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Skeletomuscular Modifications Associated with the Formation of an Additional Petiole on the Anterior Abdominal Segments in Aculeate Hymenoptera

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Abstract The skeletomusculature of the anterior abdominal segments in Aculeata was examined to discuss the relationships among Formicidae, Vespidae (s.l.) and Scoliidae, and phylogeny among Formicidae. On the basis of ground plan for Aculeata hypothesized, the present study indicated 3 types of apomorphic states associated with the formation of an additional petiole. The abdominal characters showed that Vespidae is more closely related to Formicidae than to Scoliidae. The tiphiid-like abdominal appearance of Amblyoponini may be secondary modification for increasing the length of tergal muscles. A close relationship between the ponerine tribe Ectatommini and Myrmicinae was proposed in the present study, because among the aculeates these formicid groups alone had a lobe for attachment of tergal muscles developed on the pretergum of the third segment.

Key word: Formicidae, phylogeny, petiole, skeletomusculature, Amblyoponini.

Introduction

In 1975, BROTHERS published an idea on the phylogney of the aculeate Hymenoptera, which has stimulated later investigations of the relationships among aculeates (RASNITSYN, 1988; KÖNIGSMANN, 1978; WALTHER, 1979; CARPENTER, 1981; GIBSON, 1985; SCHÖNITZER & LAWITZKY, 1987; JOHNSON, 1988; DAY, 1988; GAULD & BOLTON, 1988; KIMSEY, 1991). Most recently, BROTHERS & CARPENTER (1993) reevaluated these studies, and proposed cladograms for the superfamilies of Aculeata. However, the relationships among Formicidae, Scoliidae and Vespidae (s.l. = Masaridae + Eumenidae + Vespidae s.s.) are still doubtfull. To have more accurate understanding of the relationships among these groups, and also of aculeate phylogeny, new information based on additional morphological characters is required.

Like other apocrita Hymenoptera, aculeates are characterized by having a constriction and articulation between the first and the second abdominal segments (i.e., petiole). Furthermore, in some aculeates the flexibility of the abdomen is augmented by an additional constriction between the second and third adominal segments, and even the third and fourth segments. In Scoliidae, Tiphiidae and Mutillidae, for instance, the posterior margin of the second abdominal segment is slightly constricted. In Vespidae and Formicidae, the second segment is strongly constricted posteriorly and differentiated as a petiole. Within Formicidae, an additional constriction is developed between the third and fourth abdominal segments. The skeletomuscular study of the additional petiolar structures is of interest not only for the implications for functional morphology, but also for better understanding of true phylogenetic relationships among Formicidae, Vespidae and Scoliidae. Nevertheless, relatively few studies have dealt with the skeletomusculature of these body parts in the aculeates.

Furthermore, the skeletomuscular study of the additional petiole can also shed new light on phylogeny among the formicids, because the abdominal characters present a major puzzle to formicid systematists (cf., HÖLLDOBLER & WILSON, 1990). The ponerine tribe Amblyoponini is widely acknowledged as a "primitive" formicid group, since the group has the second abdominal segment attached broadly to the third segment, like tiphiids. In contrast, Sphecomyrminae, the oldest fossil ant subfamily, has the second segment attached narrowly to the third segment. A major question in formicid phylogeny is whether the abdominal structure of Amblyoponini represents an evolutionary reversion of Sphecomyrminae, or whether Amblyoponini (and possibly the remainder of Ponerinae) is an independent clade of formicids predating Sphecomyrminae (i.e., the family Formicidae may be diphyletic).

The present study examined the skeletomusculature of the anterior abdominal segments in Aculeata to discuss the problem of relationships among Formicidae, Vespidae and Scoliidae, and the problems presented by the abdominal characters concerning the relationships among formicids.

Materials and Methods

Only female specimens were examined. In social groups, such as Formicidae and Vespidae, worker specimens were used.

To observe the musculature, specimens were dissected in 70% ethanol and dehydrated in an ethanol series ranging 70% to 99%, and then treated with hexamethyl disilazane for 10 min to prevent muscle shrinkage. Cuticular structures were examined by digesting cellular materials with 10% KOH for 8 hr. The preparations were observed with scanning electron microscope with gold coating. The taxa examined are listed in Table 1.

Different terms have been used for the part of the abdominal sclerites, so that many discrepancies have been occurred, in particular for the anterior part of the sclerites (cf., SNODGRASS, 1935, 1942; SHORT, 1959; TAYLOR, 1978; BOLTON, 1990). In this paper, I call the anterior part "pretergum" and "presternum" instead of "acrosclerites" of BROWN (1975), because the area in

Table 1. List of taxa examined.

Vespoidea
Formicidae
Formicinae: *Anoplolepis longipes* (JERDON), *Camponotus japonicus* MAYR, *Formica japonica* MOTSCHULSKY, *Lasius niger* (LINNAEUS), *Paratrechina longicornis* (LATREILLE), *Polyergus samurai* YANO, *Polyrhachis dives* F. SMITH
Dolichoderinae: *Dolichoderus bituberculatus* MAYR, *Ochetellus itoi* (FOREL), *Technomyrmex gibbosus* (WHEELER)
Myrmeciinae: *Myrmecia gulosa* (FABRICIUS)
Pseudomyrmecinae: *Pseudomyrmex triplarinus* (FOREL), *Tetraponera allaborans* WALKER
Cerapachyinae: *Cerapachys sauteri* FOREL, *Cerapachys biroi* FOREL
Myrmicinae: *Aphaenogaster famelica famelica* (F. SMITH), *Myrmecina graminicola nipponica* WHEELER, *Pheidole pieli* MAYR, *Pristomyrmex pungenus* MAYR, *Tetramorium caespitum* (LINNAEUS)
Ponerinae: Amblyoponini: *Amblyopone australis* ERICHSON, *Myopone castanea* (F. SMITH), *Onychomyrmex* sp., *Prionopelta* sp., Proceraiini: *Proceratium watasei* (WHELLER), Ectatommini: *Rhytidoponera purpurea* (EMERY), Ponerini: *Brachyponera chinensis* (EMERY), *Diacamma* sp., *Ectomomyrmex javanus* MAYR, *Leptogenys kitteli* MAYR, *Odontomachus monticola* EMERY
Tiphiidae: *Methoca japonica* YASUMATSU, *Tiphia latistriata* ALLEN & JAYNES
Mutillidae: *Mutilla europaea mikado* CAMERON, *Myrmosa nigrofasciata* YASUMATSU
Pompilidae: *Auplopus* sp., *Cyphononyx dorsalis* (LEPELETIER)
Scoliidae: *Carinoscolia melanosoma fasciata* (SMITH), *Megacampsomeris grossa matsumurai* (BETEREM)
Masaridae: *Pseudomasaris coquilletti* ROHWER
Eumenidae: *Discocelius japonicus* PEREZ, *Eumenes* sp.
Vespidae: *Polistes chinensis antenalis* PEREZ, *Vespa simillima xanthoptera* CAMERON
Apoidea
Sphecidae: *Ampulex dissector* (THUNBERG), *Ammophila infesta* F. SMITH
Megachilidae: *Anthidium septemspinosum* LEPELETIER
Anthophoridae: *Ceratina japonica* COCKERELL
Apidae: *Trigona* sp.
Chrysidoidea
Bethylidae: *Cephalonomia gallicola* (ASHMEAD)

Aculeata are not the precostal part, but the postcostal part of each segment.

The numbering of the muscles is restricted only for the second and third abdominal segments (Table 2). The numbers are just for the sake of convenience, and do not correspond to ones employed by previous authors.

To discuss the relationships among Formicidae, Vespidae and Scoliidae, hypotheses of the ground plan for the skeletomusculature of the anterior abdominal segments were based on the most widely distributed one in Aculeata where no formation of an additional petiole occurred.

Table 2. Musculature of anterior abdominal segments in Aculeata.

Muscle No.	Origin	Insertion	Function
1, 8	Dorsal median part of T2, 3	Anterodorsal median ege of T3, 4	Retractor of tergum
2, 9	Posterodorsal part of T2, 3	Apodeme of T3, 4	Protractor of tergum and holding the apodeme of posterior tergum to the side of the anterior tergum
3, 10	Dorsolateral part of T2, 3	Exterior-lateral edge above apodeme of T3, 4	Pronator of tergum
4, 11	Dorsolateral part of T2, 3	Lateral margin of S2, 3	Compressor of abdomen
5, 12	Ventral median part of S2, 3	Anteroventai median ege of S3, 4	Retractor of sternum
6, 13	Posteroventral part of S2, 3	Anterior apodeme of S3, 4	Protractor of sternite and holding the apodeme of posterior sternum to the side of the anterior sternum
7, 14	Ventrolateral part of S2, 3	Anterior apodeme of S3, 4	Pronator of sternum
15	Ventral edge of T3	Lateral apodeme of S3	Dilator of abdomen

T: Tergum. S: Sternum. 2, 3, 4: Segment numbers.

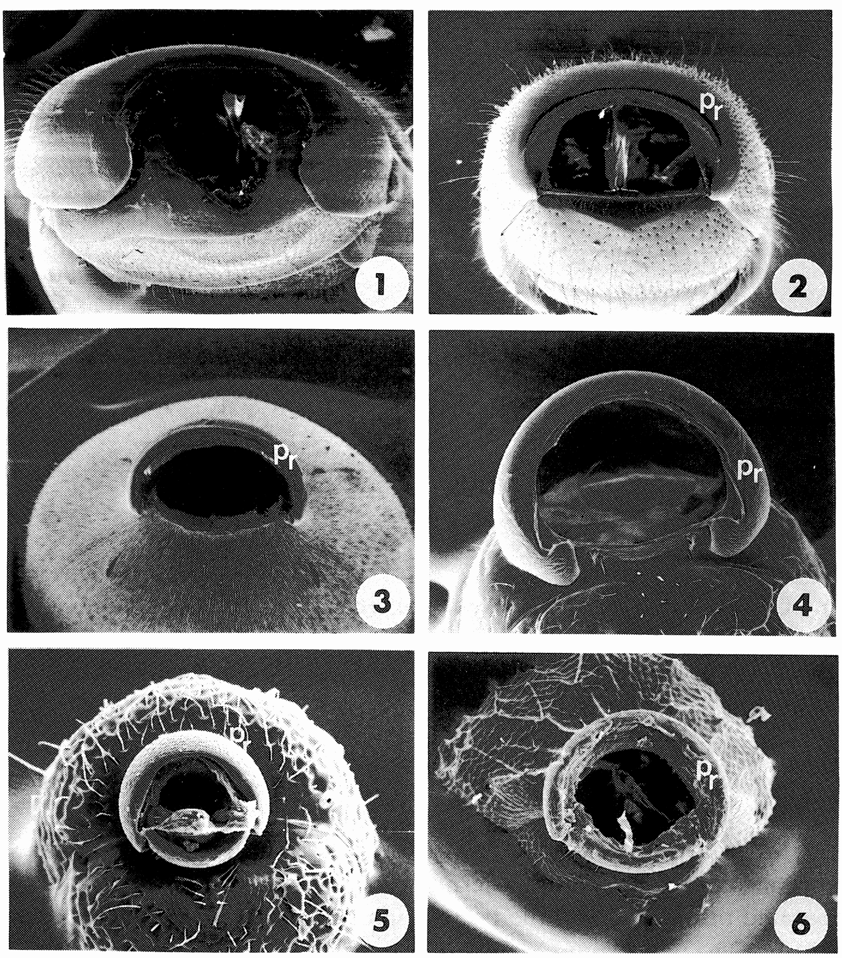
Results

Skeletal structures

1) Ground plan: In most Aculeata, each abdominal segment consists of tergum and sternum which are semicircular plates in cross-section (i.e., tergal plates from an arch above and the sternal plates form a concave floor beneath), connecting by thin flexible membrane. The presclerites are poorly developed on the abdominal segments, represented only by the thickened anterior rims (Figs. 1 & 19). Apodemes, or internal cuticular process, are well developed both on the anterior margins of the tergurm and sternum (Fig. 30).

2) Modifications: Members of Tiphiidae, Mutillidae and Scoliidae have well developed pretergum and presternum on the third abdominal segment which are separated distinctly from the posttergum and poststernum by a constriction respectively. The presternum in these aculeates forms a flat sternal plate, and the pretergum is expanded slightly below the pretergosternal juncture level (Figs. 2 & 9). The two sclerites are immovably attached, but not actually fused (Fig. 20).

In the members of Vespidae and Formicidae, the same skeletal modifications are found, but anterolateral corners of the pretergum are more broadly and roundly expanded than those of Tiphiidae, Mutillidae and Scoliidae. Furthermore, in Vespidae and Formicidae the incisions or depressions are developed on each side between tergum and sternum of the second segment, in which the anterolateral parts of pretergum of the third segment are received (Figs. 8, 10 & 11). The pretergum and presternum of the third segment in Vespidae are more tightly connected than those of Tiphiidae, Mutillidae and Scoliidae, because the ridges on the outer lateral edges of presternum and grooves on the inner lateral edges of the pretergum are developed, which fit together. In Formicidae, the



Figs. 1–6. Basal part of the third abdominal segment in frontal view; 1, *Ceratina japonica*, (Apidae); 2, *Mutilla europaea mikado* (Mutillidae); 3, *Eumenes* sp. (Eumenidae); 4, *Amblyopone australis* (Ponerinae: Amblyoponini, Formicidae); 5, *Cerapachys sauteri* (Cerapachyinae, Formicidae); 6, *Aphaenogaster famelica famelica* (Myrmicinae, Formicidae). Pr = presclerites.

third segment is tightly connected or fused completely at the portion of presclerites and even postsclerites. Pseudomyrmecinae, Myrmeciinae, Cerapachyinae and Ponerinae of Formicidae have a unique manner of fusion on pretergum and

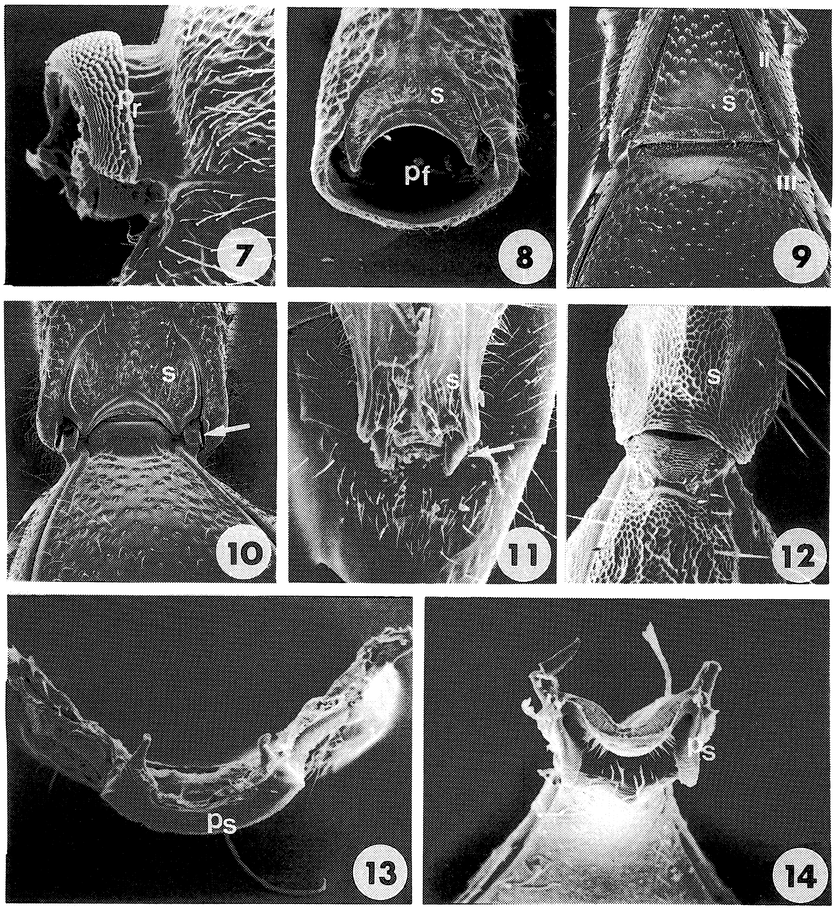


Fig. 7. Basal part of the third segment in lateral view; *Proceratium watasei* (Ponerinae: Proceratiini, Formicidae).

Fig. 8. Apical part of the second segment in ventral view; *Eumenes* sp. (Eumenidae).

Figs. 9–12. Connected part of the second and third segments in vental view; 9, *Carinoscolia melanosoma fasciata* (Scoliidae); 10, *Eumenes* sp. (Eumenidae); 11, *Dolichoderus bituberculatus* (Dolichoderinae, Formicidae); 12, *Aphaenogaster famelica famelica* (Myrmicinae, Formicidae).

Figs. 13–14. Basal part of sternum of third segment in front view; 13, *Aphaenogaster famelica famelica* (Myrmicinae, Formicidae); 14, *Tetraponera allaborans* (Pseudomyrmecinae, Formicidae). Pf=posterior foramen, Pr=presclerites, Ps=presternum, s=sternum, Roman numerals indicate segment numbers. (Arrows in Figs 10 and 11 indicate the anterolateral corners of pretergum of the third segment).

presternum of the third segment, where M-shaped presternal plate is fused broadly to the inner sides on the pretergum (Fig. 14).

In some members of Formicidae, such as Myrmicinae, Cerapachyinae and the ponerine tribe Proceratiini, a different type of skeletal modification occurs, where the presternum of the third segment is strongly convex ventrally, projecting beyond the lower margins of the pretergum (Figs. 5, 6 & 7) and the sternum of the second segment forms a concave floor without the incisions (Fig. 12).

In Tiphiidae, Mutillidae, Scoliidae, Vespidae and Formicidae, the second segment lacks apodemes on the tergum.

Development of the pretergum and presternum on the fourth abdominal segment are found only in the ceratin members of Formicidae. In the ponerine tribe Ponerini the pretergum and presternum are represented by broadly expanded anterior portions of the segment (Fig. 15). In the ponerine tribes Amblyoponini and Ectatommini, the pretergum and presternum form a convexity in profile and slightly narrow posteriorly (Fig. 24). In Cerapachyinae, Pseudomyrmecinae, Myrmeciinae and Myrmicinae, the pretergum and presternum are distinctly narrow posteriorly to form a ball-like projection (Fig. 16). In addition, in Myrmicinae pretergum is expanded ventrally so that the anterolateral parts of pretergum protrude downwards beyond the junction of the pretergum and presternum (Fig. 25).

In formicids having the developed presclerites on the fourth segment, the tergum and sternum are narrowly overlap and immovably welded together, at least on the anterior part of the segment. Apodemes on the fourth segment in these formicids exist on the anterior margins of the pretergum and presternum, though they are smaller than those in other aculeates in size.

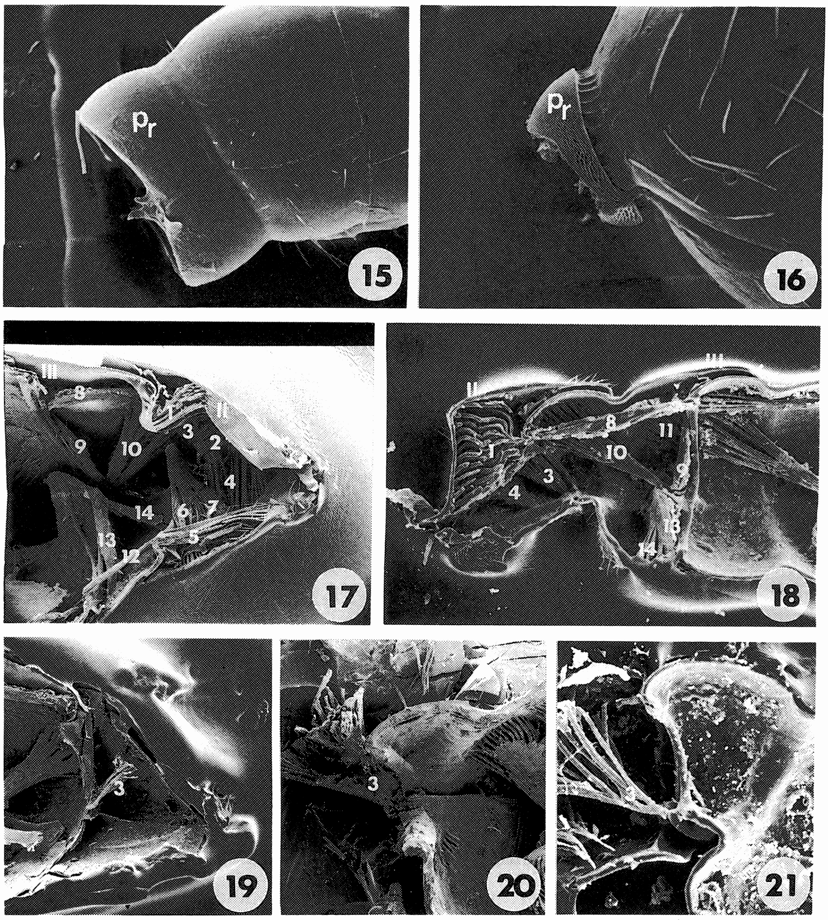
In Myrmicinae and ponerine tribe Ectatommini, an internal cuticular lobe is developed from the anterior margin of the pretergum of the fourth segment (Figs. 27 & 28).

Musculature

Musculature in the second segment to move the third segment

1) Ground plan: Seven pairs of muscles (Nos. 1 to 7) in the second abdominal segment are generally found in the Aculeata (Figs. 17, 18 and 19). In the ground plan, the positions of these muscles are illustrated in Fig. 30. The origins, insertions and functions of them are described in Table 2.

2) Modifications: In the members of Tiphiidae, Mutillidae and Scoliidae, the muscles No. 3 are inserted to the anterolateral margins of the pretergum of the third segment (Figs. 20 & 31). Because in these aculeates the anterolateral corners of pretergum slightly project below the juncture level of the sternal plates of the second and third segments, the insertions of the muscles No. 3 have the lowest point of anterior part of the third segment. In Formicidae and Vespidae



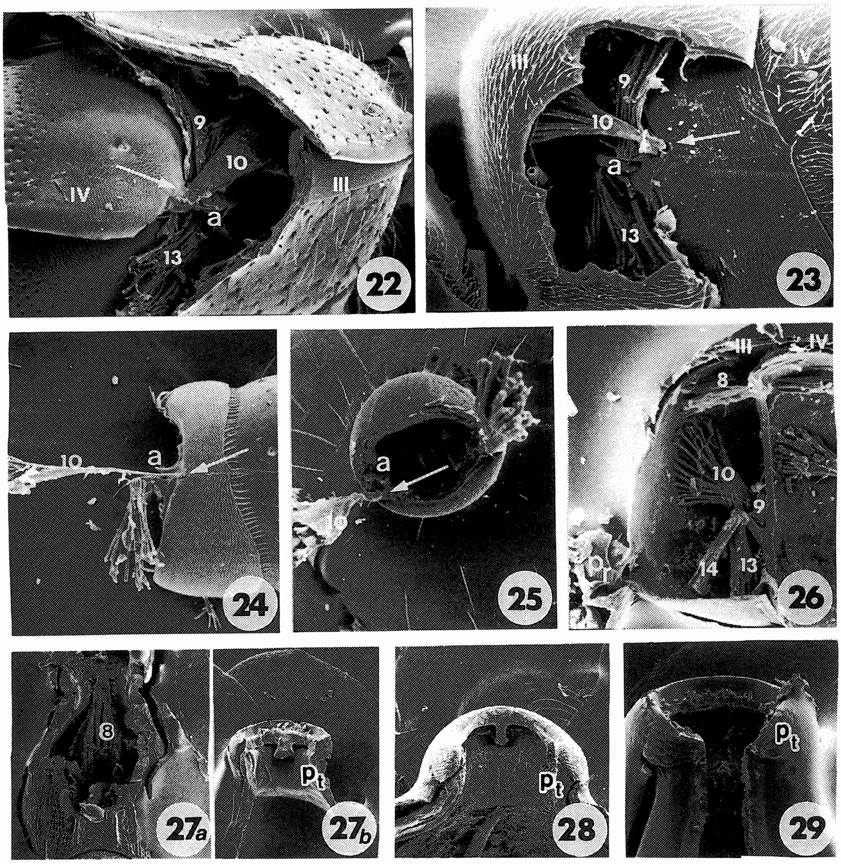
Figs. 15 and 16. Basal part of the fourth abdominal segment in lateral view; 15, *Ectomomyrmex javanus* (Ponerinae: Ponerini, Formicidae); 16, *Aphaenogaster famelica famelica* (Myrmicinae, Formicidae).

Figs. 17 and 18. Sagittal section of the second and third abdominal segments; 17, *Ceratina japonica,* (Apidae); 18, *Amblyopone australis* (Ponerinae: Amblyoponini, Formicidae).

Figs. 19–21. Position of insertion of muscle No. 3, various muscles removed to show the insertion; 19, *Ceratina japonica,* (Apidae); 20, *Tiphia latistriata* (Tiphiidae); 21, *Amblyopone australis* (Ponerinae: Amblyoponini, Formicidae). Pr=presclerites. Arabic numerals indicate the muscule numbers. Roman numerals indicate segment numbers.

having the lateral incisions of the second segment, the muscles No. 3 run through the incisions of the second segment to the anterolateral corners of the pretergum of the third segment (Figs. 21 & 32).

In Formicidae, muscles Nos. 1 and 3 are greatly increased in size, while the remaining muscles are either absent or too slender to be functional.



Figs. 22–25. Position of insertion of muscules No. 10; 22 and 23: cuticle of the third segment removed partly to show the insertion, 24 and 25: the fourth segment isolated to show the insertion, 22, *Tiphia latistriata* (Tiphiidae); 23, *Ectomomyrmex javanus* (Ponerinae: Ponerini, Formicidae); 24, *Amblyopone australis* (Ponerinae: Amblyoponini, Formicidae); 25, *Aphaenogaster famelica famelica* (Myrmicinae, Formicidae).

Fig. 26. Sagittal section of the third abdominal segment; *Brachyponera chinensis* (Ponerinae: Ponerini, Formicidae).

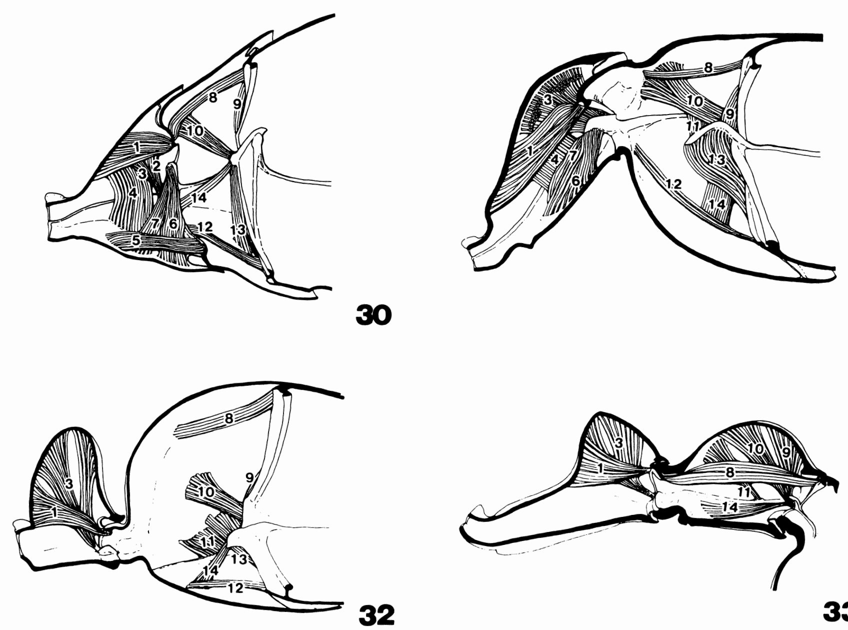
Figs. 27–29. Inner view of pretergite of the fourth segment; 27, *Aphaenogaster famelica famelica* (Myrmicinae, Formicidae), a: the position of origin of the muscle No. 8, b: the muscle No. 8 removed to show the lobe depending from the pretergum; 28, *Rhytidoponera purpurea* (Ponerinae: Ectatommini, Formicidae); 29, *Tetraponera allaborans* (Pseudomyrmecinae, Formicidae). a = apodeme, Pr = presclerites, Pt = pretergum. Arabic numerals indicate the muscle numbers. Roman numerals indicate segment numbers (Arrows in Figs. 22–25 indicate the position of insertion of muscle No. 10).

Musculature in the third segment to move the fourth segment

1) Ground plan: The third segment in Aculeata generally includes seven or eight pairs of the muscles (Nos. 8 to 15) that serve to move the fourth segment (Figs. 17 & 18). The positions of these muscles are illustrated in Fig. 30. The origins, insertions and functions of them are described in Table 2.

2) Modifications: Among the aculeates, only the members of Formicidae show the positional and functional modifications of the musculature of the third segment (Fig. 33). In Myrmicinae, Pseudomyrmecinae, Myrmeciinae, Cerapachyinae and the ponerine tribe Amblyoponini and Ectatommini, the muscles No. 10 are inserted to the anterolateral margins of the pretergum of the fourth segment (Figs. 24, 25 & 33). In these formicids, the muscles No. 8 are originated from the part of the pretergum of the third segment (Figs. 18 & 33). Additionally, in Myrmicinae and the ponerine tribe Ectatommini the end of muscles No. 8 are attached on the lobe developed on the anterior margin of the pretergum (Fig. 27).

In the ponerine tribe Amblyoponini and Ectatommini, and Cerapachyinae



Figs. 30–33. Diagrams of 4 grades of the skeletomuscular modification correlating with the formation of additional petiole or additional petioles in Aculeata, showing the musculature in right half of the second and third abdominal segments, excluding spiracular muscles; 30, ground-plan condition; 31, apomorophic condition in the first type; 32, apomorophic condition in the second type; 33, apomorophic condition in the third type. Arabic numerals indicate the muscle numbers.

the origins of muscles No. 10 are situated on the part of pretergum of the third segment (Fig. 18). In the ponerine tribe Ponerini, although the pretergum and presternum of the fourth segment are developed, the muscles No. 10 are inserted on the exterior-lateral edges above the apodemes of the tergum of the fourth segment, and the muscles No. 8 originats from the posterior part of the tergum of the third segment, like in the ground plan of aculeates (Figs. 22, 23 & 26).

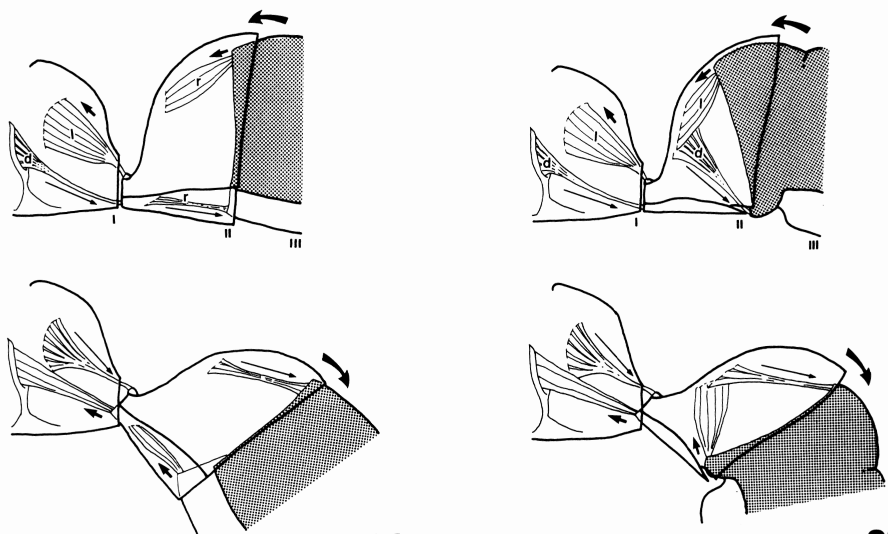
Discussion

Functional morphology

In the ground plan of aculeates, a downward movement of the abdomen is effected by both tergal protraction (relaxation of the muscles Nos. 1 & 8) and sternal retraction (contraction of the muscles Nos. 5 & 12), where the muscles Nos. 3 and 10 serve as the pronators of the tergum (Fig. 34). In Tiphiidae, Mutillidae, Scoliidae, Formicidae and Vespidae, the anterolateral parts of the pretergum of the third abdominal segment protrude downward beyond the pretergosternal junction, and the pretergum is immovably connected with the presternum. Because in these aculeates the contraction of the muscles No. 3 lifts up obliquely the lowest point of presclerites of the third segment, the muscles No. 3 change the role from the pronators to depressors of the abdomen (Fig. 35). In Tiphiidae, Mutillidae, Scoliidae, Formicidae and Vespidae, the muscles No. 1 also change the function from tergal retractors to levators of the abdomen, because the contraction of the muscles No. 1 pulls the upper part of pretergum associated with the presternum of the third segment into the posterior foramen of the second segment (Fig. 35).

Although Myrmicinae, Cerapachyinae and the ponerine tribe Proceratiini have the presternum of the third segment ventrally bulging below the lowest margins of the pretergum, muscles No. 3 also serve as depressors of their abdomen. Because the pretergum of the third segment enclosed immovably the presternum, the contraction of the muscles No. 3 provides forces for their abdominal downward movement by lifting up obliquely the lower part of the third segment (Fig. 5).

Myrmicinae, Pseudomyrmecinae, Cerapachyinae, Myrmeciinae and the ponerine tribe Amblyoponini and Ectatommini have the development of presclerites on the fourth segment. In these formicids, the muscles of Nos. 8 and 10 of the third segment also change the function to levators and to depressors of the abdomen. The origins of the muscles No. 8 in these formicids shift from the posttergum to pretergum of the third segment, thereby expanding in their size and increasing the power of the muscular contraction. Additionally, because the fourth segment preturgum of Myrmicinae and the ponerine tribe Ectatommini has a cuticular lobe which is attachment of the muscles No. 8 (Figs. 27 & 28), the



34 35

Figs. 34–35. Schematiced diagrams showing up- and downward movements of the anterior abdominal segments in Aculeata. 34, ground-plan condition; 35, apomorhic condition correlated with the formation of additional petiole: the tergal muscles in the second segment come to act as levators and depressors of the abdomen. d=depressor, l=levator, r=retractor. Roman numerals indicate segment numbers.

muscles No. 8 in these formicids increase their power by expanding area of muscular attachment. In the ponerine tribes Amblyoponini and Ectatommini, and Cerapachyinae, the muscles No. 10 also increase the power of the muscular contraction, because these muscles are expanded in length by shifting of origins from the posttergum to the pretergum of the third segment (Fig. 18).

In the case of the primary petiole (i.e., the constriction between the first and second abdominal segments), the development of presclerites includes producing new articular parts (cf., TAYLOR, 1978). This is also the case for the additional petiole, but the manner of alterations in the musculature are different between the primary and additional petioles in Aculeata. In the formation of the primary petiole sternal muscles serve as depressors, whereas in the additional petiole tergal muscles serve as depressors. Because the first abdominal segment is fused to the thorax proper in Hymenoptera (i.e., propodeum), certain sternal muscles in the frist segment can take their origin on the upper anterior edge of metafurca, which is a Y-shaped structure projecting from thoracic sternal plate. The contraction of these muscles lifts up obliquely the lower part of the anterior margin of the second abdominal segment, thereby depressing the metasoma (Figs. 34 & 35). On the other hand, because the sternal muscles in the second and third abdominal segments can not take their origin beyond the anterior margins of the sternal plates, the functions of these muscles as efficient depressors is limited (Fig. 34). This may be the reason why the muscles running obliquely in the tergal plates become the depressors in these segments (Fig. 35).

Type of abdominal structure

The present study indicates 3 types of apomorphic states associated with the formation of an additional petiole or petioles in the anterior abdominal segments (Figs. 31 to 33). The first type of the apomorphic states (Fig. 31) is found in Tiphiidae, Mutillidae and Scoliidae, where the presclerites of the third segment are developed to form a projection fitting tightly into the posterior foramen of the second abdominal segment. The pretergum of the second abdominal segment expands laterally, embracing the presternum. The second type of the apomorphic states (Fig. 32) is represented by Vespidae and Formicidae, where some accessories are added to the first type. These aculeates have more laterally expanded pretergum of the third segment than that in the first type, with the development of lateral incisions or depressions on the posterior foramen of the second segment. The third type of the apomorphic states (Fig. 33) is found in certain members of Formicidae, such as Myrmicinae, Cerapachyinae and the ponerine tribe Proceratiini, where a different type of articulatory structures is derived from the second type. The presternum of the third segment in these formicids is bulged ventrally to form a ball-like projection with the pretergum and the posterior foramen of the second segment lost lateral incisions or depressions. In addition, the third type of apomorphic states occurre on the third and fourth segments in the ponerine tribes Amblyoponini and Ectatommini, Cerapachyinae, Pseudomyrmecinae, Myrmeciinae and Myrmicinae.

In all these types of the apomorphic states, the pretergum and presternum are connected immovably at their lateral junctures and the musculature shows that certain tergal muscles are modified to act as the levators and depressors of the abdomen from as the retractors and pronators (Fig. 35).

Phylogenetic relationships among Vespidae, Scoliidae and Formicidae

Whether Vespidae is the sister group of Formicidae, or of Scoliidae is a major problem for the phylogeney of Aculeata (Cf., RASNITSYN, 1988; BROTHERS & CARPENTER, 1993). In the most recent study, BROTHERS & CARPETER (1993) supported the relationship of (Formicidae + (Vespidae + Scoliidae)). By the testing with the additional character proposed in the present study, their hypothesis requires reversal evolution in Scoliidae from the second type to the first type of the states in an additional petiole, or independent occurrence of the second type of the apomorphic state both in Formicidae and Vespidae.

A close examination of the analysis of BROTHERS & CARPETER (1993) shows that their justifications are not so strong. Firstly, among their 20 synapomorphies which support the sister-group relationship of Vespidae and Scoliidae, only 5 states are unique derivations and the remains are considered as convergent and reversal states. Second, the 3 states of these 5 unique derivations (i.e., an enlarged clypeus, a dorsal production of the pronotal angle, and a sunken prosternum) are difficult to divide into discrete states. In addition, the similar states are also found within a certain members of Formicidae (cf., BROTHERS, 1975). Thirdly, the remaining 2 states (i.e., an elongated labio-maxillary complex by production of glossa and paraglossa, and the third mesosomal phragma expanded laterally with large muscles attaching on the second phragma) are also doubtful. Seemingly these are convincing evidence for sister-group relationship of Vespidae and Scoliidae. However, these character states are considered to be modified uniquely within Formicidae, because the labio-maxillary complex is specialized for trophllaxis and thoracic condition is simplified for its mode of social life in Formicidae.

Thus the hypothesis of BROTHERS & CARPETER (1993) is less plausible. The present study shows that Vespidae is more closely related to Formicidae than Scoliidae.

The abdominal structure of the ant tribe Amblyoponini

The abdominal character of the ponerine tribe Amblyoponini presents a major puzzle to formicid systematists (HÖLLODOBLER & WILSON, 1990). The second abdominal segment of this tribe is attached broadly to the third segment, like tiphiids, which is widely acknowledged as ancestral condition of formicid group. In contrast, the second segment is attached narrowly to the third segment in the the oldest fossil ant subfamily Sphecomyrminae.

The present study indicates that the abdominal structure of Amblyoponini are different from that of Tiphiidae. Instead, the ant has more laterally expanded anterolateral corners of the pretergum of the third abdominal segment like other modern formicids. This structure is associated with the development of lateral depressions on the posterior foramen of the second abdominal segment in which the anterolateral corners of pretergum of the third segment are received. In addition, the pretergum and presternum on the fourth abdominal segment are developed in Amblyoponini.

Thus I suspect that the tiphiid-like abdominal appearance of Amblyoponini may be secondary modification from a narrowly constricted condition as in most ponerine abdomens. This might be the result of the shift in the origins of muscles Nos. 8 and 10. These muscles are usually originated from the part of posttergum of the third abdominal segment. But in Amblyoponini, they are from the part of pretergum of the third abdominal segment, so that the length is increased (Fig. 18).

In the skeletal condition of most ponerine abdomens, because the pretergum of the third abdominal segment are narrowly constricted posteriorly, it is difficult for the muscles Nos. 8 and 10 to run through the constricted part between the pre- and posttergum of the third segment (Fig. 26). In Amblyoponini this limitation may be circumvented by the secondary derivation of the broadly constricted condition of the third segment.

Consequently, the abdominal state of Amblyoponini represents neither the retention nor the reversion of plesiomorphic state of formicids. It should be considered as an apomorphic state for the tribe.

The phylogenetic position of the ant subfamily Myrmicinae

The phylogenetic position of the Myrmicinae has also puzzled students of formicid evolution (cf., WARD, 1990). Some authors relate the subfamily to Pseudomyrmecinae (WHEELER, 1920), while others to the ponerine tribe Ectatommini (BROWN, 1950; HASHIMOTO, 1991).

Recently, WARD (1990) concluded that Pseudomyrmecinae and Myrmicinae are sister groups mainly based on the unique configuration of the presclerites on the fourth abdominal segment. He mentioned that the presternum of the fourth abdominal segment was notably shorter than the pretergum and that the pretergum was protruding ventrally below the tergosternal junction. But this is only the case for Myrmicinae. In Pseudomyrmecinae, unlike the description by WARD (1990), the presternum appears to be subequal to the pretergum in length and the pretergum does not protrude ventrally.

On the contrary, the abdominal characters presented by this study indicate a close relationship between the ponerine tribe Ectatommini and Myrmicinae. Among the aculeates examined here, these formicid groups alone have a lobe developed on the pretergum of the third abdominal segment, which is an attachment of muscles No. 8. This character is an autapomorphy of Ectatommini and Myrmicinae.

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