

Phylogenetic Study of the Family Formicidae based on the Sensillum Structures on the Antennae and Labial Palpi (Hymenoptera, Aculeata)

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Abstract The present study analyzed the sensillum structures on the antennae and labial palpi of Formicidae to test hypotheses proposed for the higher-level phylogeny of this family. Sensillum structures examined were the sensilla basiconica, sensilla trichoidea curvata, sensilla coeloconica, sensilla ampullacea, setiform sensilla and button-like sensilla. A cladistic analysis of the relationships of nine subfamilies was made based on fifteen morphological characters. Plesiomorphic and apomorphic states of the characters were determined by outgroup comparison with non-formicid aculeates. The recognized patterns in nesting relationships were: (((Leptanillinae + Cerapachyinae + Amblyoponini of Ponerinae + Proceratiini of Ponerinae) + (Ponerini of Ponerinae + Odontomachini of Ponerinae) + (Ectatommini of Ponerinae + Myrmicinae) + Dorylinae) + (Pseudomyrmecinae + Myrmeciinae)) + Dolichoderinae) + Formicinae. The close relationship between Cerapachyinae and Dorylinae, and that between Proceratiini and Ectatommini of Ponerinae, both of which were proposed by earlier authors, were not supported. The validity of Ponerinae to be placed as a monophyletic taxon was questioned.

Key words: Phylogeny; Formicidae; antennae; labial palpi; sensilla.

Introduction

The Formicidae are currently divided into ten subfamilies: Myrmeciinae, Pseudomyrmecinae, Formicinae, Dolichoderinae, Aneuretinae, Dorylinae, Leptanillinae, Cerapachyinae, Ponerinae and Myrmicinae (WHEELER & WHEELER, 1972). Several authors have tried to clarify the phylogeny of these subfamilies, but the conclusions reached by these authors varied to a great extent (*e.g.*, WHEELER, 1928; BROWN, 1954; TAYLOR, 1978, etc.). It is necessary to scrutinize different hypotheses proposed for the higher-level phylogeny of Formicidae.

The scanning electron microscope (SEM) offered many new morphological characters for systematic study of insects. Sensillum structure on the antennae and other appendages are included in these characters, which can provide useful information to reconstruct their phylogeny, as has been demonstrated by KRZYWIEC (1968), MEINECKE (1975), BOHART and MENKE (1976), WALTHER (1979), BARLIN and VINSON (1981), etc. Although never has the phylogenetic significance of the sensillum structures been realized in Formicidae, these structures are expected to

be of value in phylogenetic analysis of this family (HASHIMOTO, 1990).

The present study analyzed the sensillum structures on the antennae and labial palpi of Formicidae to test hypotheses about the higher-level phylogeny of this family by new characters. Particular emphasis was placed on the subfamily Ponerinae, because the subfamily is extremely heterogeneous and poorly delineated on the traditional taxonomic criteria.

Materials and Methods

Taxa examined: The species examined were listed in Table 1. Because the worker is by far the best known and most available caste, worker specimens were investigated. Female specimens of some other aculeates were also examined for the outgroup comparison. Because the subfamily Aneuretinae cannot be examined, it was not included in this analysis.

The higher classification system of Aculeata proposed by BROTHERS (1974) and the formicid classification by WHEELER and WHEELER (1985) were used as guidelines.

Phylogenetic method: The phylogenetic analysis was made according to the Hennigian method (1966), where the phylogenetic relationships of the taxa are analyzed based on shared derived features (synapomorphies), but not on shared primitive features (symplesiomorphies), nor on independently derived features. To determine character polarities, outgroup comparison was adopted. This is summarized as follows: When two or more states for a given character were observed within a group, the most widespread state in the close relatives of the group should be regarded as a plesiomorphic state (cf. WILEY, 1981). Accordingly, the polarities of character states were assigned based on the comparison with those found in the other Aculeata.

SEM observation: The antennae and labial palpi were examined by SEM. The samples were cleaned by an ultrasonic-washer in the 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 sensillum morphology followed after WALTHER (1979).

Abbreviations used for figures were: a: aperture; am: sensilla ampullacea; b: sensilla basiconica; br: bristle; bu: button-like sensilla; ch: sensilla chaetica; co: sensilla coeloconica; d: duct; el: encircling ledge; g: groove; im: internal basal membrane; ml: middle ledge; p: sensilla placodea; s: setiform sensilla; so: socket; t: sensilla trichoidea curvata.

Table 1. List of taxa examined.

Vespoidea: Formiciformers

Formicidae

Formicinae: *Acropyga baodaoensis* TERAYAMA, *Anoplolepis longipes* (JERDON), *Camponotus haberei* FOREL, *C. japonicus* MAYR, *C. nipponicus* WHEELER, *Echinopla* sp., *Formica fukaii* WHEELER, *F. japonica* MOTSCHULSKY, *Lasius flavus* (FABRICIUS), *L. niger* (LINNAEUS), *Melophorous* sp., *Oecophylla samaragdina* FABRICIUS, *Paratrechina bourbonica* (FOREL), *Plagiolepis* sp., *Polyergus samurai* YANO, *Polyrhachis dives* F. SMITH, *Prenolepis* sp., *Prolasius* sp.

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

Myrmeciinae: *Myrmecia gulosa* (FABRICIUS), *M.* sp.

Pseudomyrmecinae: *Tetraponera allaborans* WALKER, *T.* sp.

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

Leptanillinae: *Leptanilla japonica* BARONI URBANI

Cerapachyinae: *Cerapachys biroi* FOREL, *C. sauteri* FOREL, *C.* sp.

Myrmicinae: *Aphaenogaster famelica* (F. SMITH), *Cardiocondyla nuda* (MAYR), *Cataulacus* sp., *Crematogaster matsumurai* FOREL, *Epitritus hexamerus* BROWN, *Kyidris mutica* BROWN, *Messor aciculatus* (Fr. SMITH), *Myrmecina graminicola nipponica* WHEELER, *Myrmica jessensis* FOREL, *Oligomyrmex sauteri* FOREL, *Pentastruma canina* BROWN et BOISVERT, *Pheidole pيلي* SANTSCHI, *Pheidogeton* sp., *Pristomyrmex pungens* MAYR, *Smithistruma japonica* (ITO), *Solenopsis* sp., *Strumigenys lewisi* CAMERON, *Tetramorium caespitum* (LINNAEUS), *Vollenhovia emeryi* WHEELER

Ponerinae: Amblyoponini: *Amblyopone australis* ERICHSON, *A. silvestrii* (WHEELER)

Proceratiini: *Proceratium japonicum* SANTSCHI, *P. watasei* (WHEELER), *P. itoi* FOREL, *Discothyrea sauteri* FOREL, *D.* sp.

Ectatommini: *Gnamptogenys costata* (EMERY), *Rhytidoponera purpurea* (EMERY), *R.* sp.

Ponerini: *Brachyponera chinensis* (EMERY), *Cryptopone sauteri* (WHEELER), *Diacamma* sp., *Ectomomyrmex javanus* MAYR, *Hypoponera nippona* (SANTSCHI), *Odontoponera transversa* (Fr. SMITH), *Ponera japonica* WHEELER, *P. scabra* WHEELER, *Trachymesopus pilosior* (WHEELER), *T. sharpi* FOREL, *Trapeziopelta* sp.

Odontomachini: *Odontomachus monticola* EMERY, *O.* sp., *Anochetus* sp.

Vespoidea: Vespiformes

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

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

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

Scoliidae: *Carinoscolia melanosoma fasciata* (SMITH), *Megacampsomeris grossa matsumurai* (BETEREM)

Masaridae: *Pseudomasaris coquilletti* ROHWER

Eumenidae: *Discoelius 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 japonica* YASUMATSU et HIRASHIMA

Megachilidae: *Anthidium septemspinatum* LEPELETIER

Anthophoridae: *Xylocopa appendiculata circumvolans* SMITH

Apidae: *Trigona* sp.

Bethylidae: *Cephalonomia gallicola* (ASHMEAD)

Chrysididae: *Chrysis shanghaiensis* SMITH

Cleptidae: *Cleptes* sp.

Dryinidae: *Haplogonatopus apicalis* PERKINS

Table 2. Distribution of character-states among subfamilies in Formicidae.
Character numbers and character states are denoted in text.

Character No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Formicinae	0	0	0	0	0	1	0	0	0	1 a	0	0	0	0	0
Dolichoderinae	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0
Myrmeciinae	0	0	1	0	0	1	1	1	0	1 b	0	0	0	0	0
Pseudomyrmecinae	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0
Dorylinae	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0
Leptanillinae	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1
Cerapachyinae	1 b	0	0	0	1	1	1	1	0	0	0	0	0	1	1
Ponerinae															
Amblyoponini	0	1	0	0	0	1	1	1	0	0	0	0	0	1	1
Proceratiini	0	0	0	0	0	1	1	1	0	0	0	1	0	1	1
Ponerini	1 a	0	0	0	0	1	1	1	0	0	1	0	0	1	0
Odontomachini	1 a	0	0	0	0	1	1	1	0	0	1	0	0	1	0
Ectatommini	0	1	0	0	0	1	2	1	0	0	0	0	0	1	0
Myrmicinae	0	1	0	0	0	1	2	1	0	0	0	0	1	1	0

Results

The structural features of four types of antennal sensilla (sensilla basiconica, sensilla trichoidea curvata, sensilla coeloconica, and sensilla ampullacea) and two types of labial sensilla (setiform sensilla and button-like sensilla) were analyzed in the formicids and in other aculeates.

The morphological characteristics and character states of these sensillum structures were described as below, where (0) means plesiomorphic condition, (1), (1 a), (1 b) and (2) apomorphic conditions, and (0 to 1), (0 to 1 a), (0 to 1 b) or (0 to 2) transformation series. The distribution of the character states within Formicidae was shown in Table 2.

Antennae

Sensilla basiconica.

This type of sensilla always consists of two parts, a peg and a socket which is the membrane connecting the peg with the antennal cuticle (WALTHER, 1981; MARTINI, 1986 a) (Figs. 1 and 6).

Character 1 (0 to 1 a; 0 to 1 b)

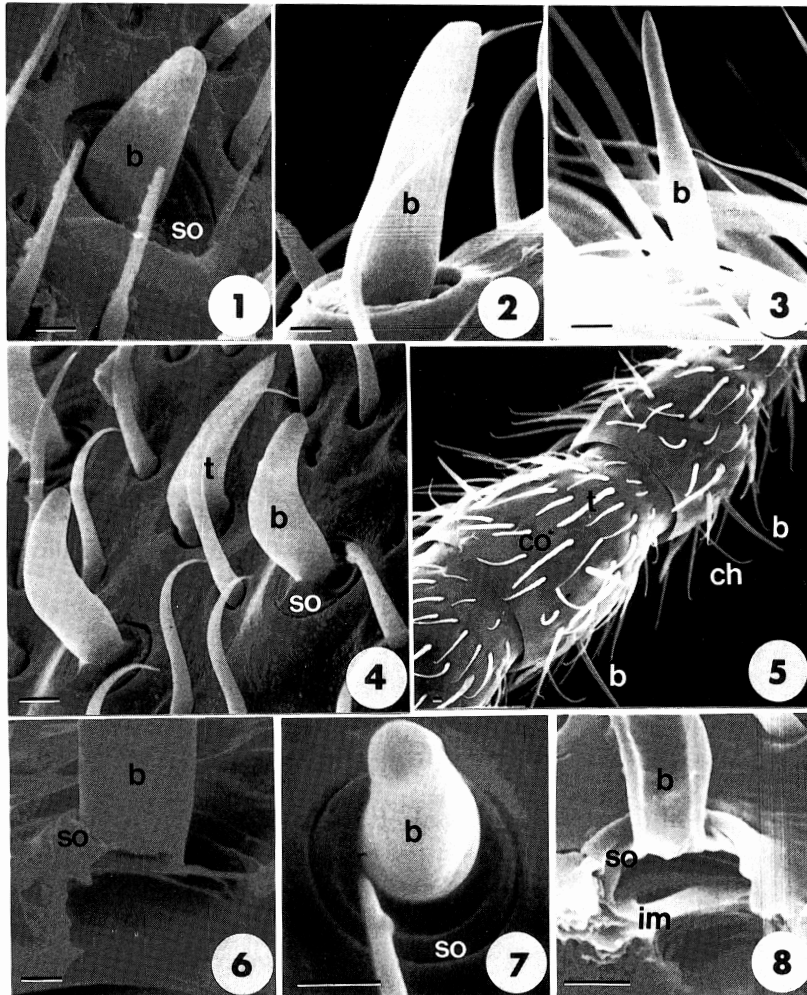
Peg stout and almost straight with a blunt tip—(0) (Fig. 2), slender, narrowed apically and basally, with the apex pointing—(1 a) (Fig. 3), or thin and greatly bent—(1 b) (Fig. 4).

Character 2 (0 to 1)

Peg short ($<20\ \mu\text{m}$)—(0), or long ($>30\ \mu\text{m}$)—(1) (Fig. 5).

Character 3 (0 to 1)

Socket flush with the antennal surface—(0), or greatly elevated above the sur-



Figs. 1–8. The sensilla basiconica. — 1–5. Pegs of the sensilla basiconica: 1, *Tiphia latistriata* (Tiphidae); 2, *Dorylus* sp. (Dorylinae, Formicidae); 3, *Cryptopone sauteri* (Ponerinae, Formicidae); 4, *Cerapachys sauteri* (Cerapachyinae, Formicidae); 5, *Pheidole pieli* (Myrmicinae, Formicidae). — 6–8. Sockets of the sensilla basiconica: 6, *Tetraponera allaborans* (Pseudomyrmecinae, Formicidae), longitudinal section of the socket; 7, *Iridomyrmex itoi* (Dolichoderinae, Formicidae); 8, internal basal membrane of the sensilla basiconica. *Cerapachys biroii* (Cerapachyinae, Formicidae), peg base longitudinally dissected to show internal basal membrane. (Scale bar = $2.5\ \mu\text{m}$)

face—(1) (Fig. 6).

Character 4 (0 to 1)

Socket flat—(0), or with raised rim—(1) (Fig. 7).

Character 5 (0 to 1)

Internal basal membrane absent—(0), or present—(1) (Fig. 8).

Sensilla trichoidea curvata.

This sensillum is a "curved hair", possessing an encircling and a middle cuticular ledges (Fig. 11). Since these ledges are features characteristic to the pore plate sensilla (Fig. 10), the sensilla trichoidea curvata can be regarded as a homologue of sensilla placodea (WALTHER, 1981; MARTINI & SCHMIDT, 1984; MARTINI, 1986 b).

Character 6 (0 to 1)

Plate type—(0) (Fig. 8), or hair type—(1) (Fig. 11).

Character 7 (0 to 2)

The basal aperture of the hair extended from the proximal end near to the upper inner corner of curved hair apparatuses—(0) (Fig. 12), showed intermediate in the state between (0) and (2)—(1), or never extended beyond the base—(2) (Fig. 13).

Character 8 (0 to 1)

Hair inserted into the antennal cuticle deeply—(0) (Fig. 14), or shallowly—(1) (Fig. 15).

Sensilla coeloconica.

The sensilla coeloconica are pegs with longitudinal groove in the chamber below the antennal surface (Fig. 18).

Character 9 (0 to 1)

Opening small (diameter $< 3.0 \mu\text{m}$)—(0) (Fig. 16), or large ($> 4.0 \mu\text{m}$)—(1) (Fig. 17).

Character 10 (0 to 1 a) (0 to 1 b)

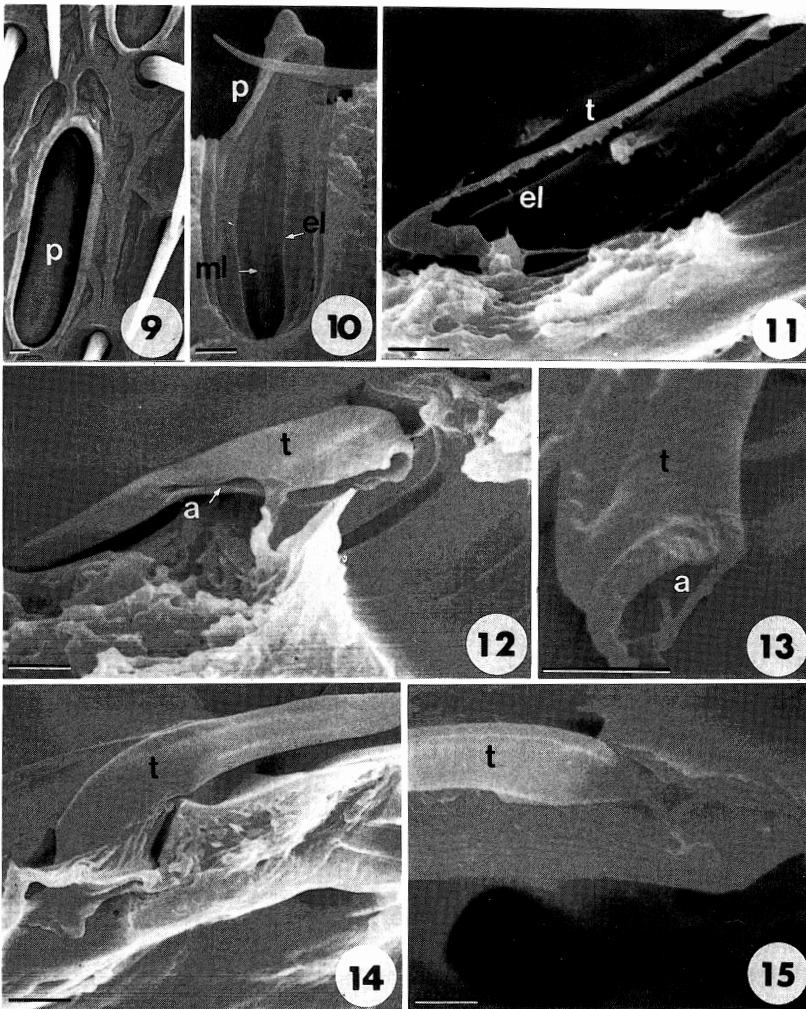
Chamber tube-form—(0) (Fig. 19), funnel-form—(1 a) (Fig. 20), or both—(1 b).

Character 11 (0 to 1)

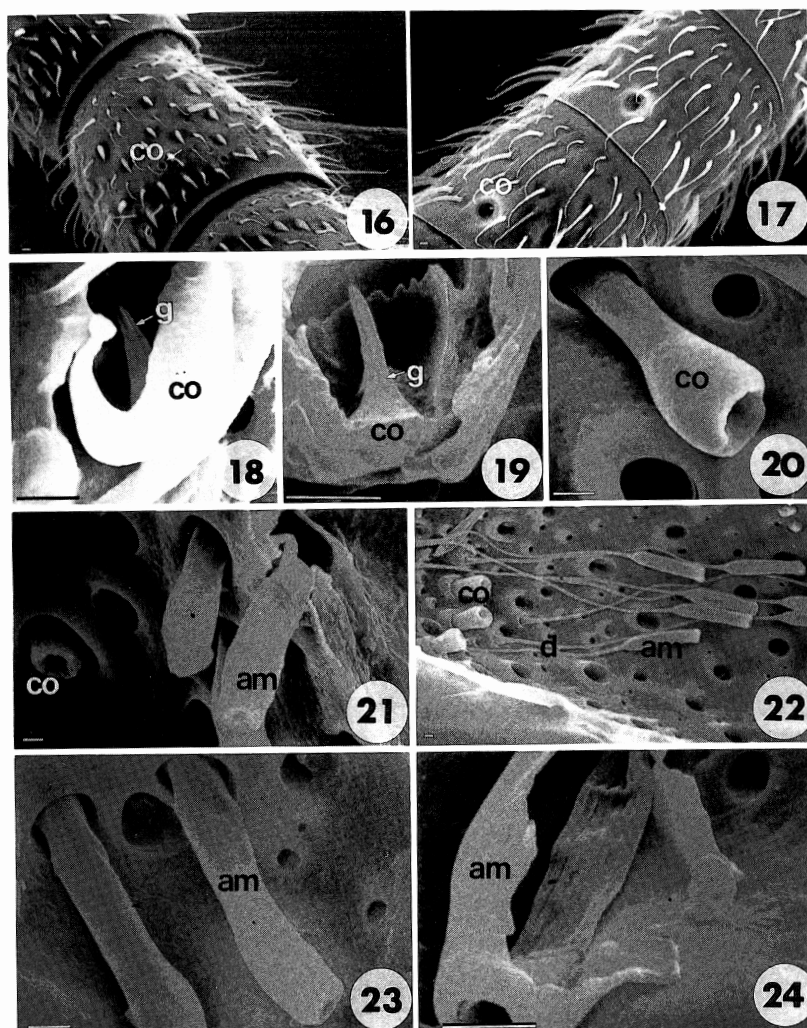
Surface grooves of the peg not extending basally beyond the midpoint—(0) (Fig. 18), or reaching nearly the base—(1) (Fig. 19.)

Sensilla ampullacea.

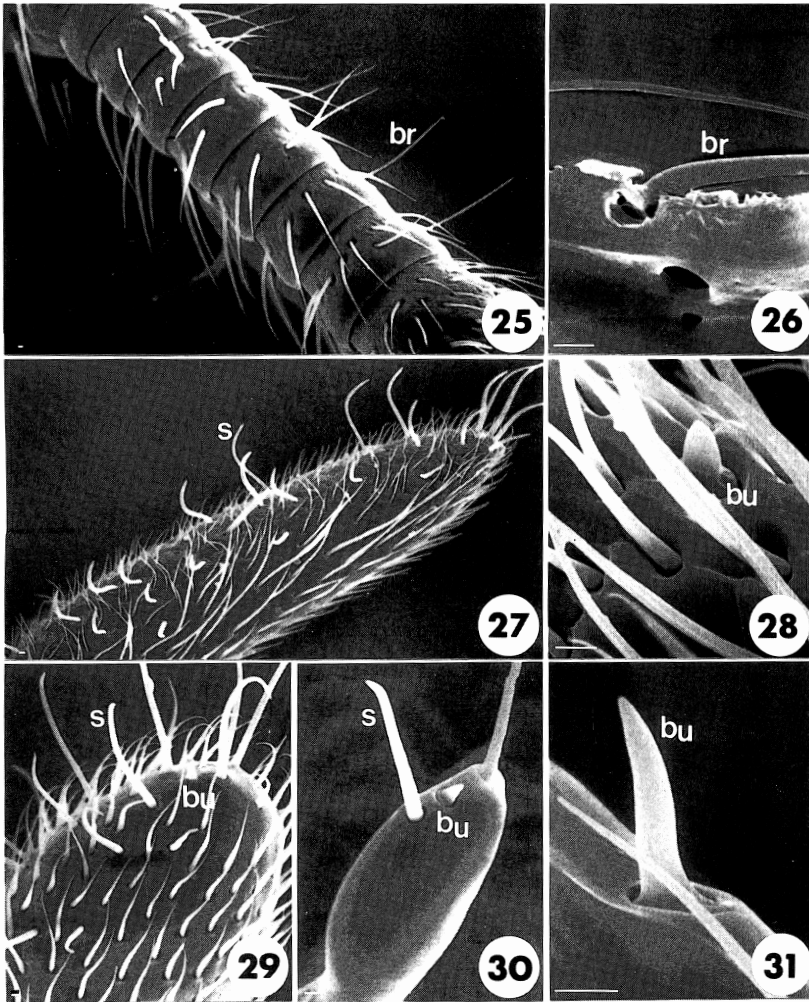
The sensilla ampullacea resemble the coeloconic sensilla, but are distinct in the chamber being more deeply situated (Fig. 21) and different surface structure of the sense hair in the chamber (Fig. 24).



Figs. 9–15. — 9–10. The sensilla placodea: 9, *Discoelius japonicus* (Eumenidae); 10, *Eumenes* sp., inner aspect. — 11–15. The sensilla trichoidea curvata: 11, *Polyergus samurai* (Formicinae, Formicidae), longitudinal section of hair; 12–13, hair base apertures of the sensilla trichoidea curvata, 12, *Camponotus japonicus* (Formicinae, Formicidae), hair base dissected to show the aperture; 13, *Aphaenogaster famelica* (Myrmicinae, Formicidae), hair removed to show the aperture); 14–15, hair insertion of the sensilla trichoidea curvata, 14, *Camponotus japonicus* (Formicinae, Formicidae); 15, *Cerapachys biroii* (Cerapachyinae, Formicidae). (Scale bar = 2.5 μ m)



Figs. 16–24. — 16–20. The sensilla coeloconica: 16–17, external openings of the sensilla coeloconica, 16, *Lasius niger* (Formicinae, Formicidae); 17, *Technomyrmex gibbosus* (Dolichoderinae, Formicidae); 18–19, longitudinal sections of inner chamber of the sensilla coeloconica showing the peg, 18, *Crematogaster matsumurai* (Myrmicinae, Formicidae); 19, *Cryptopone sauteri* (Ponerinae, Formicidae), note that peg-surface grooves run from the tip near to the base; 20, inner views of the sensilla coeloconica, *Melophorous* sp. (Formicinae, Formicidae). — 21–24. Inner views of the sensilla ampullacea: 21, *Ampulex dissector* (Sphecidae); 22, *Lasius niger* (Formicinae, Formicidae); 23–24, *Proceratium japonicum* (Ponerinae, Formicidae), 24, chamber dissected to show inner hair. (Scale bar = 2.5 μ m)



Figs. 25–31. — 25–26. Distribution pattern of sensilla: 25, basal segments of antennal funiculus, *Myrmecina graminicola nipponica* (Myrmicinae, Formicidae), note that the segments have bristles only; 26, the bristles dissected to show the base, *Smithistruma japonica* (Myrmicinae, Formicidae), note that the bristles have no apertures at the base of cuticular apparatus. — 27–31. Labial-palp sensilla: 27–28, *Mutilla europaea mikado* (Mutillidae), 28, close-up of the tip of labial palp, note button-like sensillum; 29, *Myrmecia gulosa* (Myrmeciinae, Formicidae); 30, *Cryptopone sauteri* (Ponerinae, Formicidae); 31, *Proceratium watasei* (Ponerinae, Formicidae), close-up of the tip of labial palp showing button-like sensillum. (Scale bar=2.5 μ m)

Character 12 (0 to 1)

The internal chamber flask-form—(0) (Fig. 22), or tube-form—(1) (Fig. 23).

Pattern of sensilla distribution.

Character 13 (0 to 1)

The sensilla of all types showed rather homogenous distribution—(0), or concentrated in apical segments—(1) (Fig. 25).

Labial palpi*Setiform sensilla.*

These are slender hairs pointing sharply (Fig. 27).

Character 14 (0 to 1)

The palpus covered with the setiform sensilla densely—(0) (Fig. 29), or sparsely—(1) (Fig. 30).

Button-like sensilla.

This sensillum is a peg set in a socket on the tip of last labial-palp segment (Fig. 28).

Character 15 (0 to 1)

The peg short ($< 5 \mu\text{m}$)—(0) (Fig. 30), or long ($> 5 \mu\text{m}$)—(1) (Fig. 31).

Discussion

The sensillum structures studied here provided synapomorphic states for the following nested patterns of relationships among the formicid subfamilies.

Ectatommini of Ponerinae and Myrmicinae were grouped together based on the long peg of the sensilla basiconica (character 2) and small hair-base aperture of the sensilla trichoidea curvata (character 7). Though Amblyoponini of Ponerinae also had the long pegs of the sensilla basiconica (see Table 2), this may be convergent with the two taxa mentioned above because a close relationship between Amblyoponini and (Ectatommini + Myrmicinae) was contradicted by the character states of other sensillum structures (characters 7 and 15). Ponerini and Odontomachini of Ponerinae were grouped together by a unique peg shape of the sensilla basiconica (character 1) and a unique surface groove condition in the pegs of the sensilla coeloconica (character 11). Leptanillinae, Cerapachyinae, and Amblyoponini and Proceratiini of Ponerinae were grouped together by the elongated peg of the labial button-like sensilla (character 15). Although relationships among these three groups (Ectatommini + Myrmicinae, Ponerini + Odontomachini, Leptanillinae + Cerapachyinae + Amblyoponini + Proceratiini)

were not clarified in this study, these groups and Dorylinae were grouped by a synapomorphy, *i.e.*, smooth labial palpi with reduced hairs (character 14). Myrmeciinae and Pseudomyrmecinae formed a group based on the strongly elevated socket of the sensilla basiconica (character 3), which is the sister group of Dorylinae + Leptanillinae + Cerapachyinae + Ponerinae + Myrmicinae, based on the hairs inserted shallowly into the antennal cuticle of the sensilla trichoidea curvata (character 8). Dolichoderinae was the sister group of the monophyletic component consisting of the above seven subfamilies based on the transformation series of the hair-base aperture of the sensilla trichoidea curvata (character 7), and these together constituted the sister group of Formicinae based on the hair-like plates (*i.e.*, the sensilla trichoidea curvata) (character 6). As the sensilla placodea of Hymenoptera have been believed to have evolved from hair-type sensilla (VOGEL, 1923), the sensilla trichoidea curvata were previously interpreted as precursors of the sensilla placodea (WACKER, 1925). This hypothesis, however, must assume independent origin of sensilla placodea within each lineage of Aculeata, because the plate sensilla were well developed in the other aculeates which must be earlier derived groups than Formicidae, such as Bethyloidea and Sphecoidea (cf. BROTHERS, 1974). Alternatively, if the sensilla placodea evolved once in the Aculeata, the hair-like plate of Formicidae must be the results of the reversal evolution. Thus, the most parsimonious interpretation for the restricted distribution of the sensilla trichoidea curvata only within Formicidae would be that these sensilla are derivatives of the plate of sensilla placodea, *i.e.*, the hair-like plate was an apomorphic state in the Formicidae.

The basic concept for phylogeny of formicid subfamilies had been treated in three different manners (*e.g.*, WHEELER, 1928; BROWN, 1954; TAYLOR, 1978). Based on the above nested patterns of relationships among the subfamilies, the basic concepts for formicid phylogeny were scrutinized. WHEELER (1928) hypothesized that the ponerines as the most primitive group from which the other subfamilies directly diverged. Despite no convincing evidence given by WHEELER (*loc. cit.*), REID (1941) has pointed out that ponerines display most diverse thoracic characters, which probably supports the WHEELER's hypothesis. However, there exists no reason why an ancestral group should be most diversified in morphology. Even though, for example, the fossil record suggests that the myrmicines are considered as the most recently derived group of the formicids (cf. BROWN, 1973), they display by far the greatest diversity in morphology such as of mouthpart (GOTWALD, 1969) and larval structures (WHEELER & WHEELER, 1976). The sensillum characters did not support WHEELER (1928), because accepting the hypothesis of ponerine origin for other formicids required numbers of unlikely reversions in character-state evolution of the sensillum structures (characters 1, 2, 7, 8, 11, 14 and 15).

BROWN (1954) proposed that the formicids split early in their evolution into two phylands: the Poneroid phyland including Ponerinae, Myrmicinae, Dorylinae, Leptanillinae and Cerapachyinae, and the Myrmecioid phyland including

Myrmeciinae, Pseudomyrmecinae, Dolichoderinae and Formicinae. WILSON, *et al.* (1967), supporting BROWN (1954), emphasized a possibility that the formicids may be derived twice in evolution. Though BROWN (1954) and WILSON *et al.* (1967) did not explicitly state the character data dividing the Poneroid and Myrmecioid phylands, it is most probable from their discussion that these two phylands were established by the overall similarities of the primitive members of each of the phylands, which implies that they might be based on the symplesiomorphic states. Because symplesiomorphies have no value for determining the phylogenetic relationships, the two phylands proposed by BROWN (1954) may or may not represent phylogenetic reality. The present study indicated that the members of both phylands shared the fundamental homogeneous structures in the sensilla and that all the formicids studied here were grouped together by the possession of the sensilla trichoidea curvata (see Table 2, character 6). The deep split proposed by BROWN (1954) in the formicid evolution was, therefore, not found in the sensillum structures.

TAYLOR (1978), modifying BROWN (1954), transferred *Myrmecia* of Myrmeciinae but the other myrmeciine genus *Nothomyrmecia*, and Pseudomyrmecinae from the Myrmecioid phyland to the Poneroid phyland. He proposed that his Poneroid and Myrmecioid phylands (which was renamed "Formicioid") represent separate and two major lineages in the formicid phylogeny. This modification was based largely on either fused or separate sclerites of the 4th abdominal segment. The members of Poneroid phyland and also *Myrmecia* of Myrmeciinae and Pseudomyrmecinae had fused sclerites, whereas they were unfused in the other members of Myrmecioid phyland. However, the unfused condition in the members of the Formicioid phyland may be symplesiomorphic, because this is a condition occurring in most aculeates. Though *Nothomyrmecia* were not available in this study, the monophyly of Formicinae+Dolichoderinae, at least, was not supported by the sensillum characters. Instead, this study indicated that these subfamilies were derived independently from the main formicid stock at very early time, because they shared no apomorphic characters and bore relatively few, but unique, sensillum characters in derived states (see Table 2, characters 4, 9 & 10). Consequently, each of the three phylogenies for the formicid subfamilies was not supported by this study.

The present study can also shed new light on some problems puzzling formicid systematists. WHEELER (1928) related Pseudomyrmecinae and Myrmicinae based on two segmental elements of the petiole. However, two segmented petiole occurred independently in Pseudomyrmecinae, Myrmicinae, Myrmeciinae, some Dorylinae, Leptanillinae, Cerapachyinae and some Ponerinae. BROWN (1954) related Pseudomyrmecinae to Myrmeciinae instead of to Myrmicinae, but he did not provide any convincing evidence for this relationship. Though EINSNER (1957), supporting BROWN (1954), indicated that the proventriculus of Pseudomyrmecinae was similar to that of Myrmeciinae, the similarity may be due to

symplesiomorphy because their proventriculus is the same type found in most other Aculeata. The sensillum character corroborated BROWN (1954), as indicated above (character 3).

The cerapachyines have been considered to be ancestral to Dorylinae, which serves as a transitional taxon from Ponerinae to Dorylinae (EMERY 1895; WHEELER & WHEELER, 1985), though REID (1941) did not support this view based on the thoracic structures. The present study supported neither the cerapachyine origin of the dorylines nor the intermediate placement of cerapachyines between Ponerinae and Dorylinae. The sensillum structures of cerapachyines and ponerines were more specialized than those of the dorylines. Particularly, the cerapachyines had uniquely modified pegs of the sensilla basiconica (character 1), a condition that the dorylines could not arise. Relatedness of cerapachyines with some ponerines, such as Amblyoponini and Proceratiini, was proposed by the thoracic characters (REID, 1941) and the mouthpart characters (GOTWALD, 1969). This was supported also by the sensillum characters as in character 15.

Ectatommini of Ponerinae was considered as the ancestral relative of Myrmicinae, because Myrmicinae retained some primitive characters of the ectatommines and a fossil genus *Agroecomyrmex* may provided a transitional form (BROWN, 1954). However, no apomorphic states were found to indicate a sister-group relationship between them. The present study provided two synapomorphies for Myrmicinae + Ectatommini (characters 2 and 7).

BROWN (1958) affiliated Proceratiini with Ectatommini, based on the morphological resemblances observed in *Proceratium* of Proceratiini and *Heteroponera* of Ectatommini. However, WHEELER and WHEELER (1976) disagreed with him (1958). They indicated that larvae of Proceratiini differed from those of *Heteroponera* and from those of any other known ectatommines. Although *Heteroponera* have not been examined, the present result was not consistent with BROWN (1958) because the sensillum structures of Proceratiini differed greatly from those of Ectatommini, particularly in the structures of the sensilla ampullacea; in no other formicid taxa the ductless chamber was found (character 12). Though the ductless chamber was common in Aculeata, the condition in Proceratiini suggested its secondary derivation, rather than a retained plesiomorphic state, because the chamber of Proceratiini had still markedly narrow part, unlike the ductless chamber of other aculeates.

Odontomachini of Ponerinae is the most distinctive and easily recognized of all the Formicidae by its unusual head and mandibles. Though the distinctiveness of the head and mandibles tends to obscure their phylogenetic relationship to the other formicids, BROWN (1976) related Odontomachini to Ponerini based on similarities observed in the larvae. The sensillum character of adult Odontomachini and Ponerini supported BROWN (1976), as in characters 1 and 11.

Based on the sensilla characters, the following subfamilies of Formicidae were delimited: Formicinae was characterized by the character 10, Dolichoderinae by

the characters 4 and 9, Myrmeciinae by the character 10, Cerapachyinae by the characters 1 and 5, and Myrmicinae by the character 13, though more comparative data were needed to determine that these structures are available throughout taxa. It should be noted that the validity of Ponerinae was questioned in this study, because the sensillum characters indicated that examined members of this subfamily should be divided into groups some of which are closely related to other subfamilies; group (1) Amblyoponini and Proceratiini which constitute a monophyletic component together with Cerapachyinae and Leptanillinae, group (2) Ponerini and Odontomachini, group (3) Ectatommini which is the sister group of Myrmicinae. Ponerinae is the most heterogeneous group of Formicidae, and the character states delimiting this subfamily may be plesiomorphic for Formicidae (cf. DALLA TORRE, 1893; REID, 1941; WHEELER & WHEELER, 1964; GOTWALD, 1969). Since extensive variations in morphology and behavior exist, CLARK (1951) even divided the ponerines into several subfamilies: Amblyoponinae, Discothyriinae, Odontomachinae and Ponerinae. Although CLARK's classification was not supported by this study and the final conclusion of taxonomic status for ponerines must await for further investigation, I am tempted to consider Ponerinae as a subfamily unwarranted.

The present results suggested that the existing concepts of phylogeny and higher taxa of Formicidae should be changed. A more realistic phylogeny can be approached by testing and retesting of new characters such as sensillum characters used in this study.

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