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ANTENNAL SENSILLA AND SETAE OF *EVAGETES PARVUS* (HYMENOPTERA: POMPILIDAE)

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Abstract.—The antennae of cleptoparasitic female *Evagetes parvus* were investigated using scanning electron microscopy. Setae and sensilla placodea, corrugated conical sensilla, pit organs, sensilla campaniformia, sensilla trichodea A, B, C, D, sensilla basiconica and sensilla spatulata were located, described and illustrated. The sensilla of *E. parvus* most clearly resemble those of two other pompilids, *Anoplius tenebrosus* and *A. viaticus*; however, spatulate sensilla were not found in either of these species. Two large zones on the flagellum of *E. parvus* are dominated by corrugated conical sensilla and placoid sensilla, respectively. The former are found only on the flattened ventral surfaces of flagellomeres 2–10, whereas the latter surround these sensilla and occur also on flagellomere 1. The corrugated conical sensilla in conjunction with the sensilla basiconica and sensilla spatulata are probably used in locating the host (buried spider) because of their ventral position on the antennal surface and their morphology.

Key Words: cleptoparasite, chemoreception, mechanoreception, proprioception

Members of the genus *Evagetes* are cleptoparasitic, ovipositing on spiders which have been captured by other genera of Pompilidae. The most distinguishing characteristic of the genus is the short antennae which are thickened and somewhat flattened ventrally in the female (Evans 1950). Females are usually observed walking on sandy surfaces while tapping the soil with their antennae, or stalking nesting pompilid wasps. Female *Evagetes* frequently enter nests being provisioned by other pompilids either before or after closure. Such a wasp is able to detect a buried spider by some clue, most likely olfactory and/or tactile, whereupon she unearths the paralyzed prey, destroys the pompilid's egg, and lays her own egg on the prey (Evans and West Eberhard 1970). The subsequent closure by a female *Evagetes* may be thorough or loose. Such cleptoparasitic behavior has been noted in *E. parvus* (Cresson) by Evans (1950) and Evans and Yoshimoto (1962). Similar activities of other species of *Evagetes* have been reported by Richards and Hamm (1939) and Evans et al. (1953) and summarized by Krombein (1979).

While searching for the buried paralyzed spider, *Evagetes* females extend their antennae outward in a stiff "V" and rapidly tap the ground with the ventrally flattened surfaces. The particular sensory sensilla used in detecting the spider are probably located on the ventral surfaces of the antennae. The intent of this paper was to examine and identify the antennal sensilla and setae of female *Evagetes parvus*, using SEM, and to attempt to determine which sensilla are used to locate the buried prey.

Methods and Materials

Female *E. parvus* were collected from a sand pit near Auburn, Cayuga County, New York, during the summers of 1981 and 1982. They were kept refrigerated in ventilated glass vials until used. Preparation consisted of excising either the antennae or heads, and immersing these in methylene chloride for two days to dissolve the waxy layer. Two pairs of antennae were then mounted with silver paint, and sputter-coated in a Technics sputter-coater with ionized gold-palladium alloy. Another specimen, kept in methylene chloride, was mounted on a stud with silver paint and coated with gold in a Kinney SC2 high vacuum metal evaporator.

One specimen was air-dried in an attempt to see if there were any differences in the final appearances of the sensilla. This specimen was then mounted on double sticky tape, grounded with silver paint, and sputter-coated with gold-palladium alloy. Specimens were then viewed on an ETEC Autoscan scanning electron micropscope, at accelerating voltages of 10 and 20 KV. There were no differences found in antennal features between this method and the first one used.

The nomenclature used to describe the various sensilla has been modified from Ågren (1977) and Alm and Kurczewski (1982).

Results

Female *Evagetes parvus* have filiform antennae, ca. 2.6 mm long, which are composed of scape, pedicel, and flagellum with flagellomeres designated 1–10 proximally to distally. The ventral surface is in contact with the substrate during host-searching, is flattened from flagellomere 2–10, and is highly sensory. The scape, pedicel, and flagellomere 1 are mainly setaceous. In describing the sensilla we refer to the antennae

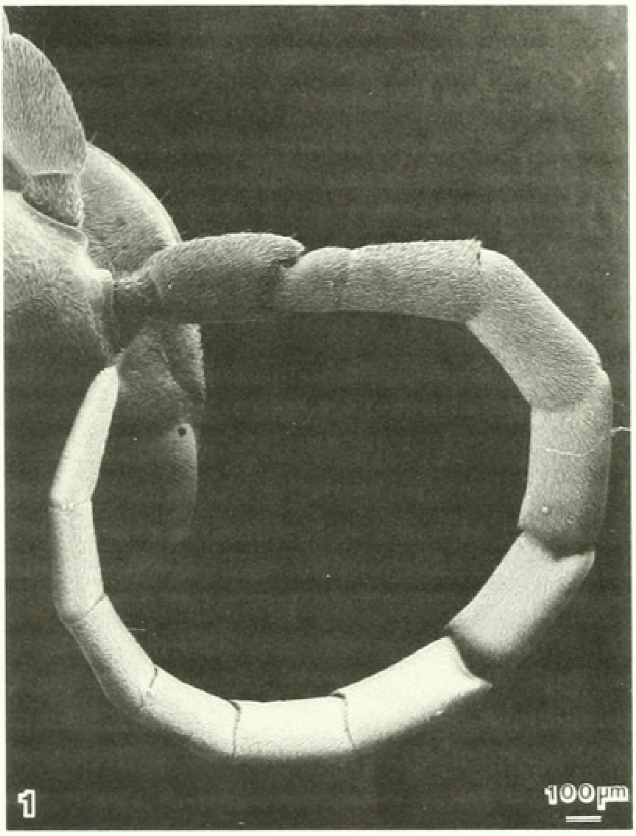

Fig. 1. Antenna of female *Evagetes parvus*, as viewed dorsally, showing the curled, resting position typical of many female Pompilidae.

being held horizontally in front of the wasp as during host-searching. When the antennae are curled back in the resting position (Fig. 1), the medial and ventral surfaces are actually facing outward away from the insect. The sensilla found are described below in order of their prominence and complexity except for s. spatulata which are described near the end because they resemble s. basiconica.

Sensilla

Sensilla placodea: A placoid sensillum is elongate, convex and has a membranous fold encircling its base (Figs. 2A, B). It is oriented parallel to the long axis of the antenna, and its dimensions are 5×15 μm. Placoid sensilla are abundant, extending from a small area on flagellomere 1 along the sides and over most of the dorsum of the remaining flagellum. They are spaced evenly and num-

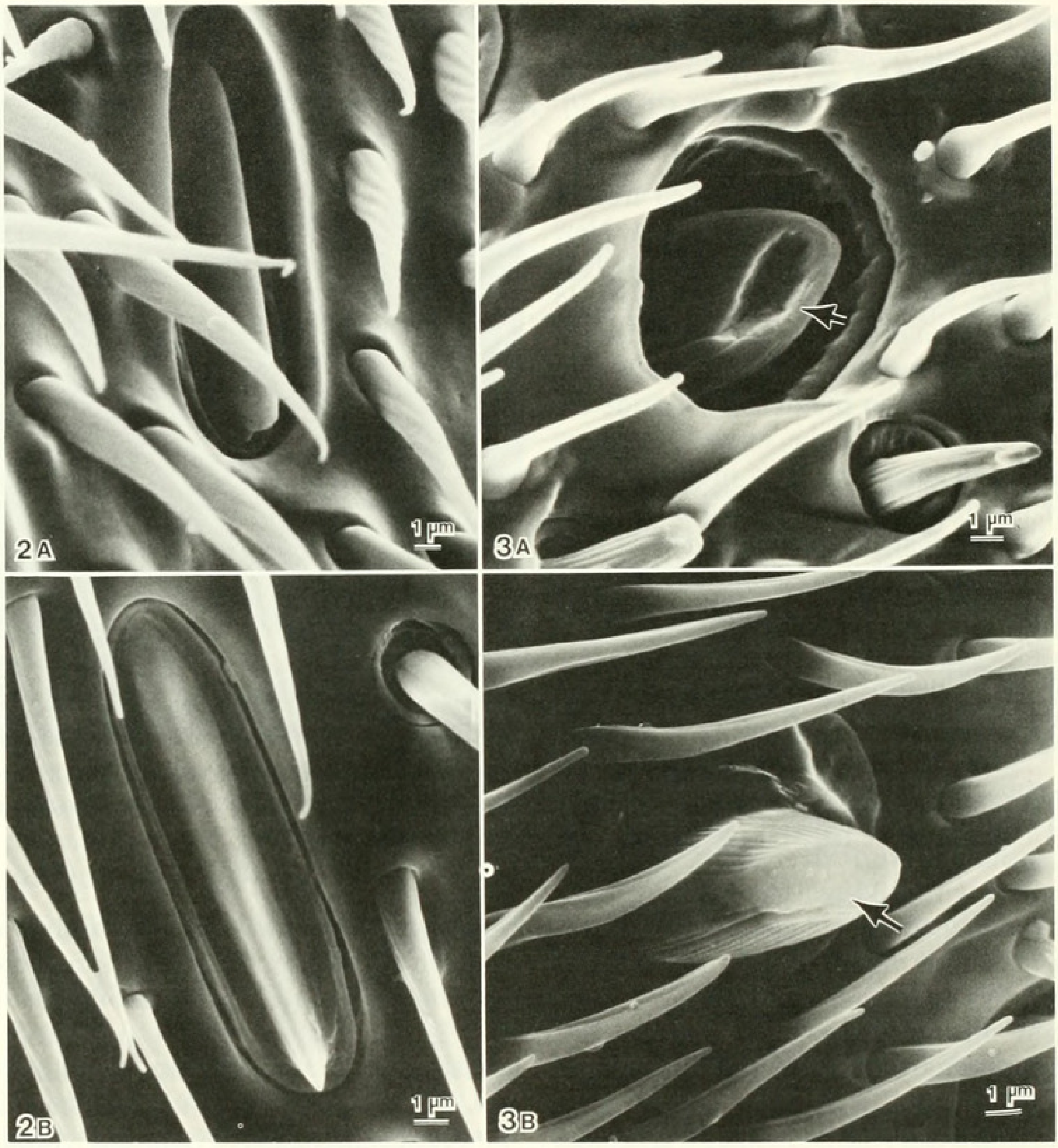

Fig. 2. A, Sensillum placodeum, flagellomere 8, sunken into cavity, with distal end projecting above antennal surface. B, Sensillum placodeum, dorsal view, showing membranous fold around base, flagellomere 4.

Fig. 3. A, Corrugated conical sensillum with subterminal furrow (arrow), flagellomere 3. B, Corrugated conical sensillum showing exudate covering furrow (arrow), flagellomere 6.

ber ca. 17 in a column down the length of a typical flagellomere.

Corrugated conical sensilla: Corrugated conical sensilla are stout, truncate receptors (Figs. 3A, B) which lean distally and are cushioned against the cuticle by a thick membrane. Numerous grooves extend from base to apex. The tip may be indented (Fig. 3A) or covered with an exudate (Fig. 3B). The sensillum is ca. 10 μm long and 5 μm wide at the base. It is found abundantly only on the flattened ventral surface of the flagellum. These sensilla form a small triangle on the underside of flagellomere 2, continue along the entire ventral surface of the flagellum, and end in a triangular area on the underside of flagellomere 10.

Pit organs: These hollowed pits resemble domes with holes in the centers (Figs. 4A, B). A smooth peg may be visible in the bot-

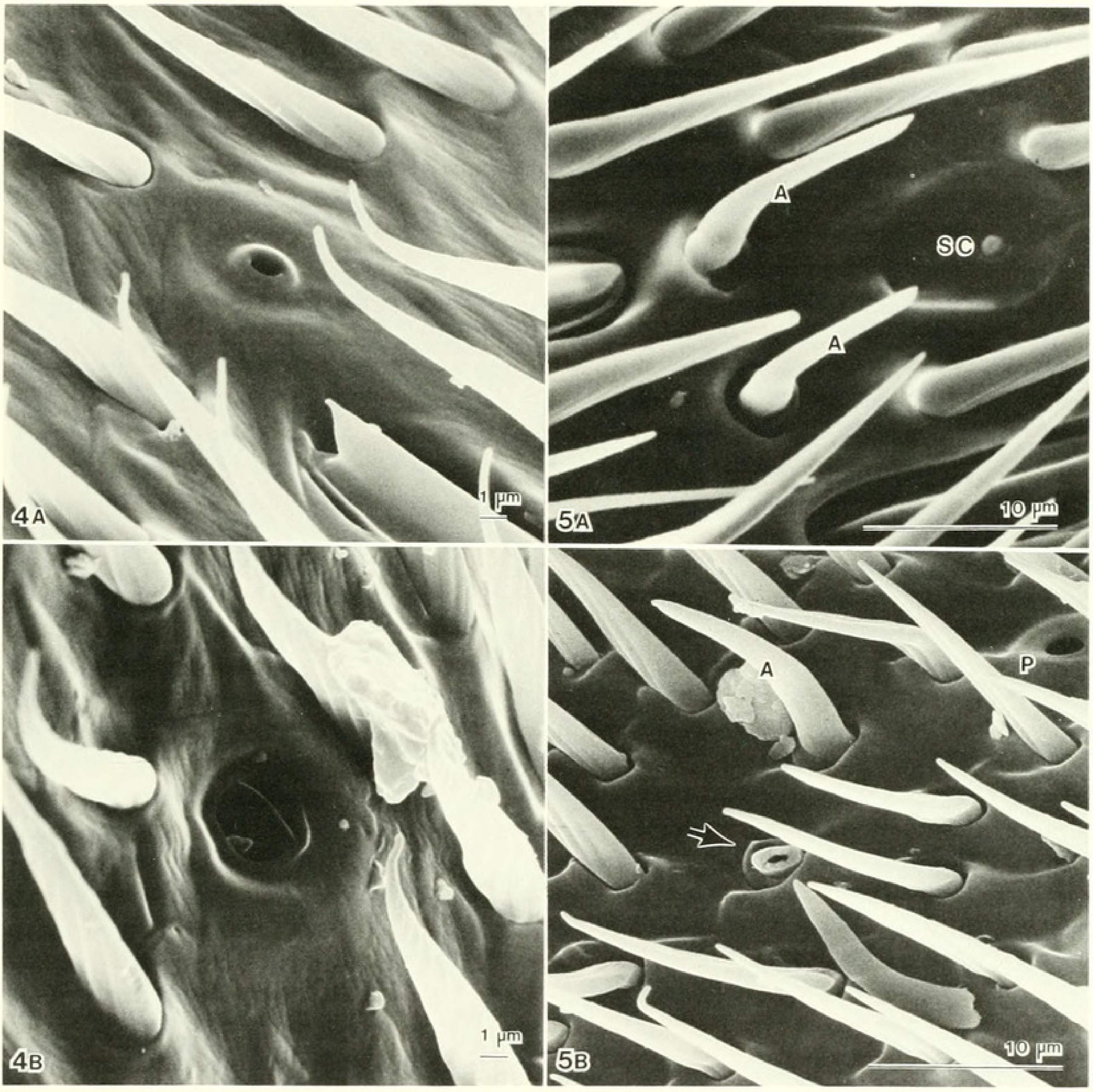

Fig. 4. A, Small pit organ, distal end, flagellomere 7. B, Large pit organ, revealing peg within pit, dorsal surface, flagellomere 10. Irregular surface may be due to fixation.

Fig. 5. A, Sensilla campaniformia (SC) and s. trichodea A (A) in asymmetrical sockets, flagellomere 1. B, Broken sensillum trichodeum A, showing hollow center (arrow), flagellomere 5. p = pit organ.

tom of the pit (Fig. 4B). Two types of pit organs are distinguished by the size of the central aperture, one being ca. 1 µm and the other, 3 µm in diameter (Figs. 4A, B). Pit organs are relatively few in number, varying from 2 to 9 per flagellomere. They are found in clusters on the medial and lateral surfaces on the proximal half of the flagellum. Toward the distal end of the flagellum the clusters are placed dorsally.

Sensilla campaniformia: This receptor has a shallow circular depression with a central papilla (Fig. 5A), is oval in shape, and has a diameter of ca. 6 × 10 µm. Campaniform sensilla occur only on the flagellum, their greatest concentration being a group of 5–8 on the ventrolateral surface of flagellomere 1. They occur in small clusters at the middle and distal ends of the remaining flagellomeres.

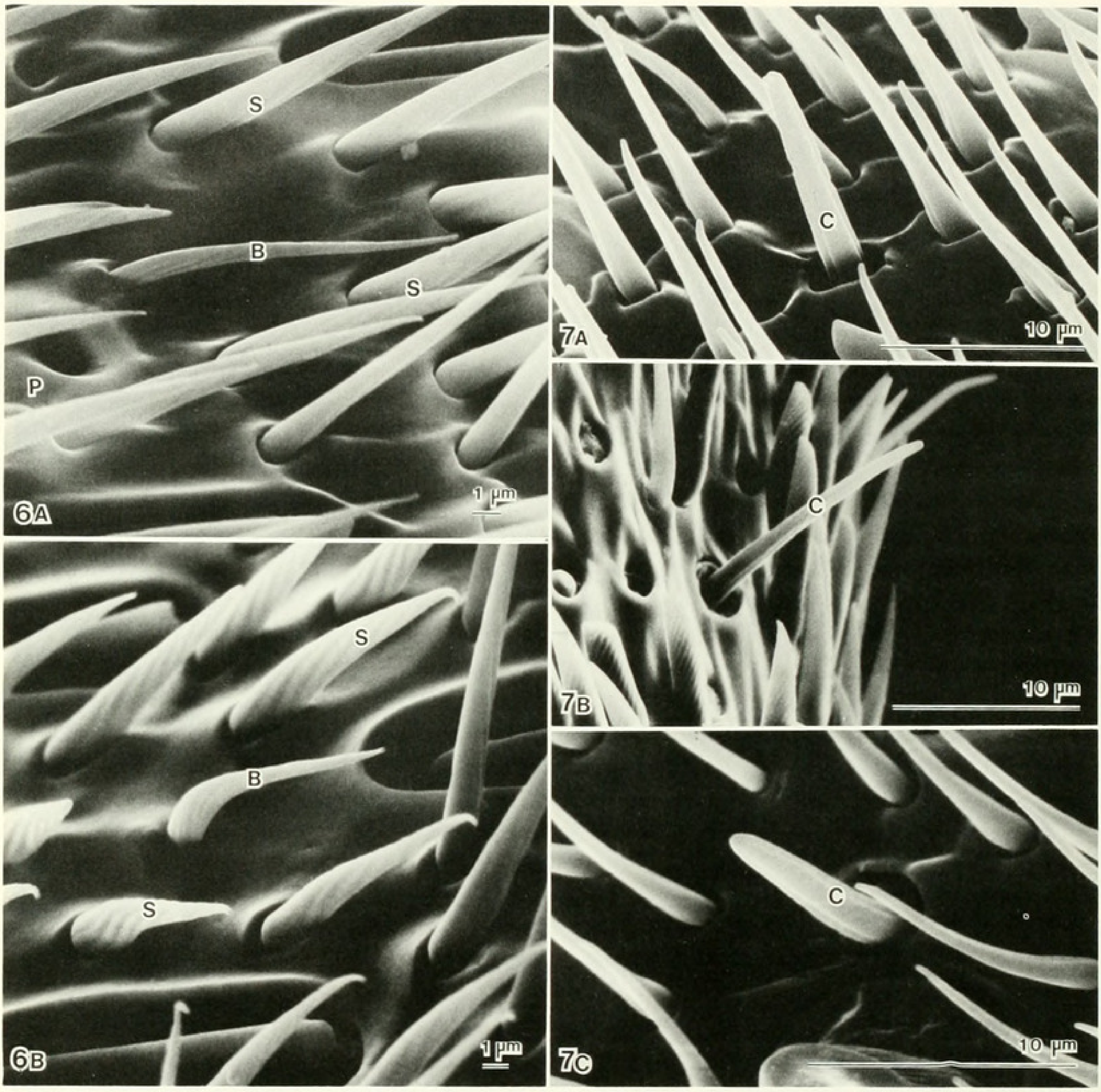

Fig. 6. A, Sensillum trichodeum B (B), flagellomere 8. p = pit organ S = setae. B, Sensillum trichodeum B (B) with heavy sculpturing, flagellomere 8. S = setae.

Fig. 7. A, Medium-length sensillum trichodeum C (C), typical form, with sunken socket, flagellomere 3. B, Long sensillum trichodeum C (C) with raised socket, ventral surface, flagellomere 1. C, Short sensillum trichodeum C (C) among corrugated conical sensilla, flagellomere 3.

Sensilla trichodea A: These hairs have abrupt tips, are ca. 12 μm long (Fig. 5A), and sit in asymmetrical sockets. The base is large and bulbous and the thick shaft bends acutely at about a 70° angle toward the distal end of the antenna. The broken sensillum in Fig. 5B shows that s. trichodea A are hollow. Trichodea A occur in patches down the center of the lateral surfaces of flagellomeres 2–9 and are scattered on the medial surfaces of flagellomeres 3–10.

Sensilla trichodea B: These slender hairs, ca. 13 μm long, taper gradually to a point, and have no visible socket at the base (Fig. 6A). Trichodea B lie parallel to the antenna and point distally. This sensillum is thinner than surrounding setae, but is similar in shape and sculpture to them. The sensillum in Fig. 6B is only 9 μm long and is scarce on the dorsum of the antenna. The sensillum shown in Fig. 6A is most dense in occurrence laterally on the flagellum and is

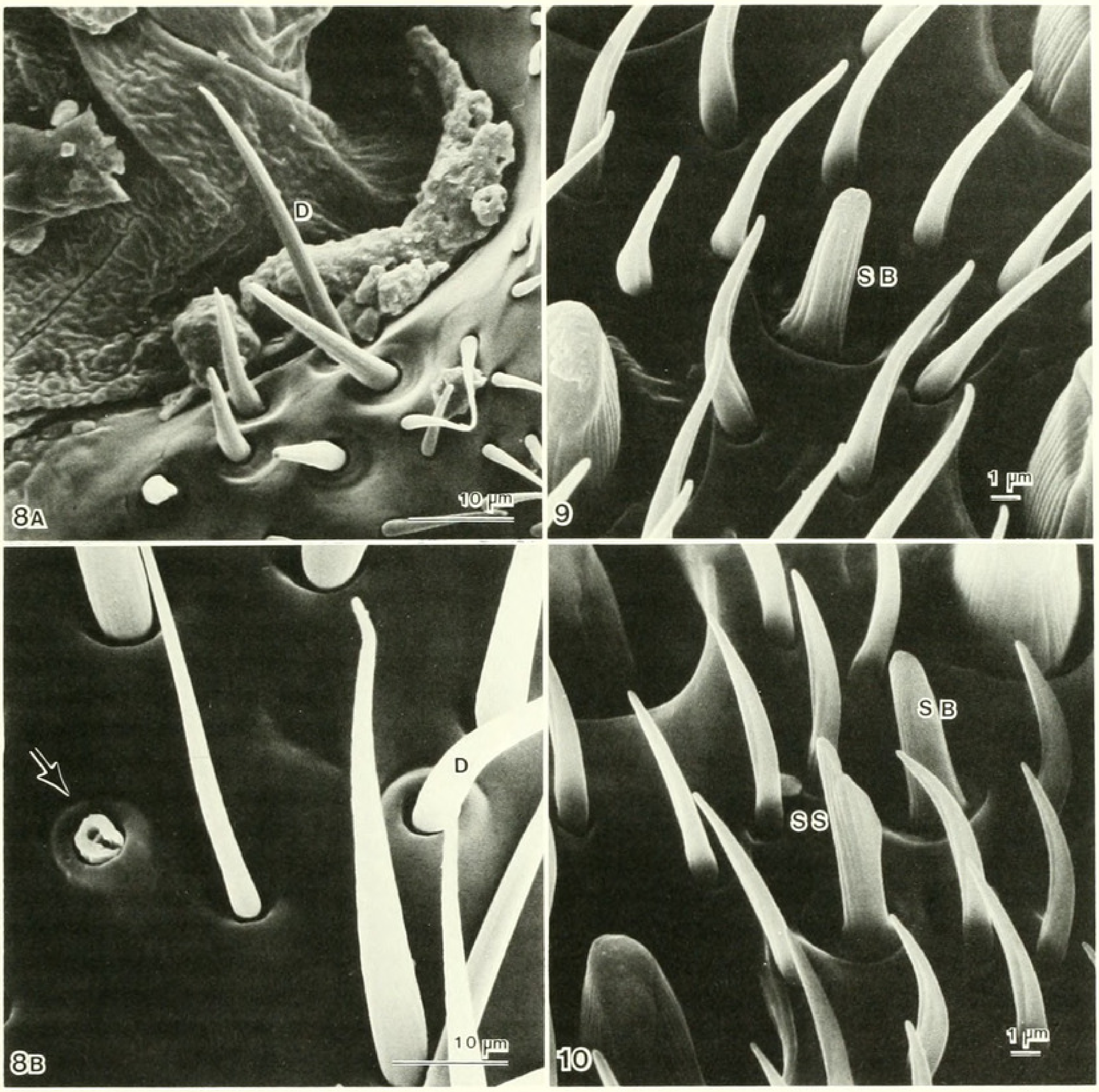

Fig. 8. A, Group of sensilla trichodea D (D), proximal end of scape. B, Broken sensillum trichodeum D, with hollow double chamber (arrow), pedicel.

Fig. 9. Sensillum basiconicum (SB), proximally set in socket, flagellomere 3.

Fig. 10. Sensillum spatulatum (SS) next to s. basiconicum (SB), flagellomere 6.

spaced evenly. Only one or two trichodea B are seen on the dorsum of the scape and pedicel.

Sensilla trichodea C: This slender, hair-like sensillum (Figs. 7A, B, C) has a blunt tip and 4–5 faint vertical furrows running from base to tip. The flexible socket has a circular, membranous collar which may be depressed or elevated. This sensillum is straight or curved slightly, 5–25 μm long, and stands nearly perpendicular to the antennal surface. Sensilla trichodea C are located on all of the flagellomeres: the longest at the distal ends, the shortest on the ventral surfaces, and medium-length ones in indistinct, widely-spaced rings.

Sensilla trichodea D: Sensilla trichodea D are similar to trichodea C, the difference being a ring around the base of the hair in trichodea D (Figs. 8A, B). The longest sensilla, 50 μm long, are located near the distal ends of the scape and pedicel. The broken trichodeum D in Fig. 8B shows a distinct double chamber internally.

Sensilla basiconica: These pegs are ca. 6 μm high, straight and stout, with a blunt, almost flat, apex (Figs. 9, 10). There are 11–12 vertical grooves on each sensillum. The socket is large, round, and rarely depressed, with the sensillum placed in the proximal side of the socket. Sensilla basiconica are distributed on the flattened ventral surface of the flagellum.

Sensilla spatulata: This unusual fan-shaped sensillum (Fig. 10) is oriented with the concave face of the fan directed away from the antennal surface. It has a large round socket and is ca. 8 μm long. It is found scattered widely on the ventral surface among the corrugated conical sensilla.

Setae.—The setae are highly variable in size and shape, commonly long and straight, smooth or fluted, and not innervated (Fig. 11A). On the extreme dorsal surface of the antenna they are short, thick, and deeply grooved (Fig. 11B). On the distal half of the flagellum the setae occur among the corrugated conical sensilla and are broadly saber-shaped with deep grooves (Fig. 11C). The setae at the antennal tip are relatively long, broad apically, and longitudinally grooved (Fig. 11D).

Sensillar zones and interrelationships.—Two large zones on the flagellum are dominated by corrugated conical sensilla and placoid sensilla, respectively (Fig. 12). The corrugated conical sensilla are found only on the flattened ventral surfaces of flagellomeres 2–10. The placoid sensilla surround the corrugated conical sensilla, extending from flagellomeres 1–10. Each zone has a characteristic sensillar composition. Sensilla basiconica and s. spatulata are distributed among the corrugated conical sensilla (Fig. 13). Pit organs, s. campaniformia, and s. trichodea A are found among the placoid sensilla (Fig. 14). The pit organs and s. campaniformia are coincidentally dispersed in two longitudinal bands which border the sides of the corrugated conical sensillar zone. There are 2–4 of each type per band per segment. On the distal half of the flagellum the two bands gradually merge dorsally into one broad band. In addition there are two specialized sensory spots. There is a concentration of 5–8 campaniform sensilla on the ventrolateral surface of flagellomere 1 within the triangular patch of placoid sensilla. There is a group of 7–9 pit organs on the medial surface of flagellomere 2.

The majority of s. trichodea A is concentrated along the border of the corrugated conical sensillar zone with the remainder widely dispersed on the dorsum of the flagellum. Sensilla trichodea D are found in small groups on the scape and pedicel, whereas s. trichodea C are evenly distributed over the entire flagellum. The last third of the terminal flagellomere is devoid of s. placodea and corrugated conical sensilla, but has an abundance of s. trichodea B and C.

Discussion

In Hymenoptera, placoid sensilla are abundant (Slifer 1970) and are thought generally to be olfactory organs (Schneider 1964). In female *Evagetes parvus* they are distributed evenly and densely in a zone directed dorsad and along both sides of most of the flagellum. The sensilla placodea of female *E. parvus* are nearly identical to those of females of the pompilids *Anoplius viaticus* (L.) and *A. tenebrosus* (Cresson) (Walther 1979, Alm and Kurczewski 1982), are smooth-walled, project from a sunken pit above the antennal surface, and are moderately elongate. In addition, s. placodea of *A. viaticus* end in a point (Walther 1979). Shapes of placoid sensilla vary within Hymenoptera. Compared to those of *E. parvus,* placoid sensilla of Braconidae and Ichneumonidae are more elongate and often extend above the antennal surface at their distal ends. In Vespidae, placoid sensilla are shorter, flatter on the surface (Callahan 1970), and similar to those of Pompilidae in size and arrangement. Higher Apoidea

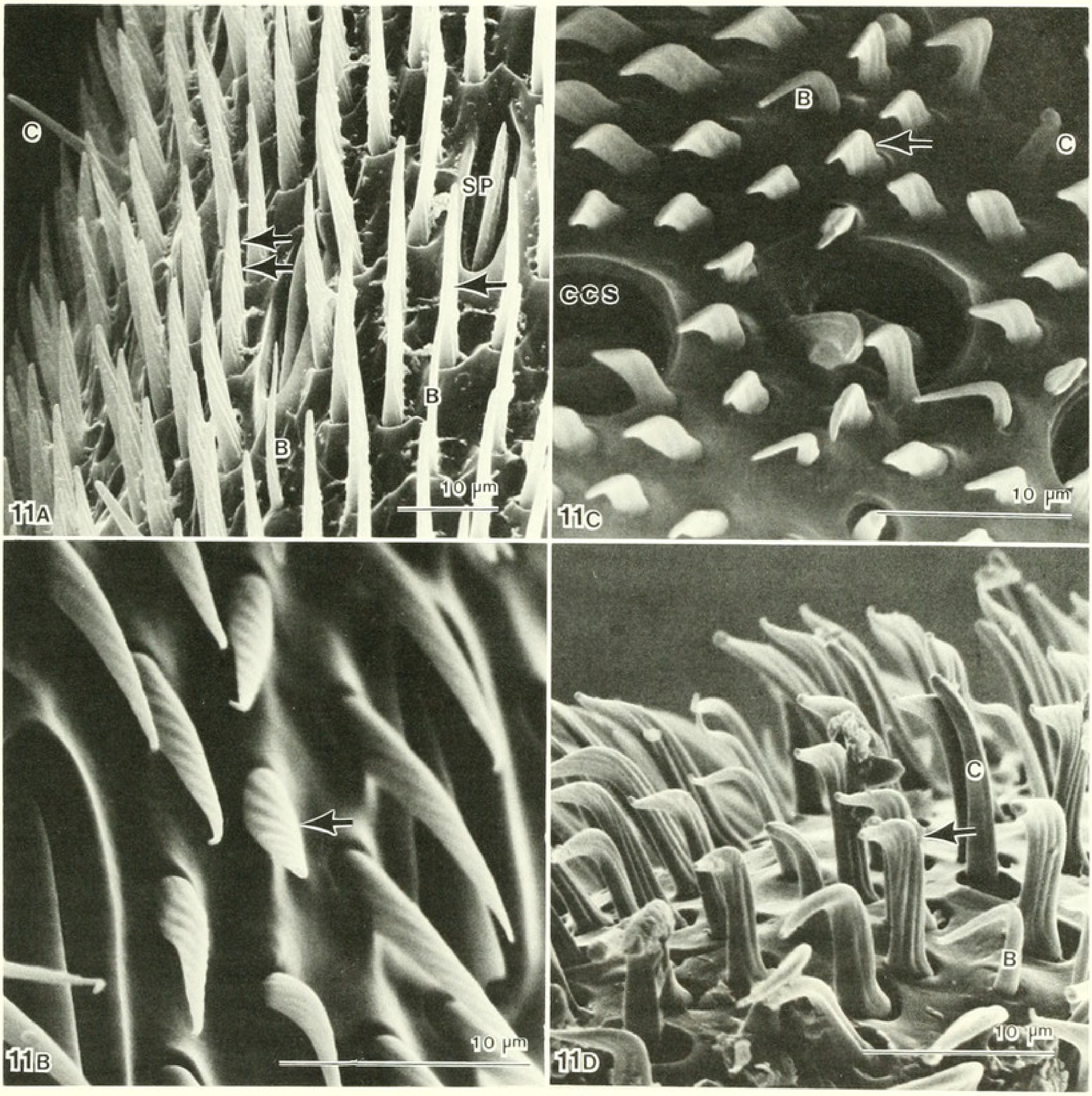

Fig. 11. A, Long and straight setae, both smooth (single arrow) and fluted (double arrow) types, flagellomere 10. B = s. trichodeum B; C = s. trichodeum C; SP = s. placodeum. B, Short, thick, spiralled seta (arrow), dorsum, flagellomere 8. C, Grooved, saber-shaped seta (arrow), ventral surface, flagellomere 10. B = s. trichodeum B; C = s. trichodeum C; CCS = corrugated conical sensillum. D, Thick, curved seta (arrow), tip of antenna. B = s. trichodeum B; C = s. trichodeum C.

have numerous circular and flat placoid sensilla (Slifer and Sekhon 1960, Dietz and Humphreys 1971, Ågren 1977, 1978). Based upon the presence of numerous small pores, Norton and Vinson (1974) suggested that elongate s. placodea of Ichneumonidae and Braconidae are chemoreceptors. Kaissling and Renner (1968) showed electrophysiologically that, in both sexes of *Apis mellifera* L., this sensillum was stimulated by the queen substance and the scent of Nasanov's gland.

The corrugated conical sensilla of *E. parvus* closely resemble those of *Anoplius viaticus* (described as s. basiconica P1) (Walther 1979) and *A. tenebrosus* (Alm and Kurczewski 1982). Callahan (1970) coined the term "conical" for this type of sensillum in the vespids *Polistes metricus* Say and *P. annularis* (L.). Those of *Polistes* species have

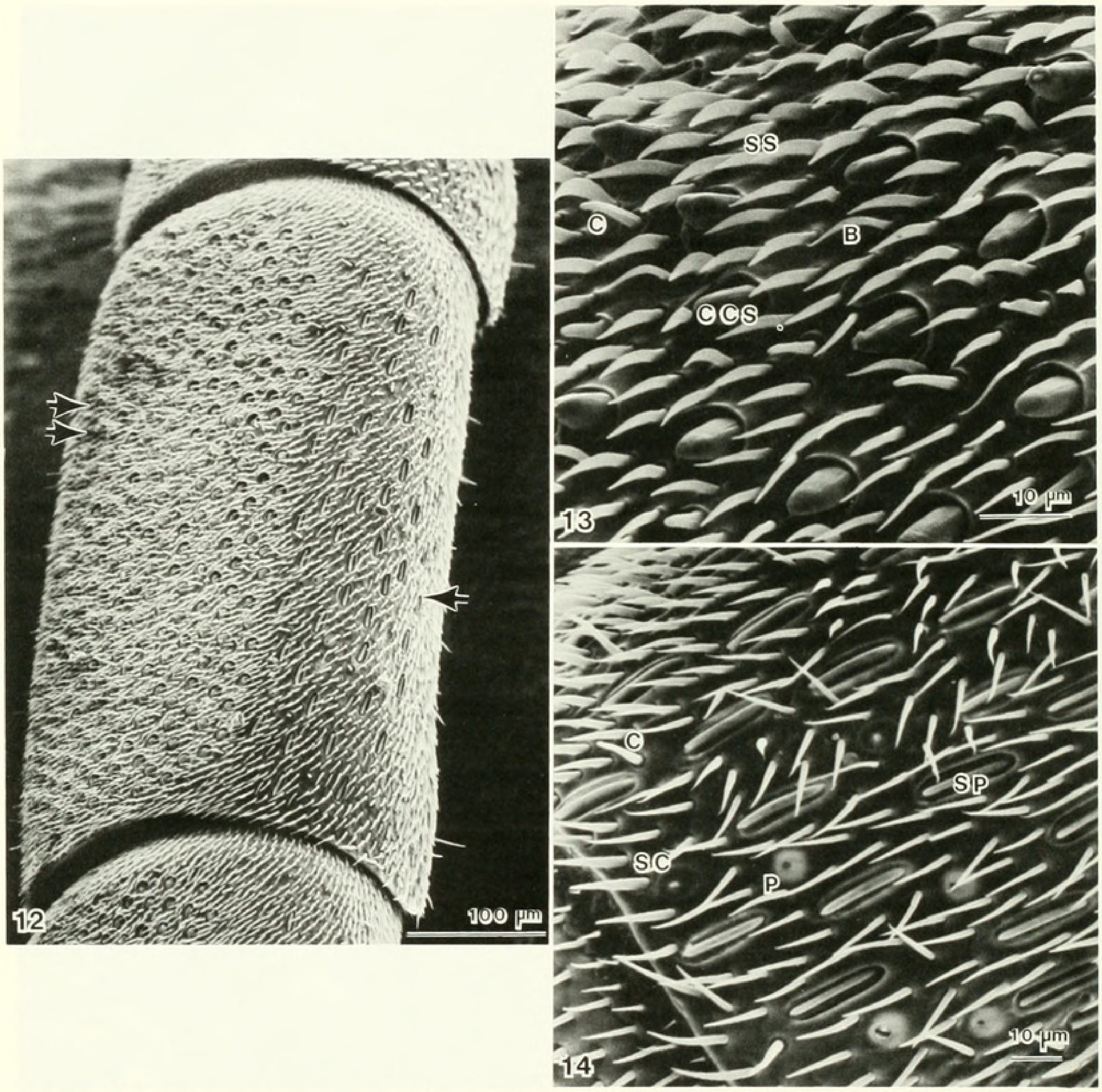

Fig. 12. Medioventral surface of flagellomere 7, showing areas containing sensilla placodea (single arrow) and corrugated conical sensilla (double arrow).

Fig. 13. Zone dominated by corrugated conical sensilla (ccs), containing s. basiconica, s. spatulata (ss), and s. trichodea C (C). B = s. trichodea B.

Fig. 14. Zone dominated by sensilla placodea (sp), containing s. campaniformia (sc), pit organs (p), and s. trichodeum C (C).

a distinct terminal pore, while those of *Anoplius viaticus* and *A. tenebrosus* (Walther 1979, Alm and Kurczewski 1982) and *E. parvus* have a deep furrow which probably indicates a terminal pore. Alm and Kurczewski (1982) reported that Kaissling and Klein (personal communication) found these sensilla to be reminiscent of gustatory bristles.

Alm and Kurczewski (1982) noted that these sensilla were found only on the antennae of female *Anoplius tenebrosus,* and Walther (1979) found the same for females of *A. viaticus.* In *E. parvus* females the corrugated conical sensilla may be used to detect buried, paralyzed spiders. These sensilla are abundant on the ventral antennal surface and their morphology suggests that they are gustatory. The corrugated conical sensilla may receive a chemical residue or heavy odor molecule from buried prey or from pompilid-manipulated sand particles, and this provides the impetus for the wasp to unearth the spider. The broad, flattened apex provides a large surface area for chemoreception. There are no long sensilla or setae on the flattened ventral surface of the antenna of *E. parvus,* thus allowing the corrugated conical sensilla to contact the ground surface without interference.

The pit organs of *Evagetes parvus* resemble those of *Anoplius viaticus* and *A. tenebrosus* (Walther 1979, Alm and Kurczewski 1982), Colletidae (Ågren 1977), and Andrenidae (Ågren 1978). They appear as different-sized apertures through which the largest reveals an internal peg. They are similar to the s. ampullaceae and s. coeloconica of *Apis mellifera* which Dietz and Humphreys (1971) differentiated as "smaller" and "larger" pores, respectively. Altner and Prillinger (1980) reported that s. coeloconica are associated with chemo-, thermo-, or hygroreception. In both *E. parvus* and *A. mellifera* (Esslen and Kaissling 1976) the pit organs lie in a zone along the lateral and medial surfaces of the antenna. In *E. parvus* there are two different-sized and shaped apertures, indicating perhaps two functions.

Campaniform sensilla have a flexible socket which, when distorted, exerts pressure on an internal mechanoreceptor. They therefore act as proprioceptors responding to exocuticular stresses. These sensilla are frequently concentrated near joints or on structures subject to cuticular distortion (McIver 1975). In *E. parvus* they are found typically in groups of 1–4 at the middle and distal parts of the flagellomeres in close association with the pit organs located on the medial and lateral surfaces of the flagellum, at which points they would be effective as proprioceptors. The antennal musculature extends only to the first segment of the flagellum, and this might explain the rather high number located on flagellomere 1. Sensilla campaniformia on the antennae of Colletidae (Ågren 1977) and *Apis mellifera* (Dietz and Humphreys 1971, Esslen and Kaissling 1976) have patterns of distribution similar to those of *E. parvus,* but structurally have a more pronounced central node. The campaniform sensilla of *Anoplius tenebrosus* (Alm and Kurczewski 1982) are similar in structure and distribution to those of *E. parvus* but Walther (1979) described s. campaniformia of *A. viaticus* to be distributed singly, not in groups.

The s. trichodeum A of *Evagetes parvus* looks similar to the s. trichodeum A 1 of *Anoplius tenebrosus* (Alm and Kurczewski 1982), trichodeum A of *Prosopis communis* (Nylander) (Colletidae) (Ågren 1977), and the sicula-type sensilla of *Odontomachus ruginodis* (Wheeler) (Formicidae) (Callahan 1975). They bend sharply over the antennal surface, and are broadest along the axis perpendicular to the surface. Sensilla trichodea A are distributed mainly on the lateral surface of the flagellum in *E. parvus* and *A. tenebrosus* (Alm and Kurczewski 1982). The trichodeum A sensillum of *E. parvus* has an asymmetrical socket which appears to be flexible in only one plane or direction. The hole in the center of the broken sensillum (Fig. 5b) indicates a chemoreceptor with a sensory dendrite extending the length of the hair-like sensillum. Although pores were not seen on the s. trichodea A of *E. parvus* the sensillum, because of its location, comes into contact with many different substances and substrates and may function as a chemoreceptor.

The thin, curved s. trichodea B are evenly distributed around the flagellum of *E. parvus.* They are usually faintly grooved but become thickened and deeply grooved on the dorsum and among the thick and spiralled setae. The s. trichodea B of *E. parvus* have no visible articulating membrane and, therefore, are probably not mechanoreceptors.

The s. trichodea C of *E. parvus* appear identical to the s. basiconica of *Anoplius* *tenebrosus* (Alm and Kurczewski 1982) and the s. chaetica of *Apis mellifera* (Whitehead and Larson 1976). Because they extend above the other sensilla, the long trichodea C at the distal end of each flagellomere may tactilely sense the adjacent segment.

There are few s. trichodea D in *E. parvus* and these are found on the scape and pedicel. They resemble the s. trichodea C, except that they have a ring of cuticle surrounding the base, rather than a broad open socket. The collar forms a narrow socket which may or may not be flexible. The double chamber observed in the broken sensillum (Fig. 8b) indicates the presence of a mechanoreceptor and a chemoreceptor, although it would be difficult to explain why a sensillum located only on the segments closest to the head would be chemosensory.

The sensillum basiconicum of *E. parvus* is stout, blunt, grooved longitudinally, and set into a broad and flattened socket. The basiconic pegs are interspersed among the corrugated conical sensilla on the ventral surface of the flagellum. Here they come into contact with, or close to, surfaces or objects and therefore may be mechano- and/or chemoreceptive.

The sensillum spatulatum has not been described in Hymenoptera. The term "spatulata" was derived from its peculiar shape and a similar sensillum described by Callahan (1975). This sensillum has a cylindrical base and the distal half fans out into a lightly grooved, concave shell. The socket is broad and flattened and nearly indistinguishable from the socket of a sensillum basiconicum. The s. spatulata occur infrequently within the corrugated conical zone. Based on the broad surface area, it is likely that this sensillum is a chemoreceptor.

Acknowledgments

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