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THE FIRST MESOZOIC ANTS, WITH THE DESCRIPTION OF A NEW SUBFAMILY

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INTRODUCTION

Our knowledge of the fossil record of the ants, and with it the fossil record of the social insects generally, has previously extended back only to the Eocene Epoch (Carpenter, 1929, 1930). In the Baltic amber and Florissant shales of Oligocene age, and in the Sicilian amber of Miocene age, there exists a diverse array of ant tribes and genera, many of which still survive today (Emery, 1891; Wheeler, 1914; Carpenter, 1930). The diversity of this early Cenozoic ant fauna has long prompted entomologists to look to the Cretaceous for fossils that might link the ants to the non-social aculeate wasps and thereby provide a concrete clue concerning the time and circumstances of the origin of social life in ants; but until now no fossils of ants or any other social insects of Cretaceous age have come to light (Bequaert and Carpenter, 1941; Emerson, 1965) and we have not even had any solid evidence for the existence of Hymenoptera Aculeata before the Tertiary.

There does exist one Upper Cretaceous fossil of possible significance to aculeate and thus to ant evolution. This is the hymenopterous forewing from Siberia described by Sharov (1957) as *Cretavus sibiricus*, and placed by him in a new family Cretavidae under the suborder Aculeata. As Sharov notes, the wing venation of *Cretavus* does resemble that of the bethyloid (or scolioid) wasp family Plumariidae, a group that has been mentioned in connection with formicid origins. The *Cretavus* wing is also similar to that of such primitive Tiphidae as *Anthobosca* (see figures, discussion and references in Brown and Nutting, 1950). But the difficulty with this fossil is that we have only the wing, and there is no guarantee that

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the evolution of venational and body traits proceeded concordantly before, during or after the transition from parasitic to aculeate Hymenoptera. In other words, we do not know from the present evidence whether the diagnostic body characters of the whole insect *Cretavus* would place it in the Aculeata or not.

The reason for the apparent absence of social insects before the Tertiary may be due at least in part to the general scarcity of Cretaceous insects. The most notable relevant Cretaceous deposit, the Cedar Lake amber from Manitoba studied by Carpenter and his associates (1934), contains moderate numbers of insects, and some are Hymenoptera, but these include no ants or aculeates of any kind. Two explanations seem possible: either the Cedar Lake amber, which has not been precisely dated within the Cretaceous,³ originates from an early part of the period, prior to the origin of the aculeates, or else the early aculeates were too large to be enclosed in the small amber pieces that characterize the deposit. Amber has been found in Cretaceous deposits along the Arctic coastal plain of Alaska (Langenheim, Smiley and Gray, 1960) but very few insects are included and no aculeates have been reported.

For many years numerous pieces of amber have been recovered from sediments exposed along the coastal plain of Maryland and New Jersey, as well as on Staten Island and Nantucket. These pieces have apparently been derived from at least two formations, the Raritan and the Magothy, both of which are referable to the lower part of the Upper Cretaceous. The first published account of this amber appeared nearly 150 years ago (Troost, 1821) but, in spite of frequent observations on the occurrence of the amber, almost no records of insect inclusions have been published. Indeed, the only account of an inclusion was that in Troost's original report on the amber (1821), which contained a "description of a variety of amber and of a fossil substance supposed to be the nest of an insect".⁴

³Langenheim, Smiley and Gray (1960, p. 135) refer to the Cedar Lake amber as of "presumed Late Cretaceous Age". However, Dr. Langenheim informed me subsequently (pers. com., 1964) that he had no knowledge of evidence dating the amber at any specific level within the Cretaceous. [F. M. C.]

⁴It is of interest to note that at the first meeting of the Cambridge Entomological Club, January 4, 1874, Professor Hermann Hagen presented an account of this specimen, concluding that it was a group of galls on a twig (Hagen, 1874). No formal description was ever published.

EXPLANATION OF PLATE 2

Sphecomyrma freyi, worker no. 2, paratype. The head is viewed obliquely from below and in front.



Sphecomyrma freyi, worker no. 2, paratype.

In 1966 Mr. and Mrs. Edmund Frey, of Mountainside, New Jersey, while collecting mineralogical specimens in the Magothy exposure at the beach bluffs, Cliffwood, New Jersey, found a relatively large piece of amber containing several insects. The amber, when discovered, was imbedded in the clay bank. Professor Donald Baird of Princeton University reported the find to one of us (F.M.C.) and eventually Mr. David Stager of the Newark Museum kindly arranged for the loan of the specimen by Mr. and Mrs. Frey. All who are interested in insect evolution are indebted to Mr. and Mrs. Frey for their alertness in discovering the amber and especially for their full cooperation in allowing the amber inclusions to be prepared and studied. Important as these insects are, the knowledge that insects actually occur in this Cretaceous amber is of even greater significance. In all probability much of the amber previously collected contained insects that were simply not detected. Efforts are now being made to examine earlier collections of the amber from the Magothy and Raritan Formations and also to obtain new material by collecting at the several exposures of these two beds.

The Magothy Formation, in which this fossiliferous piece of amber was found, has exposures in Maryland, Delaware, New Jersey, Long Island and other islands of the southern New England coast. It consists mainly of light-colored sands, with layers of gray or dark brown clays. Leaf impressions, lignite and the amber occur in the clay beds. The Magothy Formation has been referred consistently to the lower part of the Upper Cretaceous (Turonian-Coniacian stages). Resting on the Raritan, which lies at the bottom of the Upper Cretaceous, it was presumably deposited not long after mid-Cretaceous times, about 100 million years ago. The plants in the Magothy Formation have been studied chiefly by Berry (1904, 1905, 1906, 1907) but his generic determinations are not generally accepted by botanists at the present time. More recently, pollen and spores in the Magothy have been investigated by Groot, Penny and Groot (1961) and by Stover (1964). Certain cones and twigs in the Magothy clays almost certainly belong to *Sequoia* (Berry, 1905; Hollick, 1905) or related genera. There is good evidence that such trees produced most of the amber now found in the Magothy. Knowlton (1896) reported that a lignitic log about 4 feet long, which was found in the Potomac Formation (below the Magothy, in the Lower Cretaceous) and which possessed a woody structure characteristic of *Sequoia*, contained several pieces of amber. Very recently (1967, pers. com.) Dr. Jean Langenheim, of the University of California at

Santa Cruz, has informed one of us (F.M.C.) that she has tentatively concluded from her infrared studies on resins and ambers that most of the Atlantic Coastal Plain amber (including that from Cliffwood beach) was probably produced by taxodiaceous trees, very likely *Sequoiadendron* or *Metasequoia*.⁵

Among the insects in the amber which Mr. and Mrs. Frey collected at Cliffwood beach are two unmistakable worker ants. These specimens have fulfilled many of our fondest speculations about what a Mesozoic ant might be like, and thus they demonstrate to us anew the predictive power of phylogenetic reasoning (See Plate 4). We first present their formal description as a new subfamily, genus, and species and then provide a discussion of their phylogenetic significance. The other insects in the amber, all Diptera, will be turned over to appropriate specialists for subsequent study and description.

Family Formicidae

Sphecomyrminae Wilson and Brown, new subfamily

Diagnosis (worker): Mandibles peculiarly wasp-like, short, narrow, curvilinear, bidentate. Antennae 12-segmented, with a well-formed but relatively short scape and an exceptionally long (for an ant), almost filiform funiculus. The second funicular segment is longer than any other funicular segment, a rather unusual feature apparently shared with *Nothomyrmecia* (some higher ants have a long second funicular fusion segment, e.g., workers and females of *Orectognathus* and males of most *Tetramorium* and allied genera). Compound eyes large, convex, placed near the middle of the sides of the head. Ocelli present.

Body form that of a very primitive formicid. Alitrunk (=thorax + propodeum) slender, in form very much like that of *Methocha malayana* (Fig. 3), *M. stygia*, and some other species of that genus (Reid, 1941: figs. 26-27; Pagden, 1949). Sutures between pro- and mesothorax, and between meso- and metathorax, both complete, possibly movable. Mesonotum long and slender, with distinct, convex scutum and scutellum separated by a rather distinct axillary region. Metathoracic spiracles present, situated just below the limits of the scutellum on each side near its posterior margin, as in

⁵We are indebted to Mr. James Doyle of Harvard University for his assistance with this paleobotanical literature.

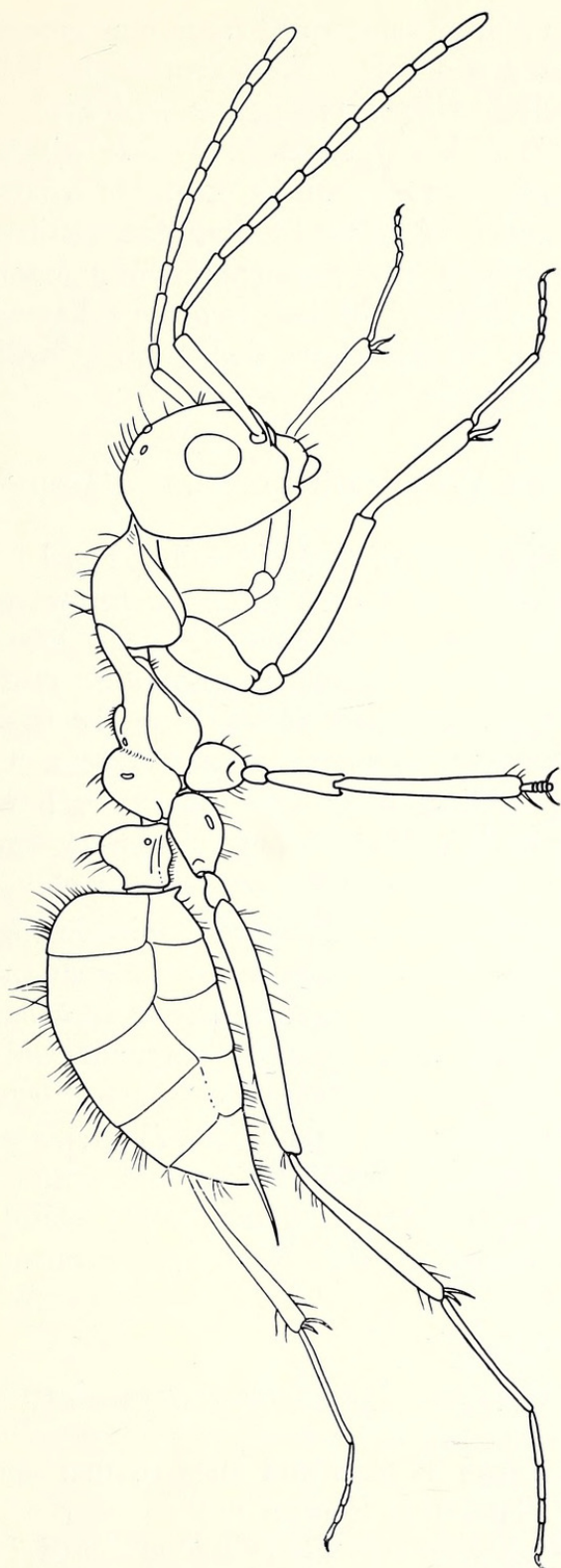


Figure 1. Drawing of *Sphecomyrma freyi*, worker no. 1. Only structures that could be clearly seen were drawn. Thus the figure is a direct rendition and not a reconstruction, although the appendages have been turned to more life-like positions.

Methocha. Metanotum a deeply impressed transverse groove between scutellum and rounded propodeum. Metapleural gland bulla and meatus present and well-developed (though it is difficult to be absolutely certain of this in amber specimens). Petiole with a distinct, raised node with strongly rounded summit, strongly separated from propodeum and first segment of gaster by deep constrictions. Gaster without a constriction behind first segment; strong exsertile sting present. Legs long and slender, the last two pairs having 2 spurs at the apex of each tibia. Tarsal claws each with a median tooth. Type and only known genus is the following:

***Sphecomyrma* Wilson and Brown, new genus**

Worker: With the characters of the subfamily. Head capsule unexceptional, more or less like that of a primitive formicine, such as *Prolasius*, *Notoncus*, or even *Prenolepis*. Clypeus broad, simply formed, convex, with broadly rounded free margin. Antennae inserted moderately far apart and well forward on the head capsule, their sockets close to the posterior margin of the clypeus. Compound eyes oblate circular in outline, large and convex, each with more than 100 ommatidia. Ocelli well-developed. Antennal segmentation and proportions unique, as shown in Figure 2A.

Alitrunk with rounded humeri. Propodeal spiracle high up, its opening elongate. Petiolar segment with a distinct node in the form of a narrowly-rounded dome, briefly pedunculate in front and behind, much narrower than the succeeding (gastric) segment, and separated from it by a broad and deep constriction. First gastric segment with an anteroventral process like that found in *Myrmecia* as well as many ponerine genera. Sting exserted, strong and acute.

Integument appearing relatively thin, not boldly sculptured anywhere; sculpture fine and superficial, body surface opaque to subopaque.

Queen and male unknown.

Type and only known species: *Sphecomyrma freyi*, described below.

***Sphecomyrma freyi* Wilson and Brown, new species**

Plates 1-4; Figures 1, 2

Holotype and paratype workers: the characters cited in the subfamily diagnosis, and particularly the form of the mandibles, antennae and mesonotum, readily distinguish this species from all other known ant species, living or fossil.

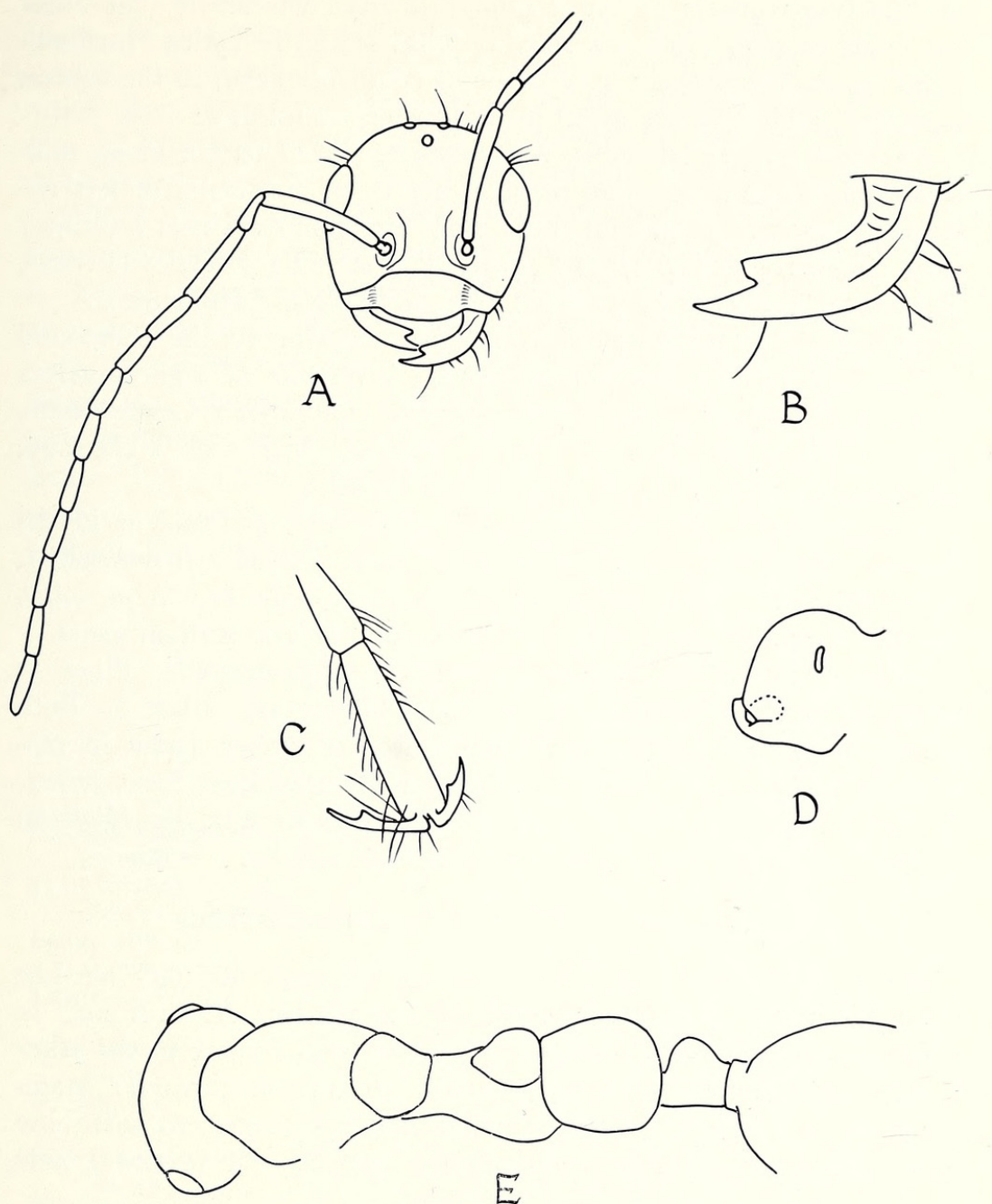


Figure 2. Drawings of various body parts of *Sphecomyrma freyi*. A, head of worker no. 2, view from below and in front. B, left mandible of worker no. 2, seen in fuller frontal view than in A so as to reveal the truncated shape of the inner tooth. C, pretarsus of left hind leg of worker no. 1. D, propodeum and metapleural region of worker no. 1. E, oblique dorsal view of body of worker no. 2.

The two workers are very similar in most characters, but differ markedly in size. Both are roughly what would be called "medium-sized" ants. Some exact measurements could be taken, to the nearest 0.01 mm, and these are given in millimeters as follows:

Specimen 1. Head width not measured; head length along mid-line 0.98; maximum length of right eye 0.32. Segments of left antenna (numbered I through XII) from insertion outward: I (scape) 0.60, II 0.16, III 0.34, IV 0.21, V 0.21, VI 0.21, VII 0.21, VIII 0.21, IX 0.21, X 0.21, XI 0.21, XII 0.26. (Holotype).

Specimen 2. Head width taken just anterior to the compound eyes, 1.00; head length not measured. Segments of right antenna (numbered I through XII) from insertion outward: I (scape) 0.68, II 0.18, III 0.40, IV 0.27, V 0.27, VI 0.26, VII 0.26, VIII 0.26, IX 0.24, X 0.23, XI 0.23, XII 0.31. (Paratype).

The details of morphology, including pilosity, are evident in the figures. Pubescence consists of scattered, short (about 0.01 mm long), appressed hairs. Both specimens are uniform light brown in color, but this means little in view of the passage of 100 million years.

Holotype: worker, labelled F1, shown in photograph, Plate 1; paratype: worker, labelled F2, shown in photograph, Plate 3. Both specimens were collected in a single piece of amber (now in separate pieces) in clay, Cliffwood Beach, on Raritan Bay, New Jersey, by Mr. and Mrs. Edmund Frey. The specimens are in the collection of Mr. and Mrs. Frey, Mountainside, New Jersey.

PHYLOGENETIC POSITION OF SPHECOMYRMA

Sphecomyrma freyi presents a mosaic of wasp-like and ant-like character states. Moreover, most of the ant-like features are, as well as we can judge the matter, primitive with respect to the other known Formicidae. Our assignments of various character states are given in Table 1. An examination of this arrangement will show that *Sphecomyrma* is truly intermediate between the primitive ants

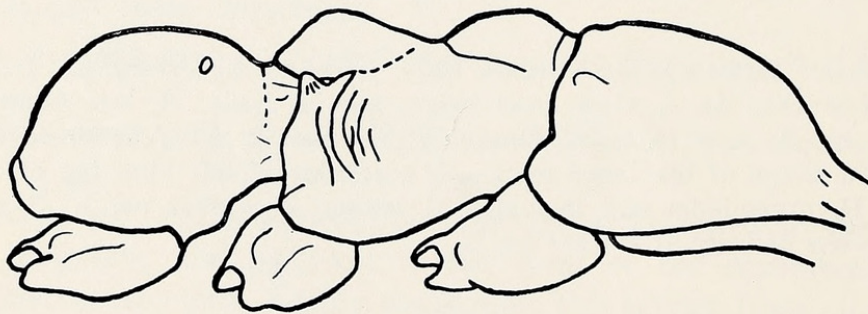


Figure 3. Alitrunk of *Methocha malayana* female in side view. (Redrawn after Pagden, 1949).

and the aculeate wasps. However, we feel that the metapleural gland, the nodiform, posteriorly constricted petiole, and the generally ant-like overall habitus place this species among the primitive ants rather than the wasps. However, if we are mistaken about the presence of the metapleural gland, it would be possible to consider *Sphecomyrma* as a wasp rather than an ant.

Which of the aculeate wasp groups might have given rise to the Sphecomyrminae? In Table 2 we present a scheme by Dr. Howard E. Evans, who has compared the Mesozoic ant with a wide range of modern aculeate families (fossil wasps are too scarce to be of much use). It can be seen that the Tiphiidae, and in particular the genus *Methocha*, come closest. (*Methocha* is impressively similar in details of thoracic structure, as shown in Figure 3). But we agree with Evans that such a comparison must be treated very carefully. The modern aculeate wasps are specialized both morphologically and ecologically: for example, *Methocha* of several species are known to

TABLE 1

Relationships of the Principal Character States
of *Sphecomyrma freyi*

	Aculeate wasps only	Other primitive ants only	Both aculeate wasps and primitive ants
Narrow bidentate mandibles	+		
Well-formed slender scapes		+	
Long, filiform funiculi	+		
Large compound eyes			+
Well-formed ocelli			+
Broad, simple clypeus			+
Reduced, apterous thorax			+
Mesonotum with separate, dis- tinctly convex scutum and scutellum	+		
Metapleural gland		+	
Petiole with node deeply constricted front and rear		+	
Gaster ovoid, unconstricted			+
Extrusible sting			+

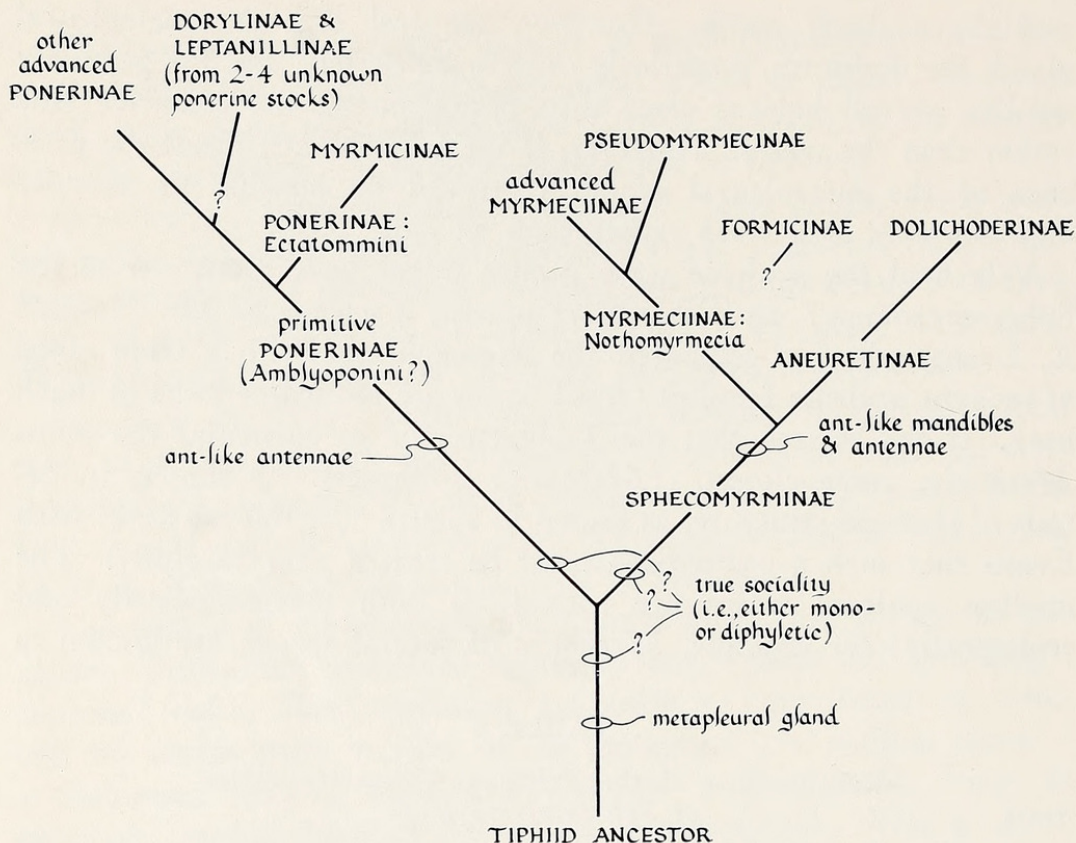


Figure 4. Hypothetical cladogram of the subfamilies of ants (Formicidae), based on all available evidence including the analysis of *Sphecomyrma*.

be parasitoids of tiger beetle larvae (Clausen, 1940: 298). There is now a greater need than ever to discover and to study in detail aculeate wasps of Cretaceous age.

The relationship of *Sphecomyrma freyi* to the other ants is clearer. The body of *Sphecomyrma* resembles that of the primitive myrmecioid ants, notably the living *Nothomyrmecia macrops* of Australia, which we regard as the most generalized member of the primitive subfamily Myrmeciinae (Brown and Wilson, 1958), and the Eocene genera of Aneuretini, which are the undoubted ancestors of the other Dolichoderinae (Wilson *et al*, 1956). Previously we had considered that the Aneuretini might have been derived from the Myrmeciinae, because we considered the long mandibles of the Myrmeciinae as primitive and the short mandibles of the Aneuretini as derived. Now the discovery of short, wasp-like mandibles in *Sphecomyrma* has invalidated this postulate.

In *Sphecomyrma*, then, we have what appears to be a good link between aculeate wasps and the myrmecioid complex of subfamilies,

Table 2. Degree of similarity of body parts of *Sphecomyrma freyi* with genera of various aculeate families. +++ , nearly identical, scored as 3. ++ , mostly similar, with minor differences, scored as 2. + , mostly dissimilar but with a few details matching, scored as 1. — , wholly dissimilar, scored as 0. These genera include those previously believed to fall closest to the primitive ants, as well as other, representative genera. Except for the Oligocene *Paraneuretus*, all are represented by living species. (The evaluation of the wasp families was provided by Dr. Howard E. Evans.)

	Mandibles	Clypeus	Antenna	Ocelli	Petiole	Alitrunk (Mesosoma)	Similarity to <i>Sphecomyrma</i> numerical score
POMPIDAE							
<i>Epipompilus</i> ♀	+++	+	++	++	—	—	8
SIEROLOMORPHIDAE							
<i>Sierolomorpha</i> ♀	+	++	++	++	+	—	8
RHOPALOCOMATIDAE							
<i>Rhopalosoma</i> ♀	—	—	+	+	+	—	3
PLUMARIIDAE							
<i>Plumarius</i> ♀	—	—	—	—	—	—	0
<i>Plumarius</i> ♂	—	+	+	+	—	—	3
MUTILLIDAE							
<i>Apterogyna</i> ♀	—	—	++	—	++	—	4
<i>Apterogyna</i> ♂	—	++	++	++	++	—	7
VESPIDAE							
<i>Gayella</i> ♀	—	+	++	++	++	—	6
<i>Alastor</i> ♀	—	++	++	++	++	—	6
THYNNIDAE							
<i>Aclurus</i> ♀	—	—	—	—	—	—	0
<i>Aclurus</i> ♂	+	+	+	++	—	—	7
<i>Diamma</i> ♀	—	+	—	++	+	+	5
<i>Diamma</i> ♂	—	+	+	++	+	—	6
<i>Rhagigaster</i> ♀	++	++	—	—	—	—	3
<i>Rhagigaster</i> ♂	++	++	+	+	+	—	10
TIPHIDAE							
<i>Anthobosca</i> ♀	—	++	—	++	—	—	4
<i>Anthobosca</i> ♂	++	++	+	++	—	—	8
<i>Glyptometopa</i> ♀	—	—	—	—	—	—	0
<i>Methocha</i> ♀	++	+	+	+	—	+	10
FORMICIDAE							
<i>Amblyopone</i> ♀	—	++	++	—	+	+	7
<i>Nothomyrmecia</i> ♀	+	++	++	++	++	++	13
<i>Paraneuretus</i> ♀	+	++	++	—	++	++	12

namely the Myrmeciinae, Pseudomyrmecinae, Dolichoderinae (including Aneuretini) and Formicinae. (See the arrangement of ant subfamilies into the "myrmecioid" and "poneroid" complexes by Brown, 1954). Where does this leave the poneroid subfamilies in the scheme of things? Among the poneroids, including the Ponerinae, Dorylinae, Leptanillinae, and Myrmicinae, the most primitive group is certainly the Ponerinae, and most particularly the ponerine tribe Amblyoponini. It is disconcerting to find that the ponerines are hardly closer to *Sphecomyrma* than they are to the primitive myrmecioids. There is no trace of the ponerine gastric constriction in the latter two groups. More significantly, the Amblyoponini have an incompletely constricted petiole (that is, the petiole is broadly attached posteriorly to the gaster), and they *also* have the constriction between the first and second gastric segments. *Sphecomyrma* lacks the gastric constriction, but has the petiole strongly constricted behind. We have long considered the amblyoponine petiolar form as primitive among the ants, and it certainly resembles that of some tiphiods as much as or more than it does that of most other ants.

One character that has never received any particular attention is the form of the amblyoponine male mandibles (Brown, 1960: figs. 8, 26) which is in fact now seen to be quite primitive. In the species of Amblyoponini so far described, the mandibles are narrow and wasp-like, sometimes bidentate, and sometimes tapering to a single acute point (the latter condition is evidently derived); they close tightly against the convex free clypeal margin, as do those of most wasps. (The more elaborate worker-female mandibles of Amblyoponini are not too difficult to imagine as derived from the bidentate wasp-like form.) When considered together, the petiole and the male mandibles of Amblyoponini certainly strengthen the general impression that this tribe is very primitive, although it shows tendencies toward specialization for life in cryptic habitats.

If the amblyoponine petiole is truly more primitive than the *Sphecomyrma* petiole, then the split between myrmecioids and poneroids must have come at a time when ants were still very wasp-like, and perhaps we should even consider the possibility that the divergence occurred before these groups had fully acquired their sociality. In the light of this last possibility, the metapleural glands assume a particular importance in our phylogenetic speculations. The fact that they are such complicated organs makes it unlikely that they were evolved independently in different ant lineages. If their function — at present unknown — is eventually shown to be primarily

social, then the hypothesis of a single origin of social life in ants would tend to be supported.

A cladogram outlining our present best guess at ant phylogeny is given in Figure 4.

RECONSTRUCTION OF FORMICID ARCHETYPE

Judging from the characteristics of the primitive ants and the tephritid wasps as we know them now, we would reconstruct the archetypal ant as follows:

Worker —

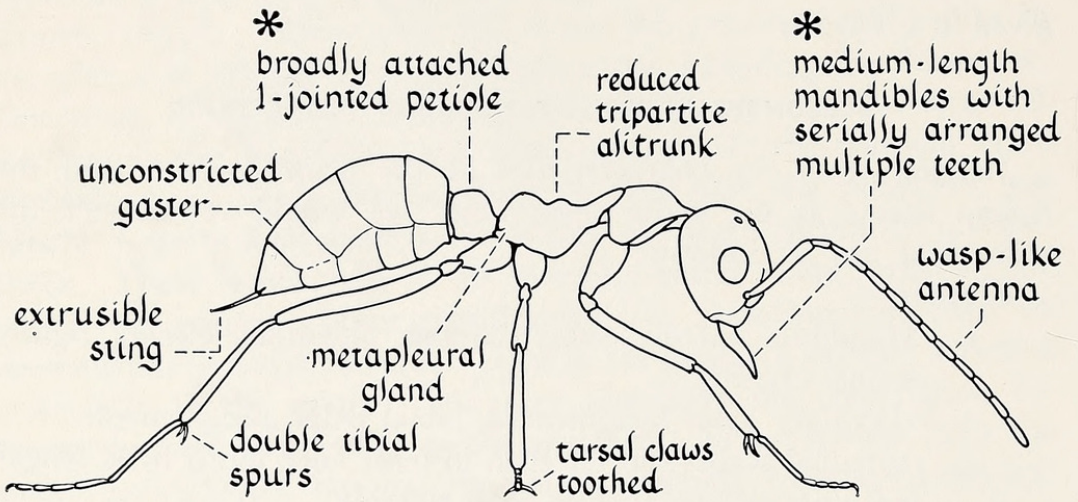
1. Mandibles narrow, short, curved, bidentate, closing tightly against clypeus.
2. Maxillary palpi 6-segmented, labial palpi 4-segmented.
3. Antennal scapes shorter than in most ants, but a little longer and more slender than in most tephritids.
4. Antennal funiculi long, slender, filiform, with 11 segments.
5. Compound eyes large, convex, oval or round, situated near middle of sides of head.
6. Ocelli well-developed.
7. Promesonotal suture complete, movable.
8. Mesonotum with scutum and scutellum separate and distinct.
9. Mesonoto-metanotal suture complete, possibly movable.
10. Metapleural gland bulla and meatus present.
11. Tibial spurs 1, 2, 2.
12. Tarsal claws toothed.
13. Petiole consisting of a single segment, sessile in front, or nearly so, sessile and broadly joined to gaster behind (with little intervening constriction).
14. Gaster unconstricted.
15. Sting strong and functional.

Of these character states, *Sphecomyrma* agrees with all but No. 13 (petiole form); its status with regard to No. 2 (palpal segmentation) is actually unknown, but we would strongly expect it to agree.

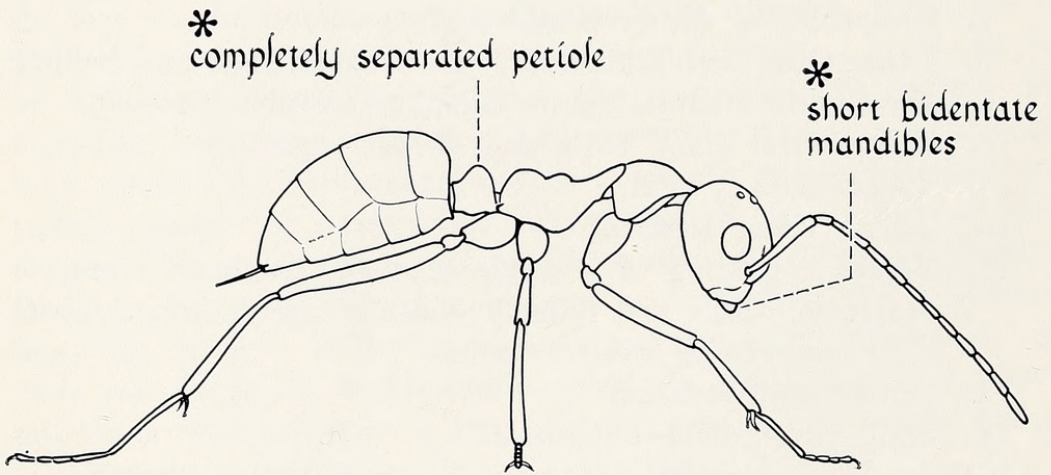
The primitive *Amblyopone* species have workers agreeing with the archetype more or less closely in character Nos. 3, 7, 10, 11, 13 and 15. Males of the larger and more primitive species of *Amblyopone* also agree in No. 1.

The *Nothomyrmecia macrops* worker agrees with Nos. 2, 4 (more or less), 5, 7, 10, 11, 12, 14 and 15.

The *Methocha stygia* female agrees well to fairly well with all character states except 10 and 12.



PREVIOUSLY HYPOTHESIZED ANCESTOR



SPHECOMYRMA

Our analysis of *Sphecomyrma*, incomplete as it must be, nevertheless suggests several promising lines of investigation in the future. First and foremost, of course, is the search for more Cretaceous ants and allied aculeate groups. Perhaps the Magothy amber will yield more material of interest. Second, we should pay closer attention in the future to comparisons in morphology, physiology, and behavior between the primitive myrmecioids and primitive poneroids. Differences should be related to the emerging new form of the formicid cladogram, while similarities should be examined with reference to the question of whether they are monophyletic or convergent. Finally, as a better idea is formed of the relationships of the ants to certain living wasp families, the biology of the latter needs to be examined more closely for clues concerning the origin of social life in ants.

ACKNOWLEDGEMENTS

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SUMMARY

Two worker ants preserved in amber of Upper Cretaceous age (Magothy Formation) have been found in New Jersey. They are the first undisputed social insect remains of Mesozoic age, and extend the existence of social life in insects back to approximately 100 million years. They are also the earliest known, certainly assignable aculeate Hymenoptera. The species, *Sphecomyrma freyi*, is considered to

EXPLANATION OF PLATE 4

A comparison of the archetypal ant as hypothesized by the authors before the discovery of *Sphecomyrma* (e.g., Brown, 1954; Brown and Wilson, 1959), with *Sphecomyrma* itself. The fine details of body shape are made the same in this drawing for convenience but do not enter into the main features to which phylogenetic speculation has been directed. This comparison is presented to indicate the degree of precision of earlier phylogenetic reasoning. Examination of the *Sphecomyrma* specimens proved the hypothesis wrong in essentially only one major respect: we had guessed that an ant-like mandible developed before an ant-like petiole, but the reverse proved to be the case.

represent a new subfamily (*Sphecomyrminae*) more primitive than any previously known ant group. It forms a near-perfect link between certain non-social tiphiid wasps and the most primitive myrmecoid ants.

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