

Unique Features of Sensilla on the Antennae of Formicidae (Hymenoptera)

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The sensillum structures on the antennae in Formicidae were examined by SEM to compare with those of other aculeate hymenoptera. While all aculeates had the sensilla basiconica, s. chaetica, s. placodea, s. coeloconica and s. ampullacea on the antennae, the sensillum structures of Formicidae were large and specialized in shape with more complex arrangement. These unique structural features reflected chemosensory specialization in formicid sensilla.

INTRODUCTION

Behavioral modifications in the host or mate selection, locomotion including flight and trail following, and defense are frequently elicited by chemical stimuli in insects. The antenna is a major sensory organ for such stimuli. The type, abundance and distribution of sensilla on this organ depend on the chemosensory needs in their behavior (CHAPMAN, 1982).

The formicids utilize most complex and diverse chemical signals to maintain higher level of organization in their colonies, which may be made possible by the development of highly sophisticated chemical sensors. The formicids can, indeed, perceive various chemical substances at lower concentrations than other insects (WILSON, 1971). Despite such a capability, very little attention has been given to their sensillum structures. Notable exception is WALTHER (1979) who pointed out that the formicids were unique among the aculeates in having "hair-like" pore plates of the sensilla placodea on the antennae.

The present study aims to characterize structural features of the antennal sensilla of the formicids. The sensillum structures on the antennae of major taxonomic groups of Formicidae were analyzed by scanning electron microscope (SEM) and compared with other aculeate Hymenoptera.

MATERIALS AND METHODS

Materials. Only female specimens were examined in this study. In social groups such as Formicidae, Vespidae and Apidae, worker specimens were used, because workers are by far the best known and most available caste. Details of the species examined were listed in Table 1.

The higher classification of Aculeata adopted here follows BROTHERS (1974) and the formicid classification follows WHEELER and WHEELER (1985).

SEM observation. The antennae were examined by SEM (Hitachi-Akashi MSM4C-102). The samples were cleaned by an ultrasonic-washer in chloroform-methanol (2:1), dried in air, mounted on stubs and then sputtered with gold. To show the inner aspect of the cuticular structures, the samples were cut with a razor blade and the cellular material were digested with 10% KOH before the gold coating was applied.

The terminology for sensilla followed WALTHER (1979).

Abbreviations used for figures are as follows.

- a: aperture
- am: sensilla ampullacea
- b: sensilla basiconica
- br: bristle
- ch: sensilla chaetica
- co: sensilla coeloconica
- d: duct
- el: encircling ledge
- g: surface groove
- im: internal basal membrane
- ml: middle ledge
- p: sensilla placodea
- so: socket
- t: sensilla trichodea curvata

RESULTS

The types of antennal sensilla of Aculeata

Aculeata have usually five to eight types of sensilla on their antennal flagellum. Five dominant types include the sensilla basiconica, the sensilla chaetica, the sensilla placodea (the sensilla trichodea curvata), the sensilla coeloconica, and the sensilla ampullacea, all of which were studied here.

Sensilla basiconica. This type of sensilla always consists of two parts, a peg and a socket (Fig. 1). They are considered as olfactory sensilla because the peg is porous on the distal end (MASSON et al., 1972; WALTHER, 1981; MARTINI, 1986a).

Sensilla chaetica. These are sensory bristles with flexible internal cuticular ring serving as articulate membrane (Fig. 6), probably being mechanosensory or contact chemosensory receptors (DUMPERT, 1972a; WALTHER, 1981).

Sensilla placodea (Sensilla trichodea curvata). The sensilla placodea have a perforated plate-like sensory cuticle (Fig. 7). The sensilla trichodea curvata are "curved hairs", possessing an encircling and a middle cuticular ledges (Figs. 10 and 12). Since these ledges are a feature characteristic to the pore plate sensilla (Fig. 9) (MARTINI and SCHMIDT, 1984; MARTINI, 1986b), the sensilla trichodea curvata may be regarded as a homologue of sensilla placodea (WALTHER, 1979). The sensilla placodea, and also the sensilla trichodea curvata, are proven to respond to a wide range of organic compounds including various pheromones (DUMPERT, 1972b; MARTINI and SCHMIDT, 1984).

Sensilla coeloconica. They are longitudinally grooved pegs in the chamber below

Table 1. List of taxa examined

Vespoidea (Formiciformes)

Formicidae

Formicinae: *Acropyga baodaensis* TERAYAMA, *Anoplolepis longipes* (JERDON), *Camponotus japonicus* MAYR, *Echinopla* sp., *Formica japonica* MOTSCHULSKY, *Lasius niger* (LINNAEUS), *Melophorus* sp., *Oecophylla smaragdina* FABRICIUS, *Paratrechina longicornis* (LATRILLE), *Plagiolepis* sp., *Polyergus samurai* YANO, *Polyrhachis dives* F. SMITH, *Prolasius* sp.

Dolichoderinae: *Bothromyrmex* sp., *Dolichoderus bituberculatus* MAYR, *Iridomyrmex itoi* FOREL, *Tapinoma indicum* FOREL, *Technomyrmex gibbosus* (WHEELER)

Myrmeciinae: *Myrmecia gulosa* (FABRICIUS)

Pseudomyrmecinae: *Tetraponera allaborans* WALKER

Dorylinae: *Aenictus laeviceps* (F. SMITH), *Dorylus* sp.

Leptanillinae: *Leptanilla japonica* BARONI URABANI

Cerapachyinae: *Cerapachys sauteri* FOREL

Myrmicinae: *Aphaenogaster famelica* (F. SMITH), *Cataulacus* sp., *Crematogaster matsumurai* FOREL, *Epitritus hexamerus* BROWN, *Myrmecina graminicola nipponica* WHEELER, *Oligomyrmex sauteri* FOREL, *Pheidole pili* SANTSCHI, *Pristomyrmex pungens* MAYR, *Smithistruma japonica* (ITO), *Tetramorium caespitum* (LINNAEUS), *Vollenhovia emeryi* WHEELER

Ponerinae: Amblyoponini; *Amblyopone australis* ERICHSON, Proceratiini; *Proceratium japonicum* SANTSCHI, *Discothyrea sauteri* FOREL, Ectatommini; *Gnamptogenys costata* (EMERY), *Rhytidoponera purpurea* (EMERY), Ponerini; *Brachyponera chinensis* (EMERY), *Cryptopone sauteri* (WHEELER), *Diacamma* sp., *Leptogenys kitteli* MAYR, *Odontoponera transversa* (F. SMITH), *Ponera japonica* WHEELER, *Trapeziopela* sp., Odontomachini; *Odontomachus monticola* EMERY, *Anochetus* sp.

Vespoidea (Vespiformes)

Tiphiidae: *Methocha japonica* YASUMATSU, *Tiphia latistriata* ALLEN et JAYNES

Mutillidae: *Mutilla europaea mikado* CAMERON, *Myrmosa nigrofasciata* YASTUMATSU

Pompilidae: *Anopilus samariensis* (PALLAS), *Cyphononyx dorsalis* (LEPELETIER)

Scoliidae: *Carinoscolia melanosoma fascinata* (SMITH), *Megacampsomeris grossa matsumurai* (BETREM)

Masariidae: *Pseudomasaris coquillettii* ROHWER

Eumenidae: *Discocelius japonicus* PEREZ, *Eumenes* sp.

Vespidae: *Polistes chinensis antennalis* PEREZ, *Provespa* sp.

Sphecoidea

Sphecidae: *Ammophila infesta* F. SMITH, *Ampulex dissector* (THUNBERG)

Colletidae: *Colletes patellatus* PEREZ

Andrenidae: *Andrena mikado* STRAND et YASUMATSU

Halictidae: *Lasioglossum* sp.

Melittidae: *Melitta* sp.

Megachilidae: *Anthidium septemspinosum* LEPELETIER

Anthophoridae: *Xylocopa appendiculata circumvolans* SMITH

Apidae: *Trigona* sp.

Bethyloidea

Bethylidae: *Cephalonomia gallicola* (ASHMEAD)

Chrysididae: *Chrysis shanghaiensis* SMITH

Cleptidae: *Cleptes* sp.

Dryinidae: *Haplogonatopus apicalis* PERKINS

the antennal surface (Fig. 19). The function of these may be olfactory because the pegs have pores at the bottoms of the grooves (WALTHER, 1981).

Sensilla ampullacea. These resemble coeloconic sensilla, but are distinct in the chamber more deeply situated (Fig. 22) and different surface appearance of the sense hair in the chamber (Fig. 26). They are probably temperature-, humidity-, or CO₂-receptor, because their sense hairs have no pores (JAISON, 1969; MASSON and FRIGGI, 1971).

The sensillum structures of Formicidae

The peculiarities found in the sensillum structures on the antennae of Formicidae were as follows:

Sensilla basiconica

The pegs of the sensilla basiconica in Aculeata were usually very uniform in size and shape. The pegs were stout and almost straight with the tips somewhat blunt or sometimes depressed, and their length did not exceed 15 μm (Fig. 1). Modifications, however, occurred in Formicidae. In Cerapachyinae, the peg was thin and strongly bent distally (Fig. 3). In ponerine tribes Odontomachini and Ponerini, it was slender, tapered apically, gradually narrowed basally, with the apex pointing (Fig. 2). Amblyoponini and Ectatommini of Ponerinae, and Myrmicinae had pegs of greater than 30 μm (Fig. 28).

The sockets in most aculeates were found at the level of the antennal surface, or slightly lower (Fig. 1). The exception was the case of Pseudomyrmecinae and Myrmeciinae where the socket was strongly elevated above the antennal surface towards the tip of the antenna (Fig. 4).

Cerapachyinae were distinct in having an additional membrane with a slit (internal basal membrane) below the socket membrane (Fig. 5). Why only cerapachyines have this peculiar structure is uncertain. Possibly, the narrow lengthwise slit of internal basal membrane guides nerves to their extraordinarily thin peg, because the nerve processes of sensory cells must pass through this slit before they reach the thin peg.

Sensilla chaetica

Usually the sensilla chaetica in the aculeates were spread over the whole surface of the antennae, but those in Formicidae were associated with the sensilla basiconica (Fig. 2). Formicinae, Dolichoderinae, some Ponerinae and Myrmicinae showed this pattern.

Sensilla trichodea curvata

All of the formicids studied here had the hair-like plates (i.e. the sensilla trichodea curvata), whereas no other aculeates had such structures. The elevated plates of the sensilla placodea occurred in many groups of Aculeata, such as Sphecidae, Mutillidae, Pompilidae, Scoliididae and Vespidae (Fig. 8), though they were attached to the antennal surface for almost their entire length, the tip being the only region that was free, unlike the hair-like plates of Formicidae.

The plates of the sensilla placodea were usually small circle or oval (5.0–9.3 μm in length along the long axis, covering 2–4% of the antennal segment) (Fig. 13). How-

ever, some Vespoidea, such as Tiphiidae, Pompilidae, Eumenidae and Vespidae, had long elliptic plates (15.2–24.5 μm , 6–14%) (Figs. 12 and 14). The elongation of the sensilla placodea is a probable evolutionary trend in Vespoidea, as that in the sensilla trichodea curvata of Formicidae. Most formicids had even longer sensilla than the other Vespoidea (Fig. 12). Each of the formicid taxa showed variation in the hair length, and the length relative to the segment which is shown in parenthesis, as follows: Dorylinae 6–10 μm , (4.5–5%); Cerapachyinae 12–14 μm , (6–12%); Pseudomyrmecinae 13–16 μm , (8–15%); Myrmeciinae 24–27 μm , (6–10%); Formicinae 19–36 μm , (11–53%); Dolichoderinae 16–30 μm , (27–40%); Ponerinae 10–40% μm , (13–63%); Myrmicinae 25–40 μm , (20–50%); Leptanillinae 21–23 μm , (77%).

The antennal segment viewed from inside showed the apertures at the base of cuticular apparatuses of the sensilla placodea and sensilla trichodea curvata (Fig. 18), where nerve processes of the sensory cells enter the sensilla (cf. WALTHER, 1981; MARTINI and SCHMIDT, 1984; MARTINI, 1986b). The sensilla placodea had apertures which nearly cover the entire outer cuticular plate, showing dome-like internal aspect, whereas the sensilla trichodea curvata had the smaller apertures in relation to the hair size and a decreasing morphocline was observed (Figs. 9, 13 and 14). This morphocline started with Formicinae, where the aperture extended from the proximal end near to the upper inner corner of curved hair apparatuses (Fig. 13), and ended with Myrmicinae and a ponerine tribe, Ectatommini which had no extension beyond the base (Fig. 14). The other formicids were in between. This is probably due to a modification associated with the development of hair-like plate (i.e. the sensilla trichodea curvata) in Formicidae, because the hair base of the sensilla trichodea curvata of Formicinae was inserted deeply, as the plates in the sensilla placodea of other aculeates, while those of other formicids were attached only to the antennal surface (Figs. 13, 15 and 16).

Sensilla coeloconica

These had external openings connecting the chambers (Fig. 17). Most formicids had the diameter of the opening between 1.5 and 3.0 μm , and the other aculeates studied here had the range overlapping this. Some groups of Formicidae, however, had much larger openings. Few Ponerinae had the diameter ranging from 3.2 to 4.0 μm , and Dolichoderinae 4.0–4.4 μm (Fig. 18).

All non-formicid aculeates examined had the chamber of tube-form (Fig. 22). Formicidae had two different forms of the chamber, tube- and funnel-like chambers (Figs. 20 and 21). The funnel-like chamber was found only in Formicinae and Myrmeciinae.

The surface of the peg of this sensillum is striated along the length. Most aculeates had longitudinal grooves running from the tip to near the middle point, beyond which they never extended (Fig. 19). Modifications occurred in ponerine tribe Odontomachini and Ponerini, where the longitudinal grooves from the tip reached nearly the base of the peg (Fig. 20).

Sensilla ampullacea

All non-formicid aculeates studied here possessed either of two chamber types, one containing duct (Fig. 23) and the other not (Fig. 22). The duct-less condition was common in non-formicid aculeates, whereas the duct-right condition was found only in Colletidae, Megachilidae, Apidae, and Anthophoridae of Sphecoidea (aphiformes),

and the Scoliidae and Eumenidae of the Vespoidea. Either condition was found also in Formicidae, but the former type occurred rarely; it was found only in a ponerine tribe, Proceratiini (Figs. 24 and 25).

Patterns in sensilla distribution

The sensilla pattern of most Aculeata was characterized by the sensilla basiconica abundantly covering at least a half of the surface of the antennae (Fig. 27). However, groups such as some Formicinae, Dolichoderinae, some Ponerinae and Myrmicinae showed more or less a radiant arrangement of the sensilla basiconica around the surface (Fig. 28).

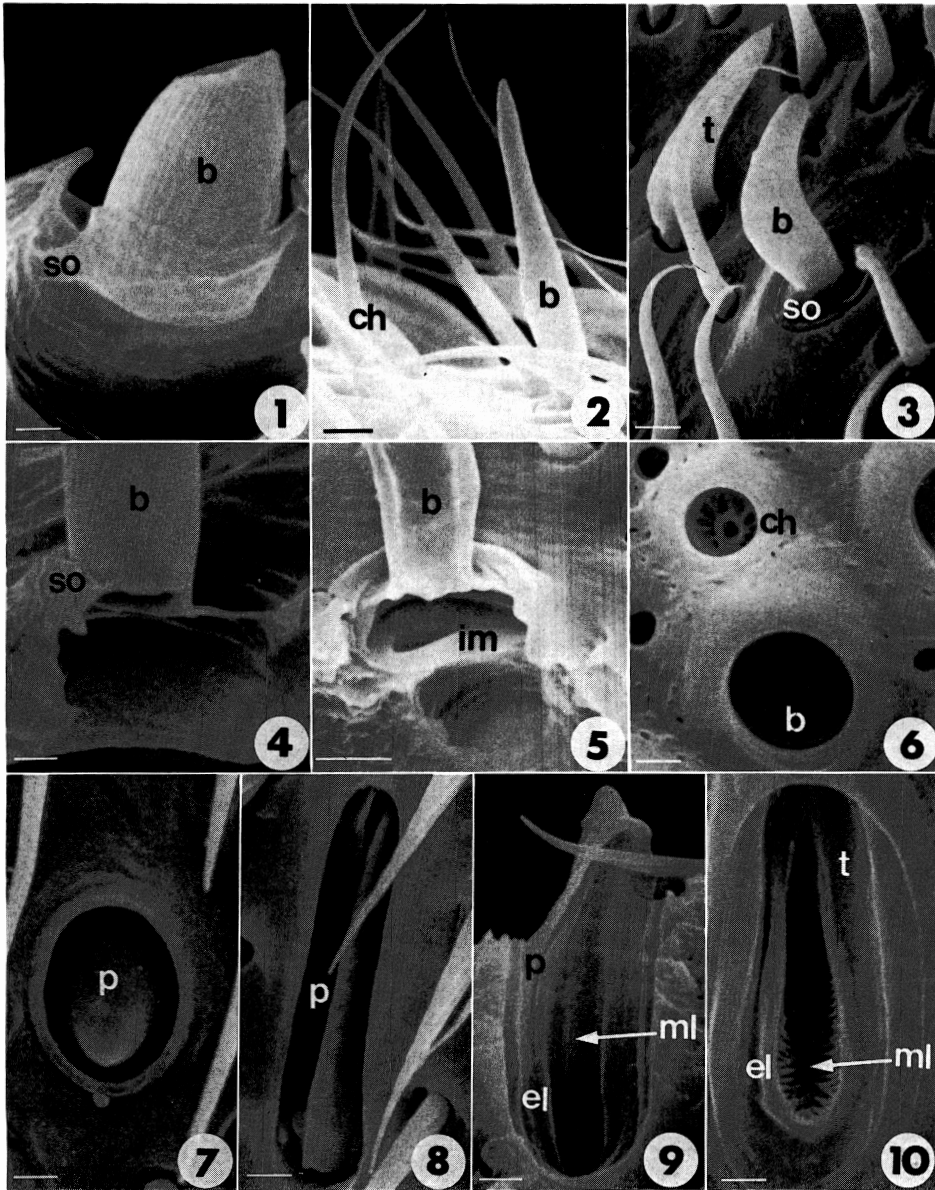
A clear increase distally in number of sensilla on the flagella was very often found in Aculeata. Nevertheless, complete loss of the sensillum structures on the proximal segments rarely occurred. Myrmicinae differed from other aculeates in having such a distribution pattern that the sensilla were concentrated on the distal 1, 2, 3 or 4 segments, and the rest of the segments had no sensillum structures but bristles which may have no sensory function, since internal aspect showed no apertures under their cuticular apparatuses (Figs. 29 and 30). All myrmicines had distinct antennal clubs, indicating that the distribution pattern may be correlated with development of club-condition.

DISCUSSION

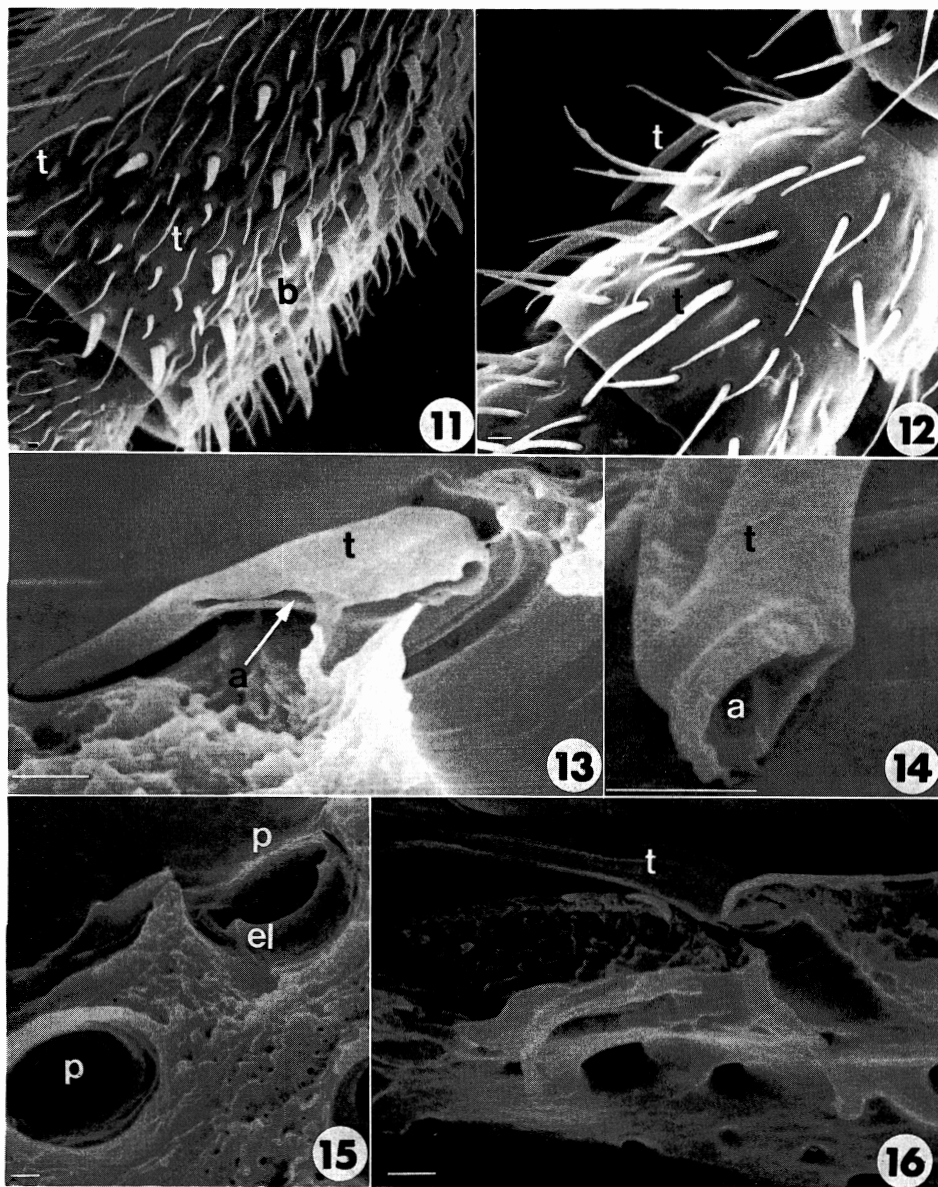
Formicidae had several unique antennal sensilla which made the family most distinctive and easily recognized of all the aculeates. Although we have, at present, no knowledge about the function, modifications in these sensilla could be associated with a high degree of olfactory sensitivity in the formicids. The protruding forms of pore plate (the sensilla trichodea curvata), for example, may provide them with higher adsorption for odorous molecules than do the flat plates. The large surface area may favor for the collection of molecules, such as in the long pegs of the sensilla basiconica, long hairs of the sensilla trichodea curvata, large openings of the sensilla coeloconica, etc. The sensilla chaetica associated with the sensilla basiconica probably act together as a functional unit which provides the animal with higher ability to distinguish more complex chemicals.

However, optimization of sensory system is probably not the only constraint in the structural features of formicid sensilla. Phylogenetic inertia is probably also a determinant of the sensillum structures, which is one of the reasons why great differences exist in the sensillum structures on the antennae of different formicid groups despite the fact that they have similar sensory needs. This may be illustrated by the sensillum structures in Dorylinae, Leptanillinae and Cerapachyinae. The members of these subfamilies are all blind "army ants" and rely exclusively on the chemosensory signals, but their sensillum structures are distinct and easily separable from one another (see Figs. 3, 11 and 12).

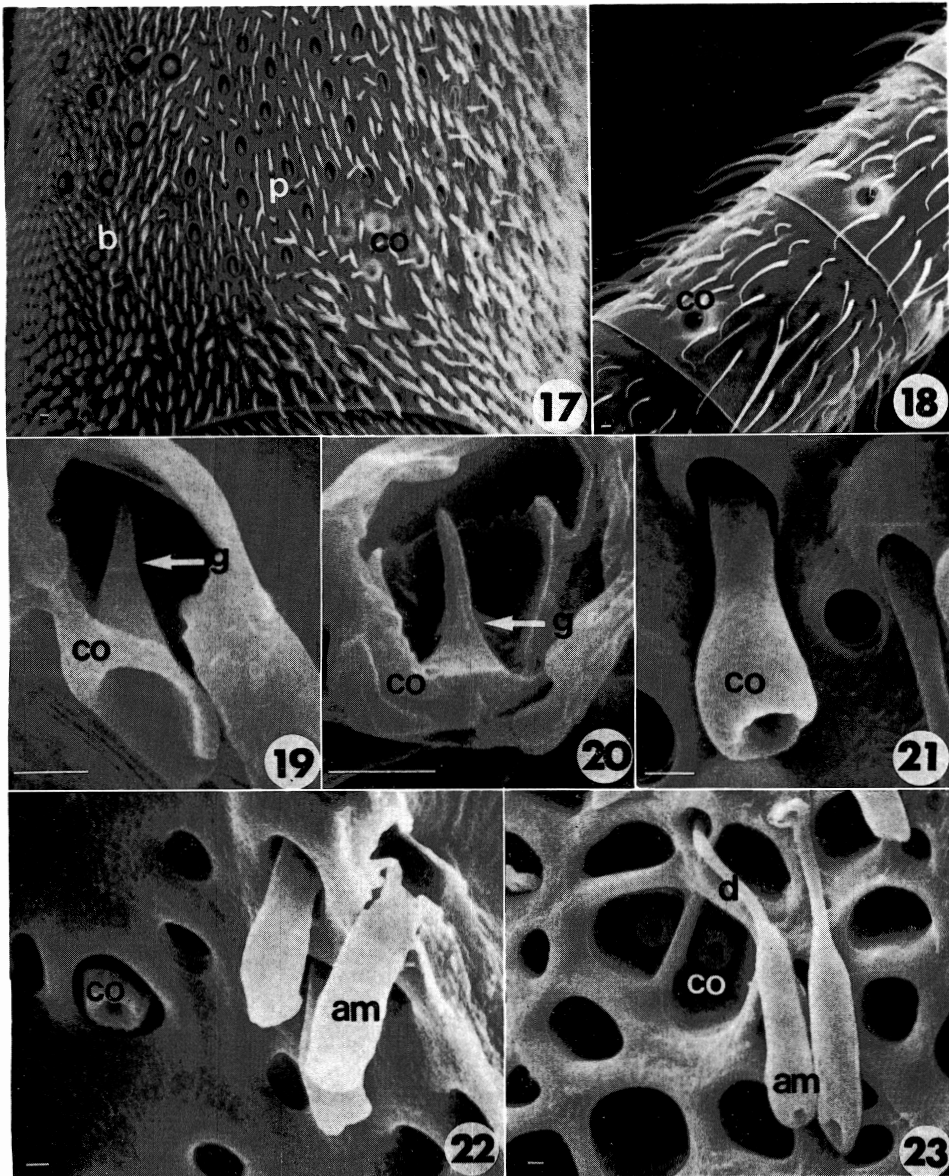
More comprehensive studies, such as those involving electrophysiology, on the antennal sensilla of Formicidae will provide new information to better understand behavior, ecology and phylogeny of this unique group of insects.



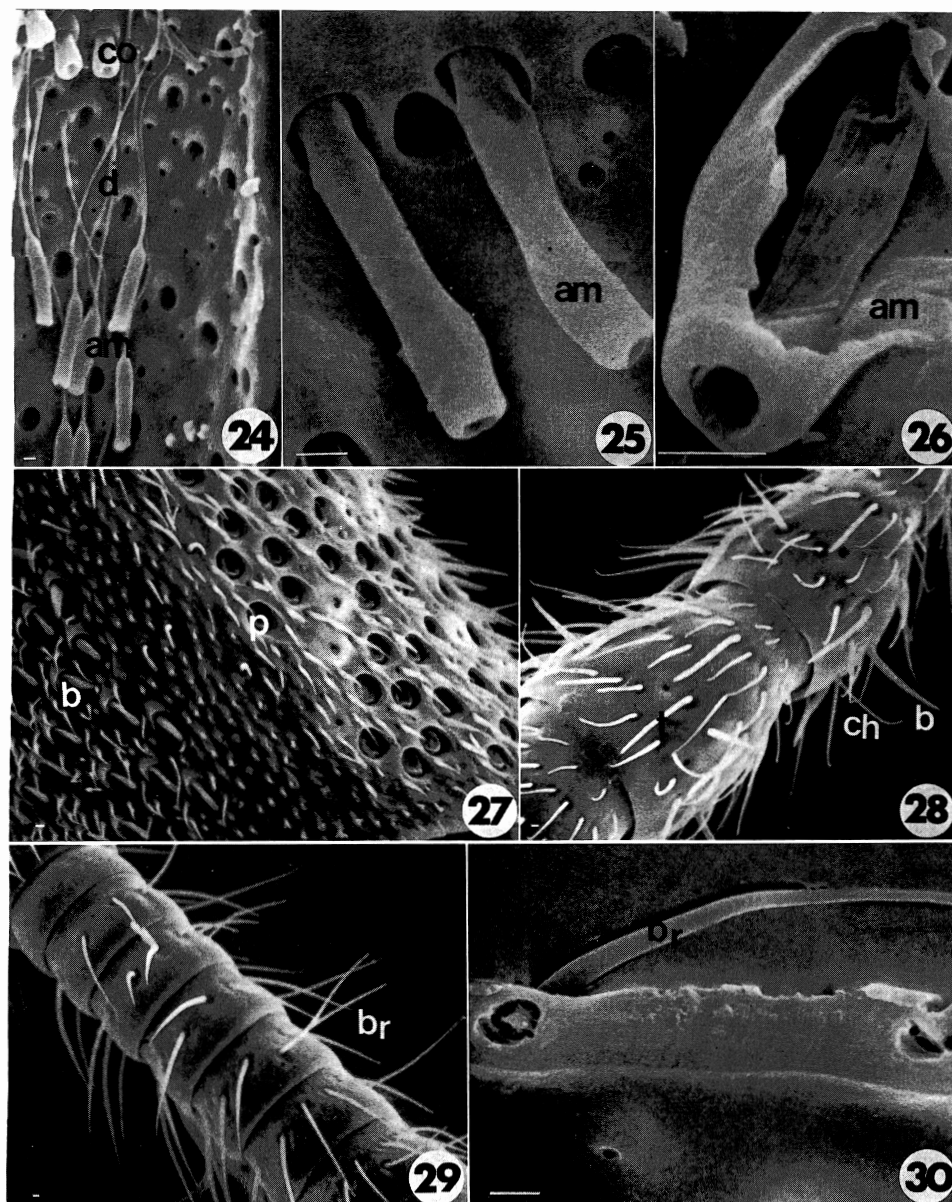
Figs. 1-10. 1-3, Pegs of the sensilla basiconica. 1, *Ampulex dissector* (Sphecidae); 2, *Cryptopone sauteri* (Ponerinae, Formicidae); 3, *Cerapachys sauteri* (Cerapachyinae, Formicidae). 4, Sockets of the sensilla basiconica. *Tetraponera allaborans* (Pseudomyrmecinae, Formicidae), longitudinal section of the socket. 5, Interior basal membrane of the sensilla basiconica. *Cerapachys sauteri* (Cerapachyinae, Formicidae), peg base longitudinally dissected to show interior basal membrane. 6, The base of the sensilla chaetica. *Oecophylla smaragdina* (Formicinae, Formicidae), internal view. 7-9, The sensilla placodea. 7, *Cleptes* sp. (Cleptidae); 8, *Anopilus samariensis* (Pompilidae); 9, *Eumenes* sp. (Eumenidae), inner view. 10, The sensilla trichodea curvata. *Paratrechina longicornis* (Formicinae, Formicidae), internal view. (Scale bar=2.5 μ m)



Figs. 11–16. 11 and 12, Different in length of the sensilla trichodea curvata. 11, *Aenictus laeviceps* (Dorylinae, Formicidae); 12, *Leptanilla japonica* (Leptanillinae, Formicidae). 13 and 14, Hair base apertures of the sensilla trichodea curvata. 13, *Camponotus japonicus* (Formicinae, Formicidae), hair base dissected to show the aperture; 14, *Aphaenogaster famelica* (Myrmicinae, Formicidae), hair removed to show the aperture. 15, The plate insertion of the sensilla placodea. *Carinoscolia melanosoma fascinata* (Scoliidae), longitudinal section of the plate. 16, Hair insertion of the sensilla trichodea curvata. *Brachyponera chinensis* (Ponerinae, Formicidae). (Scale bar=2.5 μ m)



Figs. 17–23. 17 and 18, External openings of the sensilla coeloconica. 17, *Ammophila infesta* (Sphecidae); 18, *Technomyrmex gibbosus* (Dolichoderinae, Formicidae). 19 and 20, Longitudinal sections of inner chamber of the sensilla coeloconica showing the peg. 19, *Methocha japonica* (Tiphiidae); 20, *Cryptopone sauteri* (Ponerinae, Formicidae), note that peg-surface grooves reached from the tip near to the base. 21, Inner views of the sensilla coeloconica. *Melophorus* sp. (Formicinae, Formicidae). 22–23, Inner views of the sensilla ampullacea. 22, *Ampulex dissector* (Sphecidae); 23, *Eumenes* sp. (Eumenidae). (Scale bar=2.5 μ m)



Figs. 24–30. 24–26, Inner views of the sensilla ampullacea. 24, *Lasius niger* (Formicinae, Formicidae); 25 and 26, *Proceratium japonicum* (Ponerinae, Formicidae), 26: chamber dissected to show inner hair. 27–30, Pattern in sensilla distribution. 27 and 28, The different arrangements of the sensilla basiconica. 27, *Chrysis shanghaiensis* (Chrysididae); 28, *Pheidole pيلي* (Myrmicinae, Formicidae). 29, Basal antennal segments. *Myrmecina graminicola nipponica* (Myrmicinae, Formicidae), note that the segments have bristles only. 30, The bristle dissected to show the base. *Smithistruma japonica* (Myrmicinae, Formicidae), note that the bristles have no apertures at the base of cuticular apparatuses. (Scale bar=2.5 μm)

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