half the number of bulb-shaped sensilla found on females. Rowley and Cornford (1972) hypothesized that these sensilla are used in host location and because males do not require a blood meal, they do not require as efficient an olfactory system.

The importance of the types, numbers and relative distribution of the various antennal and palpal sensilla found on biting midges has not been fully investigated. The general olfactory function of these sensilla has been inferred from their ultrastructure (Chu-Wang et al. 1975, Blackwell et al. 1992). Verification will require behavioral and electrophysiological studies. Initial studies have indicated that the number of flagellar subsegments with sensilla coeloconica (olfactory pits) and the abundance of bulb-shaped sensilla in the maxillary pits are important in host preference (Jamnback 1965, Rowley and Cornford 1972, Braverman and Hulley 1979). Jamnback (1965) showed that a number of biting midge species found in the United States known to feed preferentially on large mammals had olfactory pits on 4–6 flagellar subsegments, whereas those known to feed preferentially on birds had pits on 8–13 subsegments. Blackwell et al. (1992) stated that this hypothesis appears to be correct; the antennae of female *C. impunctatus* (mammalophagic) usually bear ≈ 7 coeloconic sensilla. Braverman and Hulley (1979) studied the morphology of 12 *Culicoides* species from southern Africa and showed that species known to prefer avian hosts had more olfactory pits and more

pit-bearing flagellar subsegments than did those known to prefer mammalian hosts. They also demonstrated that the mean number of bulb-shaped sensilla on the palpal pits were related to host preference, but that the mean number of antennal sensilla basiconica appeared to show no host relationship. Based on these previous morphological studies, *C. furens*, *C. hollensis*, and *C. melleus* would be expected to prefer mammalian hosts.

However, in a host preference study conducted by Koch and Axtell (1979), *C. hollensis* and *C. furens* were attracted to both avian and mammalian hosts. Host size and availability were major factors in host selection rather than the class of the host. Based on these data, Koch and Axtell (1979) concluded that the number of antennal olfactory pits was not necessarily an indicator of whether a species was mammalophagic or ornithophagic. Similar conclusions were reached by Tanner and Turner (1974) after studies with some species of Virginia *Culicoides* associated with forest habitats.

Additional associations have not been attempted between other biting midge sensilla and behavioral patterns. However, structurally similar sharp- and blunt-tipped sensilla trichodea occur on mosquito antennae and have been suggested to be the principal olfactory sensory organs on some species (Slifer and Brescia 1960; McIver 1969, 1971). In mosquitoes blunt-tipped sensilla trichodea mediate responses to repellents, whereas sharp-tipped setae are involved in host location (Steward and Atwood 1963). Although similar functions for these sensilla have not been identified for *Culicoides*, Blackwell et al. (1992) offered an hypothesis which suggested that the longer blunt-tipped and sharp-tipped sensilla provide an effective odor-trapping net for long-range host-derived odors. In contrast, the shorter blunt-tipped hairs might be more effective at trapping short-range, more specific odors such as those associated with nectar sources and oviposition sites.

These studies lead us to conclude that further morphological, behavioral, and electrophysiological studies are required to understand the basis of response of *Culicoides* species to particular host emanations such as octenol, and to determine how these responses relate to host preference.

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