A formicine in New Jersey Cretaceous amber (Hymenoptera: Formicidae) and early evolution of the ants

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A worker ant preserved with microscopic detail has been discovered in Turonian-aged New Jersey amber (ca. 92 mega-annum (Ma)). The apex of the gaster has an acidopore and, thus, allows definitive assignment of the fossil to the large extant subfamily Formicinae, members of which use a defensive spray of formic acid. This specimen is the only Cretaceous record of the subfamily, and only two other fossil ants are known from the Cretaceous that unequivocally belong to an extant subfamily (Browninemia and Canapone of the Ponerinae, in New Jersey and Canadian amber, respectively). In lieu of a cladogram of formicine genera, generalized morphology of this fossil suggests a basal position in the subfamily. Formicinae and Ponerinae in the mid Cretaceous indicate divergence of basal lineages of ants near the Albian (ca. 105-110 Ma) when they presumably diverged from the Sphecomyrminae. Sphecomyrmines are the plesiomorphic sister group to all other ants, or they are a paraphyletic stem group ancestral to all other ants—they apparently became extinct in the Late Cretaceous. Ant abundance in major deposits of Cretaceous and Tertiary insects indicates that they did not become common and presumably dominant in terrestrial ecosystems until the Eocene (ca. 45 Ma). It is at this time that modern genera that form very large colonies (at least 10,000 individuals) first appear. During the Cretaceous, eusocial termites, bees, and wasp species also first appear—they show a similar pattern of diversification and proliferation in the Tertiary. The Cretaceous ants have further implications for interpreting distributions of modern ants.

Long admired for their industry, the ants (family Formicidae) still capture the popular imagination and scientific attention. All species of Formicidae are eusocial, i.e., their colonies have members that are behaviorally and often highly morphologically specialized for reproduction, foraging, tending larvae, and defense. The only other highly eusocial insects are the termites (order Isoptera), two tribes of corbiculate bees (the Meliponini, or “stingless” bees, and Apini, or “honey” bees) and some social paper wasps in the subfamilies Vespinae and Polistinae (1). Eusociality vastly increases the efficiency of foraging and resource use, as well as defense (2), and it has been commonly invoked as the reason for the ecological dominance of ants, termites, and eusocial bees in terrestrial ecosystems. Ants, however, are far more diverse than these other insects: there are nearly 10,000 described species (perhaps 15,000 total) of ants, but only 3,500 species of other eusocial insects combined. Age of the ants and their niche (they were apparently the first ground-dwelling eusocial predators) have also been implicated as the basis of their remarkable diversity and biomass (2).

A Cretaceous history of ants was first revealed by the discovery of Sphecomyrmma freyi in New Jersey amber (3). Sphecomyrmines were subsequently reported in Santonian-aged amber from Taymyr, Siberia (4, 5), Campanian-aged amber from western Canada (6), and Turonian-aged amber from central New Jersey (7). The first Cretaceous record and the oldest known occurrence of the extant subfamily Ponerinae is Browninemia clavata in New Jersey amber (7); another, younger ponerine, Canapone dentata, occurs in Canadian amber (8). Dlussky (8) also reported the first Cretaceous record of the extant subfamily Dolichoderinae: Eotapinoma maculipinei, also in Canadian amber. Unfortunately, its placement in this subfamily is not definitive, leaving the two ponerines as the only Cretaceous ants definitively attributed to an extant subfamily—until now. Here we describe a recently excavated fossil worker ant in New Jersey amber that is an indisputable member of the extant subfamily Formicinae (Fig. 1).

The Formicinae is one of 16 subfamilies of the family Formicidae and contains some 48 recent genera and approximately 3,000 described species (9). This subfamily contains some very large, ecologically important genera, such as the carpenter ants (Camponotus) and wood ants (Formica). Other genera are renowned for their distinctive biology, such as weaver ants (Oecophylla), slave-making ants (Polyergus, Rossomyrmex), hon-ecystic ants (Myrmecocystus), and genera living in intimate association with plants (e.g., Cladomyrma and Dendromyrmex; ref. 2). The Formicinae is undoubtedly a monophyletic group, based on the highly modified proventriculus (10) and, more overtly, replacement of the sting with an ability to spray formic acid, a substance unique to this subfamily. All formicines have a poison gland that opens into a fringed, tubular pore at the apex of the gaster, the acidopore.

There are only two recent classifications of the Formicinae. Holldobler and Wilson (2) classified formicine genera into 13 tribes, but without providing diagnostic characteristics. Formicinae genera have also been classified into four groups, based on the positions of the coxae, petiole, and helcium (11). The phylogenetic position of the subfamily itself among all ants is somewhat uncertain. The formicines have been placed as the sister group to the rest of the ants based primarily on the putatively primitive absence of a pygidial gland (2), except in Polyergus. This gland, which is found in all other ant subfamilies examined thus far, is the source of alarm and recruitment pheromones and some defensive substances. Absence of the pygidial gland in formicines is arguably a loss related to the dramatic development of the poison gland in these ants. A recent cladistic analysis (7) confirmed the most commonly hypothesized close relationship of the Formicinae to the Aneuretinae and the large subfamily Dolichoderinae, and this lineage as sister group to the Ponerinae and various other ant tribes, including the legionary ants (Ectoninae and Dorylinae; Fig. 2). Basal to this whole assemblage are the myrmicines (a large assemblage including “gardening” or “leaf-cutting” ants), pseudomyrmecines (“acacia” ants), an Australian lineage comprised of the Myrmeccini (“bulldog” ants), as well as the primitive, monotypic

Abbreviations: Ma, mega-annum (millions of years ago); AMNH, American Museum of Natural History.

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genus *Nothomyrmecia* and the most primitive lineage of all ants, the Cretaceous Sphecomyrminae. If the Formicinae occupy this phylogenetic position, it suggests a rather incomplete fossil record of ants in the Cretaceous and indicates that the origins of basal ant lineages are even more condensed within the mid Cretaceous than previously hypothesized (7).

**Materials and Methods**

Amber was collected at a very localized outcrop of lignite and clay of the Raritan Formation (Turonian) in Sayreville, Middlesex County, New Jersey. The amber deposit is the most diverse known thus far from the Cretaceous and was formed in coastal, deltaic swamps by taxodiaceous or pinaceous trees (12).
The amber piece containing the formicine, American Museum of Natural History number AMNH NJ-1029, is clear yellow and also contains wood fragments, suggesting the ant was captured on a tree’s trunk. Preparation followed methods described previously (13). The dorsal and right surfaces of the ant are obscured by a semiopaque fracture plane running through the
center of the amber. The ventral surface is obscured by the
curled position of the specimen, but microscopic details of
exposed surfaces are observable under ×150–400 magnification.

The morphological cladogram used here was presented else-
where (7) and is based largely on the data of Baroni Urbani et al. (14), with the exception of 11 characters that were recoded and several extant and extinct genera that were added to the
matrix. Cladistic relationships of closely related aculeate families
are based on the observations of Brothers (15)—the ant clad-
ogram is rooted by the closely related families Vespidae and
Bradyrhyncha. A matrix of 62 characters and 27 taxa was
analyzed with the phylogenetic program HENNI86; the preferred
cladogram (Fig. 2) had a length of 125 steps, consistency index
= 0.48, and retention index = 0.65 (for details of the analysis, see
ref. 7). The most significant difference between this cladogram
and the original (14) is that ants do not fall into two major
lineages. Instead, the myrmicine and myrmeciine clades are
basal. Also, the Formicinae + Aneuretinae + Dolichoderinae
clade (a monophyletic group in both studies) appears as a sister
group to the large clade where Ponerinae + Adetomyrmex are the basisal members (Fig. 2). Of significance is the possibility that the
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in this large complex is beyond the scope of this study. If scape
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Table 1. Proportions of Formicidae in major deposits of Cretaceous and Tertiary insects

<table>
<thead>
<tr>
<th>Area</th>
<th>Era</th>
<th>Formation</th>
<th>Fossil type</th>
<th>Percentage of ants</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominican Republic</td>
<td>Miocene</td>
<td>La Toca</td>
<td>A</td>
<td>24% all insects</td>
<td>Grimaldi*</td>
</tr>
<tr>
<td>Dominican Republic</td>
<td>Miocene</td>
<td>La Toca</td>
<td>A</td>
<td>40% Hymenoptera</td>
<td>24</td>
</tr>
<tr>
<td>Florissant, CO</td>
<td>Oligocene</td>
<td>Florissant</td>
<td>C</td>
<td>20% all insects</td>
<td>27</td>
</tr>
<tr>
<td>Sicily</td>
<td>Oligocene</td>
<td>Ranzano</td>
<td>A</td>
<td>40% all insects</td>
<td>22</td>
</tr>
<tr>
<td>Baltic</td>
<td>Mid Eocene</td>
<td>Blau Erde</td>
<td>A</td>
<td>30–80% Hymenoptera</td>
<td>24</td>
</tr>
<tr>
<td>Wyoming</td>
<td>Mid Eocene</td>
<td>Green River</td>
<td>C</td>
<td>17% Hymenoptera</td>
<td>26</td>
</tr>
<tr>
<td>Washington</td>
<td>Mid Eocene</td>
<td>Klondike Mountain</td>
<td>C</td>
<td>2% all insects</td>
<td>25</td>
</tr>
<tr>
<td>Arkansas</td>
<td>Mid Eocene</td>
<td>Claiborne</td>
<td>A</td>
<td>1% all insects</td>
<td>6, 46</td>
</tr>
<tr>
<td>Oise, France</td>
<td>Late Eocene</td>
<td>Soissonais</td>
<td>A</td>
<td>7% all insects</td>
<td>23, A. Nel*</td>
</tr>
<tr>
<td>Sakhalin Island</td>
<td>Paleocene (?)</td>
<td>NA</td>
<td>A</td>
<td>1.2% all insects</td>
<td>42</td>
</tr>
<tr>
<td>Alberta</td>
<td>Campanian</td>
<td>Foremost</td>
<td>A</td>
<td>0.002% all insects</td>
<td>47</td>
</tr>
<tr>
<td>Taimyr</td>
<td>Santonian</td>
<td>Kheta</td>
<td>A</td>
<td>0.001% all insects</td>
<td>2sherikhin*</td>
</tr>
<tr>
<td>New Jersey</td>
<td>Turonian</td>
<td>Raritan</td>
<td>A</td>
<td>0.05% all insects</td>
<td>12</td>
</tr>
</tbody>
</table>

Fossil types: A, Amber; C, Compression. NA, not available.


have yet been found, and Armaniidae is plesiomorphic to Sphecomyrminae and other ants based on the wing venation and the barely developed petiole. The fossil record of various aculeate families extends to the Lower Cretaceous, but only one family is known from the uppermost Jurassic, the extinct Bethylonymidae, which is probably the sister group to all aculeates (18). Thus, the Barremian is probably at or very near the oldest age for the clade of aculeate families that includes the ants. This chronology establishes a lower boundary for the absolute ages of ants.

The most primitive lineage of ants is the Sphecomyrminae, putatively monophyletic on the basis of a long second funicular ant. The most primitive lineage of ants is the Sphecomyrminae, putatively monophyletic on the basis of a long second funicular ant. The most primitive lineage of ants is the Sphecomyrminae, putatively monophyletic on the basis of a long second funicular ant. The most primitive lineage of ants is the Sphecomyrminae, putatively monophyletic on the basis of a long second funicular ant. The most primitive lineage of ants is the Sphecomyrminae, putatively monophyletic on the basis of a long second funicular ant.

... in the Paleocene... and in the Middle Eocene... the boundaries between these subfamilies [Dolichoderinae and Formicinae] are uncertain.” As we have shown, their definitive separation took place at least 30 million years earlier than supposed.

Ecological Success and Species Diversity. Ants did not achieve ecological dominance until the Eocene and later. Table 1 shows the proportions of ants preserved in various amber and compression fossil insect Lagerstätte from the Cretaceous and Tertiary. Each deposit is biased by the local paleoenvironment and mode of preservation, but overall the trend is striking. The proportions of ants to all other insects ranges from 0.002 to 0.05% in Cretaceous amber and 1.2% in Sakhalin amber of probable Paleocene age; this proportion gradually increases in the Tertiary to approximately 40% (21–24). Compression remains indicate a similar Tertiary proliferation (refs. 25–27; Table 1). Ecological dominance of ants in the Eocene and later is attributed to the radiations of Myrmicinae, Dolichoderinae, and Formicinae during this time (19, 24), many of which form very large colonies (2), such as Atta, Azteca, and Formica. Many modern genera also appear for the first time in Eocene amber from the Baltic region and Oise, France (23, 28). Kyromyrmex indicates that formicines either proliferated much earlier than the Eocene and remained largely unknown in the Paleocene and Cretaceous fossil record or they inexplicably remained minor components of the insect fauna for the first 40–50 million years of their existence.

Termites and vespoid wasps originated in the Lower Cretaceous (Aptian to Hauterivian) (29–31)—only one certain and several possible records of social wasp nests occur in the Upper Cretaceous (32). Termites were apparently eusocial for their entire fossil record beginning in the Lower Cretaceous. The Cretaceous fossil record is largely based on alate (reproductive) specimens belonging to the phylogenetically basal families Mastotermitidae, Hodotermitidae, and Termopsidae (31). The first records of diverse, derived faunas of termites are in the Eocene (31). The age of the only Cretaceous bee (33) is equivocal. However, it is probably uppermost Cretaceous (34) and belongs to the recently derived tribe Meliponini (Apiidae sensu lato). The first significant record of corbiculate, social bees is in Baltic amber (Eocene), when an impressive diversity of extinct clades occurred (M. Engel, personal communication). These patterns of diversity and abundance parallel those seen in ants.

Neither age nor eusociality alone, therefore, can account for the unique success of ants—these features plus their predominant and ancestral habits as terrestrial predators must be a
significant factor. Another predominant feeding habit of ants, particularly for myrmicines, dolichoderines, and formicines, is the tending and defense of homopterans for their sugary exudates (“honeydew”). These insects particularly include aphids (Aphidoidea), scale insects (Coccoidea), plant lice (Psyllioidea), and treehoppers (Membracidae; refs. 1 and 2). Gathering honeydew is a habit clearly derived from predation and, at least for formicines, is probably related to the structure of valves in the proventriculus that allow for storage of large volumes of liquid in the crop. The earliest records of ant–homopteran symbiosis are based on two examples involving extant ant genera in Tertiary ambers: Iridomyrmex and aphids in Baltic amber (43) and several pieces of Miocene Dominican amber containing a queen Acropyga ant carrying a pseudococcid mealbug (unpublished data). Iridomyrmex today tend aphids, and Acropyga has an obligatory relationship with root-feeding pseudococcids. Aphids and scale insects are among the most abundant inclusions in Canadian and New Jersey ambers [28% (47) and 10% (12), respectively, among all insects], which are the first truly diverse fossil records. Honeydew was available in abundance to Cretaceous ants but may not have been exploited until the Tertiary.

**Biogeography.** Divergence of basal lineages of ants in the mid Cretaceous provides evidence that the distributions of major groups of ants could have been affected by Cretaceous fragmentation of Pangaea (35). Indeed, the Myrmicinae, Formicinae, Dolichoderinae, and Ponerinae are cosmopolitan lineages, whose earliest ancestors were perhaps widespread throughout Pangaea. Some geographically restricted groups, like Myrmecini in Australia and Aneuretinae in Sri Lanka, have fossils in Baltic amber (28) and thus were previously widespread. With exception of the cosmopolitan Cerapachyni, continental endemism is largely found in the tribes and subfamilies that represent the sister group to the Anomalomyrmini (Fig. 2). These taxa may have diversified when a widespread ancestor of this group became isolated on major landmasses.

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