Entomological Science, 2000, 3(3): 499–510

Cleptoparasitic Behavior and Flagellar Sensilla of *Poecilagenia sculpturata* (Hymenoptera: Pompilidae)

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Abstract. Records of specimens suggesting cleptoparasitism of *Poecilagenia sculpturata* (Kohl) on *Auplopus carbonarius* (Scopoli) are reviewed, and the cleptoparasitic behavior of this species is described. In her searching behavior, female *P. sculpturata* repeatedly uses the antennae by applying them to the substrate near where other pompilids are nesting. The flagellar sensilla of this species are observed by SEM, and the following types of sensilla are found: sensilla placodea, sensilla basiconica A, pit organs, sensilla campaniformia, sensilla trichodea A, B, C, and sensilla spatulata. The structure of the antenna and sensilla of *P. sculpturata* is compared with that of *A. carbonarius*. The female *P. sculpturata* has a shorter and stouter fusiform flagellum with denser sensilla basiconica A on its anteroventral side. Similar structures are found in cleptoparasitic pompilids, *Evagetes* species. These structures are considered to have evolved due to convergence as an adaption to the cleptoparasitic mode of life. The sensilla basiconica A are presumed to play the most important role in locating the host or paralyzed spider.

Key words: Cleptoparasitic behavior, flagellar sensilla, *Poecilagenia sculpturata, Auplopus carbonarius, Evagetes*, Pompilidae.

Introduction

Poecilagenia sculpturata (Kohl, 1898) is a distinctive species among the Japanese Pepsinae, Pompilidae, being characterized by the almost wholly black body and appendages partly with dense whitish hairs and pubescence, hyaline wings, short, stout, fusiform antennae in the female, irregularly strongly punctate head and thorax, coarsely transversely rugose and reticulate propodeum, and obviously petiolate tergum 1 in the female. This species is distributed in the Palaearctic, and has hitherto been recorded from Europe (Spain, France, Yugoslavia, Austria) (Wahis, 1970; Wolf, 1994), China (Shanghai) (Haupt, 1938), Far Eastern Russia (Lelej, 1990) and Japan (Honshu and Kyushu) (Shimizu, 2000). It appears to be rare wherever it occurs and is still poorly represented in most collections.

Nothing has been reported on the biology of *Poecilagenia sculpturata*. Wahis & Gros (1991) suspected that the European *P. rubricans* (Lepeletier, 1845) parasitizes other species of Pompilidae on the basis of its short, stout antennal flagellum and peculiar behavior. According to them, several females of *P. rubricans* were found in close proximity to nests of *Priocnemis* species. Some of them were pursued by *Priocnemis* females which were carrying their prey (*Coelotes* sp.) to the nests. Other females of *P. rubricans* entered cracks in the ground in which *Priocnemis* females nested, but soon came out. Shimizu (1994) presumed that members of *Poecilagenia* are cleptoparasitic on other Pompilidae, based on their structural specialization, e.g., the short, stout flagellum with dense sensilla on its anteroventral side, a condition also found in cleptoparasitic pompilids, *Evagetes* species, and the heavily sculptured integument of the head and mesosoma.

This paper consists of two parts, which together suggest the evolutionary relationship between sensory structures and behavior. First, records of specimens suggesting cleptoparasitism of *P. sculpturata* are reviewed and its cleptoparasitic behavior is described. This behavior is characterized by the frequent application of the flagella to the substrate and cleaning of the antennae with the fore legs, so that the flagellar sensilla are presumed to play an important role in locating the host or stored spider. Secondly, the flagellar sensilla of female *P. sculpturata* are investigated, using SEM, in comparison with those of other Pompilidae, especially *Auplopus carbonarius* (Scopoli, 1763), the possible host of *P. sculpturata*, and cleptoparasitic *Evagetes* species. Moreover, an attempt is made to determine which sensilla of *P. sculpturata* are most related to its cleptoparasitic behavior.

Materials and Methods

Field observations were made on September 25, 28 and October 5 in 1996. The study site was at Nishi-kodaira (ca. 50 m above sea level), in the southwestern suburbs of Kodama Town, Saitama Prefecture, ca. 80 km northwest of Tokyo. This field was a typical farmyard surrounded by rice and vegetable fields. There were logs, vinyl sheets and aluminum pipes, ca. 2.5 cm in diameter, all of which were carelessly piled up beside a wooden shed. At this locale I was able to observe the activities of a female of *P. sculpturata* probably in searching for the host or stored spider. I recorded part of the behavior on 8 mm videotape with VTR.

For SEM study, air-dried antennae were mounted on specimen stubs, and were coated with gold to a thickness of ca. 20 nm in a JEOL JFC-1100E ion sputter. The microscope used was a JEOL JSM-5300, at a working voltage of 10 kV.

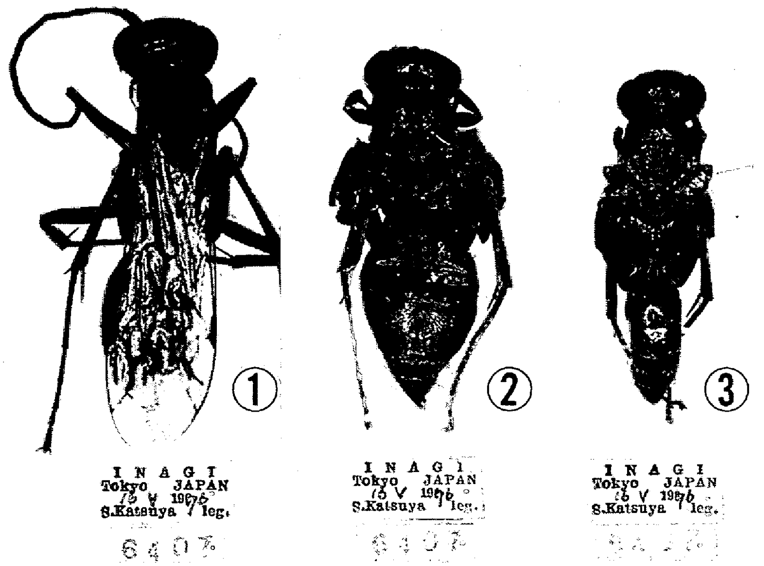
The terminology of the flagellar sensilla follows Alm & Kurczewski (1982) and Lane *et al.* (1988), although their "corrugated conical sensilla" are here designated as "sensilla basiconica A", considering the homology of these sensilla with similar organs of other hymenopteran families. Flagellar segments are designated as fl. 1, 2, etc. from proximal to distal. For positional descriptions, the antenna is considered to be extended diagonally forward. The sensilla basiconica A were counted from the micrographs of the anteroventral surface of each flagellomere as level as possible at a magnification of $\times 750$. The counted areas were $2500\,\mu m^2$, and the values were recalculated to numbers per $10000\,\mu m^2$.

Results

Records of specimens suggesting cleptoparasitism of Poecilagenia sculpturata

I had an opportunity to examine pompilid specimens of the S. Katsuya Collection and his notebook attached to it, which were deposited in the Insect Collection of the National Institute of Agro-Environmental Sciences, Tsukuba City, in 1996. In the collection I found a male and a female specimens of *P. sculpturata* arranged next to a female of *Auplopus carbonarius* (Figs. 1–3). The specimens of *P. sculpturata* were in the stage immediately before emergence, and their bodies and appendages were covered with transparent thin skin of their own pupae. In the female, especially, the skin had a slit from vertex to metanotum along the midline. The specimen of *A. carbonarius* was an adult with fully extended wings. These three specimens bore the same data labels: "INAGI Tokyo Japan 16 V, 1976 S. Katsuya leg." "6407" and "S. Katsuya Collection".

Examining Mr. Katsuya's notebook, I found that



Figs. 1–3. Specimens taken from the same nest (no. 6407) by Mr. S. Katsuya.—— 1, *Auplopus carbonarius* (Scopoli), female; 2, *Poecilagenia sculpturata* (Kohl), female; 3, ditto, male.

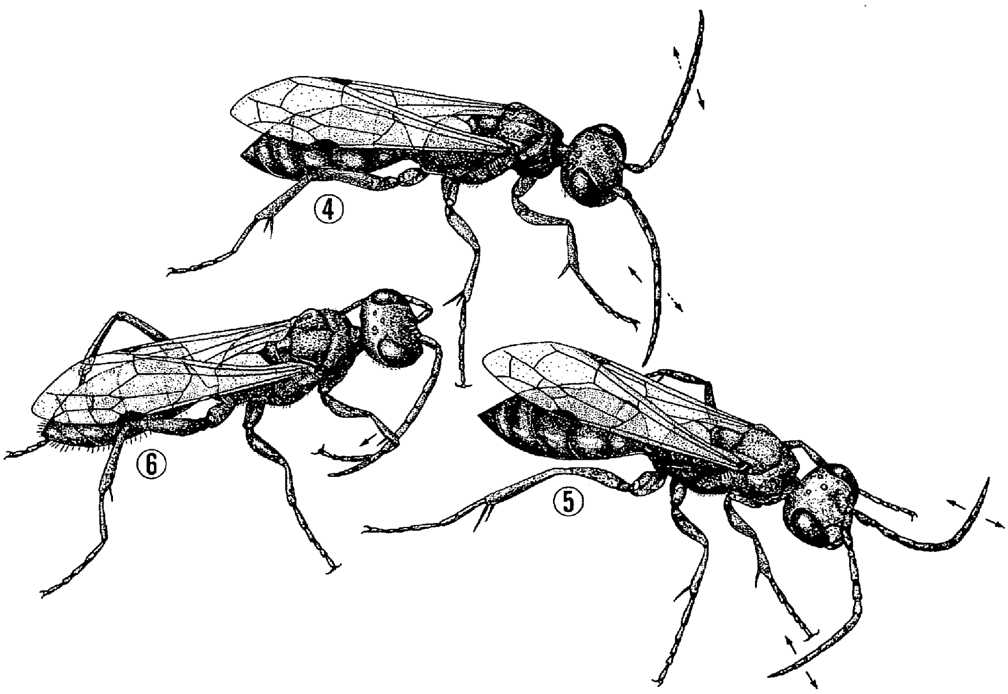
the numeral "6407" on the labels designates the code of the nest he collected. It is clear that these specimens emerged or were about to emerge from the same nest. *A. carbonarius* is well known as a species that builds barrel-shaped mud cells above ground in protected places, such as under stones and bark, and in hollow stems (Richards & Hamm, 1939; Evans & Yoshimoto, 1962; Evans & Shimizu, 1996). Thus, it is probable that *P. sculpturata* is a cleptoparasite of *A. carbonarius*.

Searching behavior

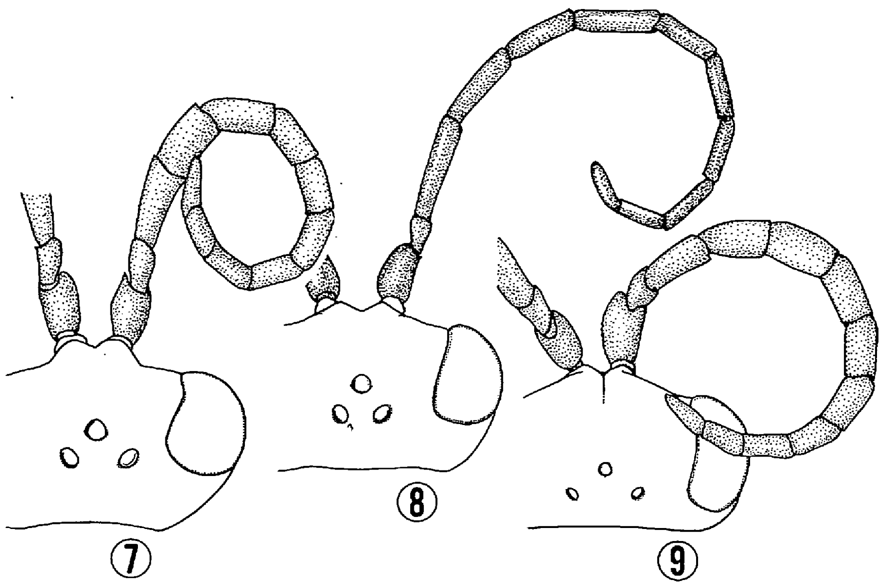
At about 14 : 00 on September 25, 1996, a female of *P. sculpturata* was walking about over piled up wooden boards and blades of grass. The wasp vibrated both antennae strongly and alternately (Fig. 4), and sometimes applied them to the surfaces of the boards and blades (Fig. 5). She then cleaned the right and left antennae with the respective fore legs simultaneously (Fig. 6), and rubbed the fore legs together and through the mouthparts. At about 15 : 10 the wasp remained motionless ca. 20 cm away from a hole on the aluminum pipe into which a female of *Auplopus* sp. was repeatedly carrying mud pellets held in her mouthparts.

At 10 : 25 on September 28, a female of *P. sculpturata* was seen walking quickly on the cut end of a log, with her antennae strongly alternately vibrating and wings constantly flicking up and down. She occasionally made flights of several tens of centimeters. At 10 : 26 she rested on one of the blades after cleaning herself, and then walked quickly over the blades, vibrating the antennae. At 13 : 30 the wasp walked over the logs, vibrating the antennae. She sometimes cleaned her antennae with the fore legs. At 13 : 39 she came out of a shallow hole ca. 1.2 cm in diameter on the log, and soon re-entered it, with the antennae tapping the bottom of the hole. At 13 : 40 she came out of it head first and again walked over the log. At 13 : 41 she cleaned herself: she held the wings vertically just outside the gaster, and rubbed the outer sides of the gaster and wings with the hindtibial brush; then she rubbed the hind tarsi with the hindtibial brush of the opposite legs.

At 14 : 19 on October 5, a female walked about over or among the vinyl sheets close to a log. The cut end of the log had a pre-existing burrow into which a female of *Dipogon* sp. transported her prey at 14 : 17. At 14 : 32 she walked on the cut end of the log, constantly vibrating the antennae. At 15 : 11 the wasp came out of a hole 8 mm in diameter on a aluminum pipe. She walked on the upper surface of the pipe, with her antennae strongly alternately vibrating (Fig. 4) and wings constantly flicking up and down.



Figs. 4–6. Female *Poecilagenia sculpturata* (Kohl) searching for host or stored spider. ——4, Walking on substrate, with her antennae strongly alternately vibrating; 5, feeling substrate with ventral surface of antennae; 6, cleaning right and left antennae with respective fore legs simultaneously.



Figs. 7–9. Antennae of female, dorsal view.——7, *Poecilagenia sculpturata* (Kohl); 8, *Auplopus carbonarius* (Scopoli); 9, *Evagetes deirambo* Ishikawa.

She then extended her antennae forward, bending them near the middle, and walked forward, while feeling the surface of the pipe with the ventral surface of the antennae (Fig. 5). After a while she stopped and polished the right and left antennae with the respective fore legs simultaneously (Fig. 6), and then rubbed the fore legs together and through the mouthparts. She repeated the above acts several times, and then flew away. As mentioned above, *Auplopus* sp. was repeatedly seen to carry mud pellets into one of the pipes on September 25.

Flagellar sensilla of Poecilagenia sculpturata

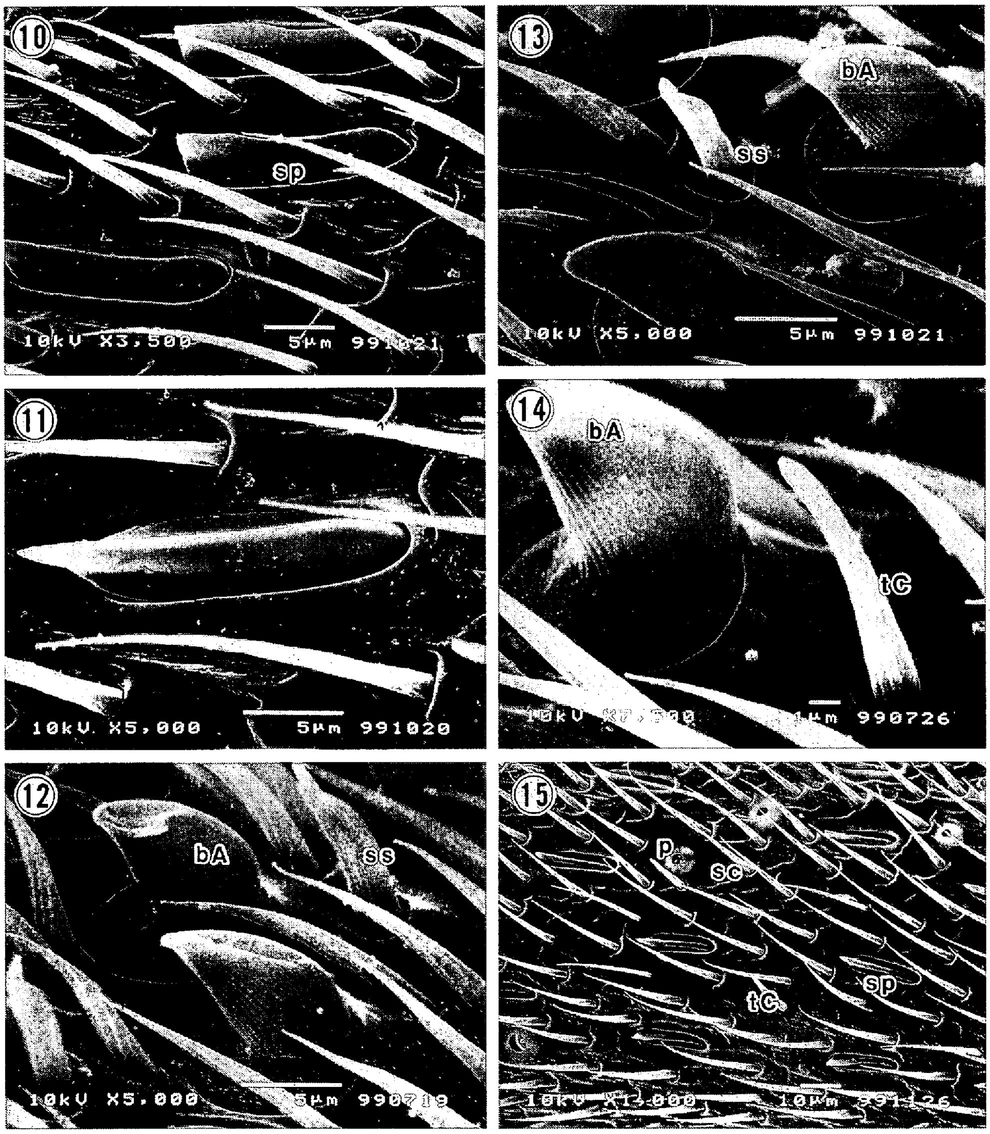
Sensilla placodea (Figs. 10–11, sp): This sensillum is an elongate, convex plate encircled by a fissure. The plate is raised longitudinally and compressed laterally, and its distal end is fairly pointed (Fig. 11) or truncate (Fig. 10). It is 4.3×16–$20\,\mu$m, and is oriented along the long axis of the antenna. Placoid sensilla are abundantly distributed from distal 2/3 of fl. 1 to fl. 10, except for the regions of the sensilla basiconica A, and form the placodea zone.

Sensilla basiconica A (= corrugated conical sensilla of Alm & Kurczewski, 1982 and Lane *et al.*, 1988) (Figs. 12–14, bA): Sensillum basiconicum A is a large, stout, peg-like receptor which leans distally and has numerous grooves from base to apex. The tip may be concave (Fig. 12) or somewhat swollen (Figs. 13–14). This sensillum is ca. 4–5 μm long and 3–4 μm wide at the base. It is located on the proximal side of a large, oval socket. The socket is 7.8–9.3 μm in long axis, and is composed of a finely granularly rugulose thick membrane. Sensilla basiconica A occur densely only on the slightly flattened anteroventral surface of the flagellum from the distal triangular area on fl. 2 to fl. 10, forming the basiconica zone (Fig. 34).

Pit organs (sensilla coeloconica and/or sensilla ampullacea) (Figs. 15–17, p): The opening of the pit is 2.5–4.3 μm in diameter and is surrounded by a slightly raised, smooth, doughnut-shaped rim. In the bottom of the pit a small peg with a surrounding circular wall may be visible. These organs occur in the placodea zone on fl. 1–10, and are few in number (their maximum number per flagellomere was 13 in this investigation).

Sensilla campaniformia (Figs. 15, 18, sc): This organ consists of a shallowly depressed oval region surrounded by a slightly raised rim and a minutely granulate central papilla. Its dimensions are 7.5–11.8 $\times$ 5.8–7.1 μm. Campaniform sensilla are found in the placodea zone on fl. 1–10, and are few in number (their maximum number per flagellomere was 11 in this investigation).

Sensilla trichodea A (Fig. 19, tA): Trichoid sensillum type A is characterized by its smooth surface, large bulbous base, thick shaft which is subbasally strongly bent toward the distal end of the antenna, and abrupt tip with a terminal papilla. It is ca. 9–13 μm long, and sits in the proximal side of a large oval socket. Trichodea A are located among the sensilla placodea on the medioventral surface of fl. 1–10.

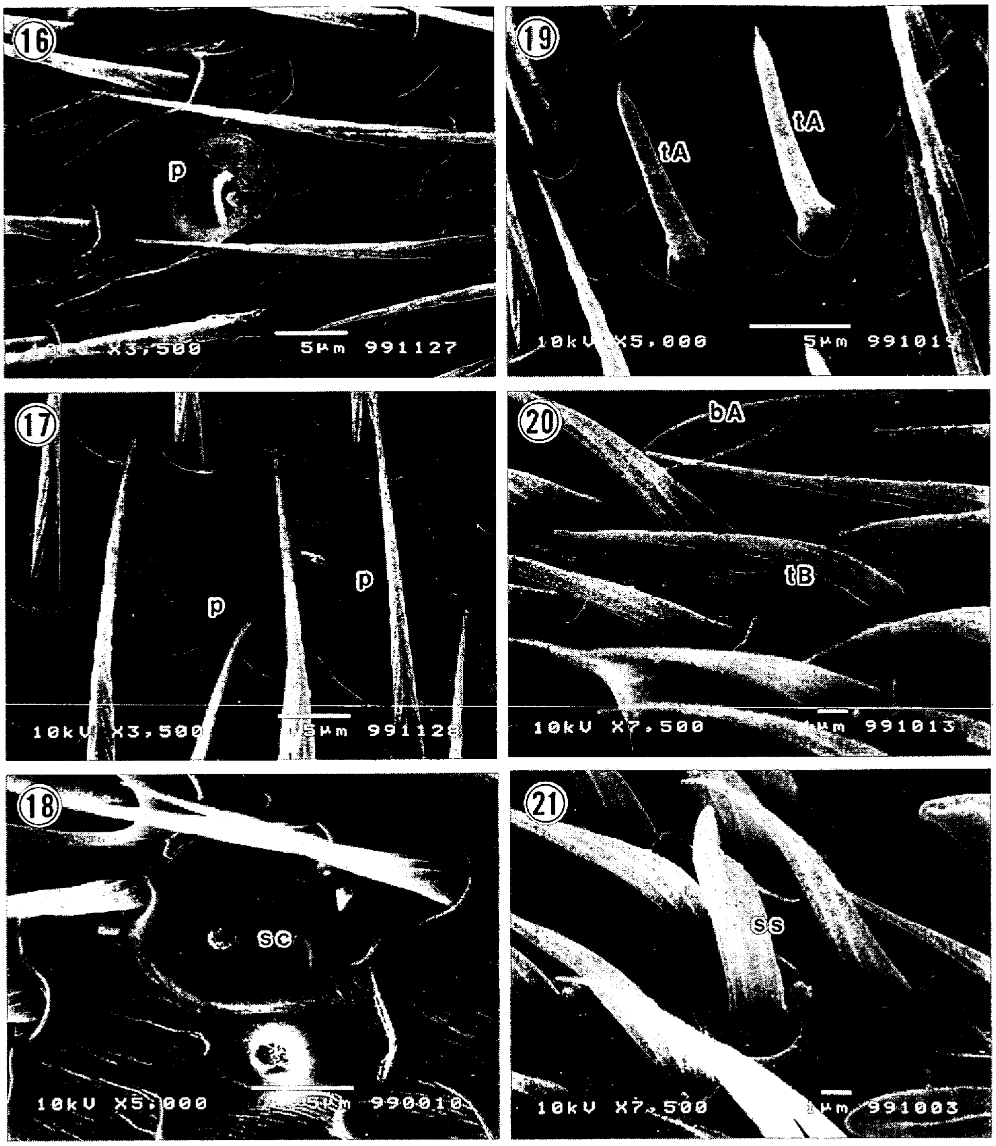


Figs. 10–15. Antennal sensilla of female *Poecilagenia sculpturata* (Kohl). —— 10, Sensilla placodea with truncate distal margin; 11, s. placodeum with pointed distal margin; 12, s. basiconica A with subterminal furrow; 13, s. basiconica A with subterminal swelling; 14, s. basiconicum A and s. tricodeum C; 15, zone dominated by s. placodea, containing pit organs, s. campaniforme and s. trichodeum C (p=pit organ; bA=s. basiconicum A; sc=s. campaniforme; sp=s. placodeum; tC=s. tricodeum C; ss=s. spaturatum).

Sensilla trichodea B (Fig. 20, tB): Trichoid sensillum type B is a slender hair tapering gradually to a point, ca. 11–12 μm long. This sensillum is thinner than surrounding setae, but is similar in sculpture to them. The hair bends at about 1/3 length of the shaft, and lies close and nearly parallel to the antennal surface. There is no visible socket at the base. Trichodea B are sparsely located in both basiconica and placodea zones on fl. 1–10.

Sensilla trichodea C (Fig. 14, tC): Trichoid sensillum type C is a straight or slightly curved hair, ca. 7–19 μm long. This sensillum gradually tapers to a blunt tip, and has ca. 6 vertical furrows running from base to tip. It stands at a 60–90° angle to the antennal surface, and sits in the circular membrane of a socket. Sensilla trichodea C are scattered in both basiconica and placodea zones on fl.1–10.

Sensilla spatulata (Figs. 12–13, 21, ss): This sensillum appears to be cylindrical basally, flattened and spatulate distally. It is ca. 7–9 μm long and ca. 2 μm wide, with the apical margin being notched or emarginate. It has more than 10 faint vertical furrows running from base to tip. The sensillum sits in the reticulato-rugose thick membrane of a large, round socket ca. 3.5 μm in diameter. Spatulate sensilla are sparsely located in the basiconica zone on fl. 3–10.



Figs. 16–21. Antennal sensilla of female *Poecilagenia sculpturata* (Kohl). —— 16, Large pit organ; 17, small pit organs; 18, sensillum campaniforme; 19, s. trichodea A; 20, s. trichodeum B; 21, s. spatulatum (p=pit organ; bA=s. basiconicum A; sc=s. campaniforme; tA=s. tricodeum A; tB=s. tricodeum B; ss=s. spaturatum).

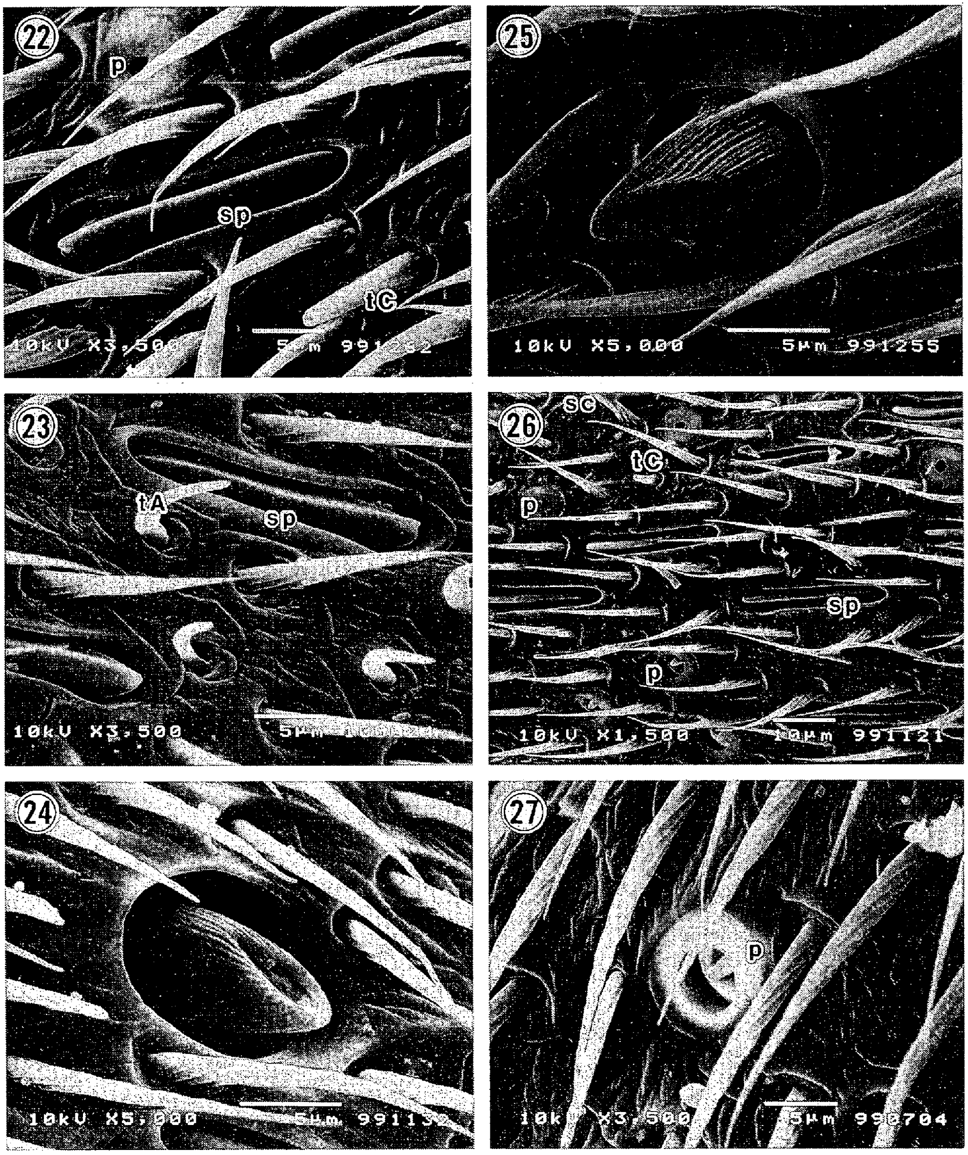
Table 1. Maximum density (/10000 μm^2) of sensilla basiconica A on each flagellomere of *P. sculpturata* and *A. carbonarius*.

	fl.1	fl.2	fl.3	fl.4	fl.5	fl.6	fl.7	fl.8	fl.9	fl.10	Number of individuals
Poecilagenia sculpturata	—	40–48	60–64	60	56–58	48–52	48	48–50	40–48	40–48	2
Auplopus carbonarius	8–10	12	16	16	16–20	20–22	20–22	24–26	18–20	18–22	2

Comparison of flagellar sensilla of Poecilagenia sculpturata with those of Auplopus carbonarius

All types of sensilla on the antenna of female *P. sculpturata* were also observed in female *A. carbonarius* (Figs. 22–33). The distribution of each type of sensillum is almost the same in both species, except for the sensilla basiconica A, which are distributed from the distal triangular portion of fl. 2 in *P. sculpturata* but from the distal half of fl.1 in *A. carbonarius*.

Further important differences lie in the density of sensilla basiconica A between the two species. Table 1 shows the maximum density of sensilla basiconica A on each flagellomere of *P. sculpturata* and *A. carbonarius*. From this table and Figs. 34–35 it is clear that the density of sensilla basiconica A is much higher in *P. sculpturata* than in *A. carbonarius* on all the respec-



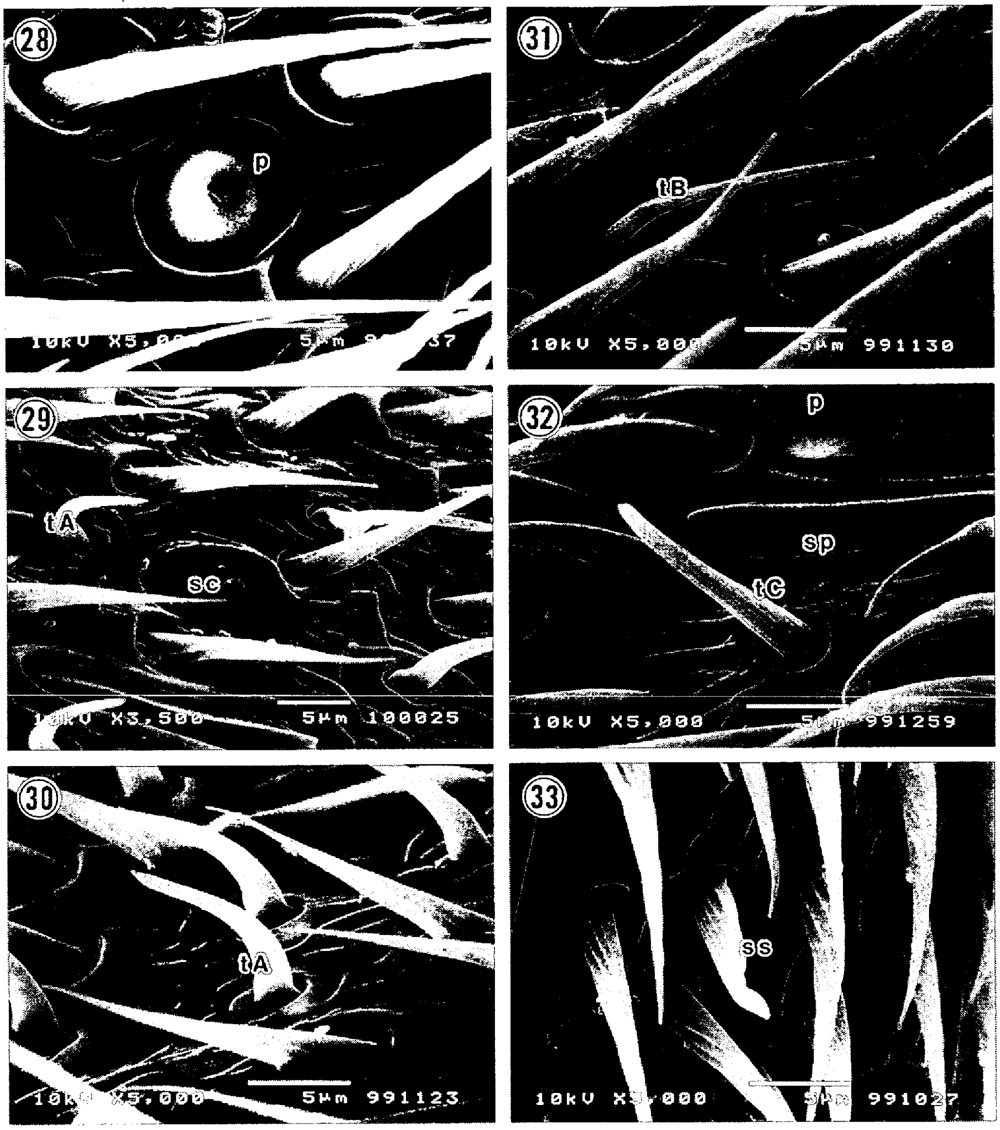
Figs. 22–27. Antennal sensilla of female *Auplopus carbonarius* (Scopoli). —— 22, Sensilla placodea; 23, s. placodea and s. trichodea A; 24, s. basiconicum A with subterminal furrow; 25, s. basiconicum A with subterminal swelling; 26, zone dominated by s. placodea, containing pit organs, s. companiformia and s. tricodeum C; 27, large pit organ (p=pit organ; sc=s. campaniforme; sp=s. placodeum; tA=s. tricodeum A; tC=s. tricodeum C).

tive flagellomeres except fl.1. Table 1 also indicates that in *A. carbonarius* the density of sensilla basiconica A tends to increase from fl. 1 to fl. 8, whereas in *P. sculpturata* the density of the sensilla tends to increase from fl. 2 to fl. 3 but to decrease from fl. 4 to fl. 10. In the latter species the variation in the density of sensilla basiconica A on the flagellomeres in a proximal to distal direction corresponds to the variation in the thickness of the flagellomeres in the same direction.

There is another difference in the structure of sensilla basiconica A between the two species. In *A. carbonarius* the sensillum sits in the membrane of a socket that is depressed below the antennal surface, hence usually the membrane is not visible and the sensillum itself does not project very high above the antennal surface (Figs. 24–25). In *P. sculpturata,* on the other hand, the sensillum sits in a membrane on almost the same plane as the antennal surface, so that usually the membrane is exposed and the sensillum projects high above the antennal surface (Figs. 12–14).

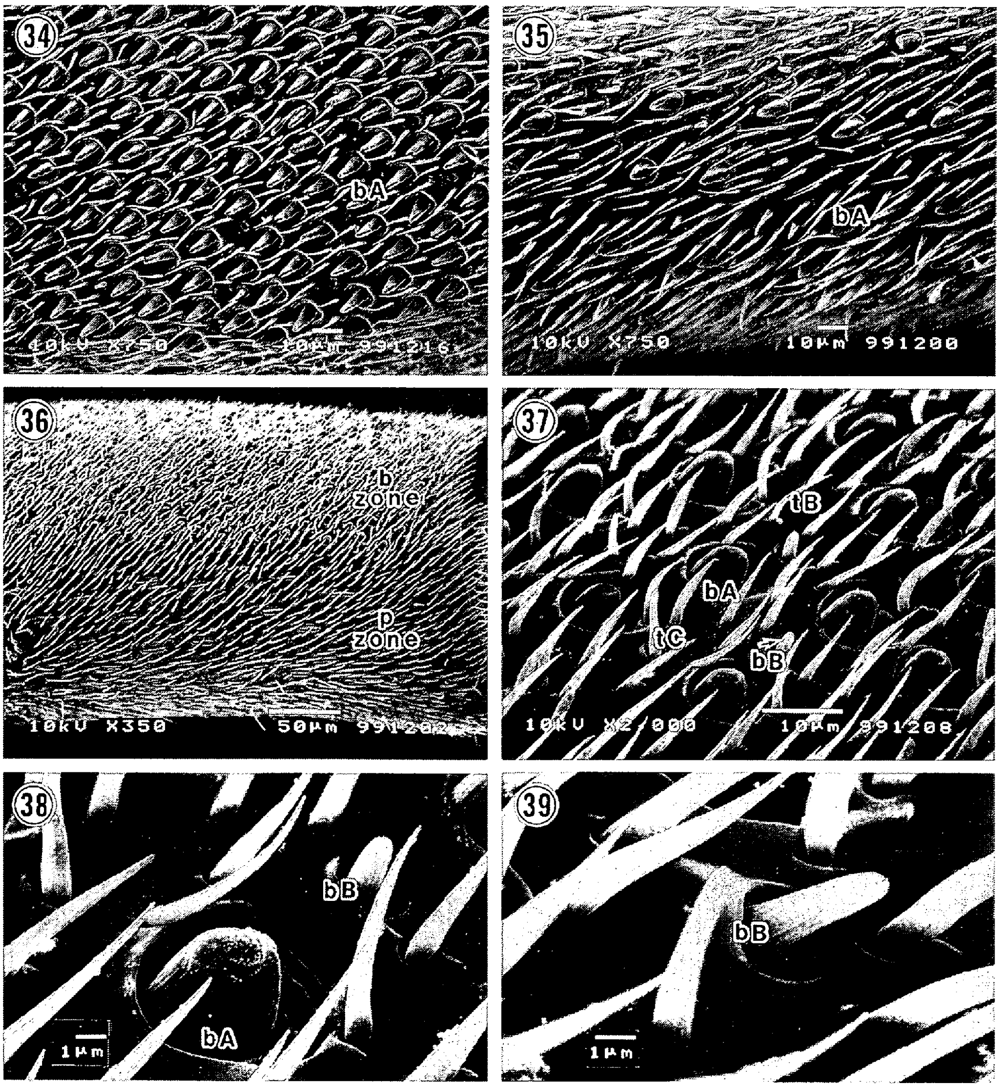
Discussion

Behavioral features of Poecilagenia sculpturata



Figs. 28–33. Antennal sensilla of female *Auplopus carbonarius* (Scopoli).——28, Small pit organ; 29, sensillum campaniforme; 30, s. trichodea A; 31, s. trichodeum B; 32, s. trichodeum C; 33, s. spaturatum (p=pit organ; sc=s. campaniforme; sp=s. placodeum; tA=s. tricodeum A; tB=s. tricodeum B; tC=s. tricodeum C; ss=s. spaturatum).

I was not able to observe *P. sculpturata* locating and entering the nests provisioned by other pompilids. However, the observed behavior of *P. sculpturata* was characterized by the strong vibration of the antennae and frequent application of the flagella to the substrate near where other pompilids are nesting. This behavior seems to be almost identical with the host- or spider-searching behavior of cleptoparasitic *Evagetes*: females of '*Pompilus pectinipes*' [=*Evagetes crassicornis* (Shuckard, 1835)] carefully explore the soil and tap it with their antennae (Ferton, 1901); females of *E. mohave* (Banks, 1933) walk over the sand, with the antennae being vibrated and applied constantly to the surface of the sand, occasionally inspecting depression and holes (Evans *et al*., 1953). [Some hunting pompilids, such as *Aporus hirsutus* (Banks, 1917), *Euplaniceps saussurei* (Kohl, 1885), *Entomobora crassitarsis* (Costa, 1887), *En. plicata* (Costa, 1883), *En. fuscipennis* (Van der Linden, 1827), *Anospilus orbitalis* (Costa, 1863), *Anoplius apiculatus autumnalis* (Banks, 1914), may exhibit similar behavior in searching for their prey spiders living in burrows in the ground (Ferton, 1890, 1897, 1901, 1902, 1909; Gros, 1983; Williams, 1928; Janvier, 1930; Evans *et al*., 1953)]. Thus, it is probable that *P. sculpturata* is a cleptoparasitic species. Moreover, the records of *P. sculpturata* and *A. carbonarius* emerging from the same nest strongly suggest the cleptoparasitism of *P. sculpturata* on *A. carbonaris,* although there still remains a possibility that one of the two species may reuse part of a nest of



Figs. 34–39. Antennal sensilla of female [34, *Poecilagenia sculpturata* (Kohl); 35, *Auplopus carbonarius* (Scopoli); 36–39, *Evagetes deirambo* Ishikawa] —— 34, Anteroventral surface of flagellomere 4; 35, ditto; 36, medioventral surface of flagellomere 4, showing basiconica zone and placodea zone; 37, zone dominated by sensilla basiconica A, containing s. basiconica B and s. trichodea C; 38, s. basiconica A and B; 39, s. basiconicum B (bA = s. basiconicum A; bB = s. basiconicum B; tB = s. tricodeum B; tC = s. tricodeum C).

the other.

In the Pompilidae there are two types of cleptoparasitism, the behavior patterns and origins of which are quite different (Shimizu, 1994). One of them (type A) is represented by *Ceropales* (Ceropalinae). The female chases the host while the latter is on its way to the nest with its prey spider. When the spider is left on the ground or after fighting and robbing the host of it, the parasite lays her egg in the book lung of the spider. The host then carries the spider into its own cell and oviposits in the usual manner, but the egg of the parasite hatches first, and the larva destroys the egg of the host, and then feeds upon the spider [behavior sequence: 'prey'-egg (Evans, 1953)]. The other type (type B) is represented by *Evagetes* (Pompilinae). The female walks over the ground, while tapping the soil with her antennae, and seeks a spider freshly stored by other Pompilidae or a pompilid female in some phase of nesting. The parasite enters the host nest, destroys its egg, lays her own egg on the spider, and then fills the burrow [behavior sequence: 'prey'-nest-egg-closure (Evans, 1953)].

P. sculpturata may exhibit cleptoparasitic behavior of type B. This reasoning is based on the fact that the female of this species repeatedly uses the antennae by applying their ventral surface to the substrate near where other pompilids are nesting (Fig. 5). The antenna of female *P. sculpturata* is unique, compared with that of other Pepsinae: it is short, stout, fusiform (Fig. 7), and the flagellum from the distal portion of fl. 2 to fl. 10 is slightly flattened on the anteroventral surface, where there are very dense sensilla basiconica A (Fig. 34). Similar structures are found in *Evagetes*, as mentioned later. The female of both genera may detect the host or paralyzed spider by olfactory and/or gustatory cues received by these sensilla.

The known hosts of *Evagetes* include *Anoplius, Arachnospila, Episyron* and *Batozonellus*, all belonging to the ground-burrowing wasps of the Pompilinae (Richards and Hamm, 1939; Evans and Yoshimoto, 1962; Wolf, 1971; Day, 1988) although, according to Schmid-Egger & Wolf (1992), it is highly probable that *Evagetes siculus* (Lepeletier, 1845) cleptoparasitizes a parasitoid pompiline species, *Aporus unicolor* Spinola, 1808. On the other hand, the probable host of *P. sculpturata* is *Auplopus carbonarius*, as mentioned before. This is understandable from the viewpoint of the phylogenetic position of *Poecilagenia* and *Auplopus*: both genera are placed in the *Ageniella* group (=Ageniellini *sensu* Banks, 1912), Pepsinae, and are considered to be relatively closely related (Shimizu, 1994; Shimizu, 2000).

Comparison of flagellar sensilla of Poecilagenia sculpturata with those of other Pompilidae

Walther (1979, 1983) investigated the antennal sensilla of the aculeate Hymenoptera, illustrating those of *Anoplius viaticus* (Linnaeus, 1758) as a representative of the Pompilidae, to test and reconstruct hypotheses about the phylogeny of the Aculeata. Alm & Kurczewski (1982) and Lane *et al.* (1988) examined the antennal sensilla of *Anoplius tenebrosus* (Cresson, 1865) and *Evagetes parvus* (Cresson, 1865), respectively, to elucidate the sensillar structure characteristic of the predatoid and cleptoparasitic Pompilidae. The result of the present study shows that the flagellar sensilla of both *Poecilagenia sculpturata* and *Auplopus carbonarius* are for the most part similar to those of the above species. The sensilla spatulata, which Lane *et al.* (1988) first described in *E. parvus*, were also found in *Poecilagenia* and *Auplopus*. Lane *et al.* (1988) described the sensilla basiconica B (as sensilla basiconica) in *Evagetes*: these sensilla are stout, blunt, peg-like receptors with 11–12 vertical grooves, and each of the sensilla is placed in a broad and flattened socket (Fig. 39); they are interspersed among the sensilla basiconica A (Figs. 37–38). However, the sensilla basiconica B were not found in *Poecilagenia* or *Auplopus*.

By comparing the antennal structure of *P. sculpturata* with that of *A. carbonarius*, it is noticed that there are several distinct differences. In *A. carbonarius* the antenna is slender and elongate, with fl.1 more than 4×as long as thick (Fig. 8). Each flagellomere is not flattened on the anteroventral surface, where there are sensilla basiconica A whose density is 8–26 per 10000 μm^2 (Table 1). In *P. sculpturata*, on the other hand, the antenna is short, stout, and fusiform, with fl. 1 at most 3.2×as long as thick (Fig. 7). The flagellum from the distal portion of fl. 2 to fl. 10 is slightly flattened on the anteroventral surface, where there are sensilla basiconica A whose density is 40–64 per 10000 μm^2 (Table 1). In addition, the sensilla basiconica A of *P. sculpturata* appear to be more elevated above the antennal surface than those of *A. carbonarius* (Figs. 12–14, 24–25). These sensilla of *P. sculpturata* may contact the substrate more easily. In fact, the female of this species was observed to use her antennae by repeatedly applying its ventral surface to the substrate (Fig. 5).

The sensilla basiconica of the aculeate Hymenoptera have been investigated by many researchers [Chrysidoidea, Vespoidea including Formicidae, and Apoidea including Sphecidae: Hashimoto, 1991, 1995; Mutillidae, Sapygidae, Pompilidae, Tiphiidae, Formicidae, Scoliidea, Vespidae and Apidae: Walther, 1979, 1981a, b, 1983; *Anoplius*: Alm & Kurczewski, 1982 (mentioned as corrugated conical sensilla); *Evagetes*: Lane *et al.*, 1988 (mentioned as corrugated conical sensilla); *Camponotus*: Masson *et al.*, 1972; *Polistes*: Callahan, 1975 (mentioned as corrugated pyramidal sensilla); *Vespula*: Spradbery, 1973 (designated as sensilla campaniformia); Sphecidae: Martini, 1986; Apidae: Agren, 1977, 1978; Agren & Svensson, 1982; *Apis*: Slifer & Sekhon, 1961; Dietz & Humphreys, 1971; Esslen & Kaissling, 1976; Whitehead & Larsen, 1976 (mentioned as sensilla chaetica?); Yokohari *et al.*, 1982]. These sensilla were considered to be olfactory (Slifer & Sekhon, 1961; Masson *et al.*, 1972; Walther, 1981b; Martini, 1986) or gustatory bristles (Alm & Kurczewski, 1982; Lane *et al.*, 1988).

After considering all the evidence mentioned above, it is reasonable to suppose that the sensilla basiconica A play the most important role in locating the host or stored spider. The sensilla basiconica A "may receive a chemical residue or heavy odor molecule from buried prey or from pompilid-manipulated sand particles" (Lane *et al.*, 1988) or other nest materials.

By comparing the antennal structure of *P. sculpturata* with that of *E. parvus* [investigated by Lane *et al.* (1988)], the following similarities were found: the antenna is stout, fusiform (Figs. 7, 9), and the flagellum from distal portion of fl. 2 to fl. 10 is more or less flattened on the anteroventral surface, where there are very dense sensilla basiconica A (Figs. 34, 36–37). Lane *et al.* (1988) stated that in *E. parvus* "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". These specialized antennal structures common to *Evagetes* and *Poecilagenia* are considered to have evolved due to convergence as an adaptation to the cleptoparasitic mode of life (type B). Moreover, the extraordinarily high density of sensilla basiconica A on the flagellum in *Poecilagenia* and *Evagetes* may support the Chapman's (1982) statement: in general, active insects that search out a specific food source or habitat using odor perception, tend to have a greater number of olfactory antennal receptors than do generalists.

Wcislo (1995) investigated and compared sensilla numbers and antennal morphology of parasitic and non-parasitic Apidae. He concluded that "females of some parasitic bees have less-dense sensilla placodea on their more terminal flagellomeres relative to their non-parasitic relatives". However, he did not examine the density of sensilla basiconica. Thus, it was impossible to compare the antennal structure of cleptoparasitic Pompilidae with that of cleptoparasitic Apidae with special reference to the sensilla basiconica.

Acknowledgments

I wish to express my sincere gratitude to Prof. Emeritus R. Ishikawa and Prof. T. Yamasaki (Tokyo Metropolitan University) for their constant guidance and improving the earlier manuscript. My thanks are also due to Prof. Emeritus H. E. Evans (Colorado State University) and Dr. M. S. Wasbauer for critically reading through the manuscript and offering useful advice. I am much indebted to Dr. T. Matsumura (National Institute of Agro-Environmental Sciences) for giving me an opportunity to examine the S. Katsuya Collection deposited in his laboratory. For the gift or loan of specimens, I thank the following persons: Dr. R. Wahis (Faculté des Sciences agronomiques de Gembloux), Dr. A. S. Lelej (Institute of Biology and Pedology, Vladivostok), Mr. T. Nambu, Dr. K. Yamagishi (Meijo University), Dr. K. Konishi (Hokkaido National Agricultural Experiment Station), Mr. Y. Haneda, Mr. H. Nagase, Dr. A. Shinohara (National Science Museum, Tokyo), Mr. Y. Nara and Dr. C. Schmid-Egger. Acknowledgments are also due to Prof. Y. Tominaga, Prof. F. Yokohari, Dr. M. Iwasaki (Fukuoka University) and Dr. T. Yazawa (Tokyo Metropolitan University) for their helpful comments on the sensilla.

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* Original not seen.

(Received February 21, 2000; Accepted July 3, 2000)