

The earliest known ants: an analysis of the Cretaceous species and an inference concerning their social organization

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Abstract.—The known Cretaceous formicoids are better interpreted from morphological evidence as forming a single subfamily, the Sphecomyrminae, and even a single genus, *Sphecomyrma*, rather than multiple families and genera. The females appear to have been differentiated as queen and worker castes belonging to the same colonial species instead of winged and wingless solitary females belonging to different species. The former conclusion is supported by the fact that the abdomens of workers of modern ant species and extinct Miocene ant species are smaller relative to the rest of the body than is the case for modern wingless solitary wasps. The wingless Cretaceous formicoids conform to the proportions of ant workers rather than to those of wasps (Figs. 1–2) and hence are reasonably interpreted to have lived in colonies.

The Cretaceous formicoids are nevertheless anatomically primitive with reference to modern ants and share some key traits with nonsocial aculeate wasps. They were distributed widely over Laurasia and appear to have been much less abundant than modern ants.

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Introduction

This article attempts to resolve a problem in systematics that bears significantly on the origin and early evolution of the ants and hence the antiquity of advanced social behavior in insects generally. Studies of four mid-Cretaceous amber specimens have established the presence of the ant subfamily Sphecomyrminae across a wide portion of present-day North America: *Sphecomyrma freyi* from New Jersey (Wilson et al. 1967a,b) and *S. canadensis* from Alberta (Wilson 1985a). Dlussky (1975, 1983) has described an important additional collection of ant-like forms from the Upper Cretaceous of the Taymyr Peninsula (extreme north-central Siberia), southern Kazakh S.S.R., and the Magadan region of extreme eastern Siberia. He erected 10 new genera to accommodate this material. In his more recent article, he also created a new family, the Armaniidae, to accommodate some of the genera while elevating the Sphecomyrminae to family rank (hence, Sphecomyrmidae) to receive others. This classification is summarized in Table 1.

Dlussky's taxonomic interpretation, which is based on careful and accurate descriptions of the new material, has sweeping consequences for our conception of the origin of the ants. First, it

presents a picture of an extensive radiation of ants or ant-like forms by the early part of the Upper Cretaceous—in other words, by no later than 80 ma B.P. Second, Dlussky suggested that the Sphecomyrmidae are not true ants or even precursors of the Formicidae but a closely related side branch, while the Armaniidae are the true ancestors of the ants. He doubted that either the Sphecomyrmidae or the Armaniidae were eusocial; in other words he questioned whether they possessed the most advanced mode of social organization in which distinct queen and worker castes form overlapping adult generations and care for the developing young (see Wilson 1971).

Because of the light that the early fossils can shed on the origin of the ants and their distinctive social systems, which are matters hitherto largely unexplored due to the exclusively eusocial status of modern ant species, I decided to reexamine closely the morphological and biogeographic evidence provided by the Cretaceous material. I have arrived at a wholly different conclusion from that of Dlussky. In essence, the differences among the fossils cannot support the separation of the two new families, the Sphecomyrmidae and Armaniidae, from the Formicidae. It is difficult to justify even the recognition of any genus other than *Sphecomyrma* on the

TABLE 1. Interpretation by Dlussky (1983) of the Mesozoic (Cretaceous) or antlike forms, classified to genus, with localities and approximate dates. Spelling of formation and estimation of dates follow van Eysinga (1978).

Taxon	Sex	Locality	Formation and age before present (million years B.P.)
Superfamily Formicoidea			
Family Sphecomyrmidae Dlussky 1983			
<i>Sphecomyrma</i> Wilson and Brown 1967	Female (wingless)	New Jersey, U.S.A.; Alberta, Canada	New Jersey: Santonian (80)
<i>Cretomyrma</i> Dlussky 1975	Female (wingless)	Taymyr Peninsula	Santonian (80)
<i>Paleomyrmex</i> Dlussky 1975	Male	Taymyr Peninsula	Santonian (80)
Family Armaniidae Dlussky 1983			
<i>Archaeopone</i> Dlussky 1975	Male	Southern Kazakh S.S.R.	Turonian (90)
<i>Armania</i> Dlussky 1983	Female (winged)	Magadan	Cenomanian (100)
<i>Armaniella</i> Dlussky 1983	Female (winged)	Magadan	Cenomanian (100)
<i>Dolichomyrma</i> Dlussky 1975	Female (wingless)	Southern Kazakh S.S.R.	Turonian (90)
<i>Poneropterus</i> Dlussky 1983	Male	Magadan	Cenomanian (100)
<i>Pseudarmania</i> Dlussky 1983	Female (wingless)	Magadan	Cenomanian (100)
Incertae Sedis (unplaced to family)			
<i>Cretopone</i> Dlussky 1975	Female (wingless?)	Southern Kazakh S.S.R.	Turonian (90)
<i>Petropone</i> Dlussky 1975	Female (wingless)	Southern Kazakh S.S.R.	Turonian (90)

basis of the morphological evidence. The most parsimonious explanation of the data is that the winged females and males from the Soviet deposits are queens and males of eusocial colonies of which the wingless *Sphecomyrma* and wingless Soviet species are the workers.

In proposing this view, I wish to emphasize that the disagreement is not over the facts assembled earlier by Dr. Dlussky and myself. There is only one exception, the supposed divided condition of the hind trochanter in the Armaniidae, to be discussed later. Instead, the disparity is due to a difference of interpretation of the facts with reference to higher classification and phylogeny. This is all to the good. By such contrasts the basic issues can be better clarified and the gathering of new data stimulated.

Materials and Methods

All of the characters known to vary among the Cretaceous species were first broken into character states. Each genus and species was then redescribed character by character in matrix form to allow close comparison of taxa. The holotypes of two of the best preserved and taxonomically most important Soviet species, *Armania robusta*

and *Pseudarmania rasnitsyni*, were studied closely in comparison with the descriptions. I also worked with all of the four known specimens of the North American formicoids, placed in *Sphecomyrma* (Wilson 1985a).

In addition, measurements were made of a wide range of contemporary queen and worker ants and the winged and wingless females of other, nonsocial aculeate families deposited in the Museum of Comparative Zoology, in order to detect consistent differences in body proportions between social and nonsocial females. A single representative specimen was taken from the series available in each species, and the species in turn were selected to provide a large amount of phyletic diversity. This information was needed to infer the level of social evolution of the earliest fossils. Further measurements were utilized from the monograph of Miocene ants of North America by Carpenter (1930). All of these fossils belong to extinct species but surviving subfamilies and in some cases surviving genera. They were considered useful because as rock fossils their shapes were likely to have been distorted in the same manner as some of the Soviet specimens, which had been similarly preserved.

TABLE 2. Character-state analysis of Cretaceous formicoid taxa based on the worker or queen castes.

Character	Worker						Queen			
	<i>Sphcomyrma freyi</i>	<i>Cretomyrma armoldti</i>	<i>Cretomyrma unicornis</i>	<i>Petrophane petiolata</i>	<i>Cretophane magna</i>	<i>Dulichomyrma longipes</i>	<i>Armania robusta</i>	<i>Pseudomyrma rasilyni</i>	<i>Pseudomyrma aberrans</i>	<i>Armanella curiosa</i>
Mandible shape	Slender, 2-toothed	Slender, 2-toothed	?	?	?	?	Slender, 2-toothed	Slender, 2-toothed	?	?
Head shape	Circular	?	?	Circular	?	About 1.5 × longer than broad	Circular	Circular	?	?
Clypeus form	Broad, simple	Broad, trapezoidal	?	?	?	Broad, simple	Broad, simple	Broad, simple	?	?
General antennal form	Scape only	?	?	?	?	?	Scape only	Scape only	?	?
	0.3 × as long as funiculus						0.3 × as long as funiculus	0.2 × as long as funiculus		
Funiculus	Flexible	Flexible	?	?	?	?	?	?	?	?
Compound eyes	Large	?	?	Medium	Large	Large	Large	?	?	?
Ocelli	3	?	?	?	?	?	?	?	?	?
Scutum/scutellum	Distinct, convex	?	?	?	?	?	?	Not applicable	?	?
Petiole	Node constricted front and rear	?	Node constricted front and rear	Node constricted in front, weakly constricted in rear	Node narrowly constricted in front, weakly constricted in rear	Node narrowly constricted in front, weakly constricted in rear	Node narrowly constricted in front, weakly constricted in rear			
Gaster	Ovoid, constricted	Ovoid, constricted	Ovoid, constricted	Ovoid, constricted	Ovoid, possibly unconstricted	Ovoid, weakly constricted	Ovoid, constricted	Ovoid, constricted	Ovoid, constricted	Ovoid, constricted

TABLE 2. Continued.

Character	Worker					Queen			
	<i>Sphecomyrma freyi</i>	<i>Cretomyrma arnoldii</i>	<i>Cretomyrma unicornis</i>	<i>Petropone petiolata</i>	<i>Cetropone magna</i>	<i>Dolichomyrma longipes</i>	<i>Armania robusta</i>	<i>Pseudomyrma raminityni</i>	<i>Pseudomyrma aberrans</i>
Sting	Extrusible	Extrusible	?	Extrusible	Extrusible	?	Extrusible	Extrusible	?
Trochanter	1-jointed	1-jointed	?	1-jointed	1-jointed	?	1-jointed	2-jointed?	1-jointed
Tarsal claws	Toothed	Toothed	?	?	?	?	?	?	?
Tibial spurs	1, 2, 2	1, 2, 2	?, ?, 2	?	?	?	?, ?, 2	?	0, 0, 2
Abdominal segment IV	Freely articulated	Freely articulated	?	?	Freely articulated	Apparently freely articulated	Freely articulated	?	Freely articulated
Metapleural gland	Present	Present	?	?	?	?	Apparently present	?	?
General comments	(See text)	(See text)	Protuberance on propodeum ¹	Poorly preserved ²	Poorly preserved ²	(See text)	(See text)	(See text)	(See text)
Source of data	Wilson et al. (1967)	Dlussky (1975, pers. comm.)	Dlussky (1975)	Dlussky (1975)	Dlussky (1975)	Dlussky (1975)	Dlussky (1983); direct study of holotype	Dlussky (1983)	Dlussky (1983)

¹ Horn-like protuberance on propodeum of uncertain nature.² Indeterminate, could be *Sphecomyrma*.

TABLE 3. Character-state analysis of Cretaceous formicid genera based on males.

Character	Species (Male)			
	<i>Paleomyrmex zberichini</i>	<i>Archaeopone kyzylbarica</i>	<i>Archaeopone taylori</i>	<i>Poneropterus sphaecoides</i>
Ratio, length of 3d antennal segment to 2d segment	2-3	?	5	3
Genitalia covered by terminal abdominal tergite, or not	Not covered	Not covered	Not covered	Covered
Petiole trapezoidal (or nearly cubical) versus tapered anteriorly (delimiting a node)	Trapezoidal	Trapezoidal	Trapezoidal	Tapered
Trochanter	1-jointed	?	?	?
Source of data	Dlussky (1975)	Dlussky (1975)	Dlussky (1983)	Dlussky (1983)

In particular, it was important to take into account the possible increase in length of the abdomen, which tends to occur when this softest of body parts is crushed laterally or dorsoventrally.

Head length was adopted as a reliable index of body size as a whole (see Wilson 1971). The size of the abdomen is critical as an indicator of reproductive as opposed to nonreproductive status in females, because it is the main part of the body containing the ovaries, organs that are proportionately large in fully social hymenopterans. The abdomen in turn was defined in two ways for the present study. First, a "functional" definition marks the abdomen as the posteriormost discrete body part, commonly called the gaster by ant specialists—the ovary-bearing portion behind the one or two segments of the waist. In addition, a strictly homologous definition of the abdomen (or, more precisely, posteriormost major body tagma) was used: all of the true abdominal segments from II posteriad, including the one or two segments of the waist in ants and a few aculeate wasps. The first, functional definition is intuitively the better, because the waist has by definition been reduced to a relatively thin, largely muscled portion that increases the mobility of the gaster. However, both measures were employed in order to evaluate the situation as fully as possible.

The results were evaluated with reference to the following criteria derived from standard systematic practice on modern faunas of insects and other animals. Individual taxa, whether species, genera, or representative of higher taxa, should be distinguished and named only if they differ by character states. The states can be relatively minor in the case of species, but should be more

substantial in the case of genera (e.g., in ants they include the number of antennal and palpal segments, presence or absence of clypeal teeth, and presence or absence of antennal scrobes; and they preferably should exist in multiples). In the case of families, traits should be truly major, as for example the presence or absence of the petiole, presence or absence of principal exocrine glands, and the pattern of wing folding—again preferably occurring in multiples. Dlussky (1975, 1983) appears to have used lighter criteria of the kind more commonly accepted in paleontology, in which it is recognized that fossils separated by large geographic distances and stretches of geological time are more likely to belong to different genera or higher categories. Add to this the fact that characters are often obscured due to imperfections in fossilization, and reliance is therefore placed on minor character states.

Because of the importance of the evolutionary issues involved, I believe the criteria employed in assessing the early ant fossils must be the stricter ones used in neontology. That is, it is preferable not to recognize taxa unless the character states separating them can be seen and are of approximately the same magnitude used in recognizing contemporary taxa of the same rank.

Results

The results of the character-state analysis for all of the Cretaceous formicoid genera are summarized in Tables 2 and 3. An inspection shows that no single character state or combination of states can be used to separate a distinct family, the Armaniidae, if neontological standards are applied. Moreover, almost none of the genera can be unambiguously supported from the existing evidence. The only exception is *Cretomyrma*,

TABLE 4. Higher classification of Mesozoic (Cretaceous) ants proposed in the present analysis.

Superfamily Formicoidea Latreille 1802	
Family Formicidae Latreille 1802	
Formicidae Latreille 1802, <i>Hist. Nat. Gen. Part., Crust. & Ins.</i> 3:352. Type genus: <i>Formica</i> .	
Sphecomyrmidae Dlussky 1983, <i>Paleontol. Zhurn.</i> 1983, no. 3, p. 65. Type genus: <i>Sphecomyrma</i> Wilson and Brown 1967. NEW SYNONYMY.	
Armaniidae Dlussky 1983, <i>Paleontol. Zhurn.</i> 1983, no. 3, p. 66. Type genus: <i>Armania</i> Dlussky 1983. NEW SYNONYMY (tentative).	
Subfamily Sphecomyrminae Wilson and Brown 1967	
<i>Sphecomyrma</i> Wilson and Brown 1967	
<i>Sphecomyrma</i> Wilson and Brown 1967, <i>Psyche</i> 74:8. Type species: <i>S. freyi</i> Wilson and Brown 1967.	
<i>Dolichomyrma</i> Dlussky 1975, <i>Trans. Paleontol. Inst.</i> 147:121. Type species: <i>D. longiceps</i> Dlussky. NEW SYNONYMY (tentative).	
<i>Paleomyrmex</i> Dlussky 1975, <i>Trans. Paleontol. Inst.</i> 147:118. Type species: <i>P. zberichini</i> Dlussky. NEW SYNONYMY (tentative).	
<i>Archaeopone</i> Dlussky 1975, <i>Trans. Paleontol. Inst.</i> 147:120. Type species: <i>A. kzytzharica</i> Dlussky. NEW SYNONYMY (tentative).	
<i>Armania</i> Dlussky 1983, <i>Paleontol. Zhurn.</i> 1983, no. 3, p. 67. Type species: <i>A. robusta</i> Dlussky. NEW SYNONYMY (tentative).	
<i>Pseudarmania</i> Dlussky 1983, <i>Paleontol. Zhurn.</i> 1983, no. 3, p. 69. Type species: <i>P. rasnitsyni</i> Dlussky. NEW SYNONYMY (tentative).	
<i>Armaniella</i> Dlussky 1983, <i>Paleontol. Zhurn.</i> 1983, no. 3, p. 71. Type species: <i>A. curiosa</i> Dlussky. NEW SYNONYMY (tentative).	
<i>Poneropterus</i> Dlussky 1983, <i>Paleontol. Zhurn.</i> 1983, no. 3, p. 73. Type species: <i>P. sphecooides</i> Dlussky. NEW SYNONYMY (tentative).	
<i>Cretomyrma</i> Dlussky 1975	
<i>Cretomyrma</i> Dlussky 1975, <i>Trans. Paleontol. Inst.</i> 147:115. Type species: <i>C. arnoldii</i> Dlussky.	
Incertae Sedis	
<i>Petropone</i> Dlussky 1975, <i>Trans. Paleontol. Inst.</i> 147:119. Type species: <i>P. petiolata</i> Dlussky.	
<i>Cretopone</i> Dlussky 1975, <i>Trans. Paleontol. Inst.</i> 147:119. Type species: <i>C. magna</i> Dlussky.	

possessing a hornlike protuberance on the propodeum (in *C. unicornis*), more compact gaster, and proportionately longer legs; a second, weaker possibility is *Dolichomyrma*, with an elongate head and slight constriction of the gaster (Dlussky 1975, 1983, and new details provided the author *in litt.*). It cannot be denied that still other genera might be represented by the Soviet fossils; we are only sure that few can be defined by neontological standards with existing data. Hence the synonymy suggested in Table 4 is for

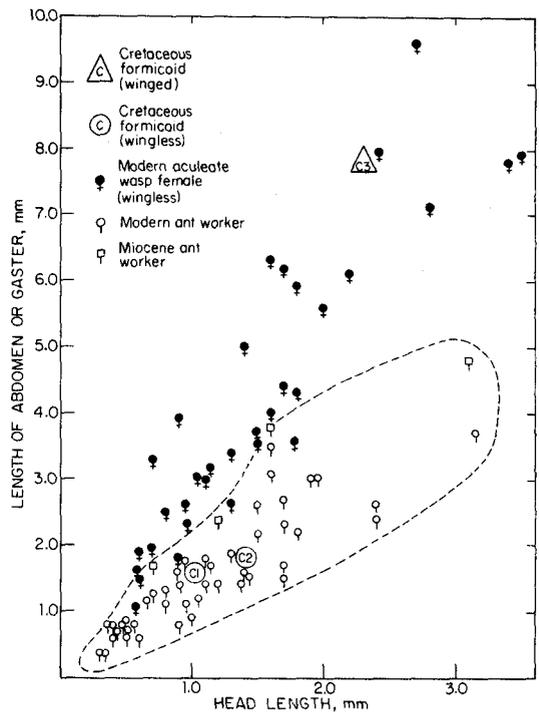


FIGURE 1. A comparison of the head length and abdomen length (functionally defined) in representative specimens of Cretaceous formicoids, modern ant workers, Miocene ant workers, and modern wingless aculeate wasps. Cretaceous formicoids: C1, *Sphecomyrma freyi* holotype worker; C2, *Dolichomyrma longiceps* holotype worker; C3, *Pseudarmania rasnitsyni* holotype winged female. The list of other specimens used is given in the Appendix.

the moment the appropriate nomenclatural arrangement.

Figures 1 and 2 show that the measurable, relatively undistorted wingless females among the North American and Soviet fossils, in other words *Sphecomyrma freyi* and *Dolichomyrma longiceps*, have small abdomens in proportion to the remainder of the body, by both the functional and strictly homologous definitions of the abdomen. In this respect they resemble the worker caste of modern ants more than they do the wingless females of modern nonsocial aculeate wasps. Moreover, the winged female type of *Pseudarmania rasnitsyni*, a relatively undistorted specimen, is within the range of the queens of modern ants (as well as the females of nonsocial aculeate wasps), as shown in Fig. 3. In sum, the wingless females among the Cretaceous fossils are best interpreted as worker ants rather than wingless reproductive aculeate wasps belonging to solitary

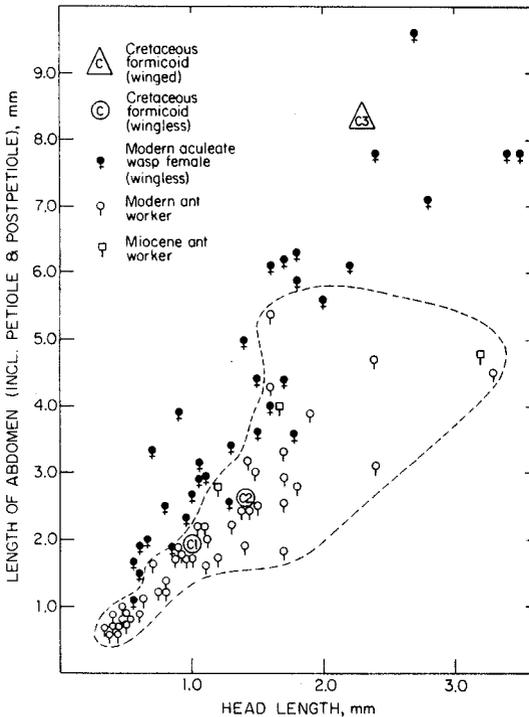


FIGURE 2. A comparison of the head length and abdomen length (defined by strict homology) using the same specimens as in Fig. 1.

species, while the winged females are probably the queens.

Several additional observations support this conclusion. In his description, Dlussky (1983) states that a diagnostic trait of the Armaniidae is the approximately equal length of the first and third antennal segments, that is, of the scape and second funicular segments. Although this is quite correct, another and more revealing way of putting the matter is to say that the scape is quite short relative to the funiculus, while the second funicular segment is long relative to the first and third funicular segments. It turns out that these are precisely the same distinctive traits used to define the Sphecomyrminae. Hence both the winged and wingless Cretaceous females share the same unusual character state in antennal form, another reason for associating them closely.

Dlussky (1983) gives as another diagnostic trait of the Armaniidae the possession of a second, free trochanter on the middle and hind legs. This condition is weakly indicated in the drawing of *Pseudarmania aberrans*, but it is wholly lacking in the drawings of all of the other ar-

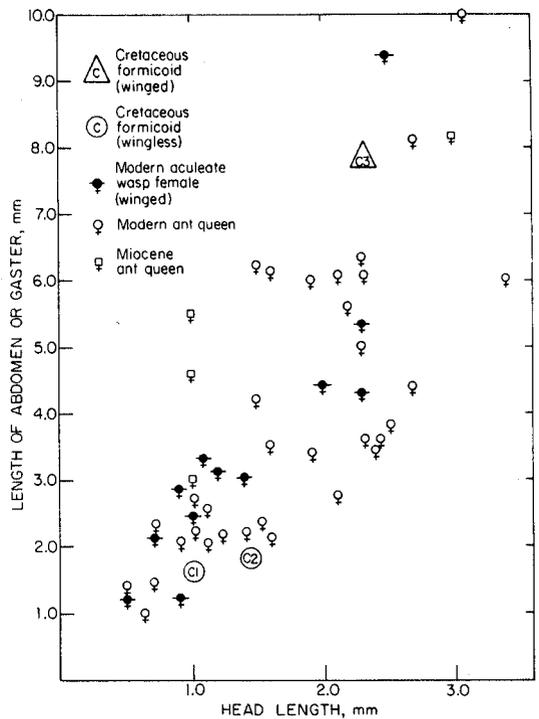


FIGURE 3. A comparison of the head length and abdomen length (functionally defined) in representative specimens of Cretaceous formicoids, modern ant queens, Miocene ant queens, and modern winged aculeate wasps. Cretaceous formicoids: same conventions as in Fig. 1. The list of other specimens is given in the Appendix.

maniids, and by direct examination I confirmed that it is indeed absent in the holotypes of *Armania robusta* (the type genus and species of the family) and *Pseudarmania rasnitsyni*.

In the winged females of the Armaniidae the petioles are more broadly attached posteriorly to the gaster than in the sphecomyrmine wingless females. But this is not a subfamilial or even species-level character. It is a common difference between the queens and workers belonging to the same species among modern ants, and hence it cannot be reliably used as a taxonomic character to separate higher formicoid taxa.

Discussion

The most parsimonious interpretation of the Cretaceous formicoid fossils, neatly joining the facts we know, is that they all belong to the subfamily Sphecomyrminae of the family Formicidae, or true ants. Furthermore, so long as contrary evidence is lacking, the Cretaceous fossils should all be placed provisionally in the gen-

era *Sphecomyrma* and *Cretomyrma*. It is entirely possible that other genera, and even taxa in additional subfamilies or still higher categories, existed in Cenomanian to Santonian times and might be represented by the existing fossils, but until supporting evidence emerges, the conservative taxonomic arrangement suggested here (Table 4) is both more accurate and heuristic.

This interpretation means that the three phases represented among the Cretaceous fossils are most reasonably interpreted to be queen, worker, and male formicoids, respectively, in other words, what we would call ants as opposed to wasps. This hypothesis is more clearly depicted by juxtaposing the best preserved representatives of the three phases as though they are members of the same colony (see Fig. 4). The hypothesis receives considerable support from the size differences between the best-preserved winged fossils and the best-preserved wingless ones, consistent with their being queens and workers. It receives additional support from the fact that the proportionate size of the abdomen in the Cretaceous ants is closer to modern ants than to modern aculeate wasps (Figs. 1, 2).

Glusky (1983) made two inferences connecting anatomy to behavior inclining him to the hypothesis that the Cretaceous formicoids were not eusocial. The first is that the tips of antennal funiculi are too far removed from the mandibles to allow the precise coordination required for social behavior: "The antennae in these insects did not permit them to control the manipulation of small objects, so that they could not have transported their brood or entered into trophallaxis with their larvae—that is, they could not have been true social insects." This supposition is surely incorrect. The eusocial vespid wasps have similarly proportioned antennae yet experience no difficulty in transporting all prey objects and placing them on the larvae. They also engage in trophallaxis, or liquid food exchange. The flexibility of the funiculi contribute to these skills, and the twists and curves of the Cretaceous ant antennae suggest that their funiculi were likewise flexible. To this may be added the fact that some modern ants, such as the primitive *Amblyopone pallipes* (Traniello 1982) and more advanced *Pogonomyrmex badius* (Wilson 1971) do not engage in trophallaxis. Hence this form of food exchange was not es-

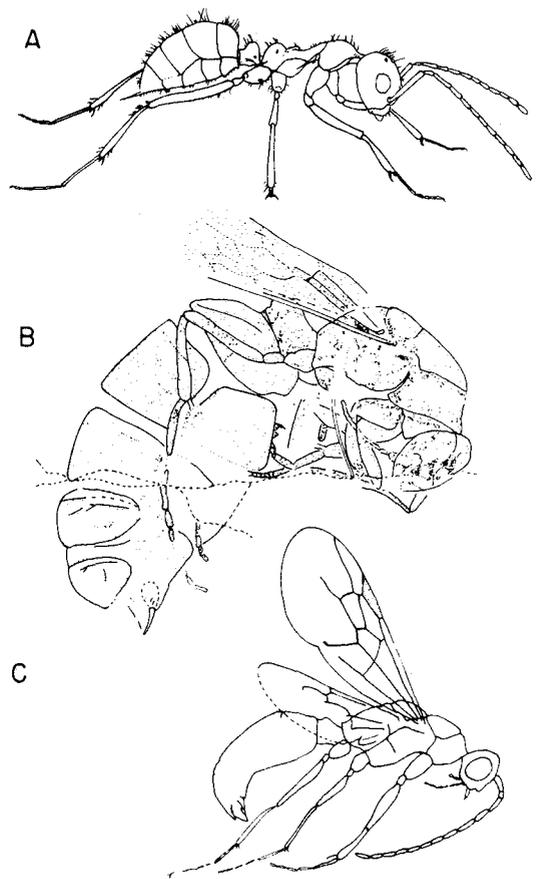


FIGURE 4. The three castes of *Sphecomyrma*, the most primitive known ants, as provisionally associated in the present study. A, Worker: the holotype of *Sphecomyrma freyi*, Cretaceous (Santonian) of New Jersey. B, Winged queen: the holotype of *Armania robusta*, Cretaceous (Cenomanian) near Magadan, northeastern Siberia. C, Male: the holotype of *Paleomyrmex zherichini*, Cretaceous (Santonian) of the Taymyr Peninsula, north-central Siberia.

sential for the evolution of eusocial behavior in ants.

Glusky also inferred that the short, wasplike mandibles of the Cretaceous formicoids "indicates that these insects did not build true nests, and could have used only pre-existing hollows." But this overlooks the fact that some primitively eusocial wasps and bees use similar mandibles to build quite elaborate nests, mostly from carton and wax. A few, such as the halictid bees, excavate soil in a very antlike fashion.

To summarize, nothing in the observable anatomy of the Cretaceous formicoids precludes their having possessed a eusocial organization, characterized by brood care, overlap of adult

generations, and division of labor between reproductive and nonreproductive castes. Although direct evidence either way is lacking on the matter, these insects could also have constructed nests in the soil, rotting wood, or arboreal cavities.

The low accumulation rate of Cretaceous formicoids to date indicates that they occurred in low densities compared with modern ants. Only two individuals (*Sphocomyrma canadensis*) have been found so far among thousands of insects in amber from Alberta Province, Canada (Carpenter et al. 1939; J. F. McAlpine, pers. comm.). Formicoids constituted just 13 of the 1,200 insect impressions in the Magadan collection and 5 of the 526 impressions in the Kazakhstan collection, in other words about 1% in both cases (Dlussky 1983). These figures contrast sharply with Oligocene and Miocene deposits. In the Florissant and other shales of North America (Carpenter 1930), as well as the Baltic amber of northern Europe (Wheeler 1914) and amber of the Dominican Republic (Wilson 1985b), the ants are among the most abundant insects, making up a large minority of all insect specimens. Thus the adaptive radiation that took place in the late Cretaceous or early Tertiary, yielding at least three of the dominant modern subfamilies (Myrmicinae, Dolichoderinae, Formicinae) by mid-Eocene times (Wilson 1985a), was accompanied by a marked increase in abundance.

The ants are seen to have paralleled the mammals by achieving dramatic increases in diversity and abundance around the close of the Mesozoic Era. How they accomplished this breakthrough and managed to sustain a dominant position in the insect world to the present time is a matter of unusual interest, which additional paleontological studies should help to illuminate.

Acknowledgments

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Literature Cited

- CARPENTER, F. M. 1930. The fossil ants of North America. *Bull. Mus. Comp. Zool. Harvard*. 70:1-67.
- CARPENTER, F. M., J. W. FOLSOM, E. O. ESSIG, A. C. KINSEY, C. T. BRUES, M. W. BOESEL, AND H. E. EWING. 1939. Insects and arachnids from Canadian amber. *Univ. Toronto Stud., Geol. Ser.* 40:7-62.
- DLUSSKY, G. M. 1975. Formicoidea, Formicidae, Sphocomyrmidae. Pp. 114-122. In: Rasnitsyn, A. P., ed., *The Higher Hymenoptera of the Mesozoic*. *Trans. Paleontol. Inst. AN SSR* 147 [in Russian].
- DLUSSKY, G. M. 1983. A new family of Upper Cretaceous Hymenoptera: an "intermediate link" between the ants and the scolioids. *Paleontol. Zhurn.* no. 3:65-78 [in Russian].
- EYSINGA, F. W. B. VAN. 1978. Geological time table (published chart). Elsevier; Amsterdam.
- TRANIELLO, J. F. A. 1982. Population structure and social organization in the primitive ant *Amblyopone pallipes* (Hymenoptera: Formicidae). *Psyche*. 89:65-80.
- WHEELER, W. M. 1914. The ants of the Baltic amber. *Schrift. Phys.-ökon. Ges. Königsberg*. 55:1-142.
- WILSON, E. O. 1971. *The Insect Societies*. Belknap, Harvard Univ. Press; Cambridge.
- WILSON, E. O. 1985a. Ants from the Cretaceous and Eocene amber of North America. *Psyche*. 92:205-216.
- WILSON, E. O. 1985b. Invasion and extinction in the West Indian ant fauna: evidence from the Dominican amber. *Science*. 229:265-267.
- WILSON, E. O., F. M. CARPENTER, AND W. L. BROWN. 1967a. The first Mesozoic ants. *Science*. 157:1038-1040.
- WILSON, E. O., F. M. CARPENTER, AND W. L. BROWN. 1967b. The first Mesozoic ants, with the description of a new subfamily. *Psyche*. 74:1-19.

Appendix

Miocene and modern species used in the measurements of Figs. 1-3 are listed here. All ants, fossil and living, are members of the family Formicidae. The families of the aculeate wasp species are listed individually.

MIocene ANT WORKERS. *Aphaenogaster mayri*, *Archiponera wheeleri*, *Hypoclinea antiqua*, *Protazteca quadrata*.

MIocene ANT QUEENS. *Formica robusta*, *Hypoclinea robwieri*, *Miomyrme impactus*, *Pseudomyrme extinctus*.

MODERN ANT WORKERS. *Acanthoclinea dentata*, *Amblyopone australis*, *Aneuretus simoni*, *Anillidris bruchi*, *Araucomyrme tener*, *Aphaenogaster longipes*, *Bothriomyrme flavus*, *Brachymyrme obscurior*, *Crematogaster parabiota*, *Diabobius coniger*, *Dorymyrme planidens*, *Engramma wolffii*, *Erebomyrma urichi*, *Forelius andinus*, *Froggatiella kirbyi*, *Gigantiops destructor*, *Heteroponera flava*, *Hypoclinea abrupta*, *Iridomyrme sanguinea*, *Lasius alienus*, *Leptomyrme fragilis*, *Liometopum apiculatum*, *Monoceratoclinea tricornis*, *Monomorium cyanea*, *Myrmecia dichospila*, *Myrmecia dispar*, *Myrmica incompleta*, *Neivamyrme bumilis*, *Neivamyrme opaciventris*, *Notoncus ectatommoides*, *Odontomachus opaciventris*, *Oecophylla smaragdina*, *Pheidole cephalica*, *Pogonomyrme desertorum*, *Proatta bustelli*, *Pseudomyrme gracilis*, *Semonius schultzei*, *Sericomyrme* sp., *Solenopsis nitens*, *Tapinoma melanocephalum*, *Techomyrme albipes*, *Thaumatomyrme zetekii*, *Typhlomyrme rogenhoferi*, *Zatopinoma* sp.

MODERN ANT QUEENS. *Amblyopone australis*, *Aenictus binghami*, *Aneuretus simoni*, *Aphaenogaster longipes*, *Brachymyrme obscurior*, *Calomyrme albertii*, *Camponotus novaboracensis*, *Eciton dulciss*, *Erebomyrma urichi*, *Formica subpolita*, *Gigantiops destructor*, *Gnamptogenys concinna*, *Heteroponera flava*, *Iridomyrme sanguinea*, *Lasius alienus*, *Leptomyrme fragilis*, *Liometopum apiculatum*, *Myrmecia dichospila*, *Myrmecia dispar*, *Myrmica incompleta*, *Neivamyrme bumilis*, *Neivamyrme opaciventris*, *Notoncus ectatommoides*, *Odontomachus opaciventris*, *Oecophylla smaragdina*, *Opisthopius* sp., *Polyrhachis gagates*, *Pogonomyrme desertorum*, *Proatta bustelli*, *Pseudolaius mayri*, *Pseudomyrme gracilis*, *Sericomyrme* sp., *Solenopsis nitens*, *Tapinoma melanocephalum*, *Thaumatomyrme zetekii*, *Typhlomyrme rogenhoferi*.

ACULEATE WASP FEMALES (WINGED). *Alphadryinus bocainanus* (Dryinidae), *Anteon gaullei* (Dryinidae), *Apbelopus varicornis* (Dryinidae), *Ceropaltes brethesi* (Pompilidae), *Clystospenella longiventris* (Scolebythidae), *Hypodynerus coarctatus* (Vespididae), *Euodynerus farguharensis* (Vespididae), *Pseudoitobranchium complanatum* (Bethylidae), *Psorompula mongana* (Pompilidae), *Scolebythus macedassus* (Scolebythidae), *Sphaerophthalma auripilis* (Mutillidae), *Yclopoca evansi* (Scolebythidae).

ACULEATE WASP FEMALES (WINGLESS). *Acrodoxochelys cubensis* (Dryinidae), *Aelurus gayi* (Tiphidae), *Aglyptacros eureka* (Tiphidae), *Apenesia browni* (Bethyidae), *Aripbron tryphonoides* (Tiphidae), *Bruesiella formicaria* (Tiphidae), *Chyphotes attenuatus* (Mutillidae), *Dasymutilla arenivaga* (Mutillidae), *Dromopompilis* sp. (Pompilidae; a brachypterous rather than completely apterous species), *Elaphroptera* sp. (Tiphidae), *Embolemus nearcticus* (Embolemidae), *Ephuta* sp. (Mutillidae), *Eurycros furtivus* (Tiphidae), *Glyptacros angustior* (Tiphidae), *Glyptometa americana* (Tiphidae), *Gonatopus frequens* (Dryinidae), *Hemithyn-*

nus sp. (Tiphidae), *Leucospilomutilla cerbera* (Mutillidae), *Methocha californica* (Tiphidae), *Myrmosa unicolor* (Tiphidae), *Myrmosula parvula* (Tiphidae), *Nealga banksii* (Rhopalosomatidae), *Olixon* sp. (Rhopalosomatidae; an extremely brachypterous species), *Photopsis zenobia* (Mutillidae), *Plumarius* sp. (Plumariidae), *Pristocerca cockerelli* (Bethyidae), *Pseudomethoca ocoela* (Mutillidae), *Reedomutilla* sp. (Mutillidae), *Rhagigaster laevigatus* (Tiphidae), *Thynnoides* sp. (Tiphidae), *Timulla leona* (Mutillidae), *Typhoctes peculiaris* (Mutillidae), *Proberthylus* sp. (Sclerogibbidae), unidentified sp. no. 3 (Tiphidae).