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**Ant worker:** the wingless, typically sterile, female caste of an ant colony; sometimes differentiated into major and minor workers

**Eusociality:** a quality of some animals with (a) a reproductive division of labor, (b) overlapping generations, (c) cooperative care of young

**Crown group:** a recently evolved, monophyletic lineage

**my:** million years

**mya:** million years ago

**myo:** million year(s) old

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## INTRODUCTION

Ants are among the most successful, some would argue *the* most successful, groups of insects to ever live. In terms of both sheer species diversity (7, 81) and ecological impacts on terrestrial systems, the importance of ants cannot be overstated. Ant colonies are often called superorganisms (53) because of the collective functioning of a colony. In tropical forests, ants can comprise upward of 15%–20% of the animal biomass (52). Owing to their eusociality, the impact of ants on their surroundings far exceeds that expected from the relatively small size of individual workers. However, despite their presence on Earth for over 100 million years and despite their current ubiquity, it was apparently not until approximately 50 million years ago that ants achieved the ecological dominance we observe today (9, 28, 76) (**Figure 1**). From beautiful pieces of amber, sometimes with spectacularly preserved specimens entombed within showing the finest details of cuticular sculpturing, to the often shadowy outlines hinting at a structure that seems just out of view provided by an imprint fossil, the ant fossil record offers a tantalizing glimpse of ant diversity at various points in the past.

## HISTORY OF PALEOMYRMECOLOGY

The study of fossil ants began primarily with inclusions in Eocene Baltic amber, with the first fossils illustrated as early as 1742 by Sendel (101) in his magnificent folio volume “*Historia Succinorum*.” Following this pioneering work, the first series of papers to discuss this fossiliferous deposit, which were published during 1819–1840 (e.g., 39, 98), were of rather poorly described species of uncertain generic placement. Heer (49) described in 1850 the first fossil ants from Radoboj (Croatia) and Oeningen (Germany), which Mayr (69) later revised. In 1868, Mayr (70) published the first large treatment of Baltic amber ants. It was this publication that stimulated other myrmecologists to study amber ants as well as imprint fossils. In 1915, Wheeler (111) produced his now classic monograph on the ants of the Baltic amber.

Following Wheeler’s comprehensive monograph, several studies between 1915 and 1937 investigated ant imprint fossils. The most interesting faunas were described from the Late Eocene–Early Oligocene deposits of Florissant and Bembridge Marls and from the Oligocene deposits of Kleinkems and some localities in eastern France. Cockerell (15) first studied the ant fossils of the Bembridge Marls, followed later by the work of Donisthorpe (32). In 1930, Carpenter (13) reviewed fossil ants described from North American deposits. In the 1930s, Théobald (106) described a diverse Oligocene ant fauna from Aix-en-Provence, France, and Kleinkems, Germany, and also revised several species described by Förster (37) from Brunstatt, France. For the next 30 years, however, fossil ant work basically came to halt, probably due in part to the fact that the deposits known at the time were no older than the Late Eocene and most of the species in these deposits belonged to extant genera. In fact, some species in these deposits do not appear much different from extant species. As a result, the fossil record from that time period told us little about the early evolution of ants, and interest in fossil ants waned.

This changed in 1967 with the discovery of *Sphecomyrma freyi* from Cretaceous (Turonian, ca. 92 mya) New Jersey amber. Wilson et al. (115) described an intriguing combination of morphological features that did start to tell us something about how early ants evolved. It also sparked renewed interest in fossil ants. Since then, a diversity of Cretaceous ants have been discovered. These include species described by Dlussky from Taimyr (18–20) and Canadian ambers (23), discoveries from New Jersey amber (35, 41), and surveys of the ancient ants of Burmese and French ambers (22, 35, 43, 77, 84, 118). More recently the oldest definitive crown-group ant was discovered